The nature and rate of vocalisation by southern right whales (*Eubalaena australis*), and the evidence for individually distinctive calls

by

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SUMMARY

Southern right whale vocalisations recorded in Walker Bay, South Africa, between June and November 1999, were analysed to investigate the acoustic repertoire, the relationship between calling behaviour and whale presence, the proportions of vocal and silent whales, and of recorded calls from unseen whales, and the evidence for vocal individuality. This marks the first study of right whale vocalisation in South African waters.

A simple matrix system with the axes acoustic contour and onset frequency described twelve call types. Analysis of call use over time indicated that some calls, as well as broadband *gunshots*, clustered strongly in bouts of differing lengths, and that their relative use varied over the season; the repertoire and its classification was compared with other accounts of right whale vocalisation [*chapter one*]. A generalised linear model explained the variation in the overall call rate in terms of the numbers of whales present, month and wind direction. The overall call rate, for each month and in all wind conditions, rose with increasing whale numbers to a plateau at between ten and fifteen whales, and then declined as whale numbers rose further, suggesting that the social motivation for vocalising was progressively reversed. An inverse linear relationship between call rate per whale and whale abundance was clearly demonstrated over the whole season, indicating that call rates were unreliable as an indicator of whale numbers [*chapter two*].

A dual-axis, three-element hydrophone array suspended at 5m from floating buoys was designed to assign whale vocalisations to calling whales. The array was calibrated with an overall mean error of 3°. Bearings to calling whales were calculated using correlelograms, and compared with the observed positions of whales. On average 31% of *low up* (upwardly inflected) calls and 11% of *medium and high down* (downwardly inflected) calls came from whales not sighted from the boat; up to just under half of the whales sighted from the boat were silent. This indicates the importance of integrating visual and acoustic data when estimating whale numbers [*chapter three*].

In characterising individuality in vocalisations, we used cluster analysis of acoustic properties of whale calls to derive the Euclidean distances (a measure of similarity) between each possible pair of calls within a continuous recording session. Calls clearly from different whales (distant call pairs) were more dissimilar than calls possibly from one whale ('close' call pairs), lending support to the hypothesis of vocal individuality. The similarity between 'close' *up* calls was greatest when the calls were within 0.5 minutes of each other, and declined progressively, up to a separation of 6.5 minutes, as the likelihood of both calls being from one whale declined, indicating individual bout-calling. *Medium and high down* (downwardly inflected) calls, associated with surface active groups (SAGs), and thought by other researchers to be produced by the focal female, were more similar within any given SAG than when compared across SAGs. This evidence strongly suggests that southern right whales produce individually distinctive vocalisations [*chapter four*].

ACKNOWLEDGEMENTS

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ACRONYMS

CPW   call rate per whale

DVV   difference between variable values

FD   frequency domain

FFT   fast Fourier transform

GLM   generalised linear model

OCR   overall call rate

TD   time domain

WT   wavelet transform

CHAPTER ONE

ACOUSTIC REPERTOIRE OF SOUTHERN RIGHT WHALES IN SOUTH AFRICAN WATERS

1. Introduction

Whatever the range over which mammals communicate, their repertoire almost invariably includes the use of sound. In human society this truth is self-evident, but it applies throughout the mammals, and beyond to other classes. Collectively, mammals use a wide spectrum of sound. The smallest rodents and bats produce ultrasonic messages beyond human hearing. Elephants, the largest living terrestrial mammals, communicate over long distances using infrasonic rumbles (Payne et al., 1998). In the underwater ocean environment, sound persists far beyond the limits for light (Urick, 1986), as the most effective medium for the wide range of signals used by marine mammals in acoustic communication.

Attempts by human researchers to interpret the signals of another species often follow a similar course. Answers are sought to a series of questions of increasing complexity, but the first step is to catalogue the repertoire of sounds produced by the species (Bain, 1986; Richardson et al., 1995; Barklow, 1997). This is the task of this chapter. Thereafter, specific sounds produced may be linked with concurrent activities, and inferences drawn as to the functions of the sounds (Clark, 1982; Clark, 1983; Tyack, 1998; Riede & Zuberbuhler, 2003). These are sometimes tested by playing back recorded sounds to observe the reactions elicited (Clark & Clark, 1980; Tyack, 1983; Seyfarth & Cheney, 1992; Hopp & Morton, 1998; Fichtel & Hammerschmidt, 2003; Parks, 2003a; Parks, 2003b). The vocal characteristics that separate one species member from another also facilitate the recognition of kin, neighbours and strangers. Identifying these characteristics leads to a more intimate knowledge of the mechanisms at work in acoustic communication (Reby et al., 1998; Tyack, 2000; Illman et al., 2002; Phillips, 2003).

The sounds produced by right whales *Eubalaena* sp. have attracted interest since at least the late nineteenth century (Scammon, 1874). In the southern hemisphere, research has proceeded since the early 1970s, when the repertoire was first described (Cummings et al., 1971; Payne & Payne, 1971; Cummings et al., 1972; Saayman & Tayler, 1973; Cummings et al., 1974). In the following decade, calls were associated with behavioural states (Clark & Clark, 1980; Clark, 1982; Clark, 1983; Clark, 1984).

In the northern hemisphere the vocalisations of *Eubalaena glacialis* received attention earlier (Schevill, 1962; Schevill et al., 1962; Schevill & Watkins, 1962; Schevill, 1964) with a blossoming of marine acoustic research. Recent concern about the conservation status of northern right whales (Fujiwara & Caswell, 2001) due *inter alia* to threats from entanglement in fishing gear and vessel

strikes (Knowlton & Kraus, 2001), has led to a renewed focus on right whale acoustics in the northern hemisphere, as an advertisement of presence. More recently, the behaviour surrounding surface active groups (SAGs), including vocal activity(Kraus & Hatch, 2001; Parks, 2003b; Parks & Tyack, 2005a; Parks et al., 2005b) and call rates of northern right whales(Matthews et al., 2001) have attracted attention.

There is apparent consensus on the three broad signal types used by right whales; calls, blows and slaps. There have been many attempts to break down these large groups of right whale calls according to various criteria. Some are descriptive (Schevill, 1962; Schevill et al., 1962; Schevill & Watkins, 1962; Schevill, 1964; Cummings et al., 1971; Payne & Payne, 1971; Cummings et al., 1972; Saayman & Tayler, 1973; Cummings et al., 1974; Kraus & Hatch, 2001; Matthews et al., 2001). Others are more quantitative in nature (Clark & Clark, 1980; Clark, 1982; Clark, 1983; Clark, 1984; Wright, 2001; Parks, 2003a). These have generated call descriptions with many names, encompassing overlapping sets of calls. In general, calls have most of their energy between 50 Hz and 500 Hz, though energy sometimes persists into the 2000 Hz region and beyond. Calls tend to be either more tonal (closer to pure sine-wave, harmonic, and with a clear pitch) or more pulsed (and broadband, with more non-harmonic elements caused by vibration of obstructions in the vocal tract), but these categories are not absolute, and many sounds are apparently points along a continuum, with adjacent calls having very different sound qualities (Payne & Payne, 1971; Clark, 1982). Some existing classification systems encompass extremely diverse calls within a singly named call type, which of necessity glosses over the many differences between calls falling within that group, so that call classification is ambiguous.

In this chapter, southern right whale vocalisations are classified using a simplified system derived from and compared with existing methods, but employing a categorical matrix to allocate thirteen call types based on onset frequency and acoustic contour (12 call types within the matrix, one call type, the *gunshot*, excluded by it). The system is offered with the intention of providing an objective tool for locating and assessing the many and varied calls produced by southern right whales, some of which could conceivably fall into several previously described, overlapping call groups. The system is intended to be effective independent of visual observations of the whales which may be producing the sounds, as remote sensing of acoustic signals (a growing area of interest in whale acoustics) normally precludes the presence of observers.

Distinct call types are identified and compared with existing call categories, and their relative densities over the short and long term are determined, in an attempt to understand the dynamic use of the acoustic repertoire over time. This description of southern right whale acoustic repertoire is the first documentation of the vocal activity of southern right whales in South African waters.

2. Materials and Methods

In this study the initial objective was to create a working map of the recorded sounds from southern right whales. Calls recorded on digital audio tape (DAT) from a single hydrophone, as mono signals with the best signal-to-noise ratio, were located and selected. They were then matched with the same calls, recorded on cassette tapes from a three element array for localisation, where each call was recorded as two somewhat noisier stereo signals. The intention was to create a simple but effective classification method which would identify each call unequivocally. The call class was defined by the initial, or starting, frequency and the acoustic 'shape' or contour of the signal. Southern right whales produce harmonic calls with four principal acoustic contours. These are *up* calls, with a frequency modulated upward 'chirp' or upsweep; *down* calls, with a frequency modulated downward sweep, sometimes associated with female courtship display; *flat* calls, with minimal or no frequency modulation; and *variable* calls, frequency modulated with one or more inflections. *Gunshots* are short, non-harmonic, broadband, explosive sounds, and *blows* are principally non-harmonic and broadband, although some blows contain harmonic elements, and they are generally produced in air, although they are sometimes heard underwater. In this chapter only harmonic and partially harmonic water-borne signals and gunshots are considered.

2.1 Data acquisition

Recording equipment

Underwater acoustic recordings of whale vocalisations were made in Walker Bay (see *Introduction, fig. 1.1*) in 1999. Recordings were made from a drifting 6m, semi-rigid, inflatable, twin-engine boat. A mono recording system utilised a hydrophone custom-built for naval detection exercises. Due to equipment constraints it was not possible to calibrate the hydrophone below 2 kHz; it was calibrated between 2 and 20 kHz, and received from 2 Hz to at least 20 kHz. with a sensitivity of -146.5dB re 1V/uPa at 2kHz, with decreasing sensitivity to -169dB re 1V/uPa at 20kHz (volume of recording device set at 50, reduced by approximately 7dB across the frequency range when volume set at 25). The hydrophone was deployed such that, depending on the prevailing wind and current, it drifted away from the boat. To minimise vertical movement of the hydrophone, a spar buoy was attached to the cable at a distance of approximately 5 metres from the hydrophone, and several tennis balls acting as mini-floats were loosely connected to the cable running to the boat using fine mesh netting. An additional gain of 7dB was used when the signal was very faint. The signal was recorded on an Aiwa portable DAT recorder (model HS-JS165), with a flat response between 20 Hz and 20 kHz at 85 dB (or better), modified to run on a 12V alarm battery.

Acoustic recordings

Between June and November, 1999, 63 hours of underwater recordings were made in Walker Bay in 69 continuous sessions (66 usable) over a total of 19 days. Of these, 4 days were in June (12 recording sessions, 11 usable), 5 in July (22 recording sessions), 2 in September (2 recording sessions), 4 in October (19 recording sessions) and 4 in November (14 recording sessions, 12 usable). In addition a record was kept of time listening and vocal activity during periods of acoustic monitoring outside recording sessions.

On days with an acceptable sea state (< 4, Beaufort scale) we launched from Gansbaai Harbour and traversed the inshore area of Gansbaai, Walker Bay, principally to the north-east of the harbour, looking for whales. When one or more whales were spotted we approached the group and stopped at a distance of approximately 50 metres from the animals. Thereafter we anchored with the engine off or drifted with wind and current until the weather changed or we were blown too close to the shore or the whales. On arrival at a location, we were frequently approached by curious whales. The impact or bias introduced by our presence can not be overlooked. Generally, however, by the time we had deployed our equipment, with the engines off, and commenced recording, the whales appeared to have lost interest in us, and resumed their normal behaviour. Recording sessions were held in water of up to 27.5 meters (with the hydrophones at 5m depth), depending on the position of the boat, currents and wind, depth of water column and distance from shore (*fig. 1.1*), and sea state. Recording commenced immediately, and continued during lulls in vocalisation; the whales regularly ceased all vocal activity for considerable periods. Sessions (n=66) lasted between 4 minutes and 150.5 minutes (*fig.1.2*). Over 61% of the sessions were >45 minutes long, and over 86% were >15 minutes long.

2.2 Acoustic analysis

Classification into call types

Given the large number of calls recorded (n=3887), all 27 DAT tapes were initially analysed aurally for onset frequency and acoustic contour, using covered-ear *Sennheiser* headphones (Matthews et al., 2001), with frequent reference to independent, external, stable frequency sources (tuning fork, fixed resonant frequency resonators). Both the frequencies of external reference sources and the frequencies of randomly selected calls were independently verified by digital sampling and computerised signal analysis to validate this method of determining their onset frequencies. The acoustic contours of calls (*up*, *down*, *flat* and *variable*) were determined by listening and by visual inspection by human operators of spectrogramsr produced using custom-written software calling on Matlab signal processing routines, with sampling rate 11025 samples per second, FFT size 2048, frequency resolution 5.3780 Hz, 95% overlap in the display of each individual fast Fourier transform (FFT)).

Tonal calls with a harmonic and partially harmonic structure were grouped according to a simple matrix system described by two axes: [*high*, *medium* and *low*] and [*up*, *down*, *flat* and *variable*]. The first axis was the onset frequency of the call fundamental, falling within one of three frequency bands (*fig. 1.3*). Calls were either *low* (55 – 110 Hz, or A1 – A2 in musical notation); *medium* (110 – 220 Hz, or A2-A3 in musical notation); or *high* (220 – 440 Hz, or A3-A4 in musical notation). The standard musical reference is to the equal tempered chromatic scale (American Standard Pitch, adopted by the American Standards Association in 1936). We divided onset frequencies into octave band categories rather than using the onset frequency of each call as a quantitative parameter, so as to have a measurable, standardised framework with which to approach each of the many different calls in the whales' repertoire. Defining each call quantitatively by a specific onset frequency would have resulted in an unmanageably large number of call types (one for each onset frequency). The second axis defining the matrix was the acoustic contour of each call *(up*, *down*, *flat* and *variable*), based on and building upon existing call classifications. These two axes, each encompassing either three (onset frequency-defined) or four (acoustic contour-defined) call types, together described twelve groups of calls (*low up*, *medium up* and *high up*; *low down*, *medium down* and *high down*; *low flat*, *medium flat* and *high flat*; and *low variable*, *medium variable* and *high variable*). 'Gunshots' comprised a further category. For many call types there was a continuum of sound quality, ranging from pure tonal, with a harmonic structure, through to mixtures of tonal and more broadband, sometimes with rapid pulsed repetitions caused by vocal tract obstructions, adding a more complex acoustic structure, or 'growly' quality ('pulsive', *fig.1.4*), and the occurrence of plosive, rapid-onset gunshots was also noted (*fig. 1.4*). Within the matrix system (*fig 1.3*), *medium down* and *high down* calls (also referred to as *SAG* calls) and several *low flat* calls were pulsive, and while this was of interest, the matrix was defined only by acoustic contour and starting frequency.

Relative frequencies of call types over the whole season

We scored the thirteen call types according to the relative frequency of each call type over the whole season, and noted their proportional contributions to the calls in total.

Monthly occurrence of call types and call rates

The monthly frequencies of all thirteen call types were assessed, to explore the variation in relative frequency of each call type at different times of the year. Continuous recording sessions falling within monthly periods were grouped together, including those where no calls were recorded ('silent' sessions). Calls were grouped separately for June, July, September/October and November. September and October were combined because the available data for these months were collected on the last few days of September and the first few days of October. The relative frequencies of each call type to the call total were assessed for each monthly group. Mean call rate for calls of each acoustic contour and monthly period were plotted as mean calls per minute. This method allowed for comparisons between
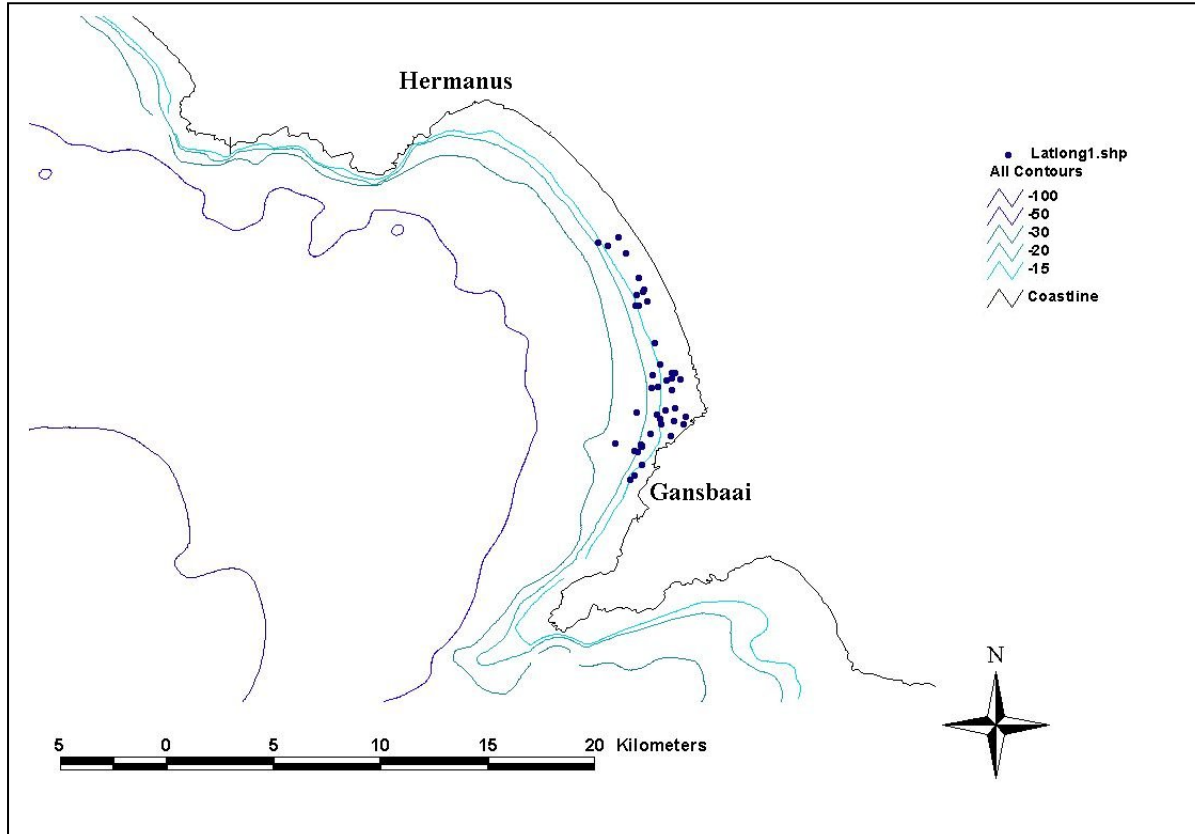
Figure 1.1 Walker Bay and positions of recording locations from the boat, with depth profiles for the bay.
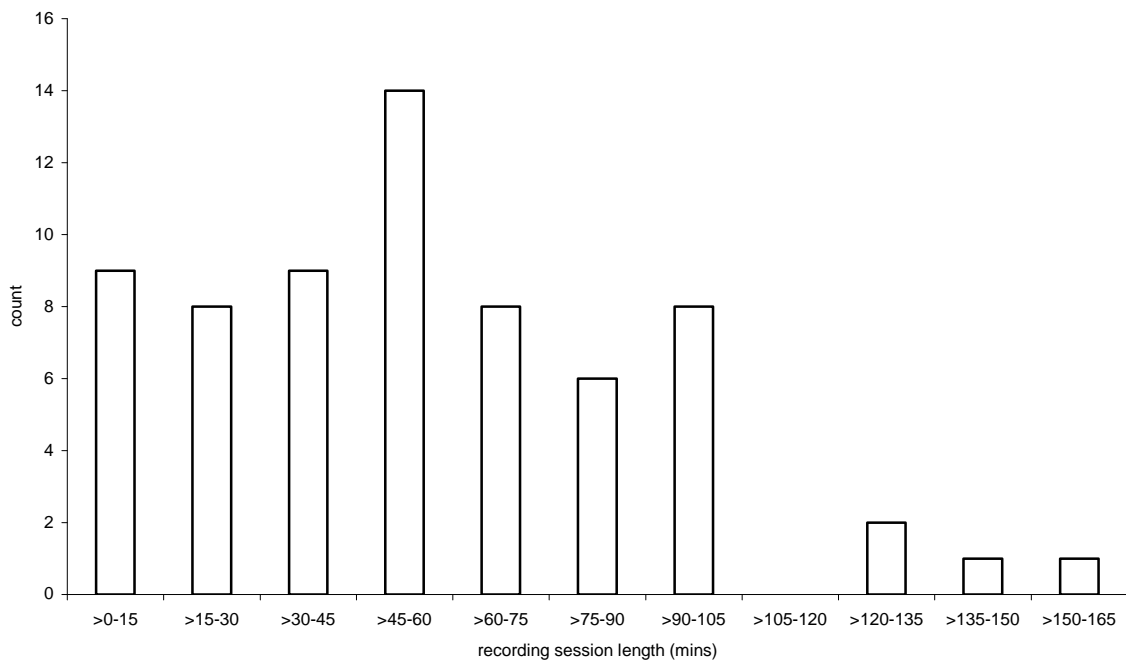
Figure 1.2 Distribution of recording sessions of varying lengths (N=66), ranging between 4 and 150.5 minutes (bin size 15 minutes).
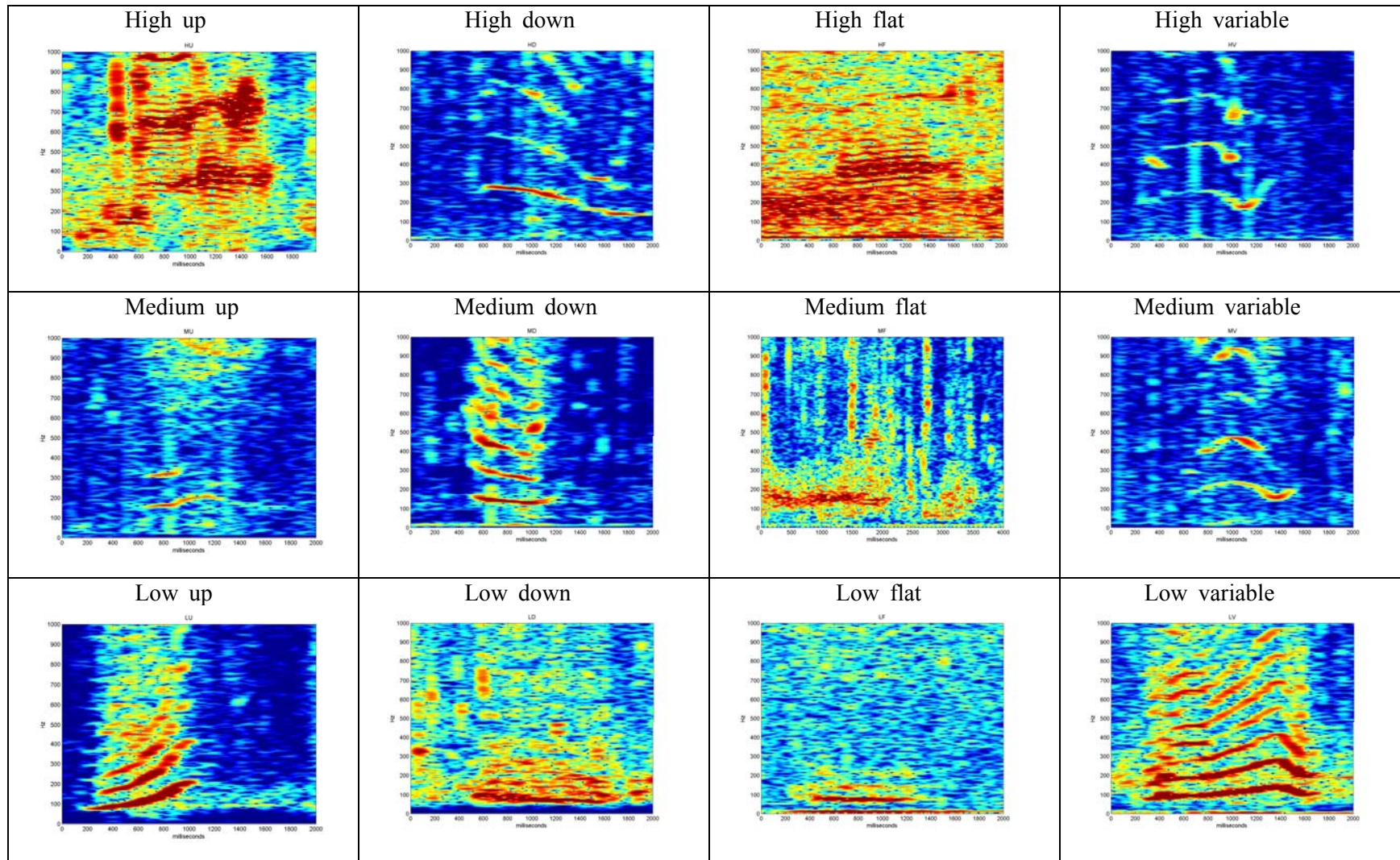
Figure1.3 Twelve tonal or mixed tonal and pulsive calls, classified by acoustic contour (*up*, *down*, *flat* and *variable*), and starting frequency (*low*=55 Hz–<110 Hz, *medium*=110 Hz–220 Hz, and *high*=220 Hz–<440 Hz). Y-axis for each spectrogram frequency range 0–1000 Hz.

call frequencies at different times of the year relative to research effort (silent sessions were included). No attempt was made in this particular analysis to account for the number of whales present in any single continuous recording session (see *Chapter 2* for call rates per whale, based on combining absolute call rates with numbers of whales sighted). The focus fell rather on distinguishing the types and numbers of calls recorded, according to the matrix criteria, as would be possible from 'blind' recordings, where observers to note the presence and abundance of whales would be an unlikely luxury in inaccessible locations, inclement weather or after dark, and where autonomous systems were more likely to be the only available option. Our equipment dictated that, for suitably clear calls, bearings to caller were not calculated in real time *in situ*, but rather *post hoc* when ashore. For many calls at low received frequency or poor signal to noise ratio (SNR), it was not possible to determine the bearings to caller (and so assign calls to a particular whale group); additionally, not all whales sighted from the boat were vocal, and some calls were made by whales not seen by observers onboard. In this study, rather than limit the analysis to a smaller subset of calls for which bearings to caller could be calculated, we used the entire set of recorded calls to quantify proportional occurrence and call rates of all call types encountered.

Clustering of call types in 'bouts'

Intercall intervals (ICI) for various call types were measured within continuous recording sessions. Only intervals bounded on either side by a call were used in the analysis. While removing the silent periods before the first and beyond the last call in each recording session may potentially have biased the ICI results through the exclusion of longer-than-normal intervals, such bias must have been very small (maximum of two intercall intervals per recording. (Call rates were calculated as calls per minute,, and took account of the entire period of each recording, including silent sessions.) Relative frequencies of the thirteen call types present (*Results, Table 1.1*) were assessed. Based on these results, intercall intervals for the most prevalent calls within the matrix were represented separately as cumulative percentage curves, where the percentage of intervals greater than the current x-value (R(x)) fell as the intercall interval increased. Of calls with *down* and *variable* acoustic contours, those with two starting frequencies (medium and high) apparently acted together (*medium down* and *high down* calls and *medium variable* and *high variable* calls). For both these acoustic contours, the *medium* and the *high* intercall intervals were considered both separately as two groups (*medium down* and *high down*; *medium variable* and *high variable*) and together as one group (*medium and high down*; *medium and high variable*). Intercall intervals were drawn from all the recording sessions throughout the season.

The log of R(x) was also plotted to test for the presence of an inflection point, indicating the extent of bouts in clustered calls. The inflection point was determined by iteratively including larger intercall intervals and calculating linear regression correlation until the correlation coefficient reached its

highest value, followed by a consistent drop. A non-linear log-survivor plot of the log proportion of intercall intervals > x has been used as evidence of clustering (Cox & Lewis, 1966; Matthews et al., 2001). This approach assumes that a Poisson distribution of intervals yields a log-survivor plot with a straight line, and deviation near low values of x (small intercall intervals) indicates clustering. When the log-survivor plot approaches a straight line near the longer intercall intervals a normal distribution of clusters is indicated.

3. Results

Proportional contribution of each call type over the whole season

When viewed over the entire season, the most common calls were *up* calls (39.2%), followed by *down* (24.8%), *flat* (19.7), *variable* (10%) and finally *gunshot* calls (6.3%) (*table 1.1*). The usefulness of the matrix may be understood in part by whether there was a significant difference in the relative proportions of calls with each onset frequency. *Up* calls with different onset frequencies showed marked differences, even when lumped over the whole season, with *low up* calls dominating strongly (*table 1.1*). Within the acoustic contours of both *down* and *variable* calls, those with both *medium* and *high* onset frequencies apparently co-occurred: *medium down* and *high down* occurred in similar numbers and were significantly more abundant than *low down* calls when viewed over the season; likewise, *medium variable* and *high variable* calls occurred in similar numbers and were significantly more abundant than *low variable* calls (*table 1.1*). This suggested that *medium down* and *high down* calls may operate as one functional unit; the same was true for *medium variable* and *high variable* calls. Of calls with a *flat* acoustic contour, there was a clear preponderance of *medium flat* calls (*table 1.1*). Sequences of two calls associated with surface active groups – *medium down* and *high down* calls (*table 1.1*) sometimes occurred together (see subsequent analysis, *figs 1.10, 1.11*).

Table 1.1 Call types, occurrence and percentages over the whole season.

acoustic contour	starting frequency	low 55-110 Hz	medium 110-220 Hz	High 220-440 Hz	total
up		987	391	146	1524 (39.2%)
down		39	482	442	963 (24.8%)
flat		215	398	153	766 (19.7%)
variable		38	170	180	388 (10%)
gunshots					246 (6.3%)
total		1279	1441	921	3887

Sound characteristics

The sound quality (more tonal vs more pulsive, *fig. 1.4*) was not relevant to the definition of the matrix (*fig. 1.3*). It was nonetheless interesting to note the presence of growl-like sounds, found almost exclusively with *low* or *medium* starting frequencies, and predominantly *flat* in acoustic contour.

Low   Down
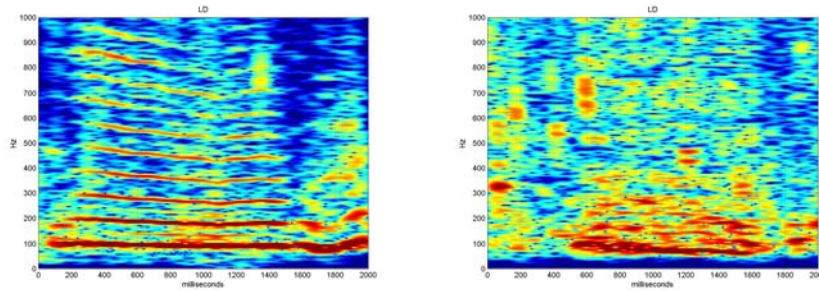
Low   Flat
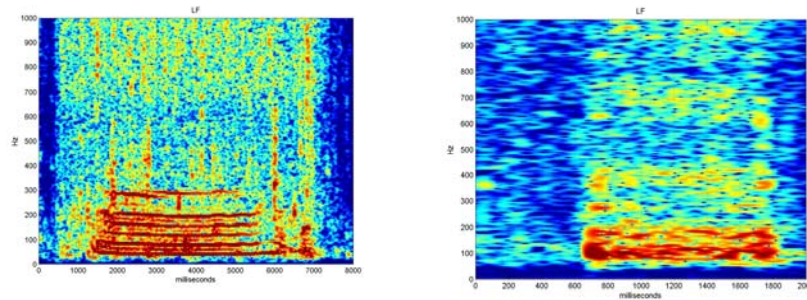
High   Down
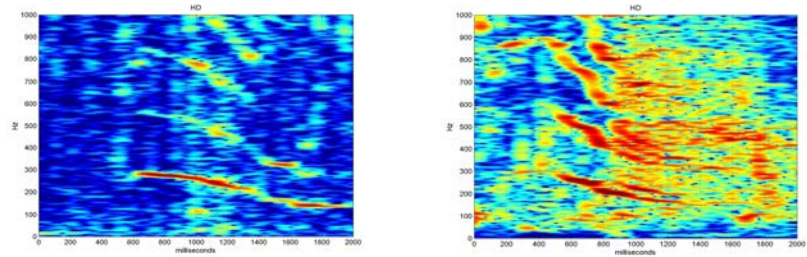
High   Variable
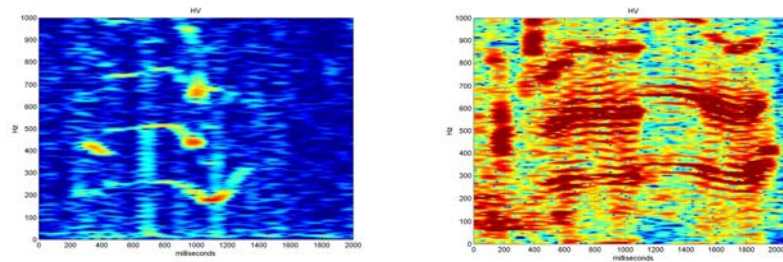
Gun   Shots
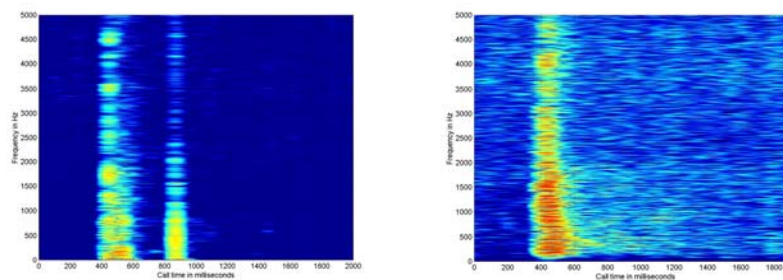
Figure 1.4 Paired calls (right and left); top three with similar starting frequencies and general acoustic contours, but with highly contrasting sound qualities: more tonal on the left, more pulsive on the right; various observed combinations of these qualities suggested a tonal/pulsive continuum (Y-axis 0–1000 Hz). Bottom left and right: gun shots (Y–axis 0-5000 Hz) Frequency resolution 5.3780 Hz.

Trumpet-like sounds were predominantly found with *medium* or *high* starting frequencies, and were mostly *variable* and *down* calls. A few very quiet *low flat* calls with a growl-like quality were detected below 55 Hz, the lowest starting frequency of the matrix (*figs 1.5, 1.6*). Two calls were detected with peak frequencies of 22 Hz, near the lower limit of the DAT recording equipment used.

Monthly occurrence of call types

The occurrence of all call types was considered over four monthly bins, both as proportions within each month (*fig. 1.7*), and as frequencies of each call type within and between months. The distributions for all thirteen call types (finest resolution by both acoustic contour and onset frequency band, smallest groups), for *up*, *down*, *flat* and *variable* calls only (medium resolution by acoustic contour only, larger groups) and for *low*, *medium* and *high* calls only (low resolution by onset frequency band only, largest groups) all differed significantly between months. This result was consistent for every month compared with every other month or combination of months. For June only, *down* calls made up the majority of calls (almost 35%), followed by *up* calls, gunshots, *flat* calls and *variable* calls. Interestingly in the month where *down* calls predominated, *medium* and *high down* calls made up the majority of this call group and occurred at almost equal levels. June was also the month within which gunshots made up the highest proportion of calls within any monthly period (18%). For all other months the pattern found in the call proportions for the whole season was mirrored in the proportional contributions within each month (in descending order, *up*, *down*, *flat* and *variable* calls, and gunshots).

When the call rates for June, July, September/October and November were considered relative to each other (*fig. 1.8*), the overall call rate rose steadily from June to September/October, dropping off sharply in November. Within call types, only *up* calls (peaking in July and September/October) and gunshots (peaking in June and September/October) differed from this pattern.

Clustering of call types and intercall intervals

In the short term, calls clustered in time, occurring in bouts. Based on the frequency of occurrence of calls (*table 1.1*), the cumulative percentage intercall interval distributions were plotted for the five most prevalent tonal call types (*low up*, *low flat*, *medium flat*, *medium* and *high variable*, and *medium* and *high down*), and for gunshots (*fig. 1.9*). *Medium down* and *high down* calls were initially considered together, as one call group (*medium and high down*), due to similar occurrence frequencies and apparent co-occurrence of both: *medium variable* and *high variable* calls were treated in the same way (*medium and high variable*). The more steeply the plot of the curve of each cumulative percentage intercall interval fell (the closer it stayed to a zero intercall interval on the χ axis before curving away to larger intercall intervals), the more closely in time that call type clustered. The deeper the plot of the curve before it changed direction (the closer it dropped down to zero cumulative percent
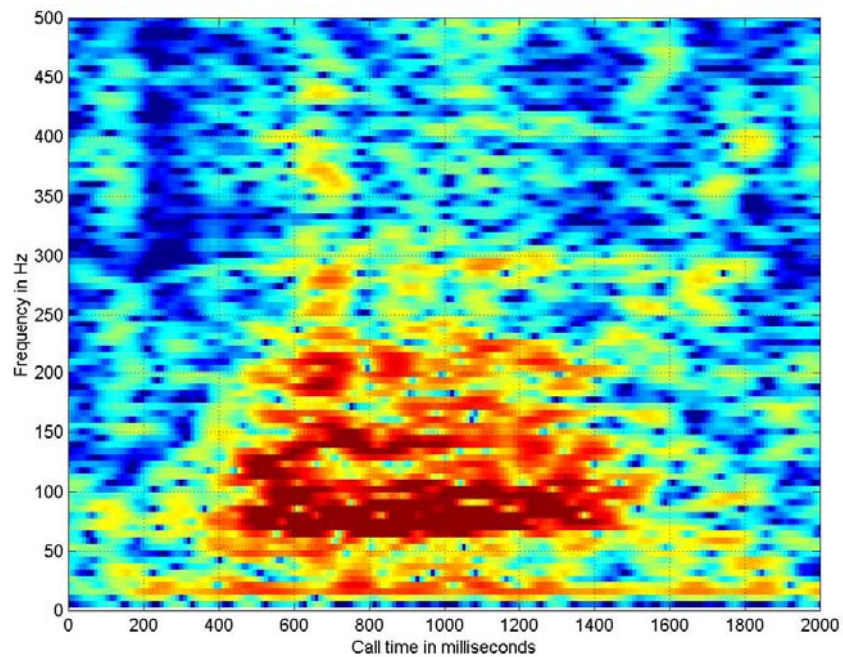
Figure 1.5 Low frequency growl around 70 Hz. Note element near 20 Hz, possibly associated with the growl, starting just before it, and continuing after it (cf. *fig. 1.6*)
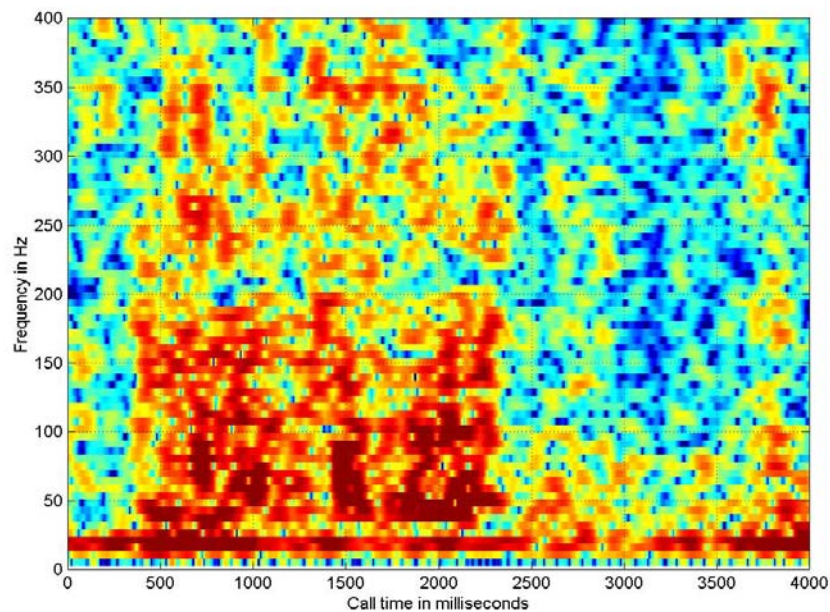
Figure 1.6 Low call with a growl-like quality, and a peak frequency shifting from 22 Hz, where it overlaps with ambient noise in that frequency range, through 65 Hz, and to 86 Hz, dropping again to 43 Hz. Ongoing low-frequency noise is independent of growl (cf. *fig. 1.5* above).
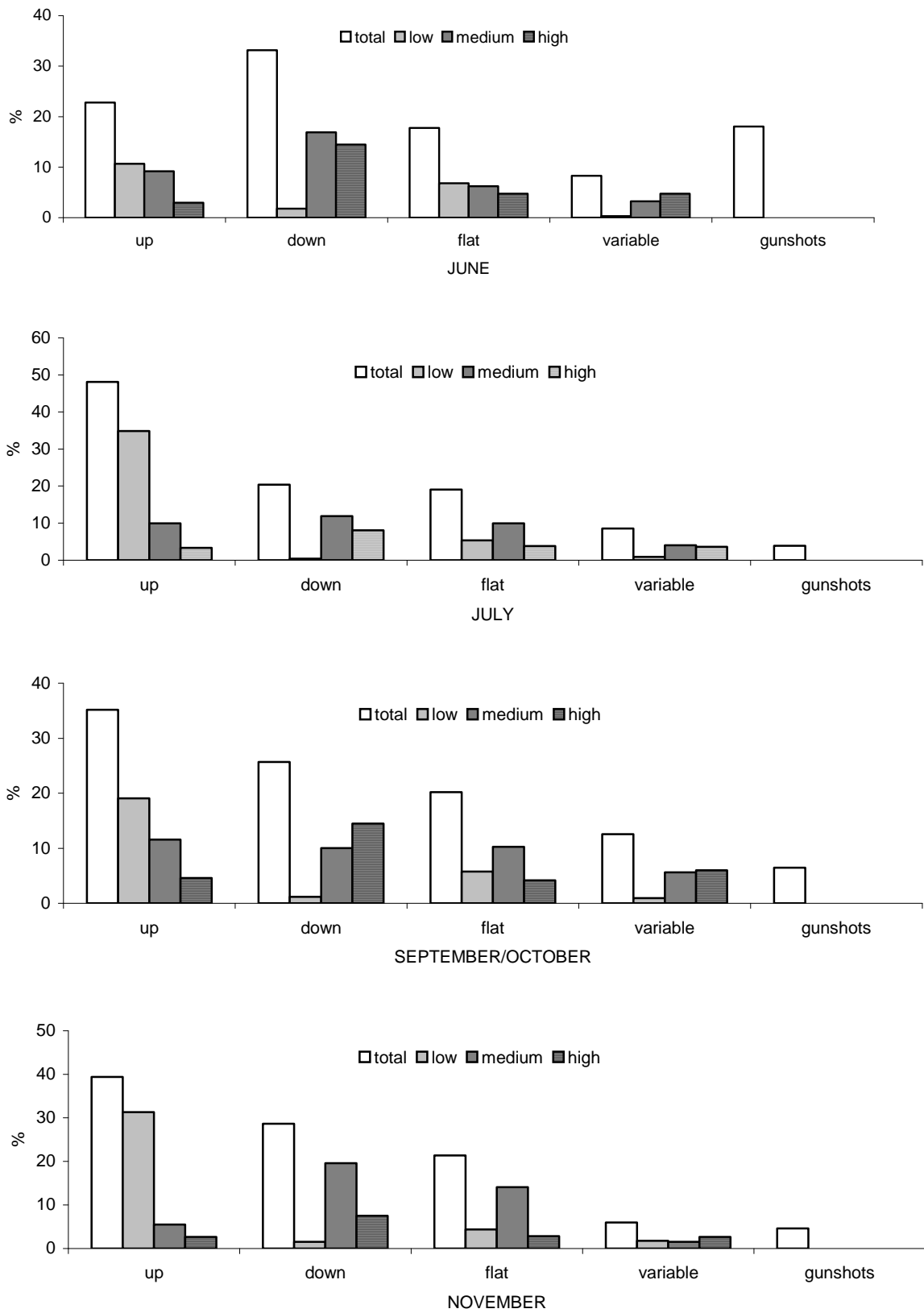
Figure 1.7 Proportional contributions of call types within each month group.

of the intercall intervals on the γ axis before curving away), the greater the proportion of the intercall intervals were small. Call types showed two separate patterns. *Low up* and *medium down* and *high down* calls both had the steepest, deepest curves, indicating the highest degree of clustering. The gunshot curve initially fell even more steeply than either of these groups, indicating shorter intercall intervals, but straightened out slightly earlier, suggesting a higher proportion of slightly longer intercall intervals (fewer calls per bout). Fifty percent of these three call types occurred at intervals of <50 seconds. *Medium and high variable* calls, *medium flat* calls and *low flat* calls had a more even distribution and fewer very short intercall intervals, suggesting a smaller degree of clustering: fifty percent of these calls occurred at intervals of <100 seconds.

The log-survivor function, log R(x), is the log of the cumulative proportion of intercall intervals >x, where x is the intercall interval. In a normally distributed series of x, log R(x) produces a straight line. The degree of deviation at low intervals of the log-survivor function indicates the extent of clustering of calls, while at large values of x, deviation indicates less long intervals than expected in a normal distribution (Cox & Lewis, 1966; Martin & Bateson, 1993; Matthews et al., 2001). In order to test the effects of combining, on the one hand, *medium down* and *high down* calls, and on the other, *medium variable* and *high variable* calls, the log-survivor function was plotted for each of these call types, first separately, and then when combined as *medium and high down* calls and *medium and high variable* calls (*figs. 1.10, 1.11*). In each of these paired call types, similar bout structures alone would not have indicated similar behavioural context; however, each pair shared an acoustic contour, and apparently co-occurred; intercall intervals were therefore recalculated, treating each paired type as one call type. If clustering were improved in combination this would indicate that both *medium down* and *high down* calls were being produced in the same context; likewise for *medium variable* and *high variable*. For *medium down* and *high down* calls, even though both clustered well at small intervals, the clustering was increased in combination. This suggested that *medium down* and *high down* calls occur in association and may operate as one functional unit (*fig. 1.10*). In contrast, the combination of *medium variable* and *high variable* calls only marginally affected the curvature of the plot of the log survivor function for intercall intervals (*fig. 1.11*), which was far less pronounced than for *high down* and *medium down* calls. These results suggest that both *medium variable* and *high variable* calls (1) are less likely to occur in bouts and (2) are less strongly linked than are *high down* and *medium down* calls. This conclusion is, however, mediated by the low occurrence in general of *variable* calls, the scarcest call group other than gunshots.

The log survivorship function was calculated individually for the most prevalent call types (*table 1.1*) as defined by starting frequency and acoustic contour, and for gunshots. The inflection point for each call type was calculated by iteratively including log R(x) for increasingly larger intercall intervals until
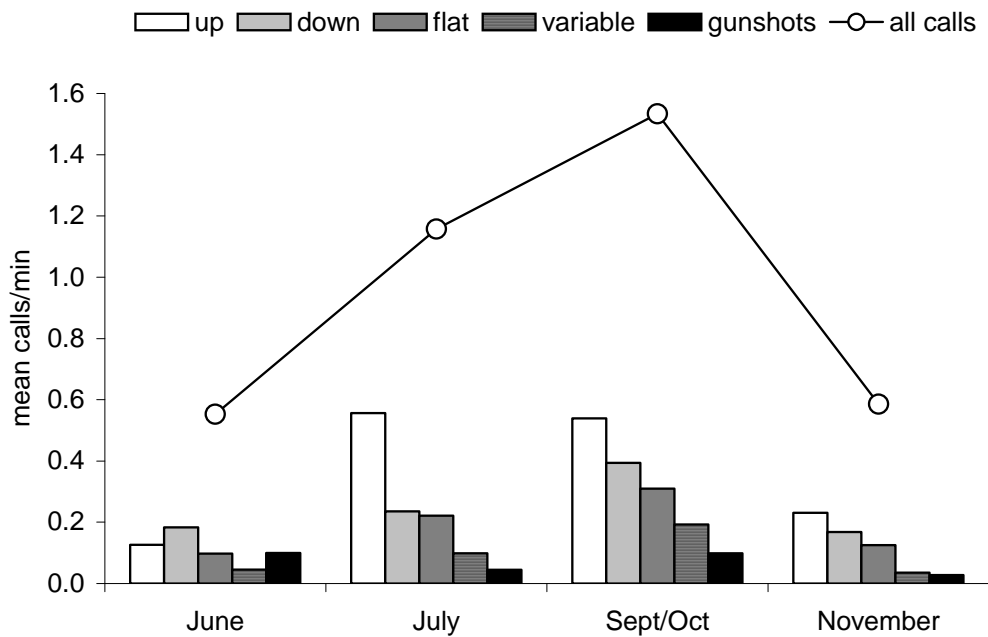
Figure 1.8 Mean overall call rate (all calls), and call rates for tonal calls (*up*, *down*, *flat* and *variable*) and gunshots, calculated for each monthly period.
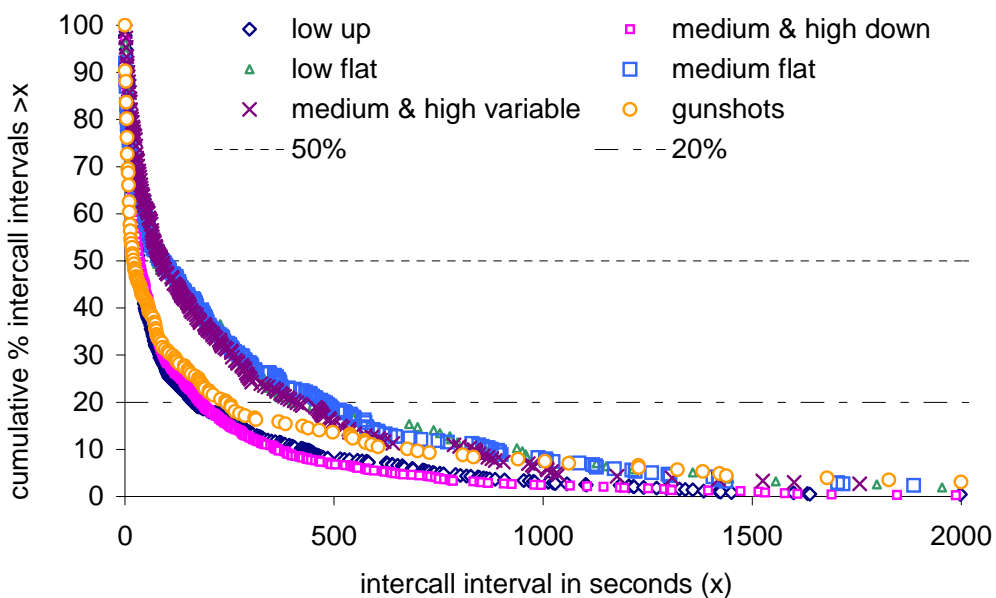
Figure 1.9 Cumulative percentage intercall interval distribution for the most prevalent call types, as defined by starting frequency and acoustic contour, and for gunshots.

Table 1.2 Distribution of intercall intervals for major call types

	low up	gun	medium down	high down	low flat	medium flat	medium variable	high variable
n	936	227	425	392	155	339	131	143
50% of intercall intervals (seconds)	>33	>22	>60	>69	>77	>90	>180	>181
20% of intercall intervals (seconds)	>162	>243	>332	>366	>399	>480	>638	>591

Table 1.3 Temporal extent of clustering for major call types

call type	range of log R(x) data included to determine inflection point	greatest R^2 value before consistent fall
low up (LU)	up to 28 seconds	0.9984
gunshot	up to 14 seconds	0.9959
medium down (MD)	up to 37 seconds	0.9839
high down (HD)	up to 10 seconds	0.9893
medium & high down (MHD)	up to 38 seconds	0.9736
low flat (LF)	up to 77 seconds	0.9837
medium flat (MF)	up to 82 seconds	0.9597
medium variable (MV)	up to 19 seconds	0.9916
high variable (HV)	up to 44 seconds	0.966
medium & high variable (MHV)	up to 44 seconds	0.99

the linear correlation coefficient R^2 reached its highest point before falling consistently. The linear correlation of these data, representing the extent of calling bouts for each call type, is indicated (*fig. 1.12*, *table 1.3*).

Intercall interval statistics (*table 1.2, table 1.3, fig. 1.12*) support the presence of clustering to some degree for all call types. The greatest degree of clustering was evident in *low up* calls and gunshots, with 50% of their intercall intervals at <33 seconds and <22 seconds respectively, only 20% of their intercall intervals at >162 seconds and >243 seconds respectively, and strong inflection points at 28 seconds and 14 seconds respectively. Next were *medium down* and *high down* calls. They clustered less strongly, with 50% of their intercall intervals at <66 seconds and <69 seconds respectively, 20% of their intercall intervals at >332 seconds and >366 seconds respectively, and inflection points at 37 seconds and 10 seconds respectively (38 seconds in combination). These were followed by *low flat* and *medium flat* calls, with 50% of their intercall intervals at >77 seconds and >90 seconds respectively, 20% of their intercall intervals at >399 seconds and >480 seconds respectively, and inflection points at 77 seconds and 82 seconds respectively. Finally *medium variable* and *high variable* calls clustered far more weakly than *medium down* and *high down* calls, with 50% of their intercall intervals at >180 seconds and >181 seconds respectively, 20% of their intercall intervals at >638 seconds and 591 seconds respectively, and inflection points at 19 seconds and 44 seconds (44 seconds in combination). This suggested that *variable* calls may be produced in a wider variety of social contexts, in patterns more random than those of other calls, or at levels far lower than for other acoustic contours. This contrasted sharply with the patterns demonstrated for the abundant *low up*
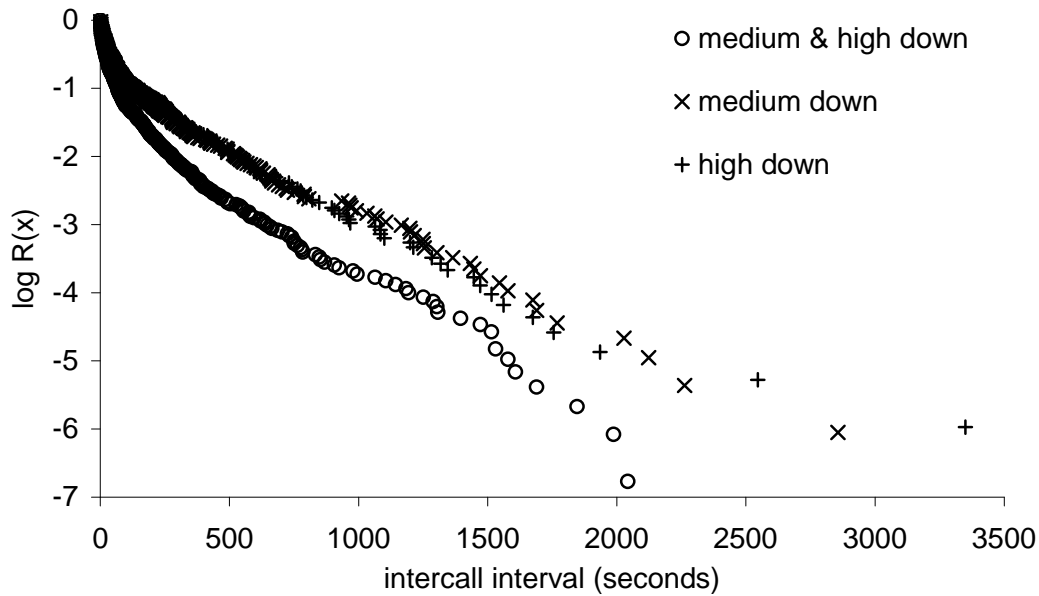
Figure 1.10 Log-survivor function, log R(x), for *medium down* (diagonal crosses), *high down* (upright crosses) and *medium and high down* (circles) intercall intervals. *Medium and high down* intercall intervals are the intervals between both *medium down* and *high down* calls, considered together as one call group.
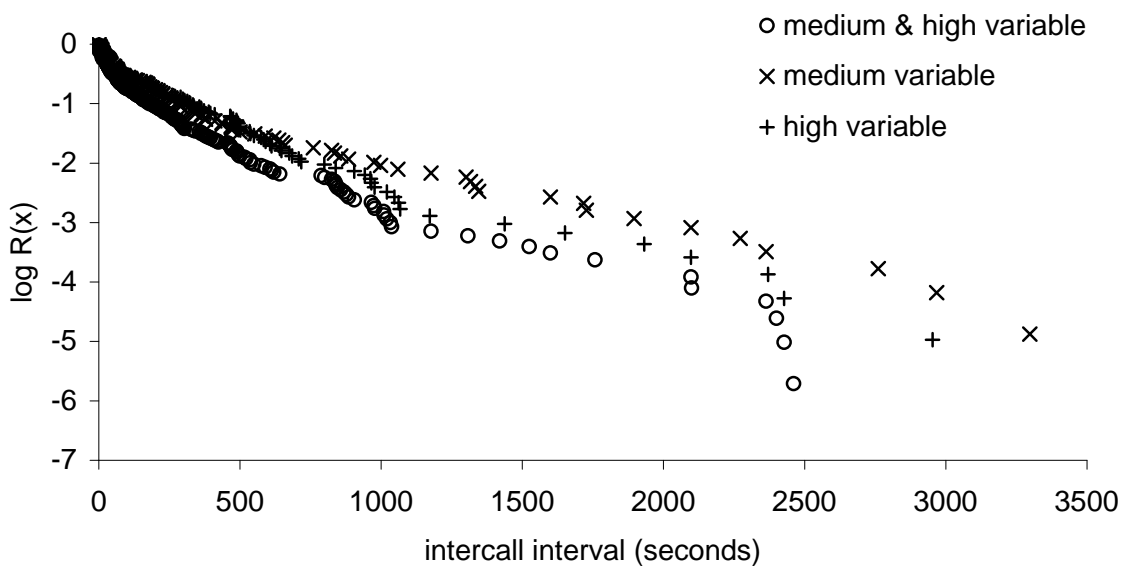
Figure 1.11 Log-survivor function, log R(x), for *medium variable* (diagonal crosses), *high variable* (upright crosses) and *medium and high variable* (circles) intercall intervals. *Medium and high variable* intercall intervals are the intervals between both *medium variable* and *high variable* calls, considered together as one call group.
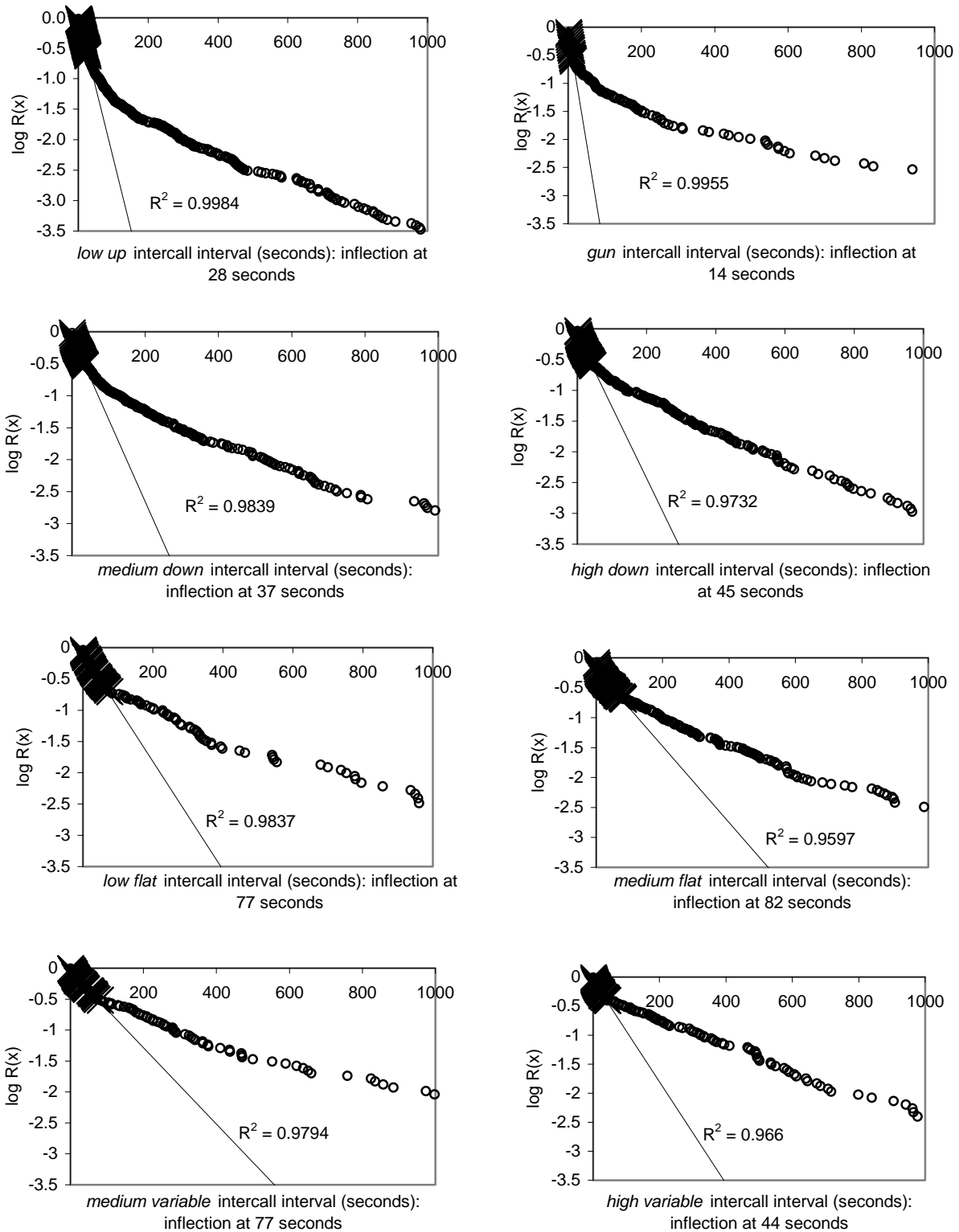
Figure 1.12 Log survivorship function (small circles), log R(x), for intercall intervals for the eight call types most prevalent within their respective acoustic contours. For all figures: X-axis: intercall interval in seconds (left to right, 0 to 1000); Y-axis: log cumulative frequency of (x) (top to bottom, 0 to −3.5). Bout length (large diagonal crosses) bounded by an inflection point iteratively determined by the highest linear correlation value followed by consistently falling correlation values as longer intercall intervals are included.

calls, and for gunshots. The slight tail-off at longer intervals was due to differing session lengths rather than some inherent factor within the call sequences.

4. Discussion

Acoustic repertoire

An understanding of the acoustic repertoire of right whales from both hemispheres has been gaining pace since the latter half of the twentieth century, although descriptions date back to at least the preceding century (Scammon, 1874). Table 1.4 summarises the call types, their characteristics and possible functions as described by different authors for different right whale populations worldwide. Importantly, in column two, the table also lists, for each call type defined by other workers, the several call types defined in this study that could fall into that one call type. This is due to the more wide-ranging definitions of call types employed in other studies. Nevertheless, the repertoire encountered off the coast of South Africa in Walker Bay encompassed the right whale sounds described in Table 1.4, from both hemispheres.

The categorical matrix defining 12 call types (excluding gunshots, which were easily identified) was developed to simplify the classification of calls recorded during fieldwork; pre-existing call descriptions were sometimes not specific enough about acoustic contour or onset frequency to adequately describe every call encountered. While we were strongly guided by these descriptions, we wished to separate calls that clearly sounded different from each other, but would have fallen under one (or another) predefined call description. This was primarily of use in distinguishing one call from another in long call sequences with a range of onset frequencies and acoustic contours. These two call properties were the ones used to define the categorical matrix described here.

Clearly, a system using 13 call types is in some ways more unwieldy than one using five or six, and when the study focuses on only one or a few call types(Parks et al., 2005b), may be unnecessarily detailed. Although one homogenous system may be simpler to standardise call descriptions and categories for all researchers involved in acoustic studies of right whale vocalisations, it may also serve to blunt the perception of subtler differences which could emerge in a system of finer resolution, which allows for a fresh appraisal of right whale acoustics from a different perspective.

Corresponding to gunshots in this study, 'pulses' (Cummings et al., 1971; Cummings et al., 1972), 'gunshot slaps' (Clark, 1990), 'gunshots' (Parks, 2003a) or 'underwater slaps' (Clark, 1982; Clark, 1983) were simple to identify and clearly equate throughout all systems. The other calls were divided in different ways in various studies (*table1.4*) but essentially covered the same ground.

Low up (LU) calls, forming the majority of *up* calls, and of the repertoire, were analogous to 'belch-like utterances of rising pitch' (Cummings et al., 1974), 'Up calls' (Clark, 1982; Clark, 1983), and

'Upcalls'(Parks, 2003a; Parks & Tyack, 2005a). These were the most stereotyped calls, and the subject of a search for individuality in the calls of southern right whales (*chapter four*). *Low up* calls were the call type most likely to be purely tonal, although pulsive *low up* calls occasionally did occur, as in Argentina (Clark, 1983). Pulsive *low up* calls, while extremely rare, correspond to a minority of 'Pulsive calls' (*table 1.4*). When harmonic, they were closest to the simple harmonic upsweep.

Medium up (MU) and *high up* (HU) calls were more likely than *low up* calls to contain some pulsiveness, harshness or strident quality. Some *medium up* calls correlate with the higher ranges of some harmonic 'Upcalls' (*table 1.4*), (Clark, 1983; Parks, 2003a), but *high up* calls (HU) are excluded from at least two definitions of 'Upcalls' as their bandwidth is higher than the upper frequency limit (Clark, 1983; Parks, 2003a). Both *medium up* and *high up* could in some cases correspond to 'Hybrid' and 'High' calls (Clark, 1983), which are defined as '*often*' ending with rapid frequency downsweeps (ie not always). *Medium up* and *high up* could likewise be described variously as 'screams' (Parks, 2003a), 'belch-like utterances' (Cummings et al., 1971; Cummings et al., 1972), and 'moans' (Schevill et al., 1962; Schevill & Watkins, 1962; Schevill, 1964; Cummings et al., 1971; Cummings et al., 1972; Matthews et al., 2001), depending on call definition. This ambiguity arises from the leeway in acoustic contour descriptions for so many call classes. The use of language such as 'may contain', 'and/or', and 'usually', in call class descriptions, while reflecting biological variation, makes call classification in certain contexts imprecise.

Down calls of all starting frequencies may be purely harmonic or contain pulsive or strident elements. The lower calls, when not purely harmonic, tend towards a 'growly' sound quality, while the higher calls tend toward a more strident character. *Low down* (LD) and *medium down* (MD) calls are equivalent to some 'Pulsive' calls (Clark, 1983). *Low down*, *medium down* and even *high down* calls may be analogous to 'Down' calls when more harmonic, depending on the various reported bandwidths (*table 1.4*) (Clark, 1983; Parks, 2003a). *Medium down* and *high down* (HD) calls fall comfortably within the definition of 'High and Hybrid' calls (Clark, 1983), and 'Screams'(Parks, 2003a; Parks & Tyack, 2005a). These two call classes co-occurred (*figs. 1.9, 1.10*), and were often heard in the presence of SAGs. The starting frequency of each successive call in bouts of down calling was often noted to rise for a time, and then to fall again, thus placing the call at different times in a bout within the *medium variable* or the *high variable* call type of this study. Thus *medium down* and *high down* represent calls in a continuum. They co-occur in similar contexts, as suggested observation and by the improved clustering curve (*fig. 1.10*) when they are considered together.

The prevalent *high down* and *medium down* calls encountered near SAGs in South African waters and the 'High' and 'Hybrid' calls recorded in the presence of Argentinean SAGs are clearly similar. If there is a difference, it may lie in the higher incidence of calls with unambiguously descending

frequencies in the South African population, with a corresponding scarcity of obvious 'multiple frequency shifts' observed in the Argentinean population (Clark, 1983) (*figs 1.3, 1.4, table 1.4*).

Flat calls also contain varying degrees of pulsiveness. When harmonic, *low flat* (LF), *medium flat* (MF) and *high flat* (HF) calls correspond to 'Constant' calls (Clark, 1983), while *low flat* calls also equate with 'Low-frequency (LF)' calls (Matthews et al., 2001).The majority of calls with a 'growly' quality were *low flat* calls.

Variable calls, as their name implies, are the hardest calls to define precisely, but in this study the term implies one or more frequency inflections (the slope of the frequency contour changes sign at least once during the call). Sound quality, as with most other call types, is also, to varying degrees, pulsive and harmonic (*fig.1.4*).

When not purely harmonic, *low variable* (LV) calls often displayed a 'growly' quality, while *medium variable* (MV) and *high variable* (HV) calls tended to be more trumpet-like. Both 'High calls' and 'Screams' (*Table 1.4*)(Clark, 1983; Parks, 2003a) may include *medium variable* and *high variable* calls, while some 'Pulsive' calls, with a lower starting frequency range (Clark, 1983), would additionally be analogous to *low variable* calls.

Classes such as 'Moans' (*table 1.4*) serve as catchalls. They include most (Schevill et al., 1962; Schevill & Watkins, 1962; Schevill, 1964; Cummings et al., 1971; Cummings et al., 1972), or all (Matthews et al., 2001) calls except for *low flat* (that is, *low up*, *medium up* and *high up*, *low down*, *medium down* and *high down*, *medium flat* and *high flat*, and *low variable*, *medium variable* and *high variable*. Only *low flat* calls would in some cases fall into the 'Low frequency' class (*table 1.4*). There are unfortunately few existing classes where membership is unambiguous. Because frequency modulation is often rather loosely defined, allowing for considerable variation in both frequency contour and onset frequency, the call types defined in this study could conceivably fall into various previously defined call descriptions.

In summary, all previously defined sounds for right whales of both hemispheres, apart from the call with a fundamental starting frequency of 1500 Hz (Payne & Payne, 1971), apparently occur in South African waters. There is some evidence of lower frequency growls in this study that are unreported elsewhere which merit further investigation. Reports of these occurrences should be regarded as opportunistic, and definitely not representative, as these calls were extremely quiet and difficult to detect aurally. The signal to noise ratios of these calls were very low, and it was beyond the scope of this thesis to examine every part of all recordings digitally. That we may have recorded the upper frequencies of infrasound is an intriguing possibility worthy of future research with dedicated equipment.

Table 1.4 Right whale acoustic repertoire

Call type: TONAL, PULSIVE, BROADBAND	May correlate with some calls from this study	Bandwidth (major energy)	Duration (sec)	Acoustic contour/sound quality/other	Function	Population	Source
Bellowings and moans of rising pitch	LU, MU, HU	Unknown	Unknown	Most common utterances (August 1972)	Mating whales, breeding	Argentinean	(Cummings et al., 1974)
Up call	LU, MU	50-200 Hz	0.5 to 1.5	Low tonal fm upsweep Simple, uniformly tonal, intensity increases towards end of sound	Contact call, swimming or mild activity, not mating	Argentinean	(Clark, 1983)
Upcall	LU, MU	50-200 Hz	0.7 to 2.2	Low, tonal fm sweeps	Male or calf, searching for female or during SAG	North Atlantic	(Parks & Tyack, 2005a)
Down call	LD, MD	100-200 Hz	0.5 to 1.5	Low, tonal fm downsweep. Simple, uniformly tonal	Swimming or mild activity	Argentinean	(Clark, 1983)
Downcall	LD, MD, HD	100-400 Hz	0.5 to 1.5	Low frequency tonal downsweep – tonal	SAGs	North Atlantic	(Parks & Tyack, 2005a; Parks et al., 2005b)
Constant	LF, MF, HF	50-500 Hz	0.5 to 6	Simple, uniformly tonal with very little fm	Swimming or mild activity	Argentinean	(Clark, 1983)
Low frequency (LF)	LF	60-80 Hz	~0.5-10	Constant frequency or slightly modulated - Quiet, only recorded with DTAGs	Unknown	North Atlantic	(Matthews et al., 2001)
High call	MU? HU? MD, HD, MV, HV	200-500 Hz	0.5 to 2.5	High, tonal, fm sweeps; multiple frequency shifts, often end with rapid frequency downsweeps	Fully active and sexually active	Argentinean	(Clark, 1983)
Hybrid sounds	LU, MU, HU, LD, MD, HD, LF, MF, HF, LV,MV, HV	50-500 Hz	Unknown	Complex sounds - points along a continuum	No behavioural correlations observed	Argentinean	(Payne & Payne, 1971)
High sound	No correlate	150 Hz	Unknown	Fundamental at 1500 Hz	Unknown	Argentinean	(Payne & Payne, 1971)
Hybrid call	MU,HU, MD, HD, MV, HV	50-500 Hz	0.5 to 2.5	Complex mixtures of fm sweeps and amplitude modulation - usually begin like a high call but become pulsive at the end	Fully active and sexually active	Argentinean	(Clark, 1983)

Warble	MU, HU, MD, HD, MF, HF MV, HV	100-2000 Hz	0.5-3.5	High, tonal, frequency and amplitude modulation signals – like Hybrid calls (Clark, 1983)	Juvenile calls in SAGs	North Atlantic	(Parks & Tyack, 2005a)
Pulsive call	LU, MU, LD, MD, LF, MF, LV, MV	50-200 Hz	0.5 to 3.5	Complex mixtures with amplitude modulations of noise and/or an fm signal - usually very harsh, strident or growly	Fully active and sexually active	Argentinean	(Clark, 1983)
Scream	MU, HU, MD, HD, MF, HF MV, HV	200-2500 Hz	0.3-5.1	Highly variable tonal calls with harmonic structure. May contain rapid frequency modulation. Part of call may mix broadband and tonal signals	Sexual advertisement by focal animal in SAG	North Atlantic	(Parks & Tyack, 2005a)
Blows	not analysed	100-400 Hz	0.5-26	Noisy, broadband, sometimes tonal like a long moan, sometimes noisy and pulsive	Produced during breathing out at the surface	Argentinean	(Clark, 1983)
Bellowing	LU, MU, HU, LD, MD, HD, LF, MF, HF, LV, MV, HV	Unknown	Unknown	Pulsive? ('like a mammoth bull')	During the hunt (alarm?)	North Pacific	(Scammon, 1874)
Belch-like utterance	LU, MU, HU, LD, MD, HD, LF, MF, HF, LV, MV, HV	30-2,200 dominant <500 Hz	1.4	Pulsive - source level (dB re 1μPa at 1 m)172-187. Most common utterances (June-July1971)	Unknown	Argentinean	(Cummings et al., 1971; Cummings et al., 1972)
Moans	LU, MU, LD, MD, LV, MV	Unknown	Unknown	Low frequency	Courtship? Not feeding	North Atlantic	(Schevill et al., 1962; Schevill & Watkins, 1962; Schevill, 1964)
Moan	LU, MU, HU, LD, MD, HD, LV, MV, HV	30-1250	0.6-4.1	Tonal, simple and complex moans	Unknown	Argentinean	(Cummings et al., 1971; Cummings et al., 1972)
Moans	LU, MU, HU, LD, MD, HD, MF, HF, LV, MV, HV	50-500 Hz	0.4-1.5	Vary widely in amplitude and frequency modulations	Unspecified	North Atlantic	(Matthews et al., 2001)
Miscellaneous	LU, MU, LD, MD, LF, MF, LV, MV	<1950 Hz	0.3 to 1.3	Low frequency	Unknown	Argentinean	(Cummings et al., 1971; Cummings et al., 1972)

Call type: PURELY BROADBAND NON TONAL	May correlate with some calls from this study	Bandwidth (major energy)	Duration (sec)	Acoustic contour/sound quality/other	Function	Population	Source
Pulse	GUNSHOT	30-2100 Hz	0.06	Pulse resembling a gun shot	Unknown	Argentinean	(Cummings et al., 1971; Cummings et al., 1972; Cummings et al., 1974)
Underwater slaps	GUNSHOT	50 – 1000 Hz	0.2	Noisy broadband sharp onset. When produced underwater very intense and painful	Mild to full activity, sexual activity	Argentinean	(Clark, 1983)
Gunshots	GUNSHOT	broadband	0.2	Broadband, impulsive. Correspond to 'slaps' (Clark, 1982), 'gunshot slaps' (Clark, 1990)	Mild to full activity, sexual activity	North Atlantic	(Matthews et al., 2001)
Gunshot	GUNSHOT	50 to 2000 Hz	0.2 to 0.3 (echo 1 to 3)	Noisy, broadband, sharp onset	Male agonistic interactions in SAG. advertisement display to attract females	North Atlantic	(Parks & Tyack, 2005a; Parks et al., 2005b)

It was also beyond the scope of this study to relate call types directly to behaviour (Clark, 1982; Clark, 1983). Recording was not targeted to any one behavioural context, as it was for North Atlantic right whales, where research centred on SAG activity(Parks, 2003b; Parks et al., 2005b), and screams were the most common call types (Parks & Tyack, 2005a). In this study the call profile was derived from calls recorded in a range of behavioural contexts in one location as they were encountered, sometimes concurrently, and included SAGs, cow-calf pairs and single whales. Given our equipment, bearings to caller were not calculated *in situ*, but on land post recording, and then for only the clearest *low up* calls and a few *medium down* and *high down* calls (*chapter four*). Many calls of all types were unsuitable for bearings analysis due to poor signal to noise ratio (SNR) or low received level. Of the calls for which bearings to caller were calculated, a notable proportion came from directions where whales were not sighted; of whale groups sighted from the boat, a sizeable proportion were silent (*chapter three*). For this study the whole recorded call set was thus analysed in a categorical matrix determined by two objective acoustic axes (onset frequency band and acoustic contour), rather than sacrificing the majority of calls so as to place the remainder in behavioural context.

Relative densities of various call types represented the summed acoustic output of whales engaged in a range of activities, between June and November. This sampling protocol is one likely to be applied in remote sensing applications, where behavioural context is unknown and calls must initially at least be taken at face value. An analysis of 'blind' recordings would reveal the relative densities of call types, which could then be compared to those presented in this study. Future studies of southern right whale calls of the southern coast of Africa, which link all call types to their behavioural contexts, will require appropriate technical equipment.

Within the matrix, the call classes represented the graded continuum of calls along the axes of starting frequency, acoustic contour and sound quality (degree of tonality or pulsiveness). Harsh calls were often interspersed with less harsh and purely harmonic calls, making an absolute condition for sound quality untenable. Many calls, such as those defined here as having a *high* starting frequency, but with a purely harmonic quality, did not apparently fit into any previously defined category, or could conceivably have fallen into more than one within one existing classification system (*column two, table 1.4*). In this study, calls were not related to activities, sound quality was not a determining factor in the matrix definition, and the calling rate was an absolute mean rate unrelated to whale numbers. (For the relationship between calling rate and number of whales, see *chapter 2*).

Relative overall and seasonal contributions and suggested behavioural significance of call types

Low up calls were the most frequently occurring overall during the study period. Based on previous studies of right whale calls (*table 1.4*), *low up* calls suggested the presence of single whales seeking

other whale groups, and cow-calf pairs maintaining contact (Clark, 1983), although they were also reported as central to SAG activity in North Atlantic right whale studies(Parks & Tyack, 2005a). *Medium* and *high* down calls were the next most abundant call types. Based on the observation that these two call types frequently occurred in the presence of SAGs, and the behavioural profile reported for the analogous 'High' and 'Hybrid; calls (Clark, 1983), the profusion of these calls indicated SAG activity. *Medium flat* calls were common, ranging from tonal 'Constant; calls to growly 'Pulsive' calls. Additionally, *medium* and *high variable* calls, though relatively scarce, were often encountered in the presence of SAG activity. They were also similar to some 'High' and 'Hybrid; calls, although it is difficult to give a comprehensive list of calls possibly contained within some previously defined classes, due to acoustic contour variability in definition (*table 1.4*). Gunshots, while the least abundant call type noted, were a distinctive feature of the acoustic profile recorded, and indicated the presence of SAGs(Clark, 1983; Parks, 2003a; Parks & Tyack, 2005a; Parks et al., 2005b), although they are reported in various behavioural contexts.

The changing proportions of call types which was observed as the season progressed is best understood in the context of the dynamics of the inshore right whale population. Walker Bay has been identified as being dominated by unaccompanied adults, rather than as a prime nursery site, with numbers reaching their peak in October, and in recent years being more abundant between June and September than in November (Best, 1981; Best & Scott, 1993). Their dominance in the area does not exclude cow-calf pairs, which are present in numbers later in the season.

In South African waters the numbers of whales participating in SAG aggregations tends to increase throughout the season. A possible reason for this is the 'declining availability of receptive females', with 90% of conceptions taking place around a window of 118 days, centred in mid-July (Best et al., 2003). The early season is consequently dominated by receptive (though not necessarily fertile) females and single males seeking copulations. (Intriguingly, available data suggests that South African SAGs largely involve sexually immature females which presumably do not come into oestrus (Best et al., 2003), but these groups may still be related to breeding, if only on a 'training' basis; other functions suggested for such behaviours include play and maintenance of social bonds(Parks et al., 2007a). Later in the season, the composition of the whale groups changes, with more cow-calf pairs present along with single males looking for the dwindling supply of available females, many of which will have left the area as the season progresses. The overall seasonality in the presence of right whales in Walker Bay(Best, 1970) is similar to that in nursery areas such as De Hoop Nature Reserve, where animals are first seen in April, reach peak numbers in September/October, and leave the area in early January. Most calves are born within an 118 day period with the peak of births in late August (Best & Scott, 1993). In Walker Bay the emphasis is on surface active groups (SAGs). As the season

progresses, increasing social complexity is brought about by the arrival of some cow calf pairs and yearlings.

When call types were considered for their proportional contribution within one of four given month slots, June was the only month within which *down* calls (consisting almost completely of *medium* and *high down* calls) were more prevalent than *up* calls. In this month gunshots were the third most common signal (compared with calls defined by acoustic contour alone – *up*, *down*, *flat* and *variable* calls), and the most common signal when compared to the twelve call types defined by both acoustic contour and onset frequency (*fig. 1.7*). Both these sounds have been associated with SAG activity (Kraus & Hatch, 2001; Parks, 2003a) (*table 1.4*). The decline in the presence of available females as the season progresses could explain the preponderance of *medium down* and *high down* calls in June, when available females were still relatively abundant and advertising vocally, and proportionally high levels of gunshots due to high proportions of males participating in SAGs.

The changing composition of the whale groups later in the season, with more cow-calf pairs, and more single males looking for available females, could account for the observed prevalence of *low up* calls as the season progressed. A similar pattern was noted in reports of 'belch-like utterances' (more pulsive calls) prevailing in June (Cummings et al., 1971; Cummings et al., 1972), and 'bellows and moans of rising pitch' ('Upcalls') occurring more commonly in August off Argentine (Cummings et al., 1974). Because Walker Bay is principally used by SAGs, a smaller proportion of recorded *low up* calls would be attributable to cow calf pairs than would be the case in a prime nursery area such as De Hoop. In Walker Bay the majority of *up* calls were likely to have been produced by solitary males in search of receptive females.

Monthly call rates, considering all call types together, were highest in September/October, as were whale numbers (*fig. 1.4*). *Up* call rates reached their peak in July and maintained a high level in September/October. *Down, flat* and *variable* call rates continued to rise through July, reaching a peak in September/October. Presumably as the season progressed, while high levels of surface activity persisted, the arrival of more cows, yearlings and juveniles, and the birth of calves, altered the balance within the whale population, with an accompanying modification of vocal activity. The peak in July of the more stereotyped *low up* calls and the subsequent altering balance of call types through the rest of the season may also reflect the initial dominance of solitary males urgently seeking females. The subsequent arrival later in the season of calves, yearlings and juveniles brings increased social complexity, perhaps adding to the use of the less stereotyped calls such as *flat* calls and *variable* calls, as well as *medium up* and *high* up calls, and *low down* calls. SAG activity, continuing throughout the season, would continue to contribute to *high* and *medium down* calls, accompanied by some *variable* calls.

Clustering of calls

There is strong evidence for clustering of *low up* calls, gunshots, and *medium down* and *high down* calls; these call types occur in bouts within specific contexts. This may not indicate that they are of greater functional importance (important calls may have long intercall intervals when they occur as lengthy calls or when they may attract predators), but it does indicate that, when clustering, they are produced within specific contexts. The establishment of contact with other whales (*low up* calls), sexual advertisement by receptive females in SAGs (*medium* and *high down* calls), and agonistic and advertisement displays by males in SAGs (gunshots) are the simplest behavioural contexts to be directly inferred. These calls are not found exclusively in such contexts, but the high incidence of short intercall intervals implies that they often are. Other call types show less strong evidence for clustering, and their functional importance is harder to determine. This observation is in agreement with earlier reports of the varied nature of adjacent calls in southern right whale vocal repertoire (Payne & Payne, 1971).

A variety of adjacent calls may reflect deeper subtleties in the communication system of southern right whales than we have thus far been able to demonstrate. It may transpire that the more mixed vocal patterns, harder to characterise into bouts of discrete call types, indicate increased social complexity and interactions, while the more stereotyped call sequences, which are easier to compartmentalise, represent simpler messages.

It has already been proposed that right whales use sound purposefully in social contexts (*table 1.4,* (Clark & Clark, 1980), and this study, while viewing the repertoire from a somewhat different perspective using a different system of call classification, supports this conclusion. Southern right whales use a variety of calls that, to a greater or lesser degree, cluster in bouts and differ in their relative proportions and rate of production from month to month, presumably as a result of changes in demographic composition and behavioural state at any given time. A high proportion of calls with strident, pulsive and 'growly' qualities may indicate higher levels of excitation or energy expenditure in the callers; purely harmonic calls suggest callers with calmer states.

The matrix call classification developed in this paper has several advantages over other classification systems. It has been developed independently of any behavioural context. It is simple and, by classifying three frequency octave bands for call onset, places each call more exactly than a larger 'catch-all' description could, and the proposed system is more specific in regard to onset frequency than other systems currently in use. Calls of southern right whales may move up through the frequency spectrum and embrace more than one call class along a continuum. This need not conflict with the matrix system, which, while acknowledging that there is a flow from one category to the other, at least attempts to locate the onset of each call within smaller bandwidths than previous systems have done. Where two categories appear to function as one functional unit (as with *medium* and *high down* calls),

they can easily be consolidated later, but retaining the onset frequency classification allows for consideration of calls in different contexts, based both on acoustic contour, and on onset frequency. Using either one of these axes as a basis for classification provides broader resolution in terms of either onset frequency or acoustic contour, leaving the door open to the possibility of unexpected discoveries about the importance of either parameter; using both axes allows for finer resolution of the varied and often unpredictable repertoire of southern right whales.

Improvements and topics for future research

This system deliberately avoids the quantification of sound quality because of the dynamic changes observed in this aspect of right whale vocalisations, often for consecutive calls within close proximity of each other, and apparently emitted in a single behavioural context. It would however be interesting to note the relative presence of non harmonic, broadband (pulsive, strident and 'growly') sound qualities for all calls instead of for a small subset, to assess the proportions of harmonic and non harmonic calls in any given context. The disadvantage in such an approach, however, would be an immediate doubling in call types, with accompanying loss of simplicity. Although splitting and merging of call types in the categorical matrix, discussed above, may provide new insights, the addition of 12 extra call types to account for sound quality (making 24 sound types) could become unwieldy, particularly as there appears to be a continuum of sound quality, from purely harmonic to purely broadband. One solution could be to keep the proposed 13 call types (12 plus gunshots), and to add an integer to each recorded call, from 1 to 5 (for instance, harmonic *low up* call (1) to *gunshot* (5)), along this continuum.

The analysis of aerial sounds such as blows, sometimes heard underwater and in air, would add to the understanding of the use of sound by right whales, although it would not generally be a useful class of sound for most passive detection systems because it is not always recorded underwater. Some tonal and pulsive blows (Clark, 1982), when they are detected underwater, may contain information about group membership which could be used in passive systems. In regions where whales habitually gather, aerial recordings with accompanying visual observation would simplify the identification of the source whale immeasurably, as blows are easily seen. The extent to which whales can hear aerial sounds is not known, but blow sounds audible in air to researchers are likely to be heard underwater by whales in audible range. Source levels could be calculated using ranges determined by the differential time delays in water-borne and aerial recordings (Wahlberg et al., 2002).

A detailed assessment of the progressive sequences in which calls of all types occur may reveal further insights into the use of sound by southern right whales. The analysis of each call type in isolation, or even a few call types that occur in together in specific contexts, such as *medium down* and *high down* and sometimes *medium variable* and *high variable* calls in SAGs, is by no means a comprehensive view. An emerging pattern of call type sequences, if it exists, could be used to detect group

membership and activities and to predict future behaviour, which would be an acoustic asset in whale/human interaction risk management; for instance, whales engaged in sexual activity in SAGs, or moving fast from one location to another, would be vulnerable to ship strikes in a different way than calm, placid whales, apparently resting at the surface, and may require different ship/boat approaches.

The lowest frequency band considered was 55–110 Hz, and most tonal calls had an onset frequency falling within that or a higher octave band; but a few calls starting below 55 Hz were detected. Using dedicated equipment, the low frequency sounds already detected with low received levels (and possible low source levels) both above and below 55 Hz should be further investigated. The possibility that right whales use lower frequencies than expected raises questions around the biological significance of such signals, and the impact of human-generated noise on whale communication.

Finally, the use of advertisement calls by female right whales in SAGs (Kraus & Hatch, 2001; Parks, 2003a) remains an enigma worthy of research. A terrestrial counterpart, the female elephant in oestrus has four days in every four years to attract mates, and uses a low frequency oestrus call to assist males in locating her over this brief period. A recorded low frequency oestrus call, when played over a loudspeaker, induced a male elephant to walk more than 1.5 km (Pye & Langbauer, 1998). Nothing is known about the nature or length of southern right whale oestrus. However, the duration of the breeding season, or the time window within which most conceptions are thought to occur, is currently held to be 118 days centred around mid-July (Best et al., 2003). The SAG-related calls described above may be an example of convergent evolution of call signaling, but the SAGs encountered off South Africa clearly do not always lead to conception as the focal female is usually sexually immature (Best et al., 2003). Parks identified a few examples of juvenile 'screams' as the sub-class 'warbles'(Parks, 2003a; Parks & Tyack, 2005a), but they were assigned a very broad bandwidth. The *high down* and *medium down* calls recorded in this study comprised the majority of SAG-related calls. It is therefore likely that many of these characteristic calls were, in fact, produced by sexually immature whales. Detection of potential differences in the calls of sexually mature vs. immature whales, if such differences exist, would signal to human researchers information which may already be apparent to whales.

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ACOUSTIC BEHAVIOUR OF SOUTHERN RIGHT WHALES IN SOUTH AFRICAN
WATERS IN RELATION TO NUMBERS OF WHALES PRESENT

1. Introduction

Several aspects of human exploitation of the oceans place marine mammals in danger.
Mortalities from ship strikes and entanglements in fishing gear contribute to the current
decline in North Atlantic right whales, and the prevention of just two adult female deaths per
year could reverse the trend (Fujiwara & Caswell, 2001). The military use of naval
excercises(Simmonds & Lopez-Jurado, 1991) and Mid Frequency Active (MFA) sonar for
submarine detection(Frantzis, 1998) has been linked with mass strandings of multiple
cetacean species, beaked whales being particularly vulnerable (Balcomb & Claridge, 2001;
Crum et al., 2005). At high levels, the pulses used in geo-seismic exploration, with sound
levels of up to 250 dB re 1µPa at 1m (Greene & Richardson, 1988) may damage auditory
systems, e.g. causing permanent hearing threshold shifts. At lower levels, they may affect
surfacing, breathing rates, and dive times, and result in alarm and avoidance behaviour or
cause temporary hearing threshold shifts(McCauley et al., 1994).

The ability to locate and estimate the density and movement patterns of whales present in an
area proposed for such exploitation is an important step in attempting to mitigate these
negative impacts, but such factors are often difficult to ascertain. Whales spend much of their
time submerged, and may cover long distances on a daily basis. The possibility of making
visual sightings is severely hampered by rough weather conditions, and is almost non-existent
at night. Fortunately, communication amongst individual cetaceans in the contexts of
reproductive displays, prey detection, predator avoidance, and navigation, is primarily
acoustic (MacLennan & Simmonds, 1992). The exploitation of biological sounds for locating,
tracking and estimating the density of groups of whales, affords methods suited both to the
underwater medium and the properties of the calls. Acoustic detection of whales has several
advantages over visual detection; this has been demonstrated for fin whales (McDonald &
Fox, 1999): it can be applied in remote situations and for protracted periods, where boat and
aerial surveys would be impractical or expensive. Additionally, acoustic detection covers a
greater range than visual detection, can occur under more adverse weather conditions and
during both day and night, often resulting in greater efficiency (Clark et al., 1996; IFAW,
2001).

Southern right whales in coastal waters off South Africa have an extensive acoustic repertoire
(see *chapter one*). For the purposes of remote sensing, the rate at which their sounds are
produced is measurable by remote recording of underwater sounds in the area, in the absence

of manned stations. Data may be post-processed to count and categorise the calls and to derive absolute rates of sound production. Of cardinal importance is the relationship between the absolute call rate and the number of whales present in the area. It is possible that rates of sound production may differ depending on factors such as the season, prevailing environmental factors, the time of day, the number of whales present, and their behaviour (socialising, non-socialising). This is therefore a research topic of high priority, and the 'ultimate goal of many applications of…passive acoustic systems' (IFAW, 2001). If a quantitative link can be established between the recordable calls from a local aggregation of whales, and its size and composition, an insight into the demographics of remote whale populations will be within grasp. Even an abundance index based on calling rates could provide information vital for stock management and informed industrial planning (Matthews et al., 2001).

This chapter describes an investigation into the relationship between the calling behaviour of southern right whales and the numbers of whales present. The intention is to derive a method of assessing local whale numbers using an index of whale presence based on call rate. By investigating the factors affecting the call rate in relation to whale numbers, we seek to find the conditions, defined by external variables such as time of day or time of season, wind direction and speed, where call rates may be reliable indicators of numbers of whales present.

This task presents several challenges. Firstly, 'acoustic data alone provide no information as to the numbers and distribution of non-calling whales' (Stafford et al., 1998), (see *chapter three* for proportions of silent groups). Secondly, without knowledge of individual differences it is not possible to determine how many individuals are contributing to the recorded calls (Stafford et al., 1998). (see *chapter four* for individual differences). 'A combination of passive localization and on-site observations of whales should provide a more complete picture of the animals' behaviour while calling as well as the proportion of calling animals in one area' (Stafford et al., 1998). The generalised linear model used in this study adjusts for parameters such as month, time of day, recording effort, wind speed and direction and numbers of whales in view to provide a relative index of predicted sound production by southern right whales in groups of varying sizes.

2. Materials and method

Between June and November, 1999, underwater recordings were made in Walker Bay, South Africa (*fig. 2.1*) during daylight hours, from a 6m semi-rigid inflatable boat, in the presence of southern right whales.
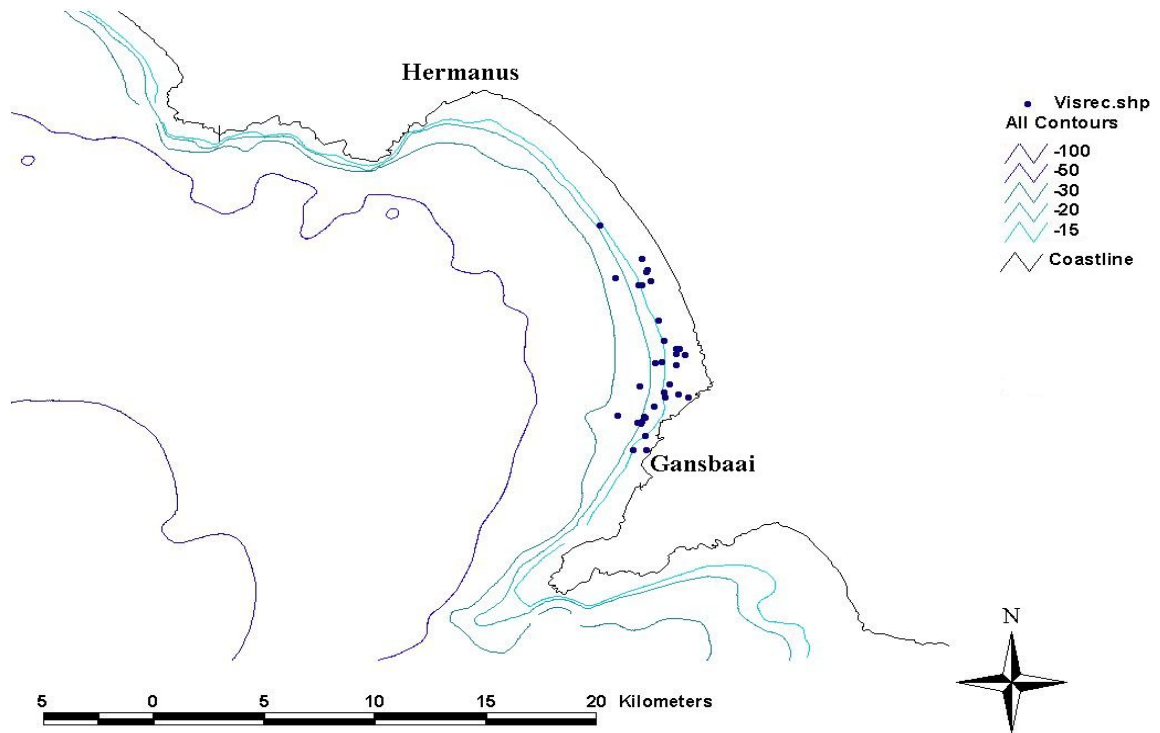
Figure 2.1 Positions (dots) from which simultaneous acoustic recordings and visual observations of whales were made from a semi-rigid inflatable boat with an elevated viewing platform in Walker Bay, South Africa, between June and November, 1999. All sampling points fell within the zone with a maximum depth of 30 metres, principally with a sandy substrate.

For 62 hours of acoustic recordings that included whale vocalisations, a record was kept concurrently of visual observations of, bearings to, and distance from, whales in the vicinity of the boat and, where possible, the number of whales in the various groups, and their composition and behaviour.

2.1 Data collection

Acoustic recordings

A mono recording system utilised a hydrophone custom built by the Institute for MaritimeTechnology. Due to equipment constraints it was not possible to calibrate the hydrophone below 2 kHz; it was calibrated between 2 and 20 kHz, and received from 2 Hz to at least 20 kHz. with a sensitivity of -146.5dB re 1V/uPa at 2kHz, with decreasing sensitivity to -169dB re 1V/uPa at 20kHz (volume of recording device set at 50, reduced by approximately 7dB across the frequency range when volume set at 25).

The hydrophone was deployed depending on the prevailing wind and current, so that it drifted away from the boat. To minimise noise arising from flow and turbulence around the hydrophone, and general water noise, a spar buoy was attached to the cable at a distance of approximately 5 metres from the hydrophone. To keep the line afloat, several tennis balls were loosely connected to the cable between the buoy and the hydrophone using fine mesh netting. The signal was recorded on an Aiwa portable DAT recorder (model HS-JS165) with a flat response between 20 Hz and 20 kHz at 85 dB (or better), modified to run on a 12V alarm battery.

Visual observations

During acoustic recording sessions a continuous watch was kept for the arrival, presence and departure of whales from an elevated viewing platform 3 metres above the deck. From this vantage point it was possible to observe whales within a radius of approximately 1 kilometer of the boat, and record absolute bearings from the boat to the whales using a hand-held Autohelm electronic compass. Distances of the whales from the boat were determined visually.

2.2 Data analysis

Continuous recording sessions

In order to determine the number of whales present during any single continuous recording session, it was first necessary to include only those periods where there was an overlap of visual observation and acoustic recording, excluding non-overlapping data from both categories. Rates of sound production were determined both directly from the number of recorded calls per unit time, irrespective of the number of whales sighted from the boat (overall call rate, or OCR), and also in relation to the number of whales sighted (call rate per

whale, or CPW). Acoustic recordings and visual observations were made between 23rd June, 1999 and 20th November, 1999, on 19 days (3 in June, 5 in July, 2 in September, 4 in October and 5 in November). After discarding non-synchronous data, 59 continuous recording sessions, covering 47 hours and 21 minutes, remained.

Counts of whales sighted from the boat

The accuracy of visually-based counts of whales from the viewing platform was dependent on the distance of the whales from the boat and prevailing weather conditions. Where possible, the size of groups was noted and specified. Only the final estimate of group size (after the group had been observed for as long as possible) was used. Where it was not possible to estimate group size due to weather conditions or distance, the presence of the group was noted, but the group size was not specified, and an averaging algorithm was applied (see below), based on the known sizes of other whale groups present.

Cumulative and non-cumulative counts and the 'clone' algorithm

During a continuous recording session, the number of visible whale groups and their composition sometimes changed as whales arrived in or departed from the region of the boat, and joined or left other groups. Whale counts were analysed in two ways. In the cumulative method, any group observed during a continuous recording session was counted and added to the number of observed whales for that recording session. The non-cumulative method was more complicated. Each session was divided into a series of subsessions (duration_1, duration_2…duration_n), defined by observed changes in the distribution of whale groups (whales_1, whales_2…whales_n). An average number of whales present, weighted according to the duration of each subsession, was derived for each complete session, using the product of the number of whales and the duration in minutes of each subsession, as follows:

Average #whales = $\sum$ (whale_minutes_i..whale_minutes_n)/$\sum$ (duration_i..duration_n)   (1)

These two methods were used to reflect two possible relationships between recorded calls and whale presence. In the cumulative method, the whales already sighted during a continuous recording session were assumed to be still within acoustic range of the hydrophone either before or after they were sighted, and thus able to contribute to the number of recorded calls. The non-cumulative method assumed that before and after sightings, whales were not contributing to the recorded calls.

For groups of unspecified size, whale numbers were determined using the "clone" algorithm, according to which the distribution of group sizes in the unspecified groups was assumed to be the same as the distribution of other observed and specified group sizes. Where all groups in a continuous recording session were of unspecified size, the weighted average group sizes of groups in the closest adjacent recording sessions on the same day were used (with greater weight given the longer sessions). When the session with unspecified group sizes was the first or last session on that day, only the subsequent or preceding session respectively was used.

Otherwise both the preceding and the subsequent sessions were used. Sessions for which group size was calculated were separated from the preceding or subsequent session by time intervals ranging from 1 to 72 minutes. The cumulative method of counting whales, when applied to the call data, gave the better statistical fit and smaller standard error, and was adopted along with the 'clone' algorithm, for the generalised linear model used in subsequent analysis.

Generalized linear model

There were 59 recording sessions, drawn from 19 research days, where visual observations were synchronous with acoustic underwater recordings. These were divided into four monthly bins: June, July, September/October, and November, separated respectively by 20, 62 and 37 research days. Within monthly bins, 3 research days in June were separated by 3 and 1 day/s respectively; 5 research days in July were separated by 1, 5, 2 and 1 day/s respectively; 6 research days in Sept/Oct were were separated by 1, 1, 1, 2, and 1 day/s respectively; and 4 research days in November were separated by 1, 4 and 4 day/s respectively. Inter-session intervals where multiple sessions occurred on one day ranged from 57 s (minimum) to 2h 58 min (maximum), with a mean duration of 41 min 42 s.s

The sessions were analysed using a generalised linear model. This technique attempts to analyse the relationships between multiple measurements made on groups of subjects or objects (Dobson, 1990). An explanation of the variation in the response variate – in this case, the number of calls recorded over time during a continuous recording session – is attempted in terms of the independent variables – in this case, month of the year, time of day, wind speed, wind direction, and number of whales sighted during an observation (*clcum*, for sizes of whale groups where unspecified groups were assigned a size using the 'clone' algorithm, and counted cumulatively).

The model developed attempted to account for the variability in observations, while adjusting for the differing lengths of the recording sessions, and incorporating information about independently variable factors influencing the number of calls produced over any given time (the dependent variable). Using mathematical formulae derived from the data, the model was used to predict the number of expected calls under varying conditions, using the arguments

Log [expected number of calls] = constant + log [observation period] + [effect due to wind speed] (range 0-5.3 knots) + [effect due to wind direction] (NE, NW, SE, SW, no wind) + [effect due to time of day] (8:00-18:00 in 2-hour slots: time1-time5) + [effect due to month of year] (June, July, September/October, November) + [linear effect of number of whales] + [quadratic effect of number of whales].

Variables found to be non-significant were time of day and wind speed, and so we adopted a generalised linear model with the arguments

Log [predicted number of calls] =constant + log [observation period] + [effect due to wind direction] + [effect due to month of year] + [linear effect of number of whales] + [quadratic effect of number of whales].

Y = all recorded calls entered into the analysis; E(Y) = predicted number of calls;

Var (Y) = S squared* E (Y); S squared = overdispersion (an estimate of the extra variation).

All effects were assessed against S squared = 25.82. The reference level was the month of June with no wind.

Given an overall call density (number of recorded calls over time), a prediction model was developed for the number of whales in visual range from the boat. Acoustic range from the boat was unquantified but presumably greater than the visual range. It was not possible to correct for the discrepancy between visual and acoustic ranges by extrapolating to increase whale number estimates for an expanded range for two reasons. The acoustic range was unknown, and overall whale distribution was unquantified and uneven. This is in contrast with a study of blue whale calling in the Rottnest Trench area, where animals were spread evenly over a large range (McCauley et al., 2001). Nevertheless as this was a relatively enclosed bay, the relationship between the recorded calls (in acoustic range) and the number of whales (in visual range) was considered as a potential index of local whale abundance.

Proportional contribution of thirteen call types in relation to observed numbers of whales
The calls were also analysed in terms of the relative contribution of their component call types (see *chapter one*), in relation to the number of whales sighted from the boat. Thirteen call types were included in the analysis: *low up*; *medium up*; *high up*; *low down; medium down*; *high down*; *low flat*; *medium flat*; *high flat*; *low variable*; *medium variable*; *high variable*; and gunshots (*see chapter one*). Call frequencies of these 13 call types (the unit of analysis) were grouped by their occurrence in the presence of a range of numbers of whales sighted from the boat (counted cumulatively using the 'clone' algorithm); whale numbers were grouped in bins of 3 whales, from [1–3] to [22–24] whales. Pearson's chi-squared analysis was performed on this data; 17 (16.3%) of the cells in the expected frequencies contained values of >5, an unacceptable portion, as the threshold for allowable expected frequencies >5 is no more than 10%. When the very rarest call types (*low down* and *low variable*), amounting to 65 calls (2.2%), were removed from the analysis, the number of expected cells with values >5 fell to an acceptable number of 7 (8%). When the four rarest call types (*high up*, *low down*, *high flat* and *low variable*), amounting to 284 calls (9.6%), were removed, there were no expected cells with values >5, and a chi-squared analysis was carried out on these two sets of call types.

A similar approach was used to explore the contribution of each call type making up the call total, first as defined by the call onset frequency (defined for *low* calls, as between 55 Hz and

109 Hz; for *medium* calls, as between 110 Hz and 219 Hz; and for *high* calls, as between 220 Hz and 440 Hz), and then as defined by acoustic contour (*up*, *down*, *flat*, *variable*). Because these grosser-resolution call groupings provided greater numbers of calls in each bin of 3 whales, a chi-squared analysis was also performed on both these groups. In assessing the difference between observed and expected call rates, the part played by both the numbers of whales present, and the various call types, was investigated by iteratively removing each bin of whales, and then each call type, from the analysis.

Call rates per whale in the presence of increasing whale numbers
The call rate per whale (CPW) was investigated because of the observation that the relationship between overall call rate (OCR) and whale numbers was non-linear. Data were grouped in bins of multiples of three whales for aggregation size (representing the number of whales sighted from the boat during any given recording session, not necessarily all in one group). Call rates per whale per minute were considered both over the whole season and according to month of the year, for all calls together and for 13 call types. Recordings during which whales were sighted, but apparently did not vocalise, were included in the analysis.

Both OCR and CPW were plotted against numbers of whales sighted to investigate the relationship between these factors, and in relation to time of day and time of year. Analysed calls included summed totals of all calls (including gunshots), *low up* calls separately, and *medium* and *high down* calls separately.

3. Results

3.1 Generalised Linear Model

Factors contributing to the observed variation in call density
There were no significant interactions between month, wind direction and number of whales. Random variation was assumed to be over-dispersed Poisson, due to the high variability of vocal patterns and calling rates encountered. The F test rejected the hypothesis of no significant regression, implying that at least one of the variables in the model influences the call rate.

Effect of month
Compared to June and adjusted for wind direction and number of whales, the predicted number of calls in July was 4.5 times that in June (p=0.085),and in September/October was 6.5 times that in June (p=0.033). The predicted number of calls in November was 2.2 times that in June (ns) (*fig. 2.2*).

Effect of wind
Compared to conditions of no wind, and adjusted for month and number of whales, the predicted number of calls with a NE wind was 31% of that with no wind (p=0.2, ns); the

predicted number of calls with a SW wind was 23% of that with no wind (p = 0.1, ns); the predicted number of calls with a SE wind was 18% of that with no wind (p = 0.05); the predicted number of calls with a NW wind was 16% of that with no wind (p = 0.2, ns) (*fig. 2.3*).

Number of whales

The effects of both linear and quadratic number of whales were highly significant (p = 0.001, p = 0.002).

3.2 Relative contributions of various call types in the presence of increasing numbers of whales

Relative frequencies of call types

Pearson's chi-squared analysis of all thirteen call types (LU, MU, HU, LD, MD, HD, LF, MF, HF, LV, MV, HV and gunshots) was impractical because it resulted <10% of cells of expected frequencies with values of >5. First the very rarest calls, *low down* and *low variable* (2% of calls) were removed, leaving an acceptable 8% of expected cells with values >5; then *low down* and *low variable* and, in addition, *high up* and *high variable* calls (10% of calls) were removed, leaving no expected cells with values >5. Pearson's chi-squared analysis was performed on each call type set and, in both of these analyses, the chi-squared statistic (p >0.00001) suggested rejection of the null hypothesis of a random distribution. Results demonstrated unequivocally that the numbers of whales present had an effect on call composition (*figs 2.4, 2.5*).

A chi-squared analysis of the contribution of gunshots and three call types defined by onset frequency (*low*, *medium* and *high*, *table 2.1*), relative to the total calls, in the presence of increasing whale numbers, tested for the constancy or otherwise of the relative call distribution in the presence of different numbers of whales. A similar process was carried out for gunshots and four call types defined by acoustic contour (*up*, *down*, *flat* and *variable*, *table 2.2*). The analysis asked the question, 'is there a fixed relationship between call types or is it influenced or determined by the number of whales present? Results of the chi-squared analysis suggested that the distribution of gunshots and call types defined by onset frequency was significantly influenced by the number of whales present (*table 2.1*, p <0.0001). Similar results were found for call types defined by acoustic contour (*table 2.2*, p <0.0001).

Figure 2.2 The effect of month on predicted number of calls E(Y), compared to June and incorporating information about the other independent variables, wind direction and number of whales (June: red; July: green; September/October: light blue; November: dark blue).
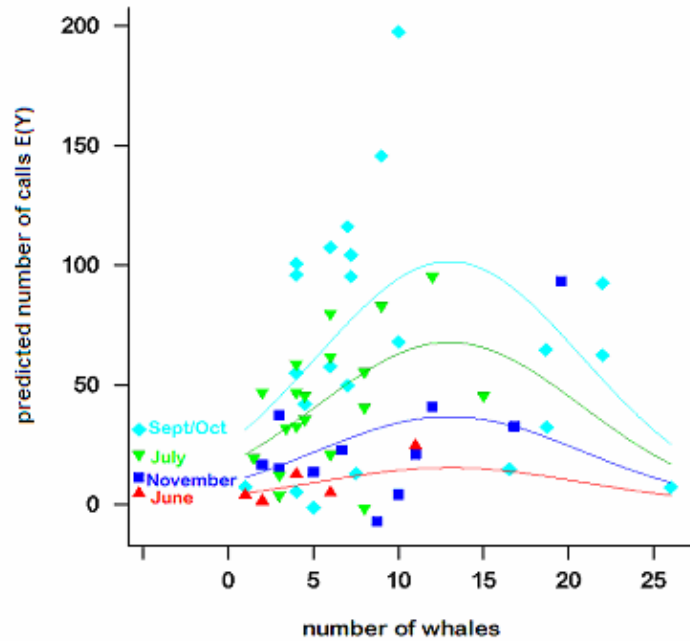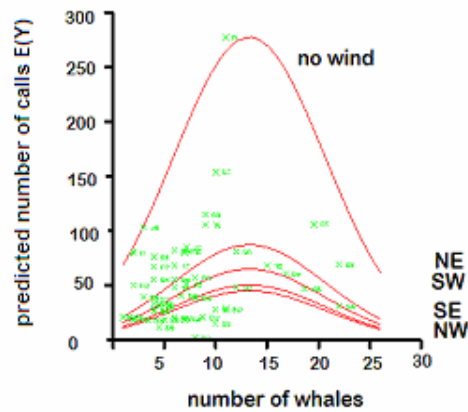

Figure 2.3. The effect of wind direction on predicted number of calls E(Y), compared to no wind and incorporating information about the other independent variables, month and number of whales.

Table 2.1 Frequency distribution of 3 call types defined by onset frequency , and gunshots, in the presence of increasing numbers of right whales.

				NUMBERS OF WHALES				
CALL TYPE	1 to 3	4 to 6	7 to 9	10 to 12	13 to 15	16 to 18	19 to 21.	22 to 24
Low calls	39	257	316	181	34	57	45	43
Medium calls	45	284	179	308	32	84	67	91
High calls	41	230	133	232	32	10	8	44
Gunshots	11	51	34	57	2	10	0	10

Table 2.2 Frequency distribution of 4 call types defined by acoustic contour, and gunshots, in the presence of increasing numbers of right whales.

				NUMBERS OF WHALES				
CALL TYPE	1 to 3	4 to 6	7 to 9	10 to 12	13 to 15	16 to 18	19 to 21	22 to 24
up calls	47	325	324	218	47	70	36	75
down calls	40	200	125	273	27	33	34	39
flat calls	28	157	112	141	12	34	39	47
variable calls	10	89	67	89	12	14	11	17
Gunshots	11	51	34	57	2	10	0	10

The impact of various aggregation sizes

To determine the relative contributions made by whale groups of various sizes to the difference between observed and predicted call type distribution, each group size (*table 2.3*) and then each call type (*table 2.4*) was iteratively excluded from the calculation.

For calls defined by onset frequency alone (*low, medium* and *high*), groupings of 7-9 whales had the greatest impact, in that the excision of this group reduced the difference between call composition for various whale group sizes by the greatest degree. This was followed by aggregations of 10-12, 16-18 and 19-21 whales (their removal most reduced the difference between observed and expected call frequencies). For calls defined by acoustic contour only (*up, down, flat, variable*), aggregations of 10-12 whales had the greatest impact, followed by those of 7-9 and 19-21 whales.

The impact of various call types

When calls were defined by onset frequency only, *low* calls had the greatest impact, followed by *high* calls and then *medium* calls (*table 2.4*). For smaller numbers of whales, *low*, *medium* and *high* calls were more or less equally distributed; when numbers reached 7-9 whales, *low* calls took a strong lead, while in the presence of 10 or more whales, *medium* calls tended to predominate (*fig. 2.7).*

Table 2.3 Determining which size grouping of whales present contributes most to variation in call type distribution. P-values after removal of a whale group class in bold indicate that its removal caused the greatest impact (suggesting that its inclusion contributed greatly to the variation in call distribution).

	low, *medium*, *high*, gunshots		*up*, *down*, *flat*, *variable*, gunshots	
	chi statistic	p value	chi statistic	p value
	199.08	5.49E-31	127.83	1.04E-14
grouping of 1-3 whales removed	195.10	9.54E-32	124.35	1.62E-15
Grouping of 4-6 whales removed	192.33	3.40E-31	125.71	9.21E-16
grouping of 7-9 whales removed	108.43	**6.18E-15**	82.74	2.21E-08
Grouping of 10-12 whales removed	154.43	1.02E-23	59.40	**7.76E-05**
grouping of 13-15 whales removed	193.66	1.85E-31	120.06	9.45E-15
groups of 16-18 whales removed	164.10	1.31E-25	123.90	1.95E-15
groups of 19-21 whales removed	161.81	3.69E-25	105.86	2.95E-12
groups of 22-24 whales removed	184.70	1.12E-29	121.40	5.45E-15

Table 2.4. Probability values and chi statistics for chi distribution of call frequency. Shown for 13 call types (onset frequency and acoustic contour), for low, medium and high calls (onset frequency) and gunshots, and for up, down, flat and variable calls (acoustic contour) and gunshots. Iterative results after removing each call type successively to demonstrate their relative impact on the result. P-values after removal of a call type in bold where its removal caused the greatest impact (indicating that its inclusion contributed greatly to the variation in call distribution).

	chi statistic	p value		chi statistic	p value
low, *medium*, *high*, gunshots	199.08	5.49E-31	*up*, *down*,*flat*, *variable*, gunshots	127.8267494	1.04E-14
low calls removed	91.00	**2.46E-13**	*up* calls removed	48.787441	**0.0005**
medium calls removed	128.06	1.64E-20	*down* calls removed	70.910489	2.51E-07
high calls removed	114.80	6.5 3E-18	*flat* calls removed	103.171298	7.90E-13
gunshots removed	182.12	2.41E-31	*variable* calls removed	124.117543	1.25E-16
			gunshots removed	112.100693	1.97E-14

Grouped by acoustic contour only, *up* calls were most influential, followed by *down* calls and then *flat* calls, in shaping the variation in relative call frequencies in the presence of differing sizes of whale groupings (*table 2.4*). For most of the size range of whale grouping, *up* calls dominated, although for gatherings of 10-12 whales, *down* calls were slightly more prolific. While *down* calls were more common than *flat* calls among smaller numbers of whales, for groupings of above 16 whales, *flat* calls became as prevalent (or more so) than *down* calls.

In other words, the relative production of various call types could potentially deliver information about the local whale density (*fig. 2.7, 2.8*). In general lower numbers of whales were most likely to produce *low up* calls more often than *medium down* and *high down* calls (*fig. 2.6*), although because of low numbers of calls in some expected call frequency

categories when analyzing all thirteen call types, the chi-squared analysis was not performed, as it was with onset frequency- and acoustic contour-defined calls (*fig. 2.7, 2.8*). Calls defined by onset frequency alone followed patterns that were easier to interpret than those of calls defined by acoustic contour alone. Similar levels of *low*, *medium* and *high* calls were recorded for smaller gatherings of whales (*fig. 2.7*). When whales were present in higher numbers, the call profile was likely to include lower levels of *high down* calls and elevated levels of *medium down* calls (*fig. 2.6*). High whale numbers would also indicate wide separations in the high levels of prolific *medium* calls, intermediate levels of *low* calls and depressed levels of *high* calls (*fig. 2.7*).

Call rates per whale over the season and by month, in the presence of increasing whale numbers

While the predicted number of calls rose and later fell with increasing whale numbers, as demonstrated by the generalised linear model (*figs. 2.2, 2.3*), the CPW, viewed over the wholeseason, tended to fall consistently in the presence of increasing numbers of whales. (y = -0.0305x + 0.2738, R^2 = 0.8957, fig.2.9). This tendency was manifest in most months throughout the season, with the exception of June, in which there was a peak in call rate per whale at 10-12 animals (fig. 2.10), probably due to small sample size. The falling pattern in CPW was clearest in July (fig. 2.11), when low up calls predominated over all whale group sizes, with a peak at 7-9 whales, and then continued to fall. There was a gradual, more-or-less steady drop in the rates per whale of the other call types.

Low up, *medium down* and *high down* calls (the three call types most influential in altering the relative proportions of call types in the presence of different numbers of whales, *fig. 2.6*), reflected the same falling CPW pattern in the presence of larger groups of whales (*fig. 2.12*). *Low up* calls, while declining overall, showed a strong peak in the presence of 7-9 whales, and a smaller peak for 13-15 whales. The gunshot CPW also fell as whale numbers rose, with a slight increase in the presence of the largest whale aggregations encountered.

The same two peaks in a generally declining call rate per whale for *low up* calls, were manifest for *low* calls when grouped by onset frequency (*high*, *medium* and *low*, *fig. 2.13*), and for *up* calls, when grouped by acoustic contour (*up*, *down*, *flat* and *variable*, *fig. 2.14*). All other call types (*medium* and *high*, for onset frequency, *fig. 2.13*, and *down*, *flat* and *variable*, for acoustic contour, *fig. 2.14*) showed a consistent decline, with the same marginal increase in gunshot calling rates per whale at highest whale numbers.
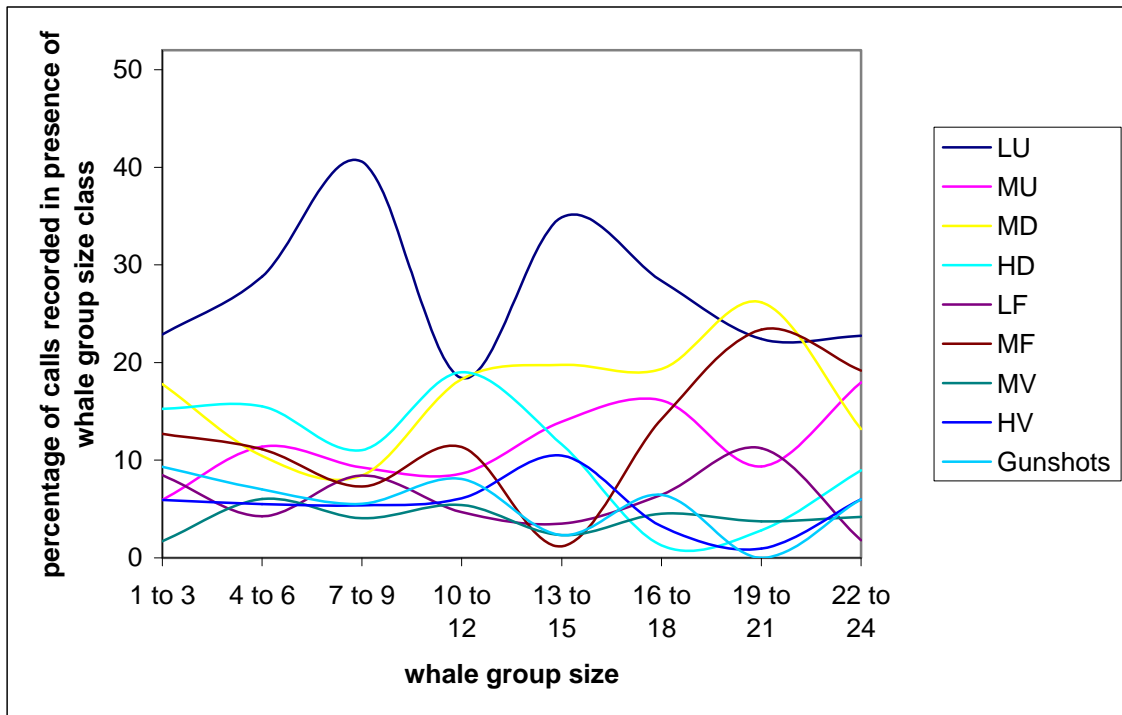
Figure 2.4. Relative call compositions of the most abundant calls recorded in the presence of a range of whale numbers (9 call types for which distribution differed significantly from a random distribution, Pearson's chi-squared test, p=>0.00001). After meeting LU calls at 20% in presence of 10 to 12 whales, MD calls increase and HD calls decrease their relative proportions of call totals in the presence of greater numbers of whales.
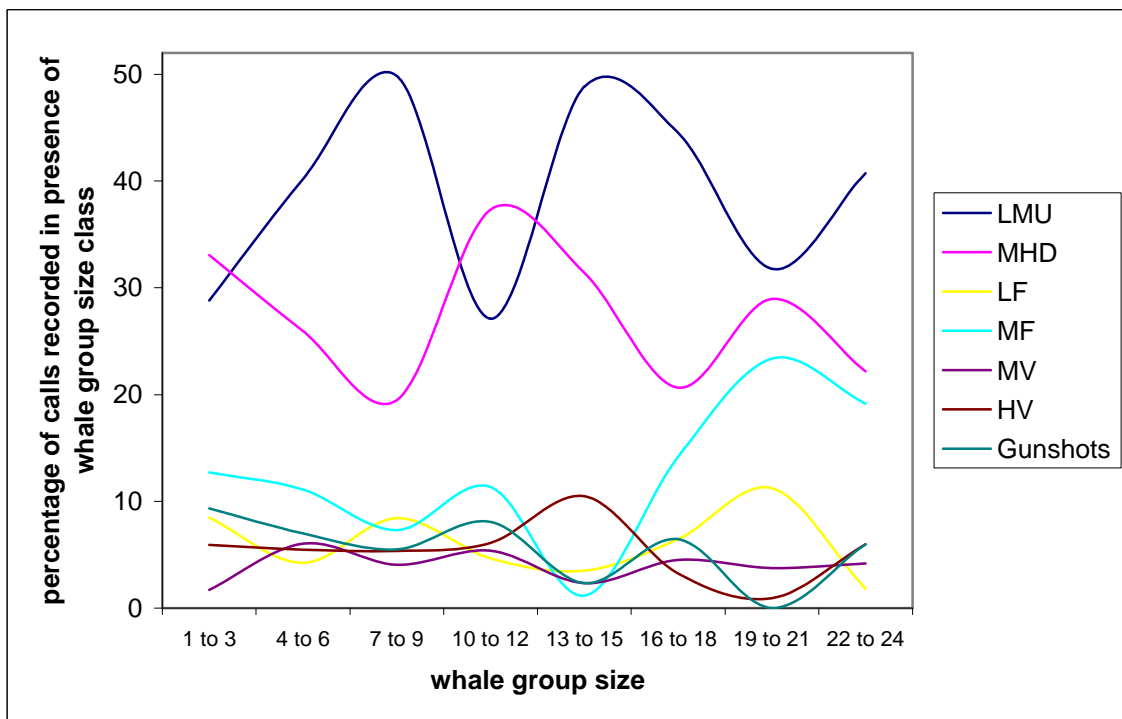

Figure 2.5. Relative call compositions of the call data from figure 2.4 (above), with [LU and MU] amalgamated as LMU, and [MD and HD], as MHD. In the presence of 10 to 12 whales, MHD calls are more abundant than LMU calls. Both dominate throughout. Note dramatic rise in MF calls in presence of high numbers of whales. Gunshots are most abundant in presence of low whale numbers.
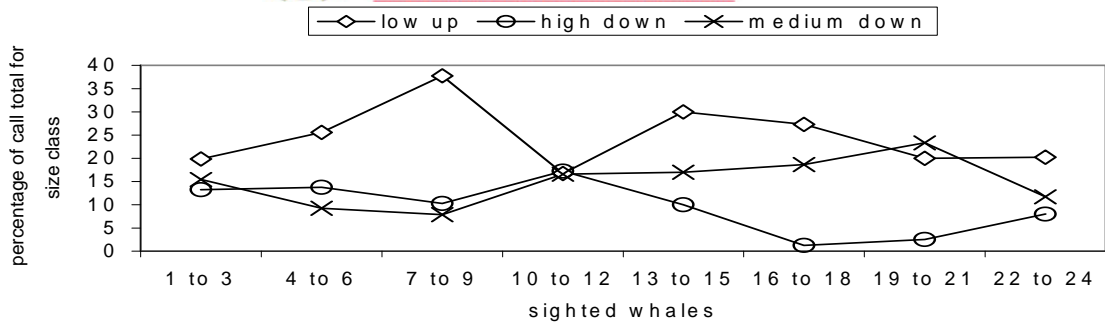
Figure 2.6 Relative contributions to the call total within size class, for the whole season, of three of thirteen call types, bounded by both acoustic contour and onset frequency (*low up*, *medium down* and *high down*). These call types exert the greatest influence on variation in the relative proportions of calls in the presence of differing whale aggregation sizes..
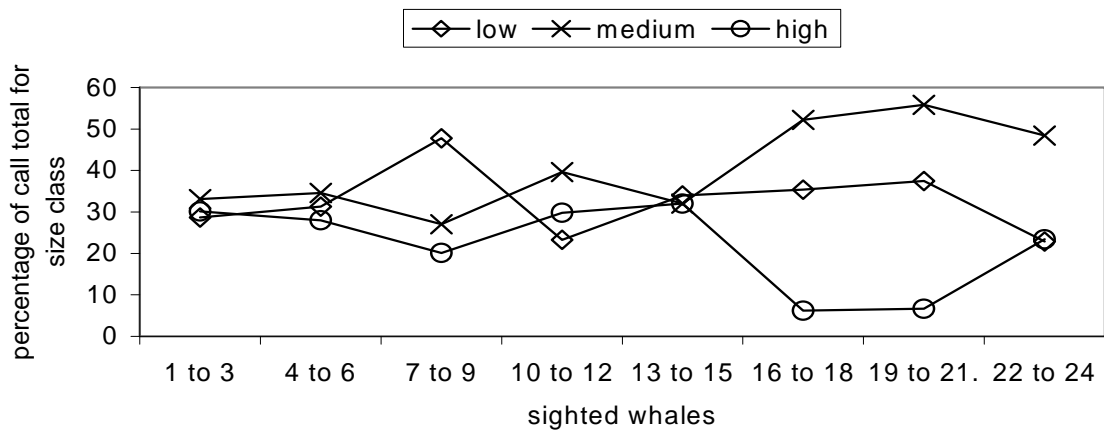
Figure 2.7 Relative contributions of call types exerting the greatest influence on variation in the relative proportions of call types in the presence of differing whale aggregation sizes, to the call total within size class, for the whole season. Call types defined by onset frequency alone (*low*, *medium* and *high*).
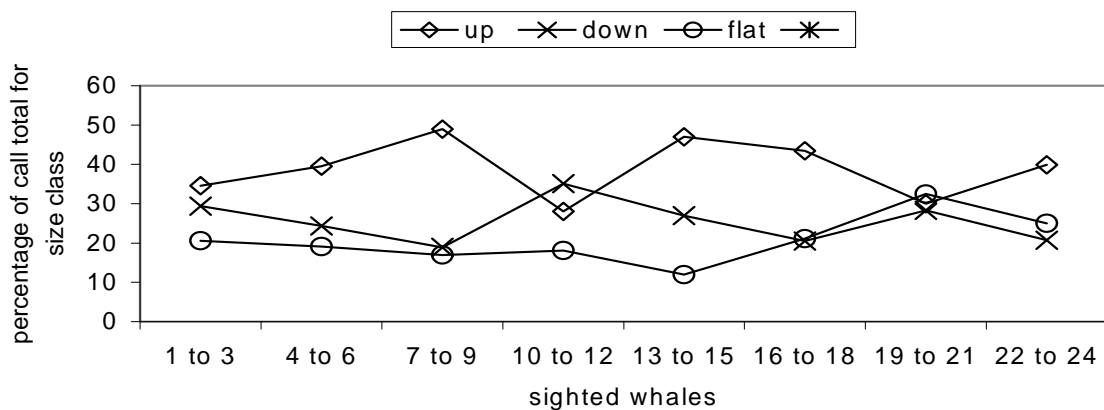
Figure 2.8 Relative contributions of call types exerting the greatest influence on variation in the relative proportions of calls in the presence of differing whale aggregation size, to the call total within size class, for the whole season. Call types defined by acoustic contour alone (*up*, *down*, *flat*).

,
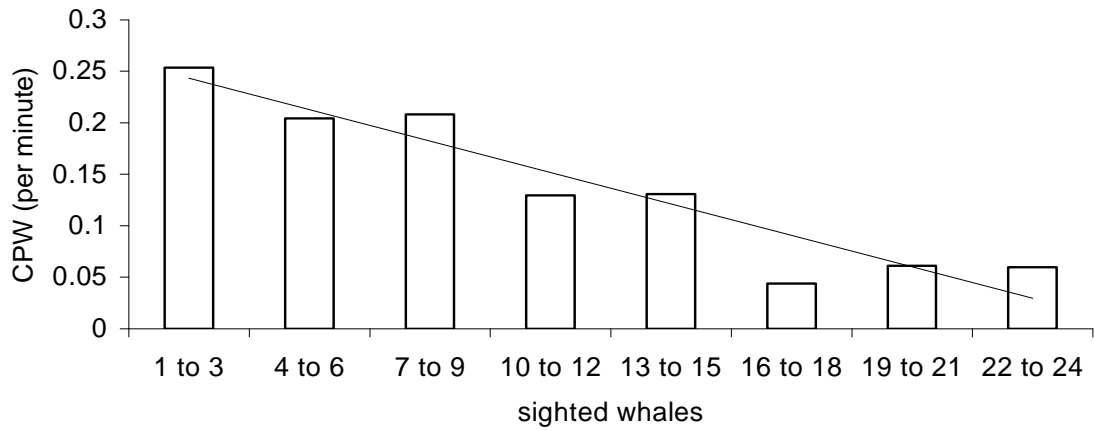
Figure 2.9 CPW with increasing numbers of whales, for all calls, over the whole season.
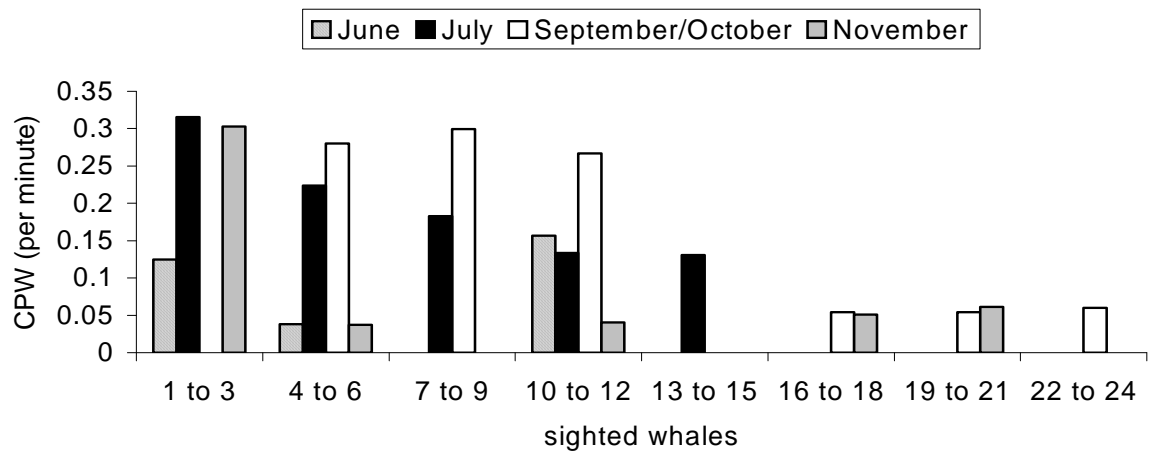
Figure 2.10 CPW with increasing numbers of whales, for all calls, viewed monthly.
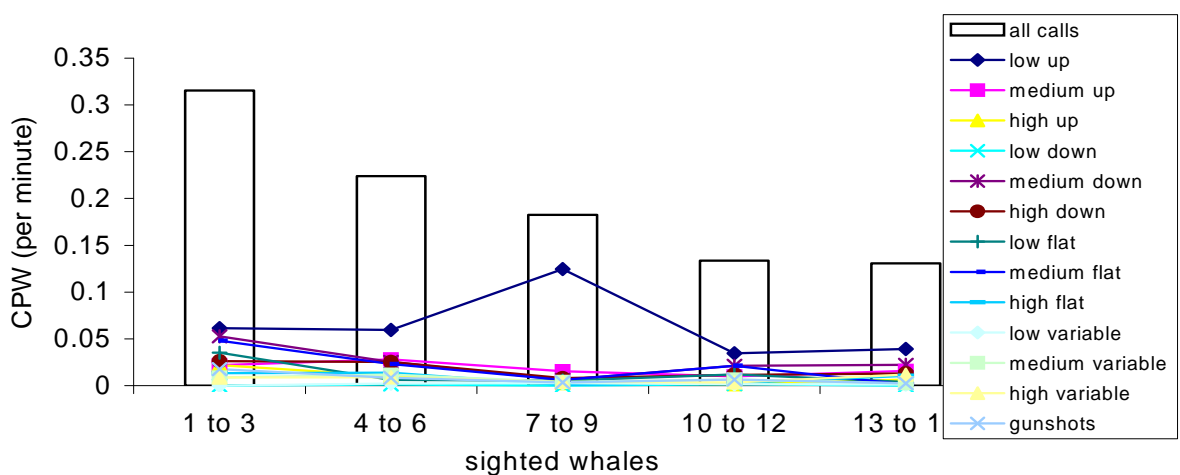
Figure 2.11. July CPW with increasing numbers of whales, for all calls and 13 call types.
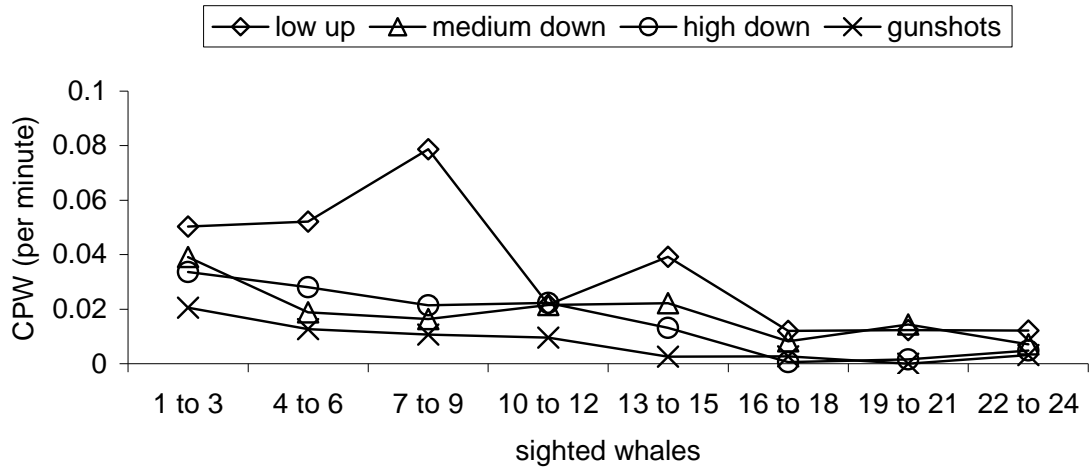
Figure 2.12 CRW of three call types responsible for the greatest variation in relative proportions of call types for different whale aggregation sizes, and of gunshots, over the whole season. Call types other than gunshots are defined by starting frequency and call shape (*low up*, *medium down* and *high down*).
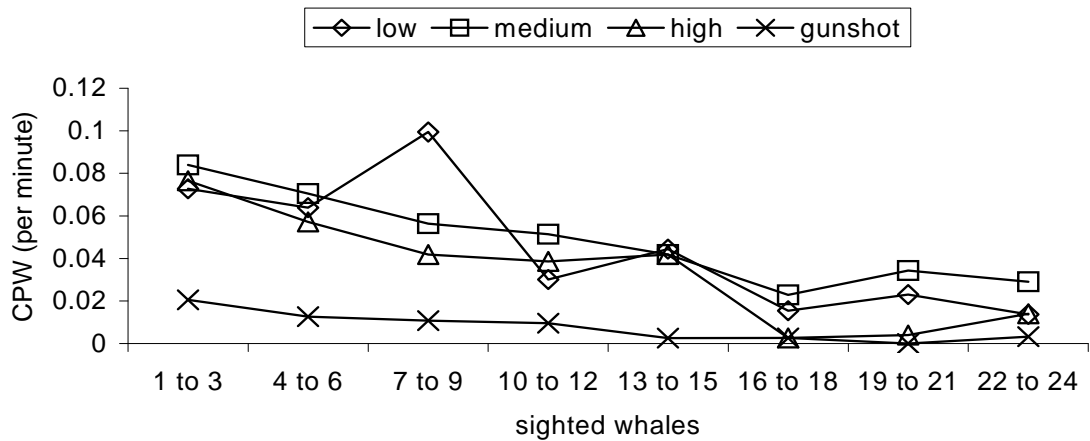
Figure 2.13 CPW with increasing numbers of whales for calls defined by onset frequency (*low*, *medium* and *high*), and for gunshots, over the whole season.
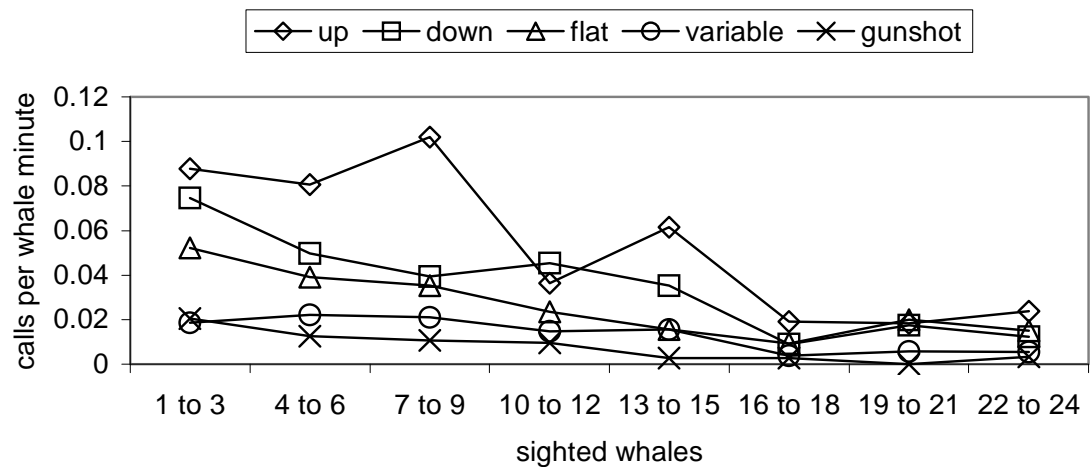
Figure 2.14. CPW with increasing numbers of whales, for calls with four acoustic contours (*up*, *down*, *flat*, *variable*), and for gunshots, over the whole season.

4. Discussion

4.1 *Generalised linear model*

This study used a generalised linear model (GLM) to investigate the relationship between the overall rate of sound production and the number of whales present. The GLM adjusted for variables such as differing session lengths, numbers of whales present, and other factors such as wind speed and direction, and time of day and of season, in modeling the data. The results revealed an interesting but confounding aspect of right whale communication: although the overall call rate (OCR) – that is, the raw call rate, calculated per unit time, irrespective of how many whales were sighted from the boat – increased as the number of whales present grew to a certain level, and then it decreased above that number. This was true for data acquired during all the sampled months and during all wind conditions, and contrary to the linear decrease in the call rate per whale (CPW) – that is, the call rate adjusted to accommodate the number of whales present.

Relationship between OCR, CPW and aggregation size

A striking feature of this study is the contrast between the quadratic rise, peak in the presence of 10–15 whales, and subsequent decline in call densities, and the linear decline in call rates per whale, with aggregation size. This difference is biologically sensible, as demonstrated in a simple model (*fig. 2.15*) that assumes linear decrease for three call rates per whale (sparse, medium and abundant) with hypothetical values in the presence of increasing numbers of whales. The three upper curves represent the three respective composite call rates with increasing aggregation size (*fig. 2.15*). For a general overview of the OCR, CPW and whale abundance over the whole season, composite data incorporating all call types were normalised for ease of comparison of trends and plotted for each monthly bin (June, July, September/October and November, *fig. 2.16*).The inverse relationship between CPW and whale abundance was clearly demonstrated; the OCR continued to rise after the CPW fell in response to an increase in whale numbers, but, as suggested both by the simulation (*fig. 2.15*) and by the results of the generalized linear model (*figs 2.2, 2.3*), dropped to a minimum as whale numbers continued to rise. This result is the natural outcome of the linear drop in the CPW demonstrated in the simulation model as overall whale numbers increase.

Importantly, the results demonstrated in the inverted parabola in the GLM (*figs.2.2, 2.3*) and modeled in the simulation (*fig. 2.15*) lead to the clear conclusion that, because call rates do not rise linearly with whale numbers, it is not possible to estimate whale numbers from call rates.
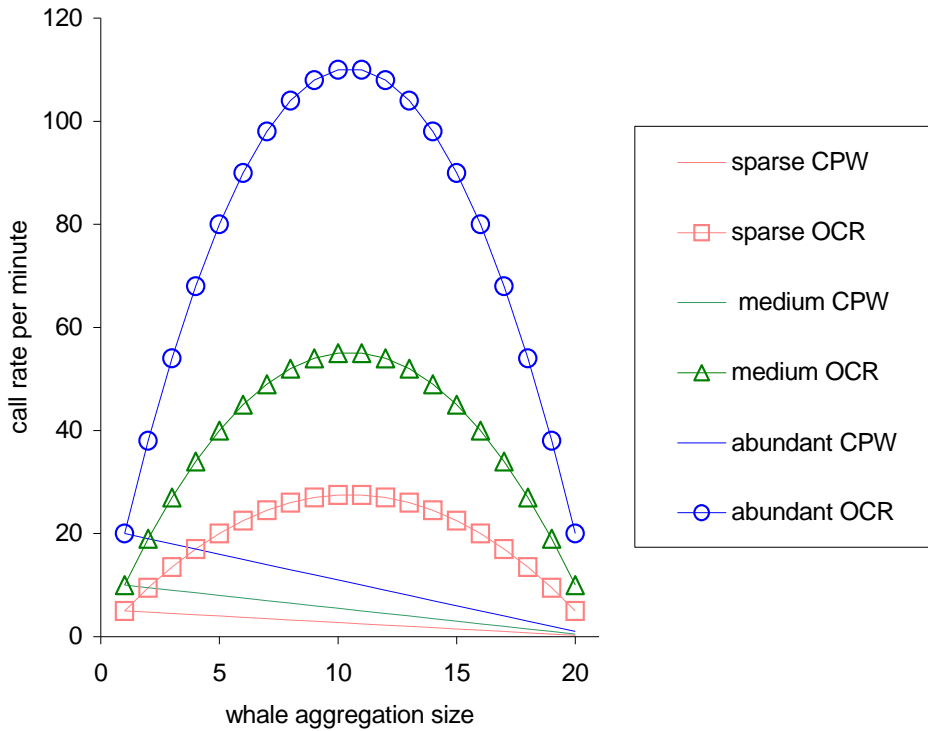
Figure 2.15 Simulated model of CPW and OCR per minute for all whales present, for increasingly large whale aggregations. Hypothetical sparse (red), medium (green) and abundant (blue) rates are modeled.
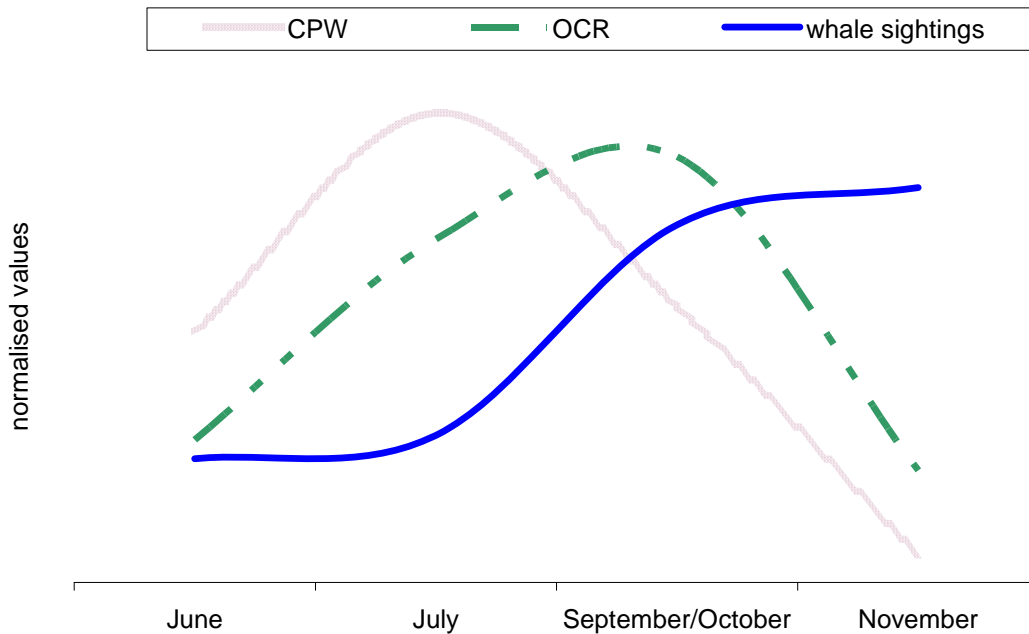
Figure 2.16 OCR, CPW, and whale abundance, for June through November. Observed data are normalised for comparison of trends. CPW clearly peaks in July, with low whale abundance, and is overtaken by OCR in September/October; both fall to their lowest levels with high whale abundance in November. (cf simulation, figure 2.15 above.)

Declining call rates in the presence of large numbers of whales

Whale behaviour incorporates many contexts and both the nature and the rate of acoustic communication is linked to specific activities and behavioural states, and is often gender-specific (Clark, 1982; Clark, 1983). This study, however, presents clear evidence for an overall tendency for large gatherings of right whales to vocalise less frequently instead of all competing to be heard. There may be several explanations for this observation. In a fully active SAG, the focal whale becomes vocally dominant (Kraus & Hatch, 2001; Parks, 2003a; Parks, 2003b; Parks & Tyack, 2005a), producing distinct calls that serve to attract males to the SAG(Parks, 2003a; Parks, 2003b). When the OCR is calculated for such a gathering, especially when there are many males present, as is increasingly the case as the season progresses (Best et al., 2003), the calls of the focal female will make the OCR appear unnaturally low due to the 'dilution' effect of assuming equal input by each whale. In reality, there are times when only one whale is vocally active. On the other hand, there is an argument for an increased rate of vocalisation when more competitive males are present; the rate of production of *gunshots* in the North Atlantic right whale was weakly correlated with the number of males present in a SAG(Parks et al., 2005b) In other contexts, such as multiple groupings of cow-calf pairs, or groups of resting whales in close proximity, the motivation to vocalise is less pressing, even though the calls may be produced by a more representative proportion of whales actually present. In such a case, the call rate per whale may be closer to the actual rate at which each whale is calling.

'Eavesdropping'

At high whale densities, silent whales can gather information about the other whales' presence and activities by listening; 'eavesdropping' has been speculated for rough-toothed dolphins, which may benefit from other dolphins' echolocation buzzes (Götz et al., 2006).

Female harassment avoidance

Low call rates may reflect a deliberate strategy on the part of females, in avoiding harassment, when alone or accompanying a calf. Female southern right whales tend to segregate themselves from other classes, possibly to avoid harassment by males (Elwen & Best, 2004). Humpback whales with calves in Hawaii also chose shallower water than whales without calves, possibly to avoid harassment and injury to calves by sexually active males (Smultea, 1994). In a visually restricted medium such as the underwater ocean environment, acoustic detection is generally the best option for suitors. Under such circumstances there would be a strong selection for the evolution of acoustic detection avoidance strategies. The higher the numbers of males present, the stronger the motivation to remain silent, which may be a factor in the dramatic decline in call density in the presence of high whale numbers. As right whales with calves move out of nursery areas and into regions of the coast such as Walker Bay late in

the season (Best et al., 2003), many of the whales present off Gansbaai in October and November may have been cow-calf pairs, accounting partly for their relative silence. Another possibility is that, to avoid detection under such circumstances, acoustic cow-calf interactions would be at a low energy level, such that many of their quieter calls would not have been detected by our hydrophones.

Predator avoidance

Predators were a second potential source of harassment, providing strong motivation for acoustic stealth. In Peninsula Valdez, southern right whales with calves chose water 5m deep or less, and for the first few weeks kept moving constantly. This may have served to elude acoustic detection by killer whale echolocation, or attack from below (Thomas, 1984). Additional acoustic benefits were conferred by the choice of shallow water, in masking or attenuating whale sounds from potential predators (Würsig et al., 1996). Parallel scars, possibly from killer whales, were observed on young calves in Argentina (Thomas, 1984). Not only are calves easy prey for killer whales, but attacks on southern right whale adults have been reported in Peninsula Valdez (Cummings et al., 1972; Thomas, 1984). To date there are only two reports of such attacks by killer whales, and observations of only a few southern right whales with rake marks possibly attributable to killer whales, in South African waters(Best et al., submitted). A more likely predator in Walker Bay is the great white shark, *Carcharodon carcharias*, which is plentiful in the area due to the nearby seal colony at Dyer island, to the south east. Opportunistic exploitation of vulnerable southern right calves may be practised by the local great white sharks, whose hearing capabilities, while currently unquantified, are believed to be good below 1000 Hz (Compagno, pers. comm.[1]).

Adults accompanying calves may avoid acoustic detection by producing less sound. The reduction in vocalisations to avoid predation is not without precedent. Playback experiments broadcasting killer whale (*Orcinus orca*) sounds to gray whales (*Eschrichtius robustus*) and belugas (*Delphinapterus leucas*) (Cummings & Thompson, 1971; Fish & Vania, 1971) resulted in significantly lower vocalisation rates from the whales (Cummings et al., 1972). More extreme forms of predator avoidance have been suggested in the hypothesis that whales leave the high latitudes of the poles and undertake their annual migrations to sheltered bays in the lower latitudes, in order to avoid predation by killer whales *Orcinus orca* (Corkeron & Connor, 1999). The reduction in rates of sound production appears a minor inconvenience when compared to a migration of several thousand kilometers, although clearly the local risk of killer whale predation is of a lower order.

Effects of month

The OCR for all monthly bins including June, July, September/October, and November, followed the pattern of rising in line with whale numbers to a maximum around 14 whales,

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[1] Dr. L. Compagno, Iziko Museums, Cape Town, telephone conversation, 31st March 2005

after which it declined. Within this pattern overall, the OCR was highest in September/October, lower in July, lower still in November, and lowest in June. Thus in chronological order, the OCR started out lowest in June, rose substantially in July, peaked in September/October, and dropped sharply to just above the June level in November. These results should be examined in the light of the changing abundance and demography of whales through the season. Between 1969 and 1979, whale numbers in Walker Bay peaked in October, and tended towards greater abundance in the early season, between June and September, than the late season, between November and December (Best, 1981). In this study, call density in June was below that for November, and higher in July, preceding October, than after it in November. In this respect at least the call density pattern followed the 1969-1979 abundance pattern.

Although the GLM results predict that the number of calls will fall with higher numbers of whales, it should be remembered that it is only the CPW that falls linearly as whale numbers increase. The relationship between whale numbers and the predicted number of calls is not directly reciprocal. It continues to increase with increasing whale numbers for some time before it declines. This parabolic curve occurs in every month, and is based on observations within recording sessions where there was a maximum of close to 25 whales present at any one time. The predicted number of calls within each month rises and then falls as whale numbers increase. It is not surprising that its highest point is higher in months where whale numbers are higher, than in months where whale numbers are lower.

The incidence of mother-yearling pairs along the South African coast (from St. Helena Bay in the west to Mossel Bay in the south) declines rapidly after early August, perhaps due to sudden weaning (Best et al., 2003). Apart from cow-calf pairs, the remaining whales are found mainly in SAGs (mean size 4.45 animals) and non-SAGs (mean size 2.57 animals) (Best et al., 2003). In Golfo San Jose yearlings were seen without their mothers throughout September, October and November (Thomas, 1984). The incidence of calves in De Hoop Nature Reserve, South Africa, increased throughout the season, from zero in June to 15-22% between August and October, when most births occur. It continued to rise to 33% in November and 42% in December (Best & Scott, 1993), by which time most other classes of whales would have departed (Best et al., 2003). The high percentage of calves present in November in de Hoop was reflected, albeit at a lower level, in Walker Bay, and this could account in part for the low call density in that month, driven by acoustic predator avoidance by cows protective of their vulnerable calves.

Walker Bay is frequented largely by single whales and SAGs, while De Hoop is a prime nursery area. The cow-calf pairs and mother-yearling pairs in Walker Bay are likely to display the same trends in their movements. Cow-calf pairs constitute an increasing proportion of the whales in the area through the season as they move in from the prime nursery areas to the

east, and mother-yearling pairs dissipate from early August. The numbers of whales participating in SAGS also increases through the season (Best et al., 2003). A picture emerges in the early part of the season of a preponderance of mother-yearling pairs over cow-calf pairs, and small SAGs, as well as non-SAG s (mainly female). By July the call density has increased to high levels, reflecting the contact calls of males in search of SAGs, and receptive females, urgently broadcasting sexual advertisement calls (most conceptions occur during an 118-day window centred on mid-July (Best et al., 2003)). Later in the season the non-SAGs maintain their group size, while SAG group size increases, and mother-yearling pairs are largely replaced by cow-calf pairs. The low call density in November relative to July may be due in part to a decreased urgency on the part of receptive females, in the presence of high numbers of interested males participating in SAGs, or a positive desire to avoid the harassment of large competitive male groups. A decreasing number of receptive females, as some leave the area, may be another factor. The higher proportion of cow-calf pairs present later in the season may further explain the drop in call density, , as communication between cow-calf pairs may be at low energy levels (more 'intimate') as the motivation to avoid predation or harassment supercedes the need to maintain contact.

Effects of wind direction

Observations of different wind conditions in Walker Bay from local boat operators familiar with local weather conditions may add another dimension to the interpretation of call rates under varying wind conditions. Mr. Rudy Hughes (pers. comm.)[2] has observed that the south-east wind in Walker Bay has the effect of flattening the sea, as it blows obliquely offshore. In gale-force conditions it produces a small, choppy sea, and clears the water, bringing a drop in temperature to as low as 12°C, and is associated with high barometric pressure. The north-east wind produces a similar flattened sea, choppy when the wind reaches gale-force, blowing directly offshore, but with a drop in barometric pressure. As the wind shifts to the north-west, the barometric pressure falls to its lowest value, and sea conditions become rough and dangerous, but the temperature is raised, and tailslapping and breaching behaviour is common among whales. When the wind comes from the south-west, it is accompanied by an extremely rough sea, with very big, long swells, creating conditions under which it is dangerous for boats to come close inshore, and a rise in temperature. Whales, especially calves, have reportedly become highly active under these conditions, breaching in the swells. When there is no wind, and the sea is calm, the whales interact more often with whale-watching boats, and they are more likely to make close approaches (>5000 observed by Hughes to date of communication).

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[2]Personal communication from Mr. Rudy Hughes, Ivanhoe Sea Safaris, balaena@kingsley.co.za, licenced boat-based whale watching operator in Walker Bay, with many thousands of hours experience on the water in Walker Bay. Communication by telephone, 29th April 2004.

In this context it is perhaps not surprising that the highest call density coincided with conditions of no wind. With calm weather maximum effort could be devoted to communication, and if whale interactions with the boat increased dramatically under these circumstances, vocal interactions between whales might conceiveably follow the same pattern. More obviously, calm conditions, in the absence of additional ambient noise caused by wind, waves and turbulence, would also be optimal for detecting more calls. This applies both to listening whales and to researchers, raising the possibility not only that we missed more calls under rough conditions than we did under calm conditions, but also that the whales called more under calm conditions because receiving signals was easier than under rough conditions. There could be a relationship between the active breaching and tailslapping observed by Hughes in rough weather, and the use of such broadband sound-producing behaviour as a more effective means of communication under such circumctances. For the GLM analysis, the standard reference condition, against which call density in other wind conditions was measured, was that of 'no wind'. The real observable contrast in call density was between conditions of no wind, and all other conditions, although only the SE vs no wind comparison was significant, due to sufficiently large sample size.

How could the GLM results be used?

The results of this study are striking and surprising, and they raise many questions about the use of sound by southern right whales; at the same time they appear unequivocally to answer the question of this chapter: is it possible to use call rates to estimate numbers of whales? These results suggest it is not. The predicted number of calls reaches its maximum and then falls again with whale numbers still on the increase. The largest aggregations of whales are accompanied by a low call rate. The only use of call rates could be in conservative estimates of minimum numbers. Minimum population density estimates were calculated in an acoustic survey of fin whale density (McDonald & Fox, 1999), using transmission loss models and multipath methods to estimate range from a single hydrophone.

4.2 The relationship between OCR, CPW and whale numbers

Methods of deriving absolute call rates

There are several methods of analysing calls in time series to derive absolute call rates. The simplest and most direct of these is to calculate a mean call rate by counting the calls produced during each recording session, and dividing the pooled number of calls by the duration of the pooled sessions, using units appropriate to the call density(Serrano & Miller, 2000), or by the product of the duration and the animal numbers (such as whale minutes) to derive individual call rates (Clark, 1982; Clark, 1983). This gives a mean call rate without reference to clustered calls, and rates within and between clusters. The mean number of calls per time-unit has also been used (Cox & Lewis, 1966), as with North Atlantic right whale calls measured in 1-minute samples (Matthews et al., 2001; Parks, 2003a) and humpback

dolphin calls per 3-minute sample (van Parijs et al., 2002) to calculate predicted intervals between and within call clusters, where they exist (Matthews et al., 2001). Intercall intervals have also been widely used to characterise call timing, using the log-survivor function (Cox & Lewis, 1966), (*chapter one*). In a study of elephant calling rates, call events, rather than single calls, separated on either side by at least 2 seconds, were counted. Only the densest 30 minute sample from each recording session was used, allowing call event rates to be established without reference to session lengths or long periods of silence, and requiring detailed attention for a dramatically reduced data set (Payne et al., 1998).

Each of these methods has advantages as well as drawbacks. When comparing the densities of several call types, some may be very much more prone to clustering in bouts than others. The use of call rates based on direct counts over time may avoid the confounding factors inherent in comparing call rates within and between bouts, with call rates with less defined bout lengths, or with none, as in this study (*chapter one*). A further source of potential confusion would be the comparison of call rates of vocalisations with widely differing within- and between-bout intervals, especially where inter-bout intervals had a Poisson distribution with a wide range. Where various call types occur together and are pooled, but have very different clustering properties, analysis of clusters is also likely to be misleading. The relative simplicity of direct comparisons of call counts over time, weighted to account for recording sessions of differing lengths, has much to commend it, particularly in the context of remote sensing, in the absence of visual observations or bearings to source.

The relationships between OCR, CPW and numbers of whales
Interestingly, the method described above for determining the call production rate for elephants, when regressed linearly with counts of elephants present, produced strikingly similar results to a linear regression using a call rate derived from direct counts of calls over time (Payne et al., 1998). In that study call rates rose in line with elephant presence, allowing for a relatively simple translation of call density into elephant numbers. Calling toadfish males (*Opsanus beta*), however, were observed to increase their call rates in response to other calls from males (Thorson & Fine, 2002). Harp seal (*Pagophilus groenlandicus*) underwater vocalisation rates were not related to group size (Serrano & Miller, 2000). These results all contrast with the observed declining trend in call rate with larger gatherings of southern right whales. In line with this study, however, in a study of killer whales off British Columbia the use of echolocation per individual by both resident and transient groups was found to decrease with increasing group size (Barret-Lennard et al., 1996).

Establishing the relationship between numbers of whales and OCR does not require a knowledge of individual call rates. Conversely, estimates of individual call rates do require measurement of OCR, and assume at least a knowledge of the number of whales present in the call origin vicinity; better still, a knowledge of the proportion of silent animals; and

ideally, the identity of the caller for each call. Conditions under which this is possible are hard to achieve in studies of non-captive animals, and even more so for cetaceans, with no obvious external sign of vocalisation, so that individual call rates per whale are often approximations rather than precise measurements.

A CPW derived from an OCR is in some respects an artefact. It assumes an equal call rate for each whale present, which is unlikely. For instance, in Patagonian waters, single southern right whales had higher rates of up calls, down calls and slaps than groups containing more than one individual, when mildly active, and up call production for single swimming whales was higher than that for those swimming in groups. Hybrid calls were produced at a higher rate by fully active groups of three, rather than two, whales. High, hybrid and pulsive calls and blows were all produced at higher rates by trios than by pairs, and by pairs than by single animals. The mean sound rate per whale was presented as sounds per whale hour (Clark, 1983). Individual call rates nevertheless remain a useful measure provided their interpretation includes the likelihood of different individual call rates within a single group and a dependence on group size, composition and activity. For instance SAG-related calls (screams (Kraus & Hatch, 2001; Parks, 2003a), high and hybrid calls (Clark, 1983), and *medium* and *high down* calls (*chapter one*)) are currently held to be produced by the focal animal in a group of right whales.

In this context the focal animal is responsible for most of the vocalisations, while for much of the time the majority of animals are relatively or completely silent. Silent whale groups have been identified in the presence of vocal groups (Clark, 1983; Matthews et al., 2001), (*chapter three*). In the Rottnest trench, calling blue whales were estimated to represent between 12-30% of the total population in the area (McCauley et al., 2001). Separation of individuals is less problematic when whales are widely spaced over a large area, as blue whales frequently are (Stafford et al., 1998). Right whales are often grouped so closely that it is impossible to assign calls to an individual (*chapter three*), (Parks, 2003a). It was conservatively estimated when analysing *up* call production in Walker Bay, South Africa, that on average over the season, at most three quarters (possible only one quarter) of southern right whale groups observed during recording sessions were vocal, though it was not possible to determine the proportion of silent whales within any group (see *chapter three*). To do so, it is necessary to ascertain the number of callers present. This in turn requires discrimination between the voices of the whales contributing to the collective calling (*chapters three, four*). The calculation of the proportion of silent whales involves a calculation for both groups, which is sometimes possible, and individuals within groups, which presents far greater challenges. Until reliable methods have been developed to establish the separate identities of multiple callers in a group, the estimated rate of sound production for individual whales should be interpreted with caution.

The relationship between call type and whale numbers

This study provides clear evidence that the numbers of whales present significantly affects the relative proportions of *up* and *down* calls, the most abundant call types produced (*chapter one*), notably *low up* (the majority of all *up* calls)*, and *medium* and *high down* calls (the vast majority of all *down* calls) or 'screams', associated with surface active groups (SAGs) (Kraus & Hatch, 2001; Parks, 2003a). *Low up* calls, usually the dominant call type, were especially prolific in the presence of 7-9 whales. Whale numbers above 13-15 produced markedly elevated levels of *medium* calls, intermediate levels of *low* calls and depressed levels of *high* calls. When the whales reached 19 to 21 in number, *medium down* calls were even more prolific than *low up* calls, possibly an indication of the prevalence of SAGs and consequent reduction in the need by (*low up* calling) males to search for them. Interestingly, as whale numbers rose the balance between *high down* and *medium down* calls, often produced in similar contexts (*chapter one*), changed. With high numbers, *medium down* calls became dominant over *high down* calls. Higher registers in vocal repertoire may indicate higher levels of arousal or excitement (Clark, 1982; Clark, 1983). The drop in vocal register from *high* to *medium* calls may have been due to the presence of large numbers of males participating in each of several SAGs, with concurrent reduction in the urgency of the female advertisement. A complementary pattern was observed for *low*, *medium* and *high* calls, equally distributed in the presence of small numbers of whales, with the same surge in *low* calls around 7 to 9 whales, as observed for *low up* calls. In the presence of higher numbers of whales, however, *medium* calls dominated strongly over *high* calls, which comprised a small proportion of the sounds. These results can only suggest trends which may be explained in terms of observed whale demographics and behaviour.

Whole season and monthly CPW for various call types

The evidence presented here for an inverse relationship between the CPW and the numbers of whales present, when all call types are considered together, extends to most call types, when they are divided according to onset frequency, acoustic contour, or both. Within the general decline in CPW, the same surge in *low up* calls in the presence of 7 to 9 whales is apparent for *low* and for *up* calls. Gatherings of 10 to 12 whales tend to produce *low up*, *medium down* and *high down* calls at the same rate, indicating a balance between the acoustic searching for SAGs by males, and within SAGs, for the focal whales by males during dives by the focal female, and contact calls between cow-calf pairs on the one hand (using *low up* calls), and sexual advertisement of receptive females on the other (using *medium* and *high down* calls). Beyond that number, while all call rates per whale continue to drop, *low up* calls still predominate, and the relationship between *high down* and *medium down* calls is reversed. The latter are produced at a higher rate than the former in the presence of larger gatherings of whales, as the need for receptive females to advertise becomes less urgent.

In July, the inverse relationship between individual call rate and whale numbers is strongest. Because most conceptions are calculated to occur during an 118-day window period centred around mid-July (Best et al., 2003), and assuming that the reproductive seasonality is female-driven, this is the month during which it is most crucial for advertising females to broadcast their status, and for lone males to locate and maintain contact with receptive females. There is likely to be strong selection around this period for females within each SAG (potentially, a large aggregation of whales) to expend a high amount of energy on communicating their availability, and for the males to spend a lot of their time calling and listening.

The falling individual call rates recorded with increasing numbers of whales are based on the assumption that all whales present contribute in equal measure to the vocalisations recorded in their presence, as discussed and qualified above.

Suggestions for future research

Playback trials broadcasting sounds of differing frequencies, at known source levels, and from various locations in Walker Bay, would extend the present study in providing a realistic estimate of the range of transmission of southern right whale vocalisations, and define the geographical area represented by each recording. Recordings opportunistically synchronised with existing aerial surveys would provide a better assessment of the effect of whale numbers on vocalisation rates, because aerial surveys provide a clearer overview of the location and the whales present. More advanced recording technology, such as autonomous bottom-mounted acoustic recorders, (Frankel & Clark, 2000), would allow for recordings at night and in rougher sea conditions, although visual observations under these conditions would be difficult or impossible.

An analysis of call density as an indicator of whale numbers, using the maximum call rate per constant time interval, rather than a mean call rate, and conducted along the lines of the elephant call study (Payne et al., 1998), would be worthwhile. Such an approach, if successful in predicting whale numbers, would dramatically reduce the time needed to analyse the large volumes of acoustic data generated by remote sensing systems, as detailed attention would only be required for a small proportion of each recording.

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CHAPTER THREE

LOCALISING CALLING SOUTHERN RIGHT WHALES IN A NOISY ENVIRONMENT, USING A DUAL AXIS SUSPENDED HYDROPHONE ARRAY

1. Introduction

In animal communication, the extent to which the sender of a signal can be located is an important feature for the signal receiver. For researchers, the first step in identifying vocal characteristics of individual callers is to assign calls to individuals. The search for intent and behavioural significance in whale vocalisations requires that they be considered within the relevant social context, which includes identifying callers and receivers. Terrestrial animals often provide visual cues when vocalising, and the location of the caller is immediately apparent to an intended or unintended receiver in visual range. Most of the vocalisations produced by southern right whales and other cetaceans occur underwater and out of sight of both underwater receivers and observers above the water. Southern right whales vocalising underwater do not normally advertise their identities with any visual clue that is discernible above water. The range of visual signals to receivers is restricted to tens of metres or less underwater, while on land it may extend to hundreds of metres. Conversely acoustic signals travel almost five times as fast in water as they do in air, and the acoustic range underwater far exceeds that in air. Acoustic methods are, in most cases, the only ones available for determining bearings to an underwater caller.

Initially the military, fulfilling a need to defend national waters from enemy presence, were leaders in the field of passive acoustic localisation. With a growing interest in cetacean acoustic systems over the past fifty years, several techniques for localising sound sources have been developed or adapted from existing technologies traditionally employed by the military for the same purpose.

A variety of different hydrophone array designs has been used for passive determination of the location of or bearings to calling marine mammals (Watkins & Schevill, 1972; Clark, 1980; Clark et al., 1986; Spiesberger & Fristrup, 1990; Miller & Tyack, 1998; Stafford et al., 1998; Clark & Ellison, 2000; Van Parijs et al., 2000). Factors such as the physical geography of the environment, the movement patterns and behaviour of the animals, the minimum useful precision level, the available manpower, the size of the available vessel and the extent of available resources, all contribute to the particular design of an array. The separation between hydrophone pairs, which provides the delay in time of a signal arriving at two hydrophones, and upon which the determination of bearing is based in many array designs, may range from centimetres (Miller & Tyack, 1998) to several kilometres (Stafford et al., 1998). Sensors may be bottom mounted (Clark, 1980; Stafford et al., 1998), towed (Miller & Tyack, 1998), fixed to a boat (Van Parijs et al., 2000) or included in (Hayes et al., 1998) or suspended from buoys, the latter a design feature of the array used in this study. Other designs, known as 'pop-ups', store data in a recoverable device programmed to surface after a given duty cycle (BRP

(Bioacoustics Research Program), 2006). Larger hydrophone separations increase the useful range of the array but are dependent upon a suitable site and may preclude simultaneous visual observations. The deployment of towed arrays introduces engine noise and, in some cases, left-right ambiguity, unless the animals of interest are known to be on one side of the vessel (Miller & Tyack, 1998), but facilitates visual observations while tracking. Free-floating buoys with in-built hydrophones, sound recorders and GPS location information, require the logistical support of transmitters and receivers, and may be lost at sea, but are easily deployed in a variety of locations. The signal may be stored within the array (BRP (Bioacoustics Research Program), 2006), physically cabled to shore-based equipment (OVAL (Orca Vocalization and Localization Project), 2006) or transmitted via satellite or VHF (Mohl et al., 2000). Other systems include the "vocalite" which lights up when the dolphin wearing it vocalises (Tyack, 1991), and the use of human ears, with the natural human ability to localise sounds, in concert with a small array mounted on a video camera with hydrophone separation scaled up to compensate for the faster transmission of sound in air than in water (Dudzinski et al., 1995).

Our research required an array system that was mobile, deployable in shallow water (<15 m depth) and recoverable from a 6m semi-rigid inflatable boat, to record free-ranging southern right whales under conditions frequently rougher than sea-state 2 (Beaufort scale). As an integral part of a study of southern right whale vocalisations in Walker Bay, South Africa (see *Introduction*), the system was developed over three field seasons, testing two mobile, deployable/recoverable array designs with several modifications. Particular attention was given to two call types. *Up* calls (Schevill, 1964; Clark, 1982; Parks & Tyack, 2005a), (*chapter one*), common to all group members regardless of age and gender, were potentially useful in the study of vocal individuality (*chapter four*). Calls associated with surface active groups (SAGs) include 'screams', many of which are thought to be made by the focal female as part of mating behaviour (Kraus & Hatch, 2001; Parks & Tyack, 2005a), and so were also potentially useful in the same study (*chapter four*).

Hydrophones were initially fixed to the boat structure via long poles, but the resulting array self-noise and water noise from flow and turbulence proved counter-productive. Real-time on-board capture of time delays was attempted using both paired two-channel oscilloscopes and a four-channel chart recorder, but ultimately abandoned because of high ambient noise levels and poor signal-to-noise-ratio (SNR) because of high seas, as well as an inability to accommodate an on-board computer. An additional difficulty was the intrinsic nature of the signal of interest, a *low up* (LU) call (*chapter one*), sinusoidal and smooth, with insufficient features to allow for easy phase determination, and with an onset that was often too soft to facilitate phase determination using signal onset as an unequivocal marker.

This development process culminated in a mobile, suspended, dual-axis, three-element hydrophone array system for assigning whale vocalisations to whales or whale groups, and required two major

phases: data capture at sea, and post-processing in the laboratory. On board at sea, the presence of whales was detected, and the underwater signal from three hydrophones making up the array was recorded, using two stereo cassette recorders. Simultaneously a signal was recorded from a separate hydrophone using a DAT recorder. A record was kept of visual bearings to the whales and the orientation of the array, using a hand-held electronic compass. In the laboratory, suitable calls were selected and digitally sampled. Time-delays between channels representing two pairs of hydrophones (A and B; A and C) were extracted and used to calculate relative bearings to the signal source with reference to the array. After correction for the orientation of the array, absolute bearings to the signal source were calculated. Finally, bearings to signal sources were compared to the observed positions of whales, in order to determine the origin of the calls. Bearings to whale calls were integrated with concurrent visual monitoring of bearings to whale groups to assess the various contributions by individuals and groups to the vocalisations recorded using the array system.

This chapter describes the design, construction and testing of the array (Part I) and presents results obtained when it was deployed at sea in the study of southern right whale vocalisations (Part II).

2. Part I: a suspended, dual-axis hydrophone array

2.1 Materials and method

2.1.1 Data capture

Between June and November 1999, recordings of southern right whale vocalisations were made in Walker Bay, South Africa (*see Introduction*), from a 6 m semi-rigid inflatable boat. Sixty hours were recorded from a custom-built, suspended, T-shaped, dual-axis, three-element hydrophone array. Two Aiwa stereo recorders (model HS-JS165) captured two sets of time delays, for determination of bearings to sound source. Visual observations of bearings to animals present at the time of recording were made from an elevated viewing platform on the boat.

Array design

The array was constructed in a horizontal T-shape, 3m by 4.24m, from 6 cm (outside diameter) reinforced PVC plumbing pipes and joints, with vertical pipes affixed to all three extremities. A custom-built hydrophone (Sonatech Model 8212, Standard ST201, with flat frequency response about 1.5 dB at about –170 dB re 1 v/μPa from about 7 Hz to about 40 kHz) was attached to the bottom end of each vertical pipe (hydrophones A, B and C). This created a dual-axis array capable of capturing maximum time delays of 2 ms for the short 3m axis, and 3 ms for the long 4.5 m axis (*fig.3.1*). Twisted, shielded coaxial cables connected the three hydrophones to two Aiwa stereo recorders (HS-JS165), recording stereo signals from hydrophone pairs A and B, A and C. The entire array was suspended at a depth of 5 m from spar buoys connected by ropes to the three extremities of the array, and was deployed at a distance of 5-10 m from the bow of the drifting vessel. The relatively small size

of this array, compared to the size of a wavelength of some of the calls detected, was a disadvantage in that bearing errors were potentially large, but adequately served the purpose of assigning calls to well separated groups of whales; it was also the largest structure that could practicably be deployed from our small vessel; whales sighted from the boat were always much further away than the small separations of the three hydrophones; uncertainty was further reduced by the dual axis design, as each hydrophone pair gave two possible source directions, but only one source direction from each hydrophone pair was common to both, which resolved left-right ambiguity.

Array theory

The process of calculating the bearing to the caller from the time delay is relatively straightforward for a fixed geometry. With reference to fig 3.1, the path delay over the short baseline is:

$$\Delta\tau_{BA} = BD = AB \sin\alpha \qquad (1)$$

where BD is the path delay at hydrophone B compared to hydrophone A, AB is the hydrophone separation (short baseline) and α is the angle of incidence between the reference axis (pointing towards 0°) and the source direction, with reference to the structural axis.

The path delay over the long baseline is:

$$\Delta\tau_{CA} = AE = AC \cos(\alpha + \beta) \qquad (2)$$

where AE is the path delay at hydrophone C compared to hydrophone A, AC is the hydrophone separation (long baseline), α is the angle of incidence between the reference axis (pointing towards 0°) and the source direction, with reference to the structural axis, and β is the offset of hydrophone C from the structural axis. The time delay between hydrophone pairs is:

$$\text{Delay } b(\alpha) = BD/c \qquad (3)$$

where delay $b(\alpha)$ is the delay at hydrophone B compared to hydrophone A for angle of incidence α, BD is the path delay at hydrophone B compared to hydrophone A, and c is the speed of sound in water (1.5 meters per millisecond)

$$\text{and Delay } c(\alpha) = AE/c \qquad (4)$$

where Delay $c(\alpha)$ is the delay at hydrophone C compared to hydrophone A for angle of incidence α.

Note, however that the relationship between time delay between the hydrophones, and bearing are approximations that only apply if the source is at a much larger distance from the hydrophones than the hydrophone spacing. The closest recorded potential source distance (to whales sighted from the boat) for these experiments was 50m; the furthest was <1 kilometre, with variation in sightings, during recording sessions where movements of whales were tracked and noted, of from 200m (500m–700m), through 300m (350m–650m), 350m (50m–400m), 400m (100m–500m) and 520m (80m–600m), to

800m (200m–1 000m) and beyond. Recorded sources were thus much further than the separation of the hydrophones.

Recordings

Prior to the recording session, animals were actively sought visually, and in the presence of whales the boat engines were turned off and the boat drifted in the vicinity of the whales. From this position the array, which was stowed on board in pieces, was assembled and deployed, with the bar of the T-shape closest to the boat (hydrophones A and B) and the single hydrophone (C) furthest from the boat. Deployment took about 10 minutes. A recording session was defined as a period of unbroken recording on the DAT recorder, accompanied by recordings on both stereo cassette recorders.

Visual observations

An observer positioned on an elevated platform on the boat about 3 m above sea level recorded the bearings to single animals and groups of whales in visual range, and monitored their movements at regular intervals. Where possible the number of animals in each group was estimated. Groups with ambiguous sizes (due to distance, weather conditions or confusing behaviour) were assumed to be no different in size from those where group size could be estimated (For a detailed description of the method used to assign size to whale groups, see *chapter two* of this thesis). The observer also kept a record of the orientation of the array as it moved in the current or with the wind, and the bearings to whales relative to the structural axis of the array were calculated. All visual bearings were measured using a hand-held electronic compass.

2.1.2 Signal processing

Signal processing involved two major steps: the extraction of time delays from the two sets of stereo recordings, and the determination of bearings to sound source from time delays. Thereafter computed bearings were compared with observed bearings to whales.

Software for extracting time delays

The standard method for determining time delays for two receivers is to perform a cross correlation of the two received signals. The stereo recordings from which time delays were extracted for use in the calculations, however, were extremely noisy due to the shallow water environment, multi-path propagation, prevailing weather conditions and array self-noise. Noise from marine organisms such as snapping shrimp (Au & Banks, 1997), turbulence and flow noise, and noise generated by the movement of the array and the slapping of water against the boat, added to the ambient sound levels, resulting in an extremely poor signal to noise ratio.

The high noise levels hampered the first step of cross correlating the two signals to determine the correct time delays, because noise extraneous to the signal of interest created confounding time delays

(a)

C
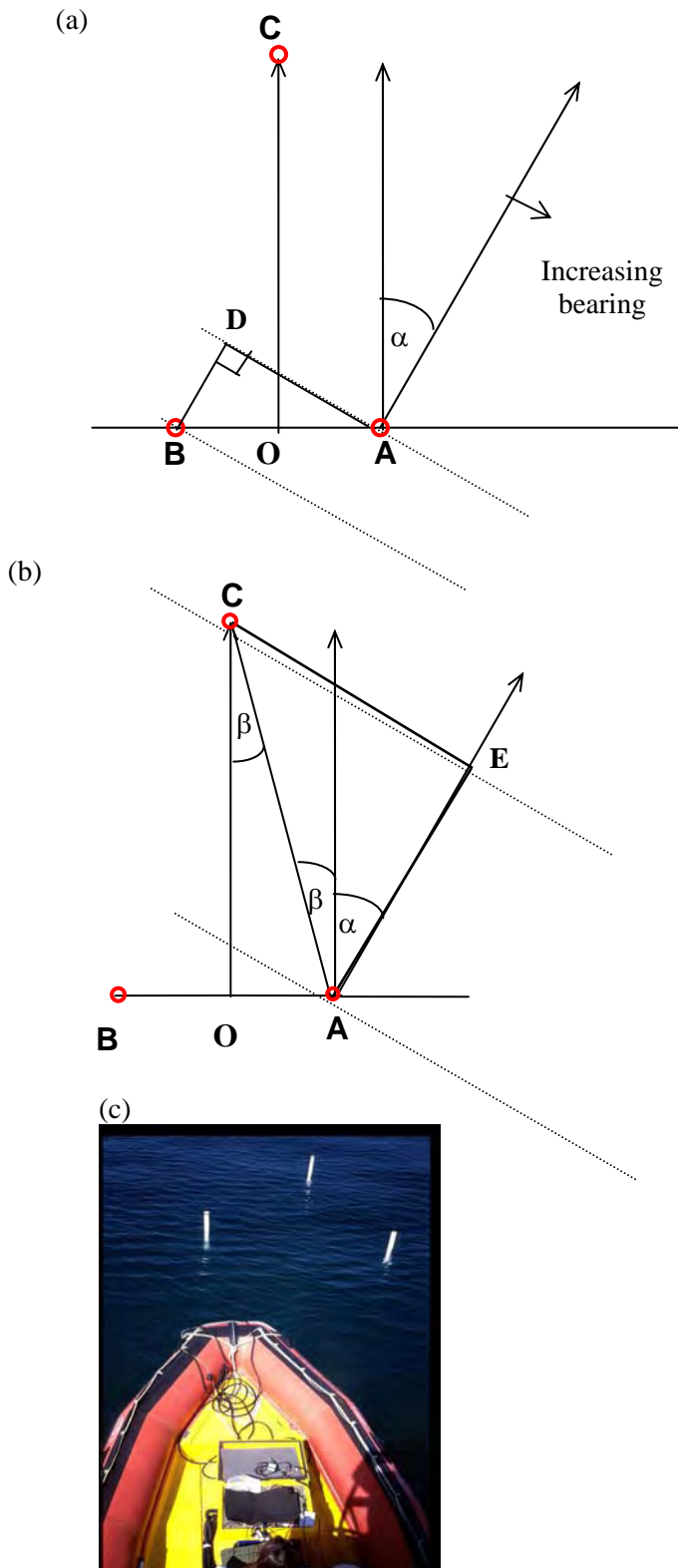
OC is the reference direction (structural axis).

Sensors are located at A, B and C.

AC is the long baseline and is 4.5 metres long (maximum delay 3 milliseconds).

BA is the short baseline and is 3 metres long (maximum delay 2 milliseconds).

Increasing bearing

D

α

B   O   A

(b)

C

β

β

α

B   O   A

E

(c)

(d)

Figure 3.1 Geometry of short (a) and long (b) baselines of array; (c) deployed array; (d) underwater configuration of array.

reflecting positions other than that of the signal source. To overcome this problem, dedicated software was developed for determining bearings to callers; it performed the standard cross correlations, and then went further by plotting cross correlation coefficients as a function of time and time delay ('correlelograms', lowest graphs in *figs 3.2* and *3.3*), together with spectrograms. Although when the signal-to-noise ratio was good (as in the bottom graph, *figs 3.2, 3.3*), the highest and lowest correlation coefficient values (indicated in red and blue) for the whale call were generally obvious, they could be ambiguous with a poor SNR (*fig. 3.5*), or where there was no clear peak delay value because of interfering noise and/or extremely faint signals; on occasion extraneous noise was actually louder than the call signal). Using the values in the correlation map (+1 = total correlation in red, to -1 = anti-phase in blue) the operator could choose an optimal time region for better SNR, to avoid confusing determination of bearings to call, with bearings to noise. The correlation had already been performed over the whole signal, and was not recalculated, but the value for the selected window (that is, the time delay and correlation value for the whale call portion of the signal) was shown in the text header of the graph (*bottom graphs, figs 3.2*).

In an environment where reflections occur, the two received signals are generally not expected to be exactly the same, apart from the delay in time. The received signal is usually the sum of the signal arriving by a direct path and the signal arriving by one or more indirect, reflected paths. (Multipath propagation is a fact of ocean sound, and certainly played a part in this study.) The sum of these signals can be zero if two signals are out of phase or larger than a single signal if they are nearer to being in phase. In a shallow sea with real whale calls, the path lengths and call frequencies are never constant, resulting in a continual fluctuation in signal amplitude. For stereo signals this fluctuation is usually not the same at the two receivers. When these signals are tested for correlation they never match perfectly.

The correlation graph is analogous to a spectrogram. Both are maps of intensity against time, but the correlation map shows on the vertical axis, instead of frequency, the delay or lead of the left channel against the right channel.

Simulation for software testing

A simulated whale call of increasing frequency against time and consisting of the fundamental and two harmonics was shown as spectrograms and as a correlation map (*fig. 3.2*). Random noise was added as background noise. A loud click, taken from an actual recording, occurred late in the two-second simulation. The delay between the two channels was -1 millisecond and the click noise was set to zero delay by using the same values in both left and right channels. The call appears in the correlation map as an area of high positive (red) correlation running horizontally across the graph. The anti-phase correlation (blue), which is half a wavelength away (thus having the lowest correlation value), appears above and below this, but the lines slant inwards with time. This is due to the decreasing wavelength of the signal with rising pitch. The click noise has some of the same

characteristics, but also shows weaker positive correlation peaks (yellow) on either side of the anti-phase (blue) correlation peaks. This indicates that there is a similar form to the click for two successive cycles.

Time delays from stereo field recordings of whale calls

When real, noisy, asymmetrical and imperfect data were analysed, the correlation maps were more varied (*figs 3.3-5*). Clear signals gave the best results, and the highest r-values. For a strong signal (*fig. 3.3*), the delays calculated from the chosen regions of the call, where high correlation coefficients coincide with the whale call, gave a well-defined indication of the bearing. Even in the presence of contemporaneous calls from different directions (*fig. 3.4*), high correlation coefficients (0.94, 0.91) for the cleanest part of the signal can be selected and sounds from a different bearing (appearing at the end of the call in *fig. 3.4*) avoided. Even amidst unfavourable SNR, with lower correlation coefficients (see left plots, *fig. 3.5*), it was possible to determine an acceptable bearing. There was a signal to noise ratio, however, beyond which the signal was swamped and no reliable bearings could be calculated.

Determination of bearing to sound

Using stereo recordings, computed bearings to the call sources were plotted for twelve continuous recording sessions. Bearings were relative to the array reference direction. Corrections for the movement of the array and its orientation were made to arrive at absolute bearings to sound source.

The algorithm used to determine the most accurate of the computed angles from the two axes took account of the higher accuracy of beam-on (broadside-on) as opposed to end-on (in-line) bearing determination accuracy. For this array the sensitivity of the bearing angle to time delay is such that if the delay changes by 0.5 milliseconds, from 2.5 to 3 milliseconds (end-on), this causes the bearing to change by 32°, from 308° to 340°, while a 0.5 millisecond change from -0.25 to +0.25 milliseconds (beam-on) causes a bearing angle change of 9°, from 65° to 74° (*fig. 3.6*). The bearing angles plotted in this figure refer to the angle of incidence between the reference axis and the source direction (α in *fig. 3.1*). It follows that the bearing angle computation is more likely to be in error for larger values of delay (in this case, for delays larger than 2.5 milliseconds). If the time delay derived from the longer baseline, AC, was close to the theoretical maximum time delay (>2.5 milliseconds to 3 milliseconds), call origin close to end-on to the array was indicated. Because end-on bearing determination is more subject to error than beam-on bearing determination, the angle computed from the short axis, AB (which would have been close to beam-on), was used, if in reasonable agreement with the end-on bearing determination. Similarly, if the time delay from the shorter baseline, AB, was close to end-on (>1.7 milliseconds to the theoretical maximum of 2 milliseconds), the angle computed from the longer axis, AC, was used. If time delays from both baselines were smaller than near end-on values, and thus more accurate, the average of the two angles was used. When the difference between angles computed from axes AB and AC was greater than 22.5° (normally from extremely faint calls), the data were
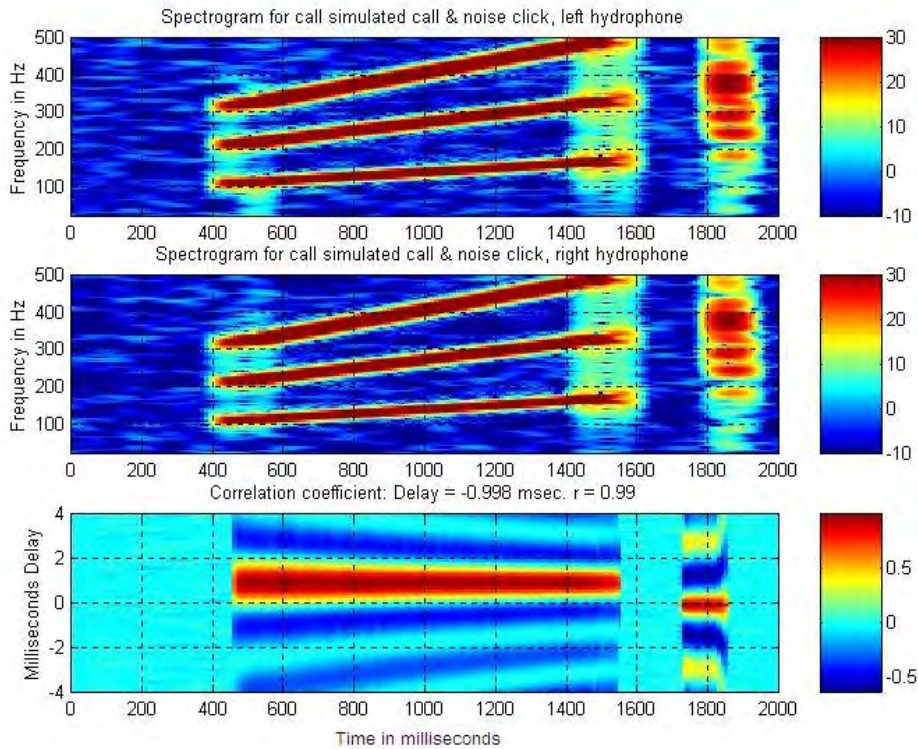
Figure 3.2 Simulated call (400 to 1600 milliseconds) with time delay of 1 millisecond, random background noise, and a click sampled from real data (around 1800 milliseconds) with a time delay of 0 milliseconds. The red areas represent high correlation; the blue regions represent low correlation.

Figure 3.3 A strong signal yielding credible time delays. Figures on the left represent the short array axis (A and B); figures on the right represent the long array axis (A and C). Red regions represent high correlation; blue regions represent low correlation.

rejected as unreliable. This cut-off point (although arbitrary) ensured that both computed angles fell within one quarter of a quadrant, or 1/16th o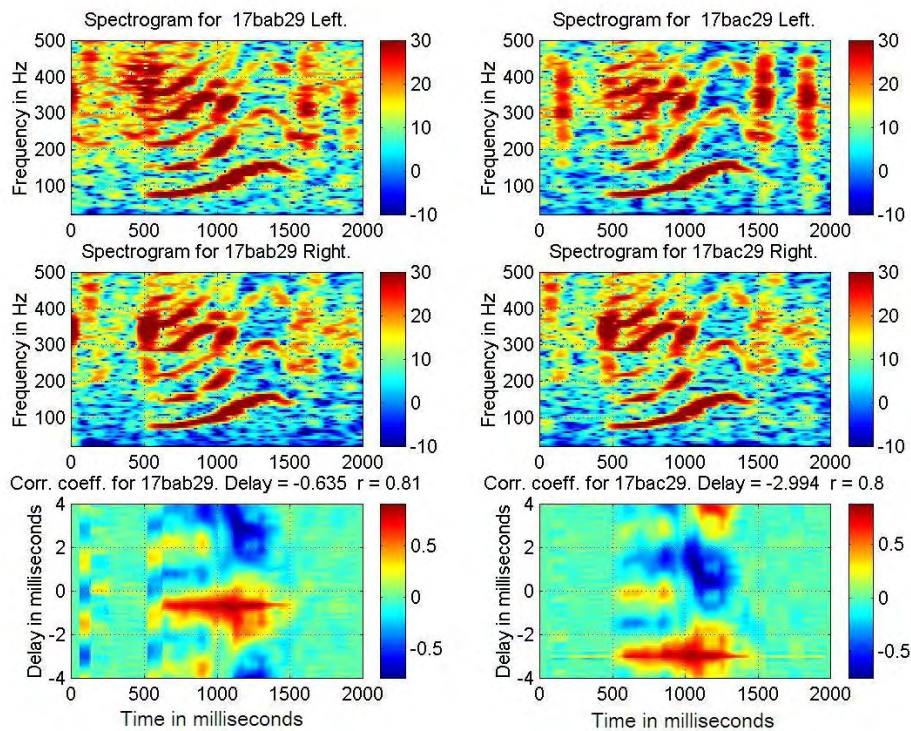f all possible sectors, while still allowing for a reasonable proportion (88.1%, or 178/202) of the total of 202 calls to be used (*fig. 3.7*).

Analysis of field recordings

The distribution of bearings to signal source calculated from field recordings of whale vocalisations was tested to determine whether signals were distributed uniformly (H_0) or came from preferred directions (H_A). For each of twelve recording sessions, the range of directions from which signals could potentially arrive (360°) was divided into 12 sectors of 30° each, avoiding the numerical anomalies of circular data, where 359° and 0° are 1 degree apart. The area was computed and graphed. Binning data according to these 12 sectors apportioned equal weight to each sector.

Bearings to signal source in degrees were then converted to radians, and the T statistic was calculated by summing their cosines. Values to compare against critical values for accepting or rejecting H_0 (directions to signal sources are distributed uniformly) were computed by multiplying T by the square root of 2/n (Cox & Hinkley, 1974). Within each continuous recording session, bearings to visually observed whale groups were compared with acoustically computed bearings to signal source to create sets of calls potentially belonging to separate whales or whale groups (*chapter four*). While such a test might have low power, as bearings were highly unlikely to have been distributed uniformly, because the whales were not, it did serve as preliminary validation that the array system was giving broadly plausible results.

In-air calibration

The calibration of the array was carried out in air, because we did not have access to an underwater transmitter capable of broadcasting signals of a suitably low frequency. Three sources of error were recognised: intrinsic error due to the architecture of the array, observer error arising from the measurement of the array orientation by electronic compass, and array distortion error resulting from the effects of wind and current on array conformation.

A sine wave with frequency rising slowly from 70 Hz to 130 Hz over one second, simulating a southern right whale up call, was used as the test signal. Initial simulations gave good correlation results. The amplified signal was broadcast on an open field at a distance of 11 metres from the array (*fig.3. 8*), using a custom-built amplifier and large Peavey speakers, at twelve stations each separated by 30°. The bearing to each station was determined using the electronic compass used in the field. The test signal (three calls) was broadcast twice at each of the twelve stations. The array was then distorted by moving the terminal end of the long axis, carrying hydrophone C, 40cm in the direction of hydrophone B (with the array directly ahead of the bow on the boat, this would equate to moving hydrophone C 40cm out of alignment, to port). The choice of 40cm as maximum displacement was based on observation of the behaviour in the field of the array, and occurred very rarely. A second
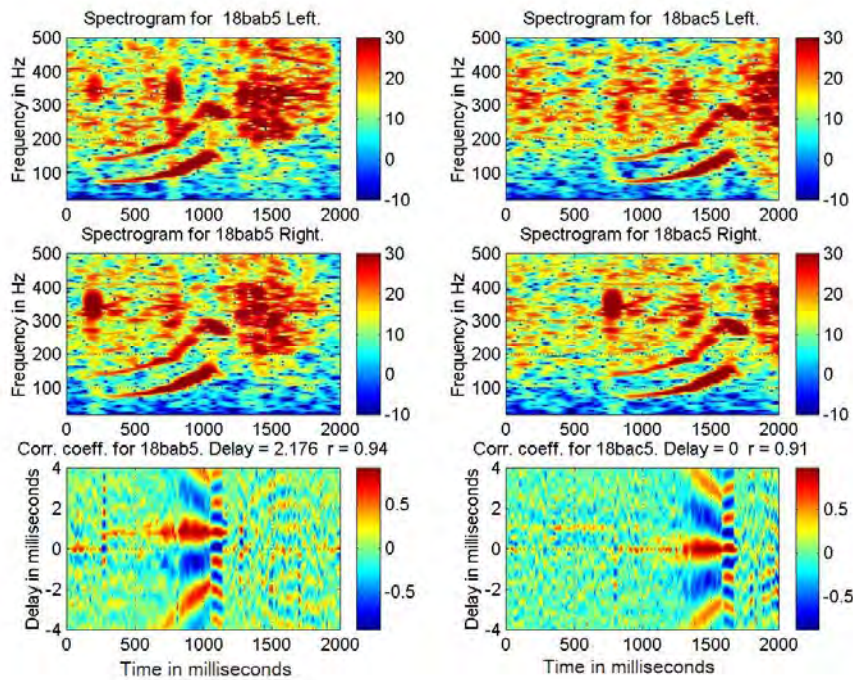
Figure 3.4 High correlation coefficients allow for distinction between the callt and a short sound of higher frequency, with shorter wavelengths and thus closer spacing of high (red) and low (blue) correlation coefficients, appearing at the end of the call at around 1 100 (ab axis) or1 600 (ac axis) milliseconds.
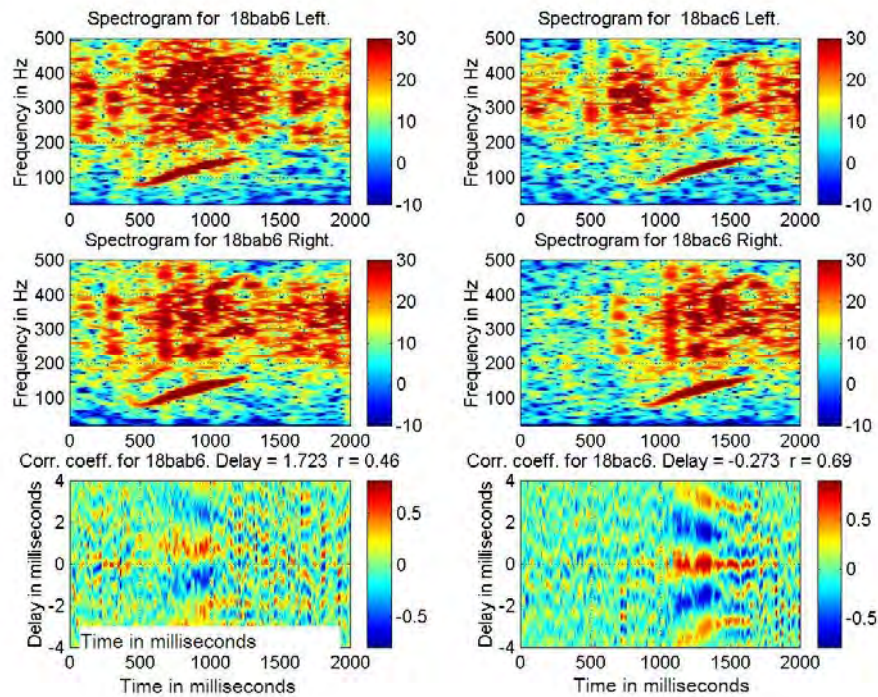
1. Figure 3.5 Determining an acceptable bearing despite an unfavourable signal-to-noise ratio.
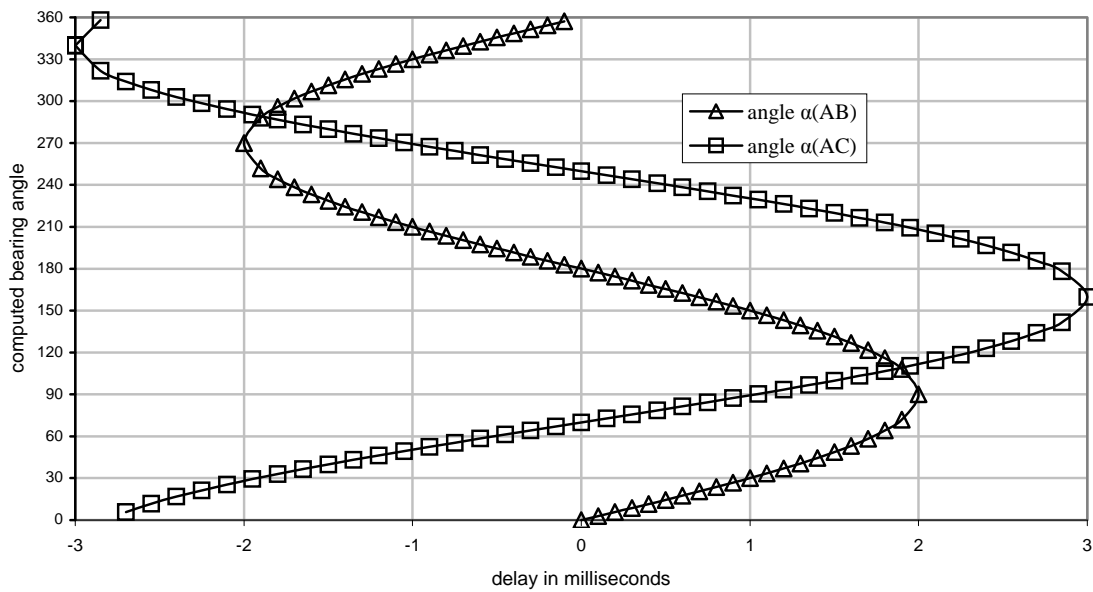
Figure 3.6 Bearing sensitivity to delay for T-shaped dual axis array. Delays for axis AB (maximum delay 2 milliseconds) and axis AC (maximum delay 3 milliseconds) refer to the angle of incidence between the reference axis and the source direction, α. (see *fig.3.1*).

Figure 3.7 Discrepancy between computed bearings to signal from axes AB and AC. Filled bars represent used data (88.1%), unfilled bars represent discarded data (11.9%).

round of tests was then performed, providing 144 calls in all for calibration analysis. This method allowed for a controlled and observable assessment of maximum likely distortion of the array. Such distortion would likely occur only, if at all, for short periods of time when the array was adju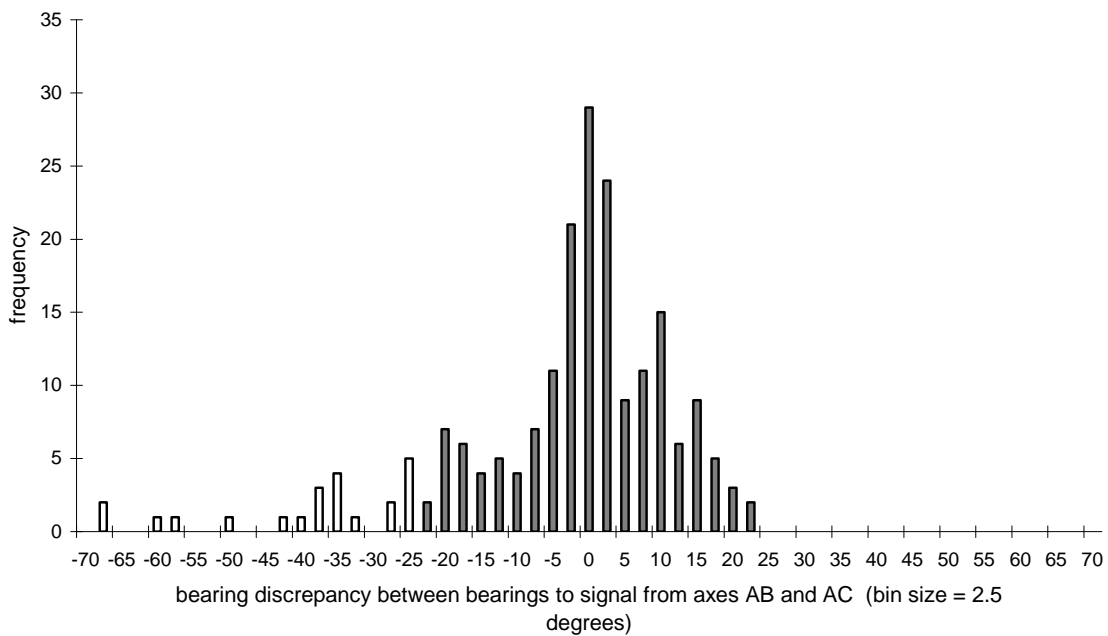sting, under severe stress from currents and wind, to a new, optimal position, after which it would resume its natural shape.

Fine-tuning of calibration analysis methods

Signal distortion by the amplifier and speaker introduced artefactual double peaks in the recorded time delays, so various methods of cross-correlating the left and right channels (hydrophones A and B, or A and C) were tested: (1) an optimal window was selected for cross-correlation, as for the bearing calculations on the recorded field data of whale vocalisations; (2) the first second of the two–second files was cross-correlated; (3) the original signal was cross-correlated with both left and right channels and the differences between results gave the delay; (4) the previous two correlation functions (original signal with left channel, and then with right channel) were cross correlated. While this latter method was the best, there remained two peaks 8 ms apart in the result, probably introduced by signal distortion. Method (4), using the full signal, was therefore adopted, with the addition of a windowing function of 6 ms around the predicted result based on prior knowledge of the test signal location, to avoid the artefactual double peaks in the cross-correlation results.

Calculated bearing error

The predicted millisecond delay per degree for all angles (for both baselines) was calculated and then used to convert the known, measured delays to equivalent bearing errors. The error in bearing was the difference between the actual bearing and the predicted bearing. The equivalent bearing errors for the distorted array were calculated. Note that the results for the undistorted array were averages of 6 tests while the results for the distorted array were the results of only one determination, but the spread between readings was relatively small, and the time period during which the array was actually distorted in the field was far smaller than the time it was undistorted.

Observed bearing error

At each of the 24 calibration stations (12 positions covering 30°sectors, for an aligned and then a distorted array), 3 measurements of bearing to the station were taken with the electronic compass, to quantify observer error.

2.2 Results

Analysis of field recordings: rejected and accepted calls

Bearing determination on a dual-axis array involves the extraction of two time delays (one for each axis), each leading to two possible, reciprocal bearings. For each pair, one of the bearings corresponds to a bearing from the other pair. When the discrepancy between the two corresponding bearings was greater than 22.5° (one quarter of one quadrant, or 1/16th of 360°, which allowed for retention of

88.1% of calls entered), the bearing was rejected (see '*Determination of bearing to sound*', p72). Of the calls which were extracted for bearings determination, the percentage of rejected calls from any one continuous recording session ranged from 0% to 22.5%. Overall 11.9% of the calls entered into the bearings analysis were rejected.

Calibration results

Various cross-correlation methods having been explored, the method used in the calibration tests was to cross-correlate first the left and then the right channel with the original signal and to estimate the delay from the two maxima obtained in this way. Correlations between channels of the calibration signals had produced two maxima (an example is one at -12 ms and another at -5 ms), probably due to signal distortion. A windowing function with an acceptance level of ±6 ms around the predicted delay (in this case, of -11.79) was implemented to exclude the artefactual second maximum. This method, while potentially questionable, was vindicated by the results obtained. Delay errors were in the region of -2 ms to 2 ms. Randomly distributed data within the ±6 ms window would have included errors of up to 6 ms. This was the most successful cross-correlation method, and was implemented in assessing the accuracy of the array in providing data to calculate bearings to a sound source.

Calculated and observed bearing error

For the undistorted array, the delay errors were converted into bearing errors of between + 8° and -5° (absolute error range 0°–8°, average, calculated using absolute values, 3°, s.e. 2°) for hydrophones (A and B), and between +9° and -5° (absolute error range 1°–9°, average, calculated using absolute values, 4°, s.e. 2°) for hydrophones (A and C). For the distorted array delay errors were resolved to bearing errors of between +3° and -13° (absolute error range 2°–13°, average, calculated using absolute values, 6°, s.e. 3° for hydrophones (A and B), and between +6° and -10° (absolute error range 0°–10°, average, calculated using absolute values, 3°, s.e. 3°) for hydrophones (A and C) (*figs 3.8, 3.9*).

Precise bearings to the array to determine its orientation were necessary for calculating absolute bearings to signal source. From the three bearings taken at each of the 24 calibration stations, an observer error of between +3° and -3° (absolute error range 0°–3°, average, using absolute values, 1°, s.e. 1°) was calculated.

When the error arising from both pairs of hydrophones, (A and B) and (A and C), for both the undistorted and the distorted array were considered together with observer error, bearing error ranged between +9° and -13° (absolute error range 0°–13°, average using absolute values, 3°, s.e. 2°).

Any source of error, arising from structural characteristics of the array when either distorted or undistorted, or observer error, could counteract or amplify other sources. Actual error combinations were impossible to predict.

Calibration Layout & Path Length Formulae:
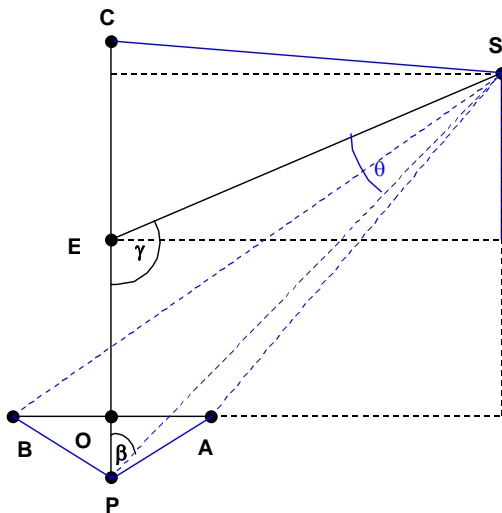
SE = 11 metres
AO = OB =1.5 metres
AC = 4.5 metres
OC = 4.2426 (= sqrt 18)
CE = EO = 2.1213   (= 0.5 * OC)
OP = 1 metre
PB = PA = sqrt(1.5^2+1^2) = 1.8028
$\angle$OPB = $\angle$OPA = atan(1/1.5) = 56.31
θ = asin(PE*sinβ/SE)
γ = 180-β - θ
SP = sinγ(SE/sinβ)
SB = sqrt(PB^2 + SP^2 - 2*PB*SP*cos(β + 56.31)
SA = sqrt(PA^2 + SP^2 - 2*PA*SP*cos(β - 56.31)
SC = sqrt(CE^2 + SE^2 - 2*CE*SE*cos(180-γ))

$$\frac{a}{\sin A} = \frac{b}{\sin B} = \frac{c}{\sin C} \text{ (Law of Sines)}$$

$$a^2 = b^2 + c^2 - 2bc \cos A \text{ (Law of Cosines)}$$

$$\frac{a-b}{a+b} = \frac{\tan\frac{1}{2}(A-B)}{\tan\frac{1}{2}(A+B)} \text{ (Law of Tangents)}$$

Figure 3.8 Test layout for in-air calibration of a portable, dual-axis, T-shaped suspended hydrophone array. The T-shaped array is defined by the symbols A, B and C, the three hydrophones creating two axes. S is the location of the speakers transmitting the signal. Visual bearings were taken from P. During trials at 12 stations, each 30° apart, S described an 11 metre full circle around E.
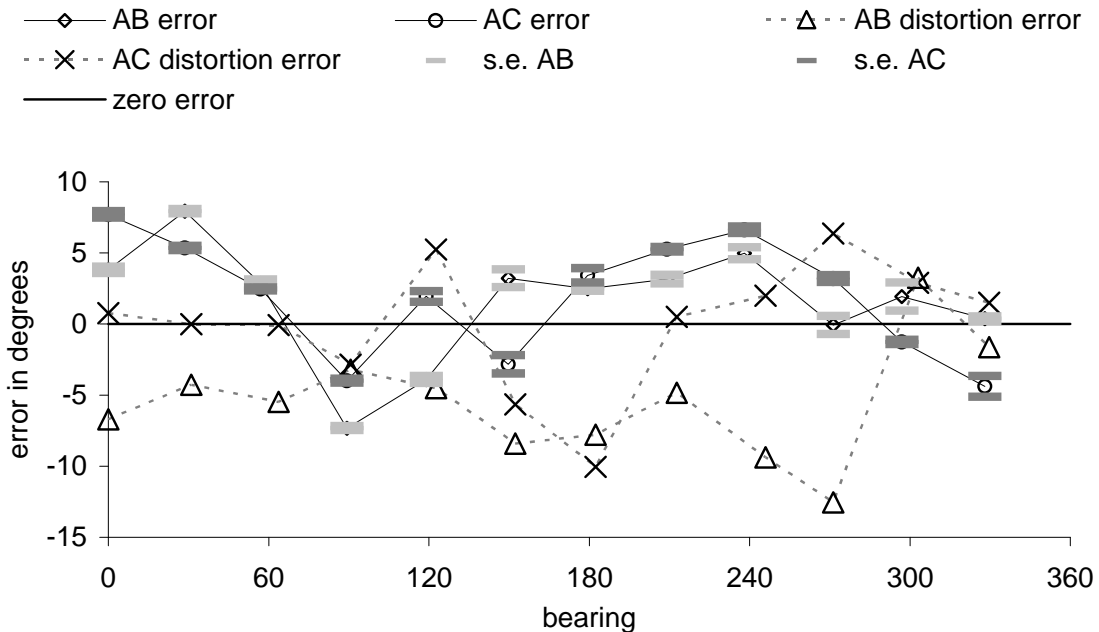

Figure 3.9 Calibration bearing errors for undistorted and distorted array, hydrophones (A and B) and (A and C). Error around bearings at each of 12 stations is shown as horizontal bars.

Because the calibration was carried out in air, and the array was deployed in water, it is worth noting that sound wave lengths in air are about 4.5 times smaller than they would be in water, for the same frequency. The test signal, an upsweep from 70 Hz to 130 Hz, would have provided the same error results as calibrating the array in water using a tone rising from 320 Hz to 590 Hz (a frequency range included in southern right whale calls and their harmonics); but strictly speaking, as error is inversely proportional to frequency, we could draw the conclusion that the average error, for the test frequency of 70 Hz to 130 Hz (2.9°), should be scaled up by a factor of 4.5 to 12°, which is unrealistically high, given that a large proportion of right whale vocalisation is above 130 Hz.

Another approach is to consider the range of uncertainty at which time delays can be read from the peak values on the correlelograms of real whale calls recorded in water (bottom graphs of *figs 3.3* to *3.5*), and then to work out the bearing error by referring to *fig. 3.6*; there appears to be an uncertainty of around 10° for baseline AB and 7° for baseline AC, for a bearing at right angles to the hydrophone pair (the most accurate direction). This translates into an effective $\pm5°$ (AB) and $\pm3.5°$ (AC), which, viewed together, are much closer to our calculated overall mean error of 3°.

Clustering of bearings for field data

The twelve recording sessions for which bearings to signal were calculated showed distinct clustering in the bearings results obtained (*fig.3.10*). A uniform distribution would have spread the bearings over the full 360° available; such a result would have been unlikely as whale distribution within any given recording session was never uniform. Viewing the available directions from which calls could arrive at the array as twelve sectors each occupying 30° of the full circle, the distribution of calculated bearings for each recording session, when graphed, showed distinct peaks in some sectors (*fig. 3.10*). This test served as an additional validation of the proper functioning of the array. Distribution, assessed for uniformity around a circle (Cox & Hinkley, 1974), was non-uniform ($p<0.05$, *Table 3.1*).

Table 3.1 Test for non-uniform distribution of bearings to calls

number of bearings		5	10	15	50 and over
critical value at 5% level		1.932	1.944	1.952	1.958
(positive or negative)					
session	T	n	T*sqrt(2/n)		
6b	-6.817	7	**-3.644**		
11a	12.906	54	**2.484**		
17b	-21.397	30	**-5.525**		
18b	-1.334	51	-0.264		
23a	-3.719	18	-1.240		
26b	5.309	6	**3.065**		
27a	-8.079	13	**-3.169**		
28b	2.674	9	1.260		
30b	7.957	13	**3.121**		
31b	-16.696	27	**-4.544**		
34a	7.158	14	**2.705**		
39a	-3.056	18	-1.019		
OVERALL	-25.094	260	**-2.201**		

2.3 Discussion

The array system comprises the physical array deployed from the boat and the recording devices used for data capture, as well as the dedicated software developed for determining time delays from the stereo recordings, and converting them into absolute bearings to sound sources. The relatively low cost of the array components and recorders makes it generally accessible. Calibration tests demonstrated the error at close range of the array, including all sources of error, to be between +9° and -13° (absolute average 3° , s.e.2°). Error associated with the bearing observation was between +3° and -3.° (absolute average 1°, s.e. 1°). These tests were in air, not sea water; our choice of in-air calibration was determined by available equipment and resources. Clearly, the multipath structure in air is very different to that in water. This limitation is offset by the fact that the 144 tests used carefully designed test calls and gave equal coverage to all areas of each quadrant. They had the advantage of being more thorough than many shipboard 'calibrations' based on small, opportunistic samples of observed sound sources with known locations. Distortion of the array was also controllable and observable. Without referring to the actual whales observed during the recording of the analysed signals, the credibility of the results obtained was further strengthened by the clearly non-uniform bearings computed for these calls (at least $p<0.05$). The bearings were clearly to specific, non-uniformly distributed sources of sound. Despite the fact that most stations were relatively close inshore, whales were still frequently encountered inshore of the boat, and we were rarely so close to shore that whales could not have been closer, so that this was not a source of bias in the non-uniform distribution of bearings.

Post-processing acoustic data for bearings information adds greatly to the time needed for analysis. It does however provide a means of accessing directional information from a small research vessel at relatively low cost. Experience of the acoustic environment in Walker Bay and the nature of the whale calls have also affirmed this approach. Southern right whales do not consistently vocalise in a predictable fashion, and relying on real-time direction finding in a location without a suitable land-based observation point with visual range to the desired study area (*fig. 3.11*) (cf. the Argentinean study(Clark, 1980)), is problematic, particularly so when the chances of missing a call in real time are high. The SNR in such shallow water ensured that the vast majority of calls were extremely faint; real-time on-board capture of time delays, using both paired two-channel oscilloscopes and a four-channel chart recorder, had been abandoned early on because the nature of the *up* call, sinusoidal and smooth, often with soft onset, displayed insufficient features to allow for easy visual phase determination on the boat in real time, and we were unable to accommodate an on-board computer.

Another limitation of the array system was that the self-noise of a suspended array also added to the ambient sound on the stereo recordings, particularly under rougher sea conditions, but this should be balanced against the added flexibility of a boat-based array system, deployable and recoverable from a small research vessel. While this array may be described as 'low-tech' when compared with many
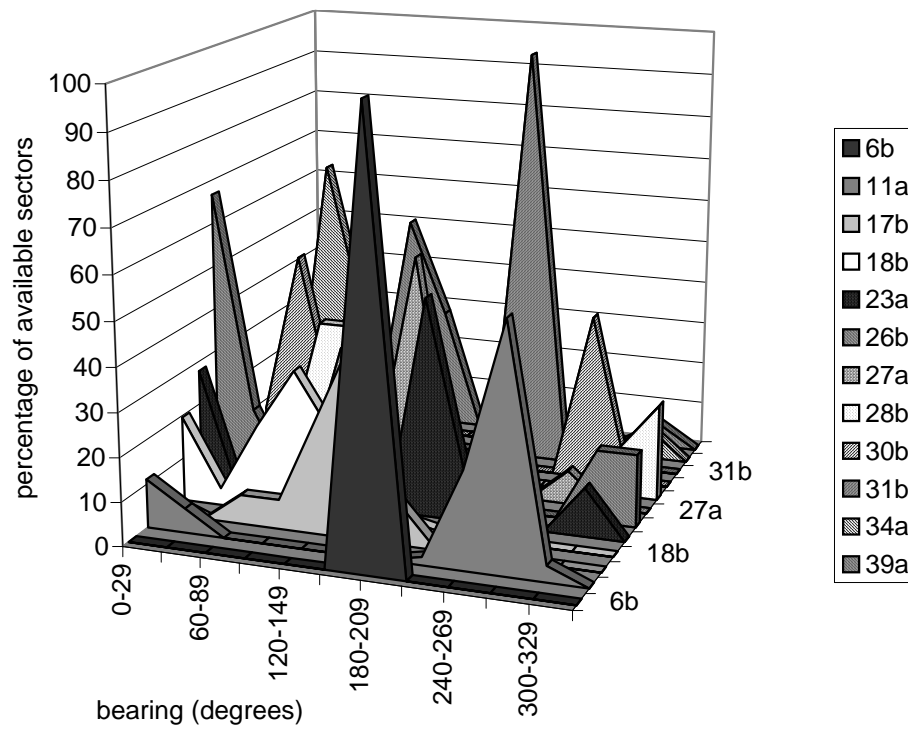
Figure 3.10 Distribution of computed bearings for 12 recording sessions amongst the twelve 30°
sectors of available space. An even distribution would have given smoother results, with mean values
for each sector of 8.3%. Instead the bearings for each recording session cluster around a few sectors.
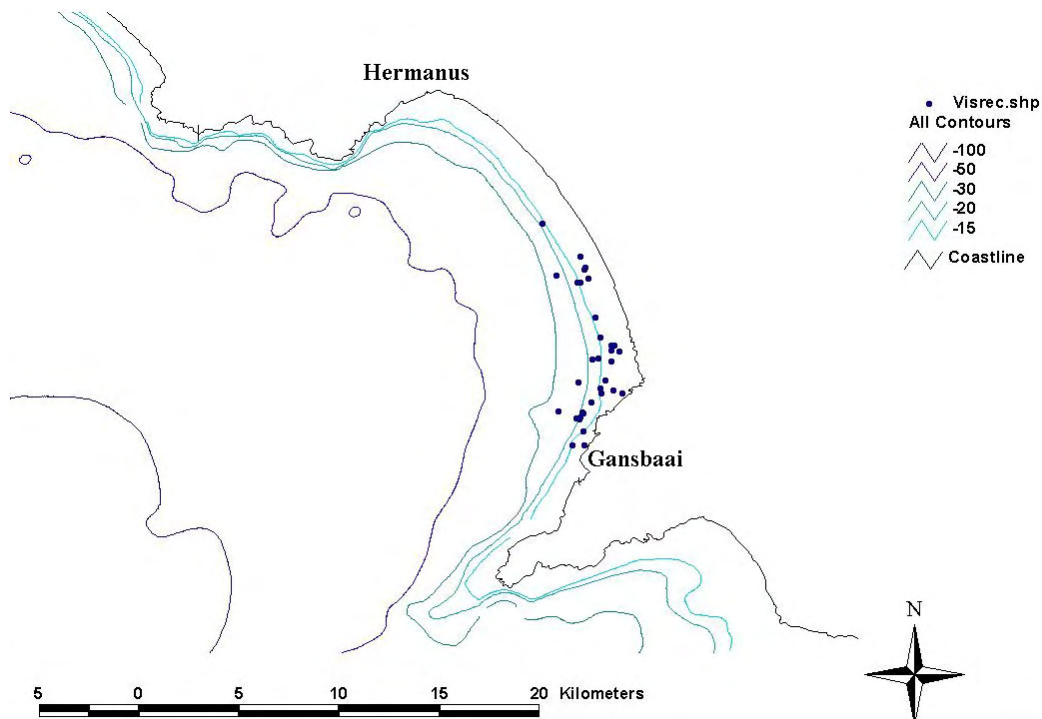

Figure 3.11 Sampling locations in Walker Bay for concurrent acoustic and visual monitoring.

more complex systems (Havelock, 2003; Macpherson & Middlebrooks, 2003), it produced results vital to the research for which it was designed.

3. Part II: Determining bearings to calling southern right whales

3.1 Materials and method

Walker Bay, South Africa, is an important concentration area for southern right whales during their winter movements to lower latitudes. Between June and November 1999, recordings of southern right whale vocalisations were made in Walker Bay (*fig. 3.11,* (Best, 2000; Best et al., 2003), from a 6 m semi-rigid inflatable boat. Sixty hours were recorded from a custom-built, suspended, T-shaped, dual-axis, three-element hydrophone array. Two Aiwa stereo recorders (model HS-JS165) captured two sets of time delays, for determination of bearings to sound source. Visual observations of bearings to animals present at the time of recording were made from an elevated viewing platform on the boat. From a separate custom-built hydrophone (*chapter four*), mono signals were simultaneously recorded onto DAT tapes using a portable DAT recorder (model HD S1), with a flat response between 20 Hz and 20 kHz, modified to run on a 12V alarm battery. An additional gain of 7dB was used when the signal was very faint.

Bearings to calling whales computed from the stereo signals were compared with observed bearings to whales located visually near the time the recordings were made, to assess the likely origin of calls and the relative proportions of vocal and silent animals.

Selection of call sequences for bearings analysis

After aural monitoring of the entire dataset of recordings, during which all calls were noted and classified (see *chapter one* for a description of call types and classification methods), twelve single track continuous recording sessions were selected for detailed analysis, based on call type and clarity. These comprised ten single-track sequences of the best examples of *low up* calls, and two of *high/medium down* calls, or SAG calls, with concurrent stereo recordings and visual observations of the whales visually located at the time of recording. Stereotypy was an important feature of the selected calls because the call types were selected on the basis of their potential to hold acoustic markers for individual signature information. Differences between similar calls from distinct individuals were sought, rather than differences due to random variation in call envelope from call to call, independently of the caller (*chapter four*). The quality of the recordings was also an important factor. Better signal-to-noise ratio allowed for greater accuracy in determining the direction of the sound source.

Bearings determination

Each call was digitally sampled as a 2 second mono file from the DAT recording, and as two matching stereo files, (A and B) and (A and C), from the cassette recordings. Bearings to sound source were calculated for each call, based on two sets of time-delayed calls captured on cassette recorder, and on the geometry and changing orientation of the array (as determined from the closest bearing in time recorded via hand-held electronic compass on the boat). Because the signal was often extremely noisy, dedicated software was developed for the study to display maps of correlation coefficients for each channel to facilitate time delay calculation.

Comparison between acoustically computed and observed bearings

This analysis was confined to periods of vocal activity, as its focus was on determining bearings to vocal whales. As a step in the process of assigning calls to individual animals, the call direction was compared with the observed directions to groups of whales in view from the boat. Where the calls came from the direction of observed whales there were often two or more animals, so that calls could only be assigned to a group rather than an individual. There was an inherent uncertainty surrounding the number of whales in some groups, and the exact location of each whale group (let alone each whale within each group) between sightings, particularly when there were many groups to track. The likely position of whale groups when not actively sighted was inferred as falling within the straightest route between sighted locations, and moving at a constant speed, even though this may not have been the case. Added to these sources of potential error were those associated with the computed bearings (structural, distortion and observer error) and observer bearing error when determining bearings to visually located whales. Computed bearings to each call were compared with visual or inferred bearings to observed whales by visual inspection of track plots showing bearings to both calls and whales. In the first of two analyses of the vocal status of the sighted whale groups, they were described as either silent or vocal. Some calls were clearly from the direction of a visually located (and vocal) whale group. Calls occurring in time before a whale group was sighted, but from a similar direction, were assigned to that group. When calls were located on a bearing similar to more than one whale group, and within around 10° of either (making it possible that the calls came from both groups, or either group) The second analysis of the data scored whale groups as either silent, vocal, or indeterminate (when it was not possible to tell which of two candidate groups was vocalising). Most groups previously described as vocal were now described as indeterminate; a group was scored as vocal only in cases where call origin was unambiguous.

Groups located acoustically but not visually were not included in the proportional analysis of vocal, silent and indeterminate groups, for two reasons: (1) to include (sometimes arbitrary) numbers of unseen vocal groups detected acoustically would, in some cases have been highly speculative without visual cues as to their number, distance and direction of movement, introducing further potential error; and more importantly(2), it would have been necessary to include an inferred number of silent, unseen

groups to avoid skewing the data. This number would have been derived from the observed proportions of sighted vocal and sighted silent groups, and so have added nothing to the analysis.

Calls clearly from a direction where no whales were seen, were scored as calls from unsighted groups; all other calls were scored as calls from sighted groups. Each plot of observed bearings to whale groups sighted from the boat, and of calculated bearings to recorded calls during the recording session (track plot) was inspected, to assess proportions of vocal and silent groups, and calls from sighted and unsighted whale groups.

Group size composition

The sizes of the whale groups encountered, weighted for relative duration in minutes of their respective recording sessions, was described. In particular, where a single animal had been observed within the twelve call sequences analysed in detail, the feasibility of assigning a call to that individual based on call bearing, was assessed. A set of calls apparently emanating from a single whale would have provided a good opportunity to characterise the variation in calls from a single individual, with a high level of confidence as to the identity of the caller. Calls from the direction of more than one animal would reduce certainty as to the caller, but still allow for separation of calls from different directions.

3.2 Results

Twelve tracks of bearings to observed whale groups compared with computed bearings to calls

For each of the twelve recording sessions, the computed bearings, without reference to observed whales, clustered non-uniformly around only a few directions in the assessed circle, a result consistent with the assumption that the calls were coming from localised sources and hence specific directions.

Bearings to ten sets of LU (*low up*) calls and two sets of HD/MD (*high down /medium down,* or *SAG*) calls, and their timing, were then compared with observed bearings to whale groups and times of sighting (*figs. 3.12-3.23*). (Note that in *figures 3.12–3.23*, calls are represented by upright crosses without lines on either side. Whale group sightings are represented by several other symbols, and are joined by lines. When a whale group symbol appears without lines either through or on either side of it (a feature which also serves to distinguish between similar symbols where there are many groups present), it represents the only sighting of that group.) Call bearings clustered non-uniformly in specific directions which were sometimes close to observed whales in space and time, and sometimes not.

Up calls

Track 11a (*fig .3.12)* was relatively straightforward to interpret. Only two groups were visually detected during or directly before the calls of interest, at ranges of 600m to 700m, and only two calls were relatively near the observed groups. Neither group was identified as a single animal. Group 1 (3

whales) was observed before and after one of the calls, and some or all the whales may have moved slightly off course from the inferred route between sightings. The bulk of the calls were clearly from whales not visible from the boat.

Track 17b (*fig.3.13*) had a greater proportion of calls from directions near sighted whales, and some from a direction where whales were subsequently seen, such as the two calls in line with group 2.

Track 18b (*fig.3.14*) calls were more difficult to assign; two groups at 500m to 600m distance could certainly have produced the first seven well separated calls, and possibly all but a few of the later calls. The bulk of these calls followed a strong trend, firstly in one direction and then in the opposite direction. As both groups were of unspecified size, it is possible that some of the calls came from a whale or whales swimming off course from the direct line between sightings of group 5. The last clustered group of calls may be a continuation of this movement, or belong to group 2, as sightings ceased 20 minutes before the calls but they are from the same direction.

Track 23a (*fig.3.15*), the joining and parting of two groups (possibly two adults and a single animal), matches well with the separation between two initial groups of calls. While the calls near 0° are not in a direct line with sightings, they are close enough for at least one of the pair to have moved away from the observed position. Later calls between 180° and 240°, and between 300° and 360°, are from whales not seen from the boat.

Track26b (*fig.3.16*) demonstrates the difficulty of keeping track of multiple whale groups visually. Whale groups 9 and 10, sighted after 13:45, are not sighted during or after the calls of interest were made, although both appear to be heading in the direction of the subsequent call location between 0° and 45°. Group 14 is the nearest group to the call direction, but the direction in which they were moving is inconsistent with the bearing to the call.

Track 27a (*fig.3.17*) presents another dilemma, with one call (near 300°) almost definitely from either group 1 or group 2, which have converged. A further seven calls (between 150° and 180°) are highly likely to belong to group 4 (a single whale). Again the calls occur between actual sightings, and call bearings are off-course from the direct line between sightings, but near enough for the whale to be the likely caller. Track 30b (*fig.3.18*) shows a clearer picture. Calls separate into two distinct groups. The first five calls may be assigned to group 1 (of unspecified size) though group 3 may also have contributed, and the calls from approximately 50° are definitely from an unseen source, although one hour later group 6 appears on the same bearing.

Track 31b (*fig.3.19*) shows four groups, all relatively stable in bearing, and all the calls aligned with group 2, of unspecified size. Group 4, starting out as four animals, becomes a surface active group (SAG) by 15:00.

20 minutes (calls occur within 14.2 minutes)
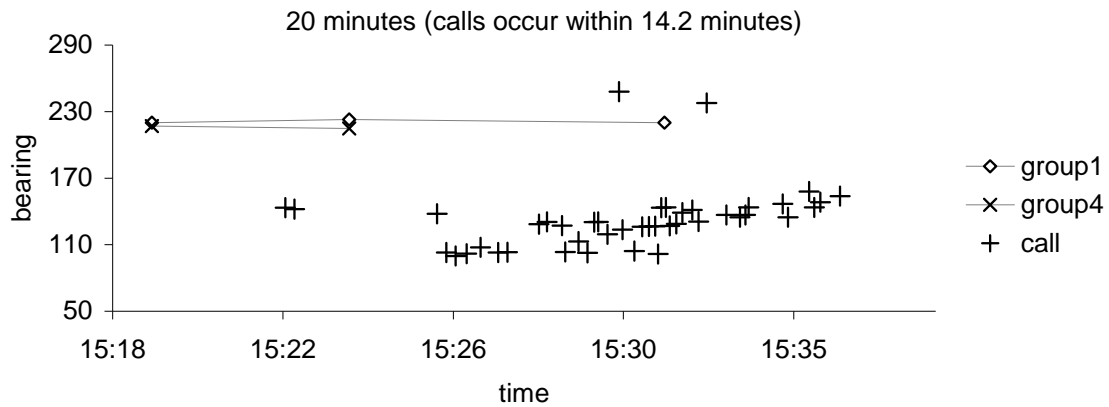
Figure 3.12 Track 11a: computed bearings to LU calls and observed bearings to whales. Only two of the calls may belong to group 1.

50 minutes (calls occur within 40.9 minutes)

Figure 3.13 Track 17b: computed bearings to LU calls and observed bearings to whales. Several calls cluster around areas where whales were observed.

60 minutes (calls occur within 45.7 minutes)

Figure 3.14 Track 18b: computed bearings to LU calls and observed bearings to whales. Several calls cluster around areas where whales were observed. Others do not.

135 minutes (calls occur within 37.4 minutes)
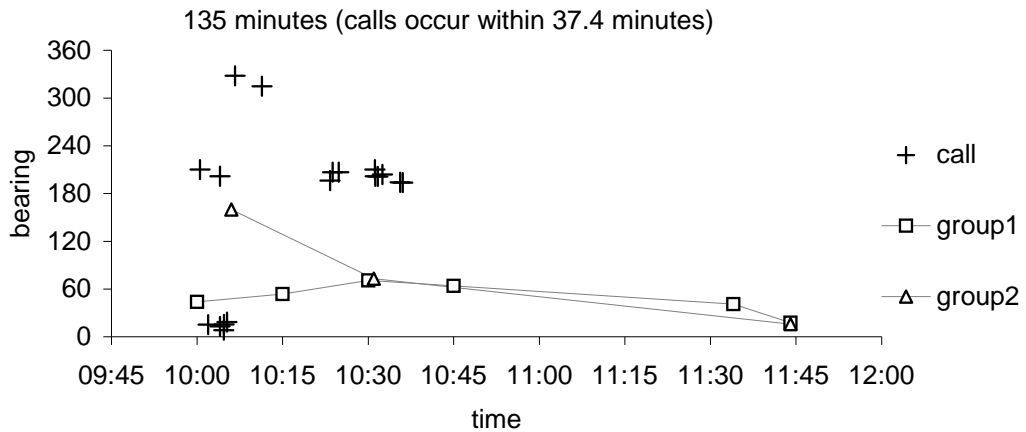
Figure 3.15 Track 23a: computed bearings to LU calls and observed bearings to whales. Only seven calls may have been made by observed whale groups.

180 minutes (calls occur within 9.1 minutes)
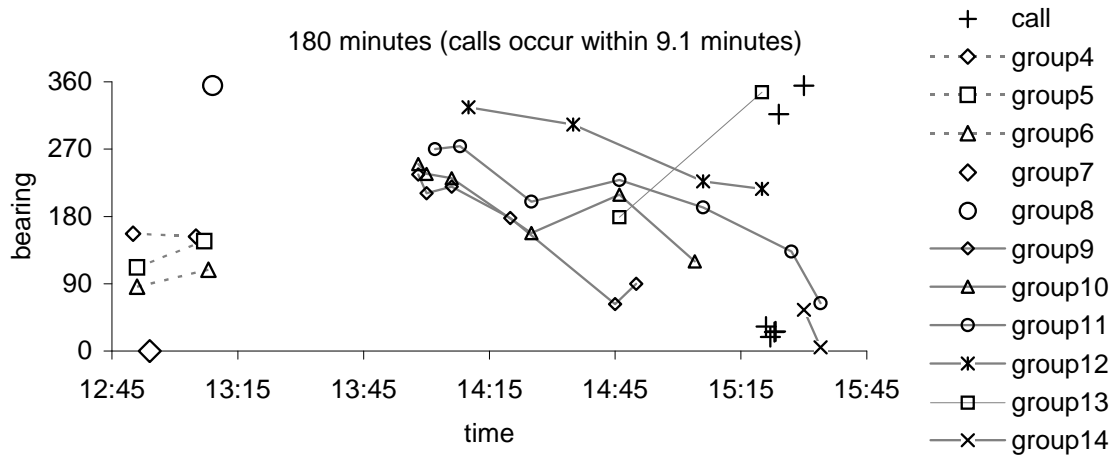
Figure 3.16 Track 26b: computed bearings to LU calls and observed bearings to whales. It is possible that all calls came from sighted whale groups.

49 minutes (calls occur within 8.2 minutes)
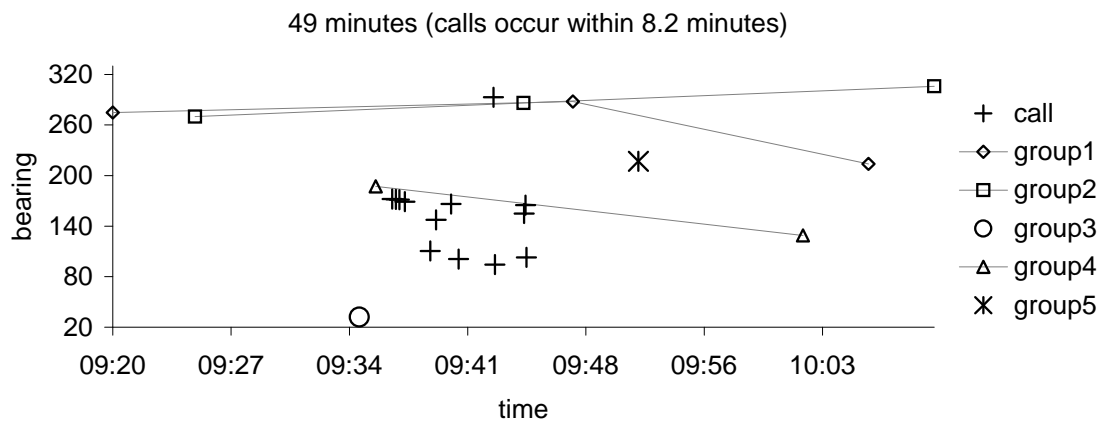
Figure 3.17 Track 27a: computed bearings to LU calls and observed bearings to whales. Several calls cluster around areas where whales were observed. Others do not.

Figure 3.18 Track 30b: computed bearings to LU calls and observed bearings to whales. Six calls are possible candidates for observed whale groups.

Figure 3.19 Track 31b: computed bearings to LU calls and observed bearings to whales. All calls apparently emanate from group 2.
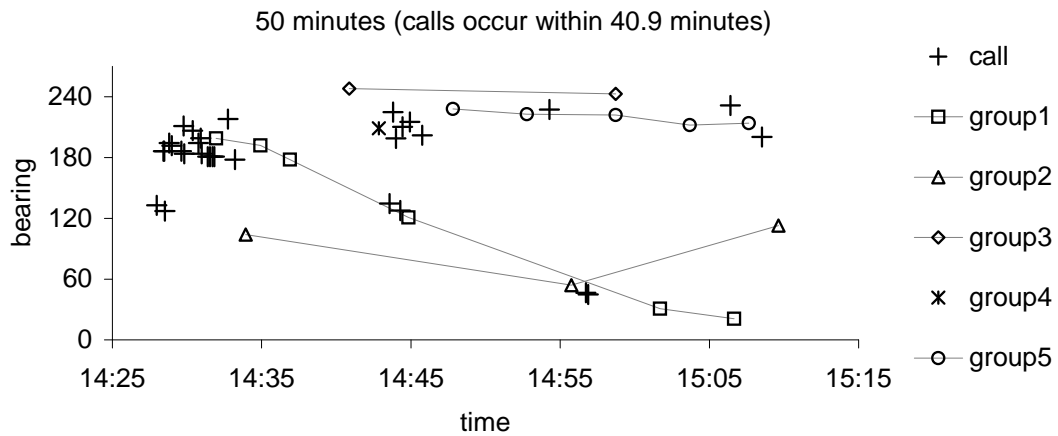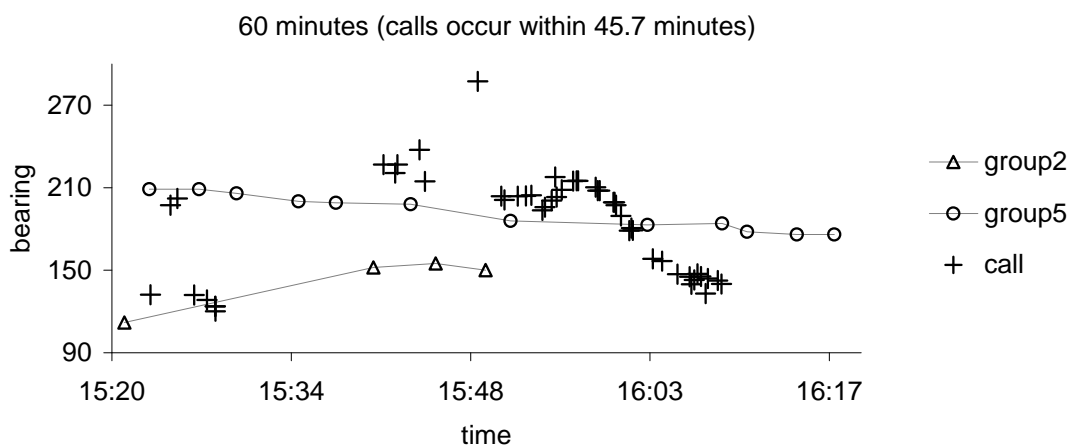

Figure 3.20 Track 34a: computed bearings to LU calls and observed bearings to whales. Several calls cluster around areas where whales were observed. Others do not.
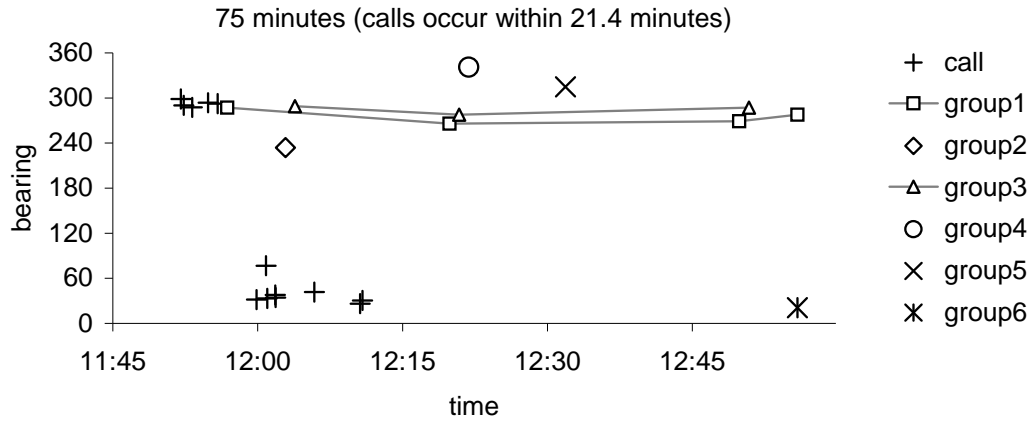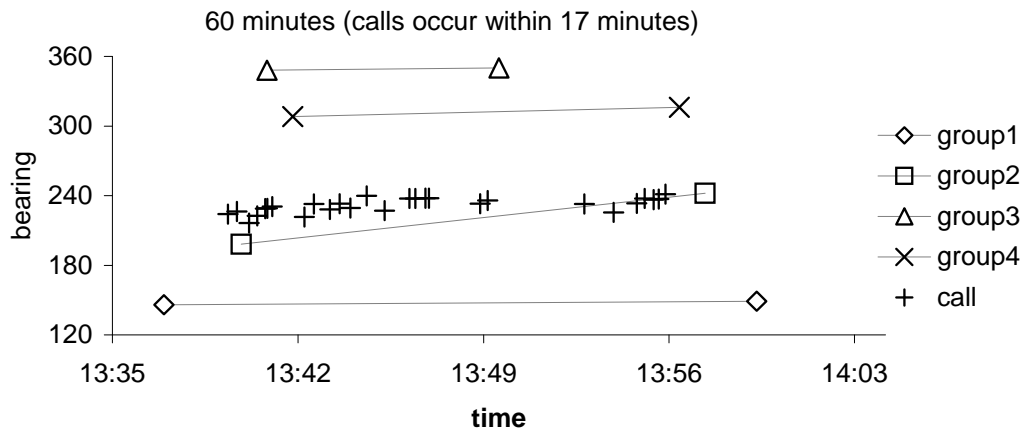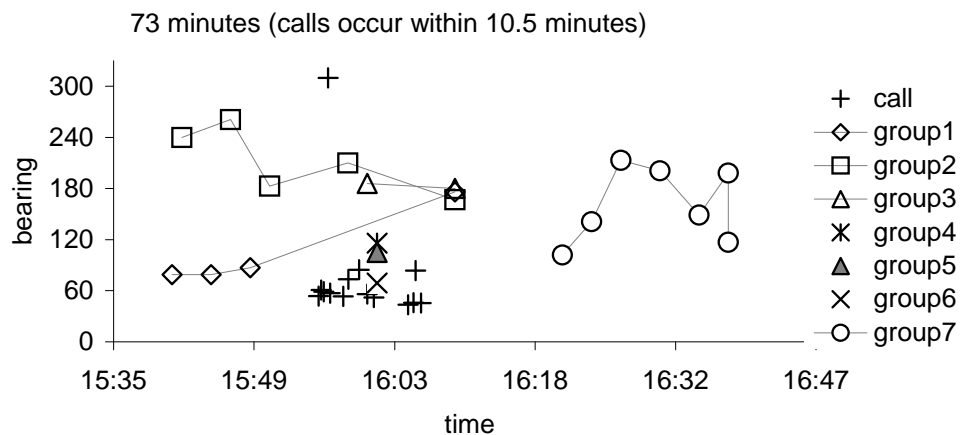
Track 34a (*fig.3.20*) shows a complex situation with several groups on close bearings and calls clustered between 30° and 90°, around group 6 (a cow-calf pair) but also close to group 5 (of unspecified size). Group 7, appearing around 16:20, also a cow-calf pair, may be the same whales as group 6.

Track 39a (*fig.3.21*), at the time of the tightly clustered, rapid succession of calls between 80° and 120°, shows the convergence of two cow-calf pairs (groups 7 and 8) coinciding with bearings to eleven calls. There are four groups present, three of them cow-calf pairs, and one a single animal. Three of the remaining four calls are close to sighted whales.

SAG calls

Track 6b (*fig.3.22*) illustrates the convergence of two groups, each of at least two whales, and a series of rapid calls at the point of their joining. The signal-to-noise ratio was very good, and the calls loud and clear, which may have optimised the accuracy of the array.

Track 28b (*fig.3.23*) gives a realistic picture of the difficulty of keeping track of the movements of nine groups of whales. The locations plotted for groups 1 and 2 suggest some confusion in allocating visual bearings to the correct sighting, although it should be remembered that the plots only show time against bearing; distance of various groups from the observation point also serves to distinguish one group from another. At the time of the calls there were six whale groups, some of which had been extremely active. The calls between 0° and 90° appear closest to group 6 (a single whale). Alternately they may belong to nearby group 3, as there were no actual sightings at the time of the call for this group and it may have moved in that direction before taking up its observed position after the calls. The remaining calls, between 90° and 120°, appear to come from group 2, made up of three whales, but the possibility that they could also come from group 4 (this group's plotted direct path is also close) cannot be dismissed without sightings.

Synthesis of track data and inferences drawn from results

To investigate the proportion of calls coming from sighted groups, calls were defined as group calls (coming from a sighted group) or calls from unsighted whales (coming from an unsighted group). Where two or more groups were close in bearing, it was not always possible to assign calls to a specific group, even though the call bearing coincided well with the previous or latter sightings of those groups, because of the uncertainty of whale movements when unobserved or out of sight. For some of the recording sessions, calls could have come from one or two different groups. Estimates of silent groups and calls from unsighted groups were therefore conservative, assigning calls to all possible groups close enough to the computed call origins to have been responsible for them. The addition of the label 'indeterminate' for scoring lowered the over-estimated number of'vocal' groups, but added to the uncertainty around vocal activity of the 'indeterminate' groups.
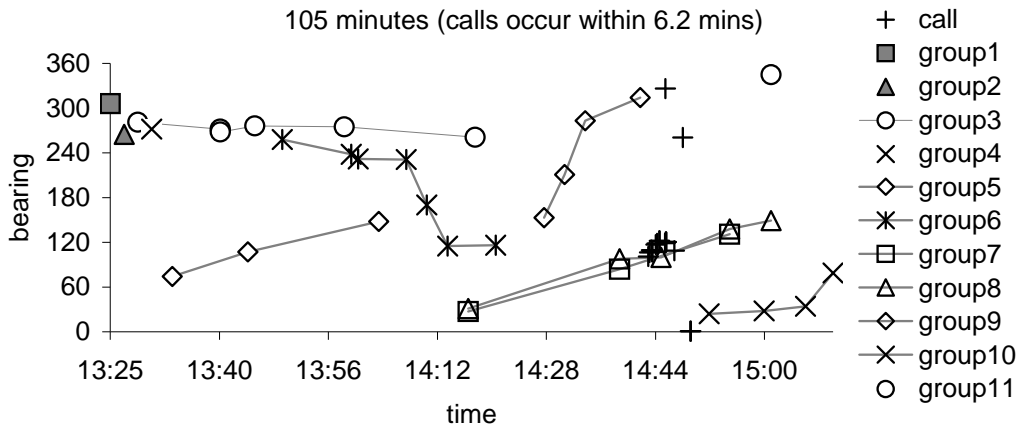
Figure 3.21 Track 39a: computed bearings to LU calls and observed bearings to whales. Several calls cluster around group 8, and groups 9 and 10 each have one call nearby.
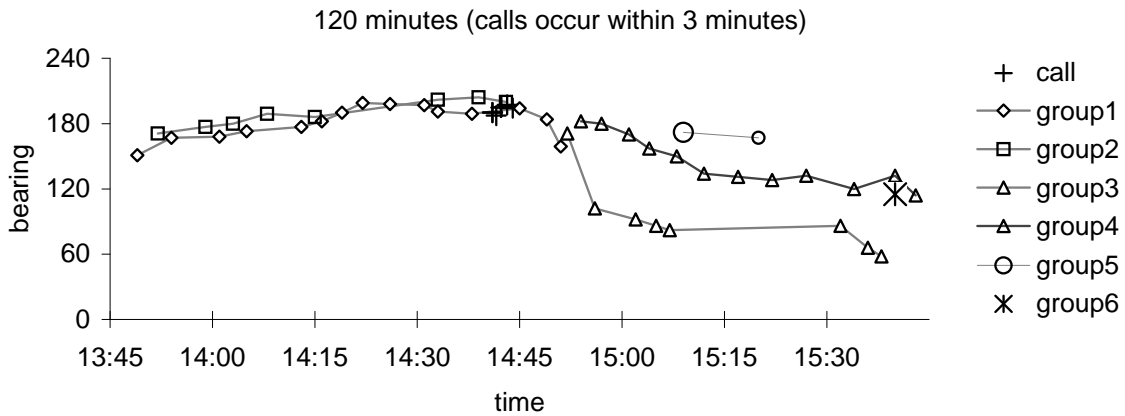
Figure 3.22 Track 6b: computed bearings to SAG calls and observed bearings to whales. All calls cluster closely around the convergence of two groups.
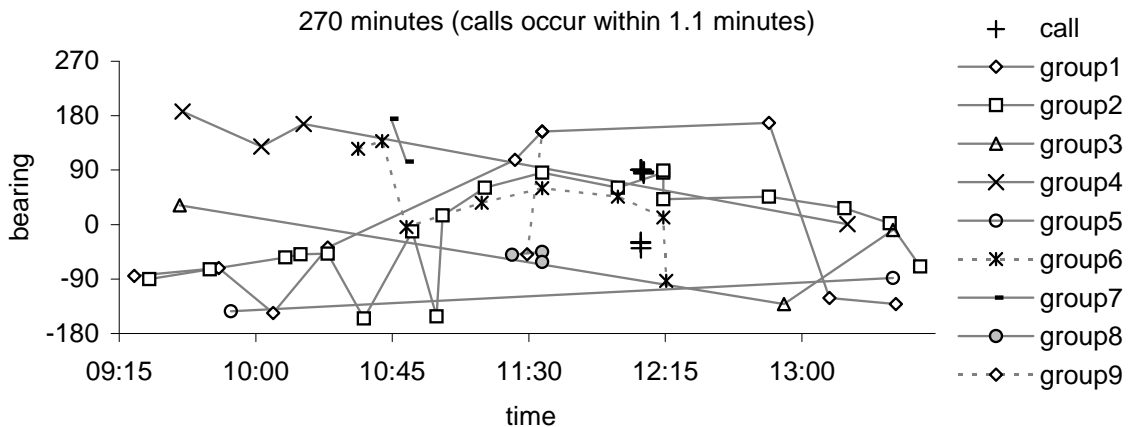
Figure 3.23 Track 28b: computed bearings to SAG calls and observed bearings to whales. Several calls cluster around areas where whale groups 2 and 4 converged. Other calls may belong to group 6.

Table 3.2 Silent and vocal groups observed both concurrently with occurrence of calls, and during entire recording sessions

recording session	GROUPS SIGHTED CONCURRENTLY WITH OCCURRENCE OF CALLS # groups	% vocal groups	GROUPS SIGHTED DURING ENTIRE RECORDING SESSION # groups	% vocal groups	# calls	% calls from sighted groups	duration (mins)
UP CALLS							
11a	2	50	2	50	32	6	14
17b	5	100	5	100	31	90	41
18b	2	100	2	100	51	74	46
23a	2	100	2	100	18	44	37
27a	5	60	5	40	13	62	8
30b	5	40	6	17	13	39	21
31b	4	25	4	25	27	100	17
34a	6	50	7	29	14	71	11
39a	4	100	11	27	18	94	6
26b	4	50	11	9	7	0	9
time-weighted mean	3.5		4.2		28		
percentage	**74 (26% silent)**		**56 (44% silent)**			**69 (31% from unsighted groups)**	
SAG CALLS							
6b	2	100	2	100	7	100	3.0
28b	6	67	9	11.1	9	66.7	1.1
time-weighted mean	3.1		3.9		7.5		
percentage	**83 (17% silent)**		**45 (55% silent)**			**89 (11% from unsighted groups)**	

Table 3.3 Groups sighted concurrently with occurrence of calls: a comparison of two analyses, one scoring groups as either [silent or vocal], the other, as [silent, vocal or indeterminate]

UP CALLS

	without indeterminate groups	with indeterminate groups
% calls from sighted groups	69	69
% calls from unsighted groups	31	31
% sighted groups - silent	26	26
% sighted groups - vocal	74	52
% sighted groups - indeterminate		22

SAG CALLS

	without indeterminate groups	with indeterminate groups
% calls from sighted groups	89	89
% calls from unsighted groups	11	11
% sighted groups - silent	17	17
% sighted groups - vocal	83	0
% sighted groups - indeterminate		83
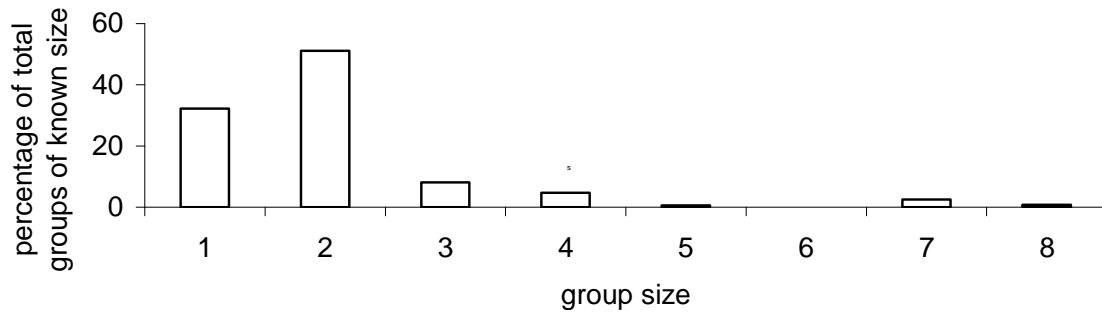
Figure 3.24 Group size distribution of whale groups of known size (n=131), encountered during overlapping recording and visual observation sessions.
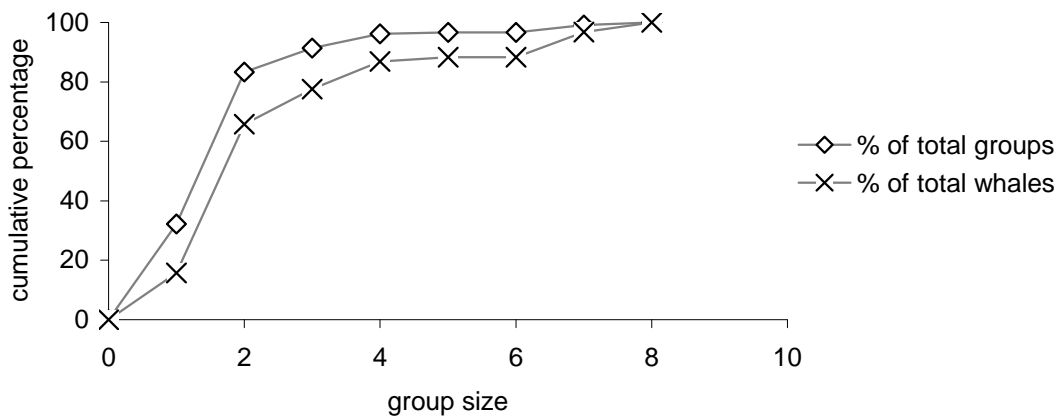
Figure 3.25 Size distribution of whale groups encountered over 63 recording sessions. Cumulative proportions of whale groups of various sizes, both known (n=131), and inferred from observed size distribution (n=90), are compared with the cumulative proportions of whales comprising the groups (n=377).

The number of groups present, and therefore potentially vocal, during calls was estimated in two ways: as the number of groups in view at the actual time the calls occurred (a conservative estimate producing a minimum number of silent groups), and as the number of groups sighted during a continuous recording session (probably still within audible range even if temporarily out of sight, giving a maximum number of silent groups). With these caveats, analysis of the plotted results led to the cautious interpretation that, of whale groups present during recording of *up* calls, between 6% (minimum) and 44% (maximum) of whale groups present were silent, depending on the whale count period; during recorded SAG calls,, between 17% (minimum) and 55% (maximum), were silent, depending on the whale count period (*table 3.2*). For *up* calls, 69% of the calls analysed for directionality came from sighted groups (% calls from sighted groups, *table 3.2*), while 31% were from unsighted groups (% from unsighted groups, *table 3.2*). For *SAG* calls, a markedly higher proportion of calls, 89%, were from sighted groups (% calls from sighted groups, *table 3.2*), and only 11% came from unsighted groups (% calls from unsighted groups, *table 3.2*).

The vocal status of the whale groups was further analysed (*Table 3.3*) by dividing the groups previously scored as vocal, into those that were definitely vocal, and those that may or may not have been vocal (indeterminate). This analysis revealed slightly more definition in separating definitely vocal groups from those that may or may not have been vocal, but the grouping 'indeterminate' had its own drawbacks, in lumping together whale groups with different probabilities of being vocal or not. There were at least four types of 'indeterminate' groups: (1) two groups, both close in bearing and time to calls, so that at least one of them had to be vocal (A and/or B) – 1 or 2 'vocal' indeterminate groups, for example, Tracks 6b, 27a, 28b and 39a; (2) two indeterminate groups and one definitely vocal group, where both indeterminate groups may or may not have been vocal along with the vocal group {[(A)and (B and/or C)], or just (A)} – 0, 1 or 2 'vocal' indeterminate groups, for example, Track 34a; (3) one indeterminate group and one vocal group, where the indeterminate group may or may not have contributed vocally [(A) or (A and B)] – 0 or 1 'vocal' indeterminate groups, for instance, Tracks 17b and 30b; and (4) one indeterminate group, possibly contributing to calls close in time and bearing, which may also be from an unsighted group [(A and/or (unsighted group)] – 0 or 1 'vocal' indeterminate groups, and 0 or 1 unsighted, but vocal groups.

In this chapter, dealing specifically with calls analysed for bearings, the emphasis was placed on the vocal periods, defined from the first to the last call within each recording session, and the spatial relationship between recorded calls and observed whales during those times. The focus was on the relative proportions of actively vocal and silent groups during vocal activity, rather than vocalisation rates over long periods. Remote sensing places a high premium on recorded vocalisation; acoustically based assumptions about the presence or absence of silent groups are flawed in the absence of any vocal groups. Even in tandem with visual monitoring, silent groups that are present but

not sighted cannot accurately be estimated, as whales spending less time at the surface may vocalise or remain silent in different proportions to whales spending longer at the surface. Silent monitoring periods are informative in the right context, and are included in the analysis of the relationship between call rates and numbers of whales (*chapter two*)). Mean values were weighted to take account of the duration of vocalisation bouts. Proportions of vocal and of silent groups, and proportions of calls from both sighted groups and unsighted groups were based on these weighted means.

Observed whale group size composition

Call type and quality were the principal criteria for the selection of the twelve call sequences, but because of the objective of assigning calls to individuals, within these selections particular attention was paid to calls from the direction where a single animal had been sighted. In the original 63 overlapping sessions (recording and visual observation), 38.4% of the groups had an unspecified size, and were assumed to be identical to the size distribution of the adjacent groups (for a description of the method for accounting for groups of unspecified size, see *chapter two*).

Of the groups with known size (*fig.3.24*), pairs were most common (51%), followed by single animals (32%). It should be noted that although, of the total groups, the proportion of single whale groups appears high, this can be deceptive: with all whales considered, the proportion of single whales is far lower (*fig.3.25*). Only 16% of the whales we encountered were travelling singly. The presence of the single whales was no indication, however, that they were vocal. Despite the relatively high proportion of single animals encountered over the 63 sessions, the twelve call sequences selected for analysis because they had the clearest signals and contained the desired call types, were made in the presence of whales travelling predominantly in groups larger than one. Out of a total of 49 groups present over the twelve sessions when the desired calls analysed for bearings were made, only 4 groups were confirmed as single whales (8%), with a further two groups possibly single (totalling 12%). Of these 6 single whales, only 4 were in positions that corresponded with computed directions for calls where there was even a possibility that the calls were made by that particular whale. Of the 260 calls within the twelve sessions for which it was possible to compute a bearing, only 21 call bearings (8%) were near a (possibly) single whale.

It is likely that even vocal groups contained silent animals, with one whale at any given time vocalising for a brief period. When all possible pairs of calls which were potentially from a single animal, were compared within recording sessions, the two calls within a pair proved to be most similar to each other when separated by the shortest time interval, suggesting 'bout' calling (*chapters one, four*). When the study of individuality in southern right whale vocalisations (*chapter four*) has advanced to the point where separate identities may be unequivocally assigned to the recorded calls of unseen whales, it will become possible to quantify not only proportions of silent groups, but also proportions of silent whales.

3.3 Discussion

The determined bearings allowed for the identification of vocal groups rather than vocal individuals because the processed calls generally came from whale groups of two or more rather than lone animals. The best outcome to hope for would have been several sets of calls close in time and bearing, each set from a different direction and likely to come from a different animal. Despite difficult field conditions and high numbers of whales, it was possible to assign 69% of the calls either to specific groups, or to one or another of a few groups close enough to qualify as likely candidates. Only 8.08% of calls were assigned either to a single whale, or in some cases, to a group which was most likely a single whale.

While these results allowed for less certainty than we would have desired, they nevertheless provided a great deal of insight into the logistics of whale communication, and the challenges inherent in tracking mobile and largely submerged animals. Southern right whales do not generally travel in large groups. The most stable association is that of cow-calf pairs (Best et al., 2003). Adult males and females without calves form temporary, fluid associations, and juveniles frequently leave adults for periods of exploration. The problems encountered in matching computed calls to whales observed in real time are not peculiar to this particular study. Similar difficulties were encountered (Tyack, 1998) by other workers attempting to associate vocalisations with dolphins (Watkins & Schevill, 1974; Freitag & Tyack, 1993), and with bowhead whales (Clark et al., 1986).

Many potentially variable factors combined to complicate the outcome of the matching.

(a) Accuracy of the array
A series of calibration tests in air showed that error associated with the bearing observation fo array orientation was between +3° and -3° (absolute error range 0°–3°, average, using absolute values, 1°, s.e. 1°) and, including possible temporary distortion, the array had an inherent error of between +9° and -13° (absolute error range 0°–13°, average using absolute values, 3°, s.e. 2. (*Part 1*). Roughly comparable errors are likely to have occurred in the field recordings, with array accuracy inversely proportional to frequency.

(b) Uncertainty about positions of whales
It was difficult to associate a call with a caller because of the uncertainty inherent in the distribution of calls around and in the vicinity of observed whales. Between sightings there was uncertainty about the movements of any particular whale, which may have been submerged and swimming slowly or rapidly, or staying precisely in the position at which it was last noted. The calls often occurred between sightings of the group closest to the signal origin. The first eight calls in track 18b (*fig.3.14*) offer a good example of this. There were also frequently situations where more than one group of whales could have been the caller, as all were more or less equally displaced by a small angle from the apparent call origins (track 34a, *fig.3.20*, and track 39a, *fig.3.21*). Sometimes a group of calls clustered

in a general area but were not as tightly distributed as at other times (compare tracks 31b, *fig.3.19,* and 39a, *fig.3.21*). Slightly dispersed calls may have come from mobile and temporarily submerged members of a group where only the whale at the surface had been noted.

(c) Uncertainty about the array orientation

The array orientation was only noted intermittently, usually when whale sightings were logged. However it was needed for every bearing calculation, because the time delays from the hydrophone pairs could only provide data for the angle to target relative to the array; the absolute bearing was calculated by correcting for the array orientation. Missing positions along the path between one logged orientation and the next were interpolated, on the assumption that the array swung from one position to the next in a smooth, even way. In reality the array movement, brought about by force exerted by wind and ocean currents, was unpredictable and non-linear. Small errors introduced in this way could translate into large discrepancies between call and whale bearings, particularly when the whale was at some distance from the boat. Human error in measuring the array orientation could have been a factor in slightly mismatched whale and call bearings, though the margin of error was small.

Despite these complicating factors in interpreting the plotted tracks of whales and matching them to bearings to calls, the suspended array system facilitated the successful location of the sources of whale calls recorded in the field. It also provided evidence of the uneven vocal production among whale groups and the relative inefficiency of relying on visual observation or acoustic monitoring alone. Visual monitoring alone (referring only to sighted whale groups) may overlook the whale groups producing almost one third of calls (unsighted groups), and acoustic monitoring alone (referring to recorded whale calls only) may overlook silent whale groups from over one quarter to almost a half (for *up* calls), and from almost one fifth to over a half (for *SAG* calls) of, at the very least, the whales present at the surface.

Silent and vocal groups: information sharing

Because some groups were silent it is likely that some of the information conveyed by the calls was shared. In a study of dolphin vocalisation, the presence of silent animals during echolocation clicks from larger groups led to the interpretation that the information gained as a result of the clicks was shared (Jones & Sayigh, 2002). A similar situation was postulated for rough-toothed dolphins(Götz et al., 2006). There is a great difference between dolphin echolocation and whale tonal calls; yet it is possible that calls and responses to calls, whether contact calls or the calls of a female adult in a surface active group, contain information useful to multiple receivers.

Future use

Establishing the location of calling whales will remain an important factor in understanding the dynamics of whale communication and exploring the function of whale vocalisations. With automation of array orientation and real-time localisation of the sound source the power of the techniques will be greatly enhanced. The attachment of D-tags for the study of whale vocalisation has

some advantages in identifying individual callers; but it is an expensive option, drastically limiting sample numbers, and does not always deliver unequivocal caller identity when a whale has close companions (Matthews et al., 2001; Parks, 2003a). The attachment of a tag may also inhibit or alter in other ways the vocal and non-vocal behaviour of the tagged whale (perhaps more so than the presence of a small research platform). Hi-tech solutions will minimise error, aggravation and time-expenditure; yet the system presented here is non-invasive and cost-effective, and produced some interesting perspectives on the acoustic behaviour of submerged and visible southern right whales.

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CHAPTER FOUR

INDIVIDUAL VARIATION IN THE CALLS OF SOUTHERN RIGHT WHALES

1. Introduction

Any attempt to decipher the communication system of a non-human species must start with the isolation of their signals, be they electric, visual or acoustic. The more precisely communicative signals may be assigned to individuals (Tyack, 1991), rather than groups (Mellinger & Clark, 2003), the finer will be the resolution of their significance in context. This holds true for both the observers (such as human researchers), and for participants in the communication (sender and receiver/s). Communication among cetaceans, occurring largely underwater, in low visibility, and often over long distances, places a high premium on the acoustic advertisement of identity. The acoustic recognition of individuals, an integral factor in binding individuals into groups, is a skill that must be acquired early on in both birds, primates and cetaceans (Clark, 1983; Fischer, 2003; Phillmore et al., 2003). Some signals between two individuals, such as right whale cow and calf (Clark, 1982), or pig mother and offspring (Illmann et al., 2002), would serve little purpose without the stamp of individuality. Such signals have implications in the survival of the most vulnerable individuals in a group. Many bird species recognise a mate's calls (Beletsky, 1983; Robisson, 1992). Individually specific signals from one signaller to many receivers, such as advertisement calls of female elephants (Pye & Langbauer, 1998) or right whales (Kraus & Hatch, 2001; Parks, 2003b) may alert potential mates to receptive females, and play an important role in reproductive strategies. Calls from strangers may alert local residents to the presence of an outsider (Brindley, 1991; Beckers et al., 2003; Slater, 2003; Hayes et al., 2004), arousing a territorial response. Vocal expressions of behavioural states gain in relevance when the identity of the signaller and the context of the signal are known to the receiver (Bayly & Evans, 2003; Rendall, 2003), and the discrimination of individuality in calls is a more challenging listening task than their mere detection (Lohr et al., 2003).

The importance of vocal individuality to the researcher lies in the access it potentially provides to the identity, behavioural state and location of individuals, encoded in their calls, particularly so in the absence of visual clues. Knowledge of caller identity is useful not only in understanding short-term behaviour (Christie et al., 2003), but also in tracking the longer-term movements, survival and demographics of individuals within populations, an objective currently achieved using visual census techniques (Best, 2000), though not without its drawbacks (Stevick et al., 2001).

The first step in characterising the vocalisations of individuals is to assign calls to their authors (see *chapter three*). The caller having been identified, a series of calls from the same caller are investigated for acoustic properties distinguishing that caller from another. The identification of call features with a high information content is central to the pursuit of vocal identity, and has been the focus of the

concerted research effort of biologists (Phillips & Stirling, 2000), bioacousticians (Goold & Jones, 1995) and information scientists (Ikeda, 1998). Attempts to characterise individual voices have met with numerous successes, amongst them for fishes (Ladich et al., 1992; Vester et al., 2004), birds (McGregor & Byle, 1992; Phillmore et al., 2003; Saino et al., 2003; Slater, 2003), insects (De Winter, 1992), amphibians (Allan & Simmons, 1994; Simmons, 2004), and numerous land mammals. The latter group has been widely studied, for species including *inter alia* baboons (Rendall, 2003), barking foxes (Frommolt et al., 2003), red deer (Reby & McComb, 2003), cattle (Ikeda, 1998) and elephants (McComb et al., 2003). Sea mammal studies (Phillips & Stirling, 2000; Sanvito & Galimberti, 2000; Phillips & Stirling, 2001), where animals spend considerable time ashore, or may be kept in captivity (Tyack, 1991) have further elucidated the salient features distinguishing vocal identity. There has been some progress in field studies of resident dolphin communities (Sayigh et al., 1998). Studies of individual features in the voices of great whales have been more problematic due to the logistics of identifying, tracking and recording large, gregarious, wild animals that spend a large proportion of their time underwater, and of limited success (Clark, 1983; Parks, 2003a). Due to the protracted and highly structured nature of humpback song (Payne et al., 1983; Cerchio, 1993; Juritz, 1996; Frankel & Clark, 2000), allowing the researcher to 'lock on' to a singing whale and follow the progression of an individual's song, acoustic studies of vocal identity are more advanced for this than for any other species of mysticete.

The acoustic repertoire of southern right whales (Schevill, 1964; Clark, 1982; Richardson et al., 1995) does not follow the prescribed patterns displayed in humpback song. Matching calls with caller, for a variety of cetacean species, has presented stiff challenges (Tyack, 1998); for instance to workers attempting to associate vocalisations with individual dolphins (Watkins & Schevill, 1974; Freitag & Tyack, 1993), or with bowhead whales (Clark et al., 1986).

During the field seasons of 1997 and 1998, we recorded the underwater vocalisations of southern right whales from a semi-rigid inflatable boat in Walker Bay, off the southern coast of South Africa (*fig.4.1*). We attempted to assign calls to callers in real-time using an array initially mounted on plumbing poles fixed to the boat, and later on a floating array. Portable oscilloscopes were later replaced by a chart recorder, to capture the two sets of time delays necessary for determining bearings to caller. This proved technically daunting due to the nature of the chosen calls, which often began quietly without a sharp onset, and had an almost random temporal occurrence, making them extremely difficult to anticipate. High levels of ambient noise (above the signal amplitude trigger threshold) caused by sea conditions led to poor signal to noise ratio, reducing opportunities for data capture. Where it was possible to determine bearings to caller in real time, there were frequently several whales in the general direction calculated. Clearly a new approach was needed.

In this chapter I describe the results achieved using a portable dual-axis floating hydrophone array, from which bearings to callers could be determined by post-processing data and relating them to whale sightings.

2. Materials and method

Between June and November, 1999, the vocalisations of southern right whales were recorded in Walker Bay (*fig. 4.1*) from a 6m semi-rigid twin engined inflatable. Two sets of dual-channel signals, (A and B) and (A and C), were recorded on three hydrophones (A, B and C) from a portable, floating, dual-axis hydrophone array, with the objective of determining bearings to the callers (*chapter three*). Simultaneously, single channel signals, with a better signal to noise ratio, were recorded with a separate hydrophone for detailed acoustic analysis. A record was kept of the compass orientation of the array, bearings to positions of whales sighted during the recording sessions, and, where possible, the numbers of animals in each group, for comparison with computed call bearings (*chapter three*). Bearings to calls were computed by post-processing signals in the laboratory, and compared with visual bearings to whale sightings.

Ten continuous recording sessions with bouts of *up* calls (*chapter one*) and two with *high* and *medium down* calls associated with surface active groups, or SAGs (*chapter one*) were first processed to determine the direction of the call origins and to match the call directions with those to whales sighted from the boat during the recording periods. We experienced difficulty in assigning calls unequivocally to individuals for two reasons. When a call bearing coincided with a whale sighting, there were generally at least two, and frequently more, animals present. It was often difficult to count the number of whales present in a group because of poor visibility or distance. It was therefore easier to assign calls to groups of whales than to individuals (*chapter three*).

In terms of characterising the vocalisations of individual whales, this left us with no ground truth of certainty as to caller identity. It was necessary to modify the approach to the problem. The revised plan was to assess the relative acoustic similarity of all call pairs within each continuous recording session in the light of the computed call bearings. The underlying assumption was that at least some of the call pairs close in time and bearing were likely to come from the same animal, while calls close in time but sufficiently far apart in bearing could not have originated from the same animal.

Acoustic features

The first step in assessing acoustic similarity was to measure acoustic features characterising the differences between dissimilar calls. Using a subset of calls from the ten continuous recording sessions with *up* calls, and the two with *SAG* calls for which bearings had been calculated (*chapter three*), two approaches to variable extraction were tested.
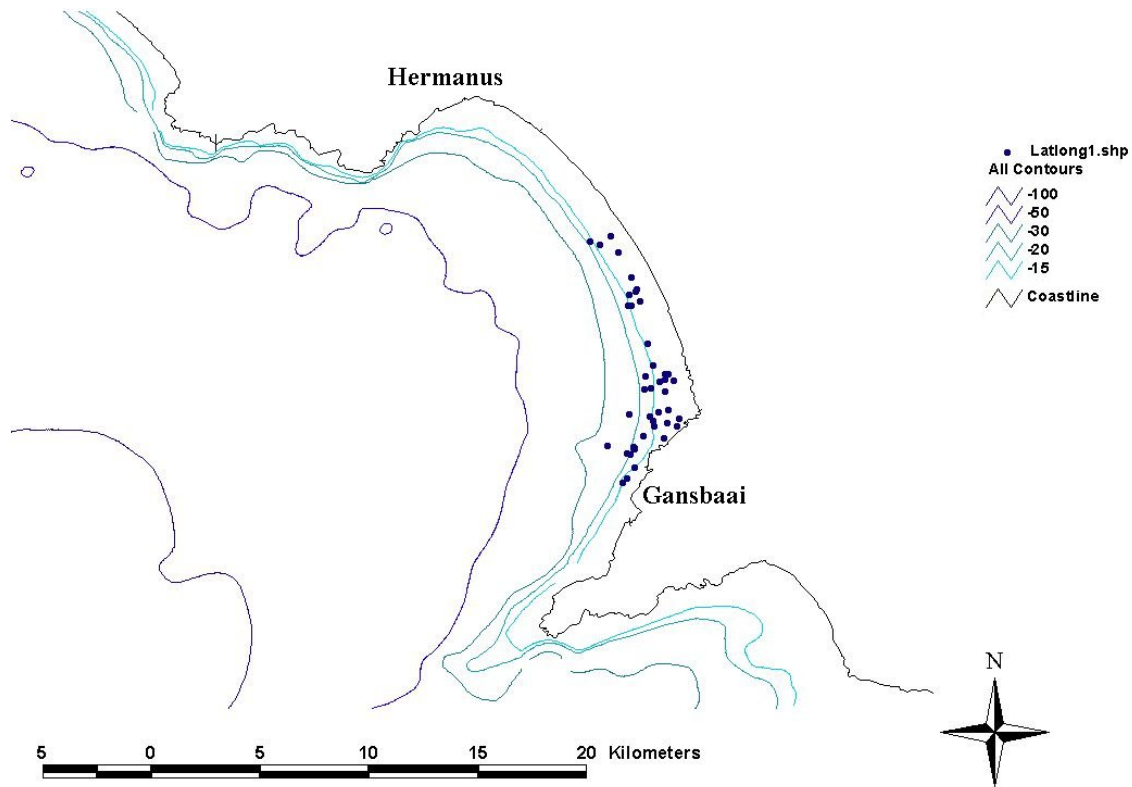
Figure 4.1 Positions from which right whales calls were recorded in Walker Bay, South Africa, between June and November, 1999.
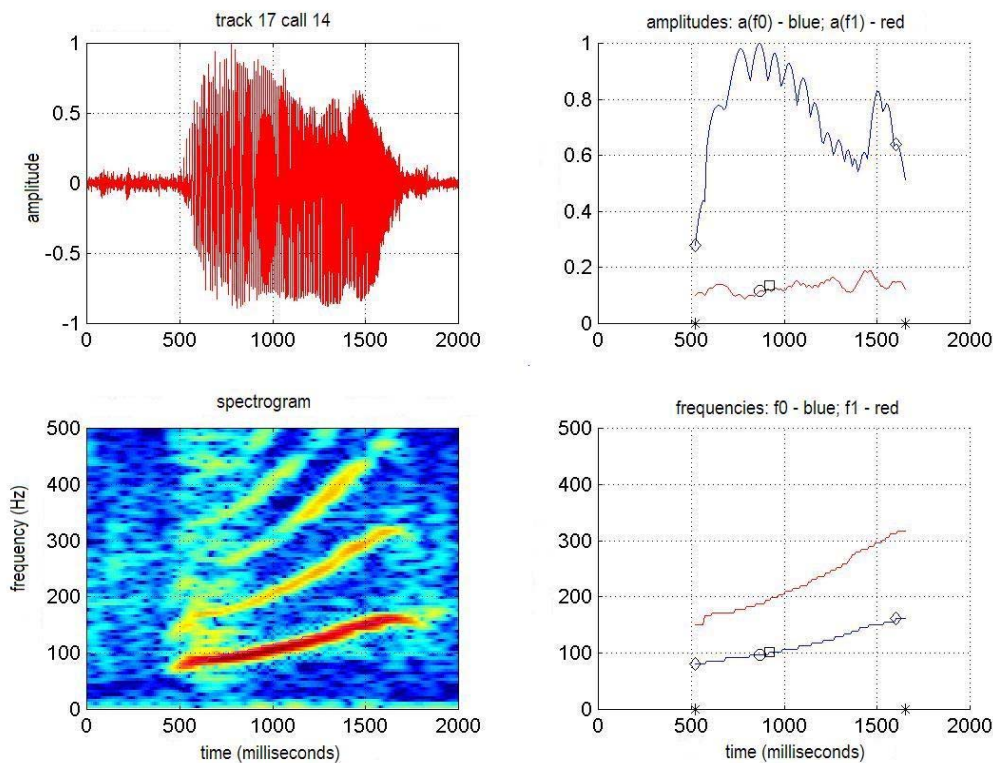
Figure 4.2 Amplitude (top right) and frequency (bottom right) measurements from a spectrogram (bottom left) of an *up* call (raw signal top left). Amplitude and frequency modulations of the fundamental, a(f0), f0, and first harmonic, a(f1), f1, in blue and red respectively. Call region between diamonds; f0 crosses 100 Hz at square, and peak frequency at circle markers.

The first approach was based on fast Fourier Transforms (FTs) of the signal and measurement of frequency and amplitude features of the first and second harmonics, f0 and f1, revealed by spectrograms, while the second approach relied on frequency-related amplitude features extracted from discrete Daubechies wavelet transforms (WTs) of the entire bandwidth.

FT-derived variables

Signals were analysed using a programme tested on synthesised signals, calling on inbuilt Matlab functions to perform FFTs and display spectrograms. For each 2-second signal, sampled at 11 025 samples per second (giving a frequency resolution of 5.3780 Hz), an amplitude graph was plotted after normalising and filtering with a Butterworth filter between 20 Hz and 1000 Hz; an FFT was performed (FFT size 2048, overlap 95%, by 1945 samples); the 'call' portion of the signal was then manually selected, and eight frequency- and amplitude-related call features were automatically extracted (*fig.4.2*).

1. minimum call frequency for first harmonic, f0 (Hz)

2. maximum call frequency for first harmonic, f0 (Hz)

3. ratio between energy in first and second harmonics, f0 and f1, for frequency of peak amplitude for f0, hereafter referred to as 'peak frequency' (Hz)

4. 'peak frequency' for f0 (Hz)

5. bandwidth of first harmonic, f0 (Hz)

6. bandwidth between signal onset and peak frequency for fundamental, f0 (Hz)

7. bandwidth from peak frequency to signal end for fundamental, f0 (Hz)

8. bandwidth between signal onset and peak frequency, as a fraction of the entire signal bandwidth, for fundamental

Confidence in the software was built up through comparing spectrograms with those produced by other programs. The Matlab program was also tested by analysing synthetic calls (with known parameters) written in Matlab.

WT-derived variables

In the time domain, call signal amplitudes were normalised to counter differences in signal amplitudes due to different distances of source from receiver. Thereafter, using inbuilt Matlab functions, admissible wavelet packets were applied to each 2-second signal deconstruction using a Daubechie discrete wavelet filter. The analysis took account of the entire available bandwidth (up to 5 512.5 Hz). Each call was divided into six bandwidths, according to the following structure (X = total signal bandwidth: 5512.5 Hz (half the sampling rate)):

1. 0 - X/16 (0 - 344.5 Hz)

2. X/16 - X/8 (344.5 Hz - 689.1 Hz)

3. X/8 - X/4 (689.1 Hz - 1378.1 Hz)

4. X/4 - X/2 (1378.1 Hz - 2756.3 Hz)

5. X/2 - 3X/4 (2756.3 Hz – 4134.4 Hz)

6. 3X/4 – X (4134.4 Hz – 5512.5 Hz)

The bandwidth X/2 – X was divided into two sub-bands (variables 5 and 6) because analysis of call spectra revealed variation in this region. The energy in each bandwidth was measured by decomposition of the signals at the appropriate scales (inversely proportional to signal frequencies).

Cluster Analysis

For each of twelve continuous recording sessions (ten with *up* calls, two with *medium* and *high down* calls), all features (8 fast FT-derived, 6 WT-derived) were entered into a hierarchical agglomerative cluster analysis (Primer5 for Windows, version 5.2.2, 2001). All data were transformed (square root) and standardised. The normalised Euclidean distance was calculated for each possible call pair within each continuous recording session, and expressed as a similarity matrix. The matrices were expressed in a multidimensional scaling plot (MDS) for each continuous recording session.

Distant and close groups

Entirely independently of the Euclidean distances in the similarity matrices, each call pair within a continuous recording session was assigned to one of two call pair groups: distant call pairs, and 'close' call pairs. Distant call pairs had to have come from separate animals, as they were close in time but separated in bearing. They occurred within a maximum of two minutes of each other, and on bearings diverging by an angle greater in degrees than double the standard deviation (i.e. >(2°*2)) of the array bearings error (*chapter three*).The majority of distant calls were located on far more divergent bearings: more than 89% of distant call pairs were separated by >13°, 80% by >20°, and 50% by >65° (*fig.4.3*). 'Close' call pairs were all the other pairs, including both call pairs close in time and bearing, and call pairs separated in time and bearing. Each call pair in the 'close' grouping therefore had the potential of being produced by either one whale or by two whales. The 'close' grouping was therefore less consistent, including call pairs both from the same animal and from different animals, while the distant grouping included only call pairs from different whales. This was unavoidable (see above) as there was no method available for unequivocally determining the origin of each call.

Assessment of Euclidean distances derived from FT- and WT-derived variables

Two sets of Euclidean distances, arising from the FT- and the WT-derived acoustic features respectively, were assessed for their efficiency in discriminating between 'close' and distant call pairs. Calls for which it was not possible to obtain a full set of variables for each method were discarded for
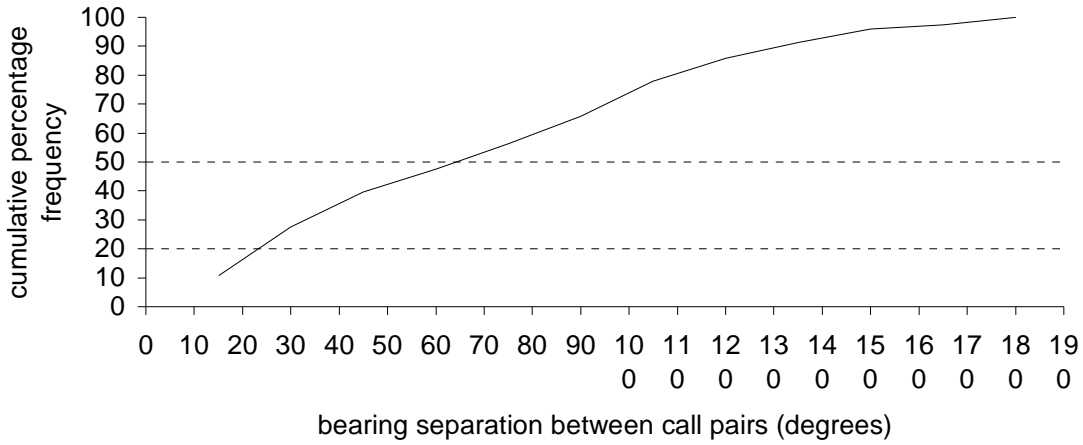
Figure 4.3 Distribution of separations in degrees between distant call pairs: 80% of call separations are greater than 20°, and 50% are greater than 60°.
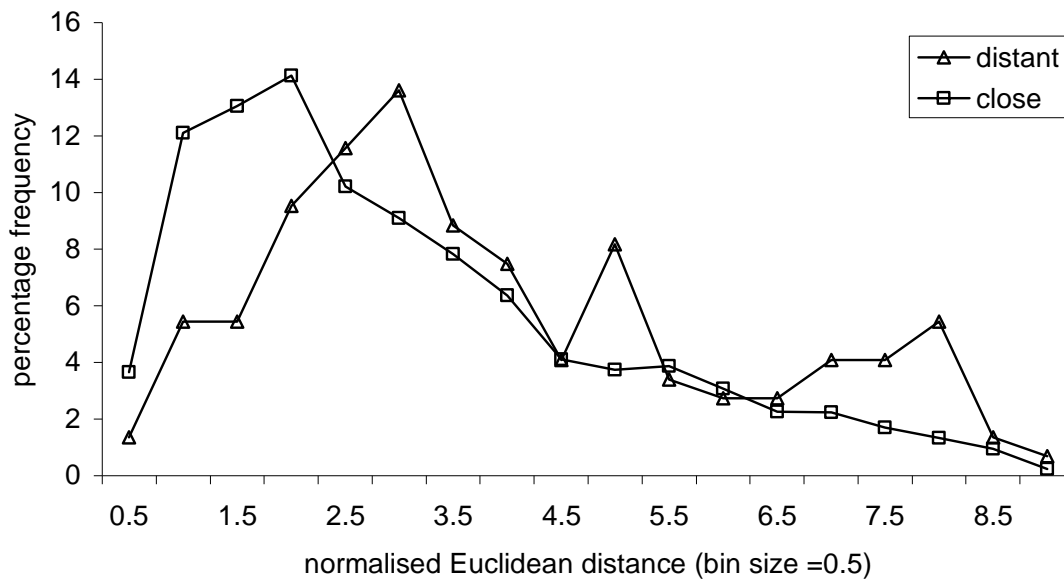
Figure 4.4 Frequency distribution of Euclidean distances between 'close' and distant call pairs.
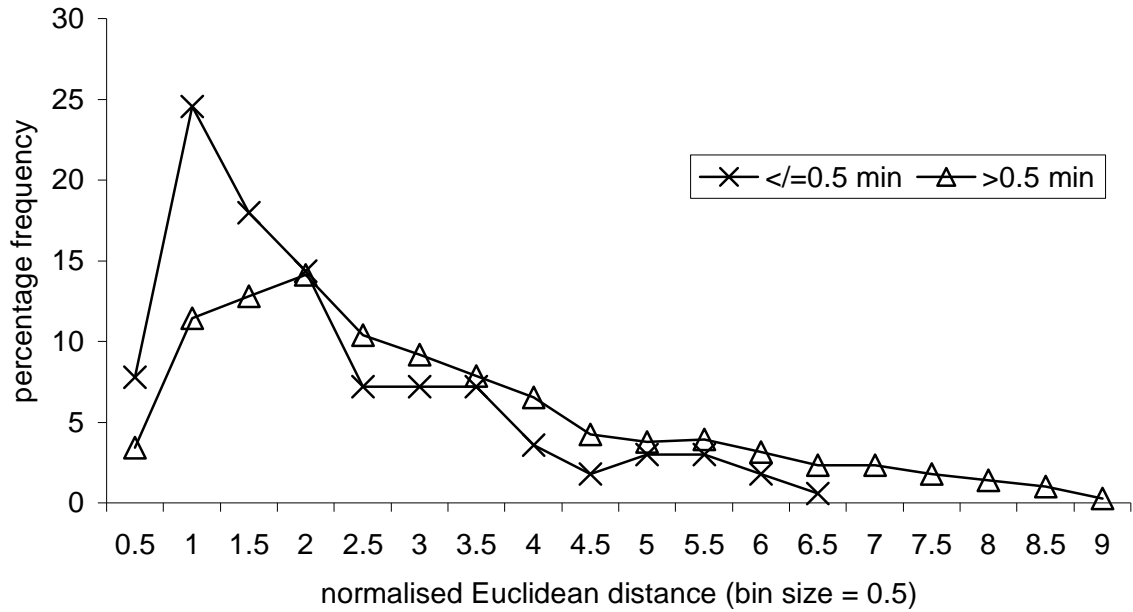
Figure 4.5 Percentage frequency distribution of Euclidean distances for call pairs (excluding distant pairs) separated by up to 0.5 minutes, and in excess of 0.5 minutes.
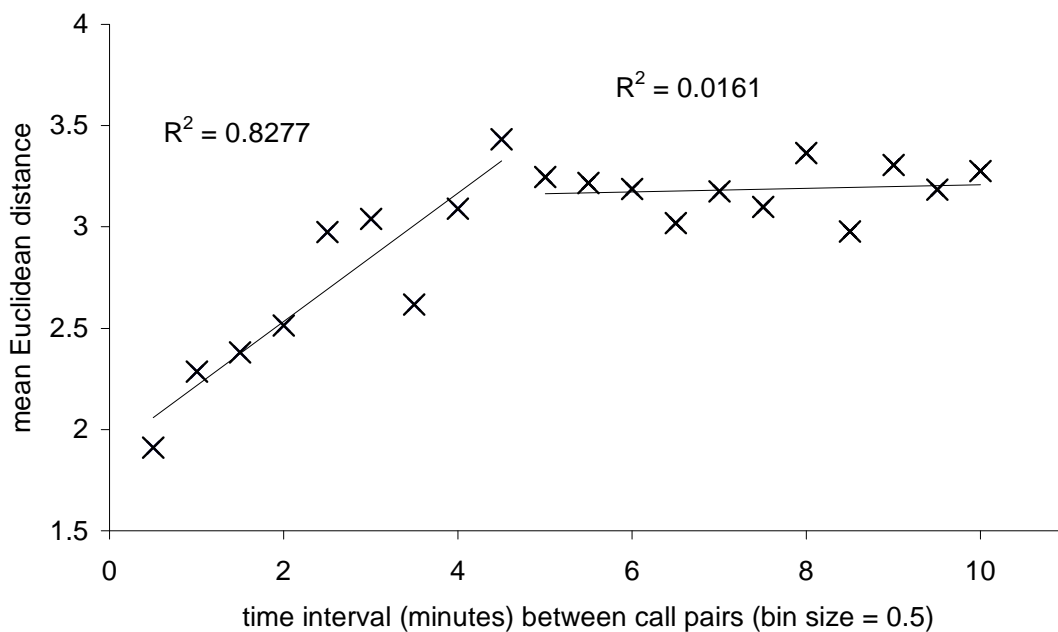
Figure 4.6 Mean Euclidean distances for call pairs (excluding distant pairs) with increasing time intervals between calls. Note the strong positive correlation up to around 4.5 minutes, after which Euclidean distances appear to stabilise, with no further correlation.

This analysis. Mean 'close' and distant Euclidean distances were compared for each method, using all Euclidean distances calculated for the ten recording sessions containing *up* calls (*table 4.1*).

Table 4.1. FT-derived and WT-derived Euclidean distances for close and distant call pairs

Transform	close			distant			close cf distant	
	n	mean	stdev	n	mean	stdev	t	p (close/distant)
Fourier	3239	3.51	1.88	145	3.44	1.93	0.44	0.661
Wavelet	3239	2.83	1.92	145	3.74	2.09	-5.55	<0.001

The smaller WT-derived Euclidean distances for 'close' call pairs and larger WT-derived Euclidean distances for distant call pairs favoured WT-derived variables for discriminating between the 'close' and distant groups . More importantly, the highly significant difference between 'close' and distant call pair Euclidean distances for wavelet results, and non-significant equivalent Fourier results, indicated the use of WT-derived variables in subsequent analysis.

Analysis of 'close' and distant call pair Euclidean distances
Having determined that the WT-derived set of variables was more useful in characterising the differences between the two groups, the Euclidean distances generated by a cluster analysis of these variables were used in three ways to answer three distinct questions. The first and central question addressed the difference between Euclidean distances for these two groups, and the subsequent questions flowed from this first question, and were confined to the 'close' group.

1. *Testing the assumption that call pairs close in time and separated in bearing are less similar than all other call pairs*
Using WT-derived Euclidean distances between call pairs from 'close' and distant groups, the means and frequency distributions of these two groups were compared. The underlying assumption was that two calls from the same animal were likely to be acoustically more similar (with a shorter Euclidean distance) than two call from two separate animals (with a longer Euclidean distance), so that the 'close' group should have more of the shorter Euclidean distances than the distant group.

2. *Testing the assumption that individual whales are likely to call in closely timed bouts*
Using WT-derived Euclidean distances between call pairs from the 'close' group, the relationship between the temporal spacing of calls, and their acoustic similarity, was investigated. Call pairs occurring within a short space of time were compared with the remaining call pairs. The time interval within which Euclidean distances of call pairs were most different from Euclidean distances of the remaining call pairs, was determined in an iterative procedure. The underlying assumption was that an individual was more likely to call in bouts (Matthews et al., 2001), so that calls close in time were

more likely to come from the same animal (and be acoustically similar) than calls widely spaced in time. With an increasing time interval between two calls came a decreasing probability that they were made by one whale. The frequency distributions of the two groups were compared, and the difference between them was tested. Mean values were plotted for Euclidean distances derived from call pairs with a range of time intervals.

3. Testing the assumption that individual whales emit multiple calls in close sequence

The importance of the positional sequence of calls in a series, in relation to their acoustic similarity, was tested by dividing the distribution of Euclidean distances of call pairs from the 'close' group (each pair of which had the potential of being from a single animal) into two sub-groups. One sub-group comprised call pairs within a few sequential positions of each other. The other sub-group comprised the Euclidean distances between the calls in the remaining call pairs. The frequency distributions of the two sub-groups were compared and tested iteratively using different sequential cut-off points.

Testing differences between 'scream' calls from two surface-active groups (SAGs)

Surface active groups are usually composed of a single focal female and several males (Best et al., 2003). It is hypothesized that *high down* and *medium down* calls (*chapter one, chapter three*; (Kraus & Hatch, 2001), also referred to as 'screams' (Parks, 2003a), from surface active groups (SAGs) are emitted by the focal female within any given SAG. On the assumption that *down* calls (or 'screams') from two SAG events were emitted by different females, the Euclidean distances between calls from the two continuous recording sessions containing *down* SAG calls (*chapter one*), were compared. In this instance, the comparison was not between 'close' and distant groups of calls within one continuous recording session (*high down* and *medium down* SAG calls generally come from one specific direction where *SAG* activity is taking place (*chapter one*)). Instead, the Euclidean distances of call pairs from two recording sessions separated by 13 weeks were compared, for intra- and inter-group differences. Given the observed seasonal distribution and movements of southern right whales (Best, 2000), the time interval between the two recordings made it extremely unlikely that calls from the two sessions were produced by the same animal. Thus each intra-group comparison potentially assessed the similarity of calls from one whale, whilst each inter-group comparison assessed the similarity of calls from two whales.

Assessing the contributions of each of the eight FT-derived and six WT-derived variables

The coefficient of variation was calculated for each variable derived using either Fourier transform or wavelet transform, and their contributions to the variability of the calls were ranked accordingly. Mean values for each normalised variable value were plotted and compared for selected call pairs close in time, bearing and Euclidean distance (i.e. each call in a given pair potentially from the same whale), to further investigate the influence of each variable in characterising the call from which it was measured. The intention was to elucidate the areas of the call which were individually distinctive.

Variable values for each call of selected call pairs were plotted to assess how closely each variable measurement was matched in similar calls.

Using wavelet variables, the difference between variable values (DVVs) for each distant call pair, comprising 2 calls, each from a different whale, was plotted against the equivalent Euclidean distance, and ranked for influence at each level of call dissimilarity. Mean DVVs within both 'close' and distant groups were then plotted against the equivalent Euclidean distances, to compare the influence of each variable for each group

Comparing pairs of calls close in time with calls close in Euclidean distance

Based on the results of tests above comparing the Euclidean distances of 'close' and distant call pairs, and of adjacent 'close' call pairs within and exceeding 0.5 minutes or adjacent positions, pairs of calls close in time were selected from the ten recording sessions with *up* calls, plotted to display bearings to both call origins, and whale groups sighted during the session (subsequently referred to as tracks). Only call pairs for which bearings to calls had been calculated, and visual bearings to whale sightings during the recordings had been noted, were eligible for selection. Each pair of calls served as potential candidates for call pairs from one distinct individual. Call pairs close in time were examined in the light of their Euclidean distances. Given the challenges outlined above in accurately assigning calls in real time or during post-processing to specific whales, each pair of calls close in time and Euclidean distance, was the closest approach in this study to two calls from the same animal.

There was no expectation that each adjacent call pair represented two calls from the same animal. Clearly many such pairs were the single calls emitted by two different animals, even when both calls originated from the same direction. We expected many instances where two calls on the same bearing, making up adjacent or near-adjacent call pairs, would be produced by two different whales, and would therefore be widely dissimilar and have large Euclidean distances. We did, however, anticipate that some adjacent call pairs, each emitted by the same animal, would be similar and separated by short Euclidean distances. This anticipation was based on comparisons of 'close' and distant Euclidean distance groups, as well as 'close' Euclidean distances from call pairs within and exceeding short time-frames and close sequential positions. A third intriguing possibility would be the similarity of calls too close in time and distant in bearing to be the vocalisations of a single whale, raising the possibility of mimicry.

3. Results

Hierarchical agglomerative cluster analysis of each group of calls for each of the 12 continuous recording sessions provided a set of Euclidean distances for each call pair. The calculation of bearings to calls for 10 continuous recording sessions containing *up* calls, and 2 containing *SAG* calls (*chapter three*), provided the basis for dividing these Euclidean distances into two groups. In the distant group,

each pair of calls had to have come from different animals, and in the 'close' group, each pair of calls may or may not have been from a single animal.

Testing the assumption that call pairs close in time and separated in bearing are less similar than all other call pairs

If calls from the same animal were more similar than calls from different animals, the Euclidean distances from the 'close' group would be smaller than from the distant group. Euclidean distances for 'close' call pairs were shorter than those for distant call pairs for six of the nine tracks where distant calls could be identified, and the two groups differed significantly for three of these tracks. Of the three tracks where the mean Euclidean distance was longer for 'close' than for distant call pairs, in only one (27a) was this difference significant. The overall result, however, suggested a highly significant difference between Euclidean distances for smaller 'close' and larger distant groups (*Table 4.2*). The difference in distribution of Euclidean distances for the two groups was easily discerned. The initial peak occurred at a smaller Euclidean distance for 'close' than for distant pairs, while the subsequent distribution of the distant group showed two additional peaks at greater distances (*fig. 4.4*).

Table 4.2 Summary statistics: Euclidean distances between close and distant call pairs. Significant results are given in bold text..

Track	DISTANT			CLOSE					
	mn	N	stdev	mn	n	stdev	t-value	ttest: p	
11a	**3.5**	**43**	**2.0**	**3.0**	**860**	**1.8**	**2.06**	**0.04**	*
17b	2.8	33	1.7	2.9	432	1.9	-0.22	0.83	Ns
18b	**5.2**	**27**	**2.4**	**2.6**	**1248**	**2.1**	**6.10**	**1.44E-09**	***
23a	4.5	4	2.1	3.0	132	1.6	1.87	0.06	Ns
26b	4.1	3	1.4	2.8	12	1.2	1.57	0.14	Ns
27a	**2.4**	**16**	**0.9**	**3.4**	**62**	**1.5**	**-2.49**	**0.01**	*
30b	N/A	N/A	N/A	3.3	21	1.2	N/A	N/A	
31b	2.8	6	1.0	3.1	345	1.6	-0.35	0.73	Ns
34a	3.9	9	1.4	3.0	82	1.6	1.59	0.12	Ns
39a	**6.4**	**6**	**1.9**	**2.2**	**85**	**2.2**	**4.58**	**1.51E-05**	***
Overall	**3.70**	**147**	**2.11**	**2.84**	**3279**	**1.92**	**5.31**	**1.18E-07**	***

Testing the assumption that individual whales are likely to call in closely spaced bouts

The time interval that might define the two sub-groups of Euclidean distances, both drawn from the 'close' group, was determined (*Table 4.3*) by iteratively testing the difference between an initial group (group 1) where calls fell within a defined but increasing timespan, and the remaining group (group 2). Results showing a significant difference between the two sub-groups are in bold. The maximum

Table 4.3 Mean Euclidean distances of call pairs occurring within and outside of increasing time intervals.

	mn gp1	mn gp2	t	df	ttest: p	n gp 1	n gp2	stdev gp1	stdev gp2
Up to 0.5 min*rem	1.91	2.89	-6.46	3277	**1.18E-10**	167	3112	1.41	1.93
Up to 1.0 min*rem	2.10	2.92	-7.52	3277	**7.05E-14**	336	2943	1.49	1.94
Up to 1.5 min*rem	2.19	2.95	-8.23	3277	**2.64E-16**	491	2788	1.56	1.95
Up to 2.0 min*rem	2.26	2.98	-8.52	3277	**2.42E-17**	632	2647	1.62	1.96
Up to 2.5 min*rem	2.41	2.98	-7.33	3277	**2.87E-13**	796	2483	1.70	1.96
Up to 3.0 min*rem	2.51	2.97	-6.34	3277	**2.68E-10**	942	2337	1.74	1.97
Up to 3.5 min*rem	2.52	2.99	-6.69	3277	**2.63E-11**	1078	2201	1.75	1.97
Up to 4.0 min*rem	2.58	2.99	-5.84	3277	**5.77E-09**	1216	2063	1.77	1.98
Up to 4.5 min*rem	2.66	2.96	-4.48	3277	**7.75E-06**	1329	1950	1.82	1.97
Up to 5.0 min*rem	2.70	2.94	-3.59	3277	**3.40E-04**	1441	1838	1.85	1.96
Up to 5.5 min*rem	2.73	2.93	-2.91	3277	**3.67E-03**	1536	1743	1.86	1.96
Up to 6.0 min*rem	2.76	2.91	-2.32	3277	**0.02**	1628	1651	1.88	1.95
Up to 6.5 min*rem	2.77	2.91	-2.00	3277	**0.05**	1723	1556	1.89	1.95
Up to 7.0 min*rem	2.79	2.90	-1.59	3277	0.11	1791	1488	1.89	1.94
Up to 7.5 min*rem	2.80	2.89	-1.31	3277	0.19	1850	1429	1.89	1.95
Up to 8.0 min*rem	2.82	2.87	-0.72	3277	0.47	1912	1367	1.90	1.94
Up to 8.5 min*rem	2.82	2.86	-0.59	3277	0.56	1964	1315	1.90	1.94
Up to 9.0 min*rem	2.84	2.84	-0.02	3277	0.98	2029	1250	1.90	1.94

Table 4.4 Mean Euclidean distance of call pairs separated by up to and exceeding an increasing number of calls in a sequence

gp1*gp2	mn gp1	Mn gp2	t	Df	ttest: p	n gp 1	n gp2	stdev gp1	stdev gp2
up to within 1 pos*rem	1.99	2.88	-5.53	3277	**3.41E-08**	147	3132	1.52	1.92
up to within 2 pos*rem	2.05	2.91	-7.36	3277	**2.28E-13**	288	2991	1.51	1.94
up to within 3 pos*rem	2.25	2.93	-6.99	3277	**3.22E-12**	440	2839	1.66	1.94
up to within 4 pos*rem	2.42	2.93	-5.79	3277	**7.65E-09**	583	2696	1.78	1.93
up to within 5 pos*rem	2.52	2.93	-5.12	3277	**3.18E-07**	728	2551	1.85	1.93
up to within 6 pos*rem	2.59	2.93	-4.47	3277	**8.19E-06**	866	2413	1.89	1.92
up to within 7 pos*rem	2.66	2.92	-3.60	3277	**3.23E-04**	998	2281	1.93	1.91
up to within 8 pos*rem	2.69	2.91	-3.09	3277	**0.002**	1126	2153	1.94	1.90
up to within 9 pos*rem	2.72	2.91	-2.86	3277	**0.004**	1244	2035	1.94	1.90
up to within 10 pos*rem	2.74	2.91	-2.44	3277	**0.01**	1366	1913	1.95	1.89
up to within 11 pos*rem	2.76	2.90	-2.08	3277	**0.04**	1476	1803	1.95	1.89
up to within 12 pos*rem	2.78	2.89	-1.60	3277	0.11	1579	1700	1.94	1.89
up to within 13 pos*rem	2.80	2.88	-1.16	3277	0.25	1675	1604	1.94	1.89
up to within 14 pos*rem	2.80	2.88	-1.15	3277	0.25	1762	1517	1.94	1.89
up to within 15 pos*rem	2.81	2.88	-1.06	3277	0.29	1846	1433	1.93	1.90
up to within 16 pos*rem	2.81	2.87	-0.82	3277	0.41	1924	1355	1.93	1.89

difference was detected between call pairs occurring within 0.5 minutes of each other, and those more than 0.5 minutes apart. The percentage frequency distribution of the Euclidean distances of these two groups (*fig. 4.5*) clearly showed a marked difference in distribution between the two groups at small distances, and an essentially similar distribution over the remaining distances. Because for each iteration there were always only two groups, group 2 became progressively smaller as group 1 increased in size to include call pairs up to and including a given time interval which increased at each iteration. In a different approach, mea Euclidean distances for 'close' call pairs, grouped non-cumulatively in discrete, consecutive time interval bins of 0.5 minutes, showed a consistent increase correlating strongly with increasingly large time intervals separating the call pairs from which they were derived (*fig. 4.6*) for time intervals of up to 4.5 minutes (R squared = 0.83), and no correlation thereafter (R squared = 0.02). This reflects the increasing percentage of call pairs with longer Euclidean distances (each call in a pair more likely to come from a different animal), added to the initially high proportion of call pairs with short Euclidean distances (both calls in a pair from the same animal). An equilibrium was reached when calls were separated by a time interval of 5 minutes or more. With an increase in the time interval separating the two calls in a pair, the mean Euclidean

distance between the acoustic properties of calls up to a given time interval (group 1) and after it (group 2) gradually declines (*fig. 4.7*).

Testing the assumption that individual whales emit multiple calls in close sequence
For this analysis all Euclidean distances between call pairs were drawn from the 'close' group, thus excluding call pairs that could not have been from the same animal. The importance of sequential position for calls (consecutive, or with varying numbers of calls between them) was tested iteratively. The results indicated that calls closer to each other in a sequence were more similar than those further apart, up to a separation of 11 calls (*Table 4.4, fig. 4.8*). The grouping with the greatest difference between sub-groups was for Euclidean distances between call pairs which were consecutive.

Testing differences between 'scream' calls from two SAGs
The similarities between call pairs for the two combined *SAG* call sets, each with tightly clustered bearings, were compared by calculating the intra- and inter-group means for Euclidean distances within group 1 (intra-group1), within group 2 (intra-group 2), and between groups 1 and 2 (inter-group). The inter-group mean Euclidean distance (3.99) was greater than either of the intra-group mean Euclidean distances (1.88, 2.73) (*Table 4.5*). This indicates that the *high down* and *medium down* calls produced by each SAG were more similar to each other than to those in the other SAG. (Although the mean Euclidean distances within each group were significantly different from each other, this was at a lower level of significance: there is no biological reason why the level of individual call variation should be constant.)

Table 4.5 Intra- and inter-group statistics for *high* and *medium down* call pair Euclidean distances

	mn	mn	t-value	Df	n gp1	n gp2	stdev gp1	Stdev gp2	ttest: p		
Intra-gp1 vs inter-gp	1.88	3.99	-5.76	55	15	42	1.024572	1.280628	3.98E-07	p=<0.001	***
Intra-gp2 vs inter-gp	2.73	3.99	-3.86	61	21	42	1.094035	1.280628	0.0003	p=<0.001	***
Intra-gp1 vs intra-gp2	1.88	2.73	-2.36	34	15	21	1.024572	1.094035	0.02	p=<0.05	*

Assessing the contributions of each of the eight FT-derived and six WT-derived variables
The contributions of the Fourier- and WT-derived variables were assessed by calculating their coefficients of variation (CV). Variables are ranked according to their increasing variability (*Table 4.6*). All but one of the WT-derived variables had higher CVs than all but one of the FT-derived variables, indicating the superior nature of the wavelet analysis in detecting variation within *up* calls. This result also confirmed earlier results in which the wavelet variables delivered significantly different Euclidean distances for the distant and the 'close' groups, while the FT-derived variables did not. Subsequent analysis has therefore been confined to WT-derived variables.

Table 4.6 Ranked acoustic variables from Fourier and wavelet signal transforms

	n	cv	Description of variable
Fmax: Fourier	192	15.56	maximum frequency(f0)
F1amax:Fourier	192	16.56	Frequency of maximum amplitude(f0)
fmin: Fourier	192	28.95	minimum frequency(f0)
df(f0): Fourier	192	45.89	Bandwidth of fundamental (f0)
df(pk-st)/df: Fourier	192	46.58	Bandwidth of onset-to-peak(f0)/bandwidth(f0)
df(mx-pk): Fourier	192	64.00	Bandwidth of peak-to-maximum(f0)/bandwidth(f0)
Ratx: Fourier	192	69.38	first harmonic(f1)/fundamental(f0)
var4: wavelet	223	71.80	X/4-X/2: bandwidth 1378.1 - 2756.3 Hz
df(pk-st): Fourier	192	75.59	Bandwidth of onset-to-peak(f0)
var2: wavelet	223	78.43	X/16-X/8: bandwidth 344.5 - 689.1 Hz
var1: wavelet	223	85.83	0-X/16: bandwidth 0 - 344.5 Hz
var3: wavelet	223	90.43	X/8-X/4: bandwidth 689.1 - 1378.5 Hz
var6: wavelet	223	96.88	3X/4-X: bandwidth 4134.4 - 5512.5 Hz
var5: wavelet	223	104.20	X/2-3X/4: bandwidth 2756.3 – 4134.4

Euclidean distance and the difference in variable values: 'close' call pairs

To determine which variables might be most useful in discriminating between individuals, they were tested on a set of pairs of *up* calls where the two calls within a pair were most likely to have been produced by the same individual. Mean normalised values for each wavelet variable, for 7 selected pairs of calls close in time, bearing and Euclidean distance (the mean of each pair thus each likely to represent calls from one whale) were compared (*fig. 4.9*). Each call pair came from a separate recording. We sought to identify the regions of the signal characterising similarities for like calls and differences between dissimilar calls. These regions would indicate the most informative variables. Normalised variable values for these selected calls showed least variation from the mean for variable 3 (energy from 689.1 Hz – 1378 Hz) and more variation in lower and higher registers. When the variable values for each call in selected pairs of similar calls, close in time, bearing and Euclidean distance, were compared, they followed similar patterns in their variable values (*fig. 4.10*). All of these pairs of *up* calls were also drawn from separate recording sessions, with the exception of two call pairs from track 18b, separated by over 35 minutes. Of all the selected call pairs with two similar calls, the two calls labelled 23a (from track 23a) showed the greatest difference between their variable values, and this difference occurred between variables 2 through 4. This supported evidence that variation at the upper and lower ends of the frequency range of the signals were the most important features characterising the calls of different individuals.
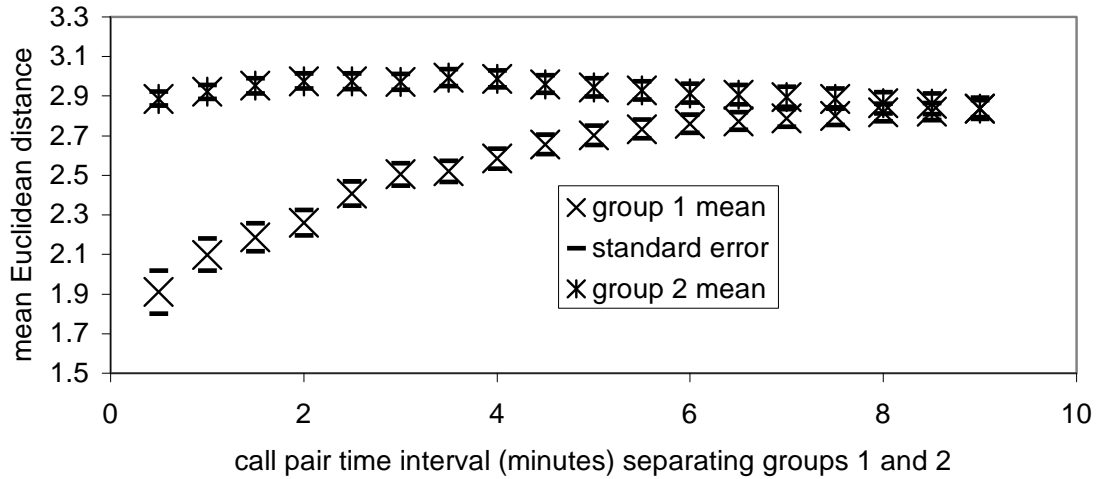
Figure 4.7 Mean Euclidean distances between call pairs, for group 1 and for group 2. Groups are separated by a defined but increasing time interval (*x*-axis), with group 1 call pairs separated by time intervals up to (*x*), and group 2 call pairs separated by time intervals exceeding (*x*).
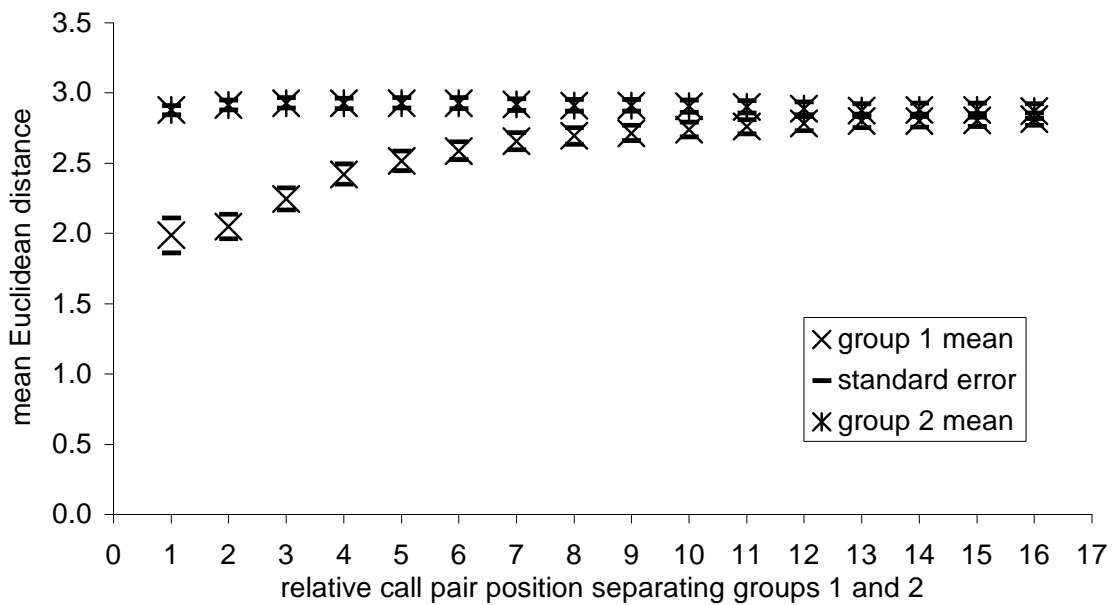
Figure 4.8 Mean Euclidean distances between call pairs, for group 1 and for group 2. Groups are separated by a defined position of one call in a pair, relative to the other call in the pair (1=adjacent). This defining position increases iteratively (*x*-axis), with group 1 call pairs positioned relative to each other from adjacent positions up to (*x*), and group 2 call pairs occurring relative to each other at positions exceeding (*x*).

Euclidean distance and the difference in variable values: distant call pairs

As an alternative test of the suitability of different WT-derived variables in discriminating between individuals, pairs of *up* calls that were most unlikely to have been from the same individuals were tested. Using distant call pairs only, the relative contribution to the variation of each variable at increasing levels of dissimilarity (Euclidean distance) was calculated (*Table 4.7*). It is assumed that two different animals produced the calls making up each of these pairs. At the higher levels of dissimilarity (Euclidean distances of 5-6, 6-7, 7-8 and 8-9, *table 4.7* column 1, lower four rows), the two highest ranked variables (accounting for the largest proportion of variation) were (in bold): variables 6 and 5 (%var6 and %var5), variables 5 and 1 (%var5 and %var1), variables 1 and 3 (%var1 and %var3) and variables 1 and 6(5var1 and %var6) respectively. Variables 1 (lowest frequency band) and 5 and 6 (highest frequency bands) therefore appeared to make the most important contributions, as in the previous analysis. Partly corroborating this observation, unfiltered calls sampled at 11050 Hz resolved frequencies up to 55025 Hz, and some call signals showed energy up into the highest frequency bands targeted by the upper WT-derived variables, which were clearly associated with the call, not ambient noise (*fig. 4.11*).

Table 4.7 Ranked contributions of distant group variables at increasing levels of call pair dissimilarity

| Euclidean distance	position 1	position 2	position 3	position 4	position 5	position 6
0-1	%var1	%var2	%var6	%var5	%var4	%var3
	29.89	17.79	15.35	14.25	13.98	8.74
>1-2	%var2	%var3	%var4	%var1	%var5	%var6
	19.63	19.05	18.30	18.29	14.57	10.16
>2-3	%var4	%var5	%var3	%var2	%var1	%var6
	19.37	19.24	19.10	16.66	15.10	10.53
>3-4	%var4	%var3	%var5	%var2	%var1	%var6
	21.34	20.28	19.77	15.64	14 .60	8.37
>4-5	%var3	%var4	%var5	%var2	%var6	%var1
	24.96	23.78	20.13	12.27	10.46	8.40
>5-6	**%var6**	**%var5**	%var1	%var3	%var4	%var2
	25.59	22.74	15.24	14.83	11.91	9.69
>6-7	**%var5**	**%var1**	%var6	%var3	%var4	%var2
	22.08	21.90	19.95	15.89	12.79	7.38
>7-8	**%var1**	**%var3**	%var5	%var4	%var6	%var2
	20.56	19.30	18.38	17.17	13.57	11.03
>8-9	**%var1**	**%var6**	%var4	%var5	%var3	%var2
	24.08	18.17	17.58	17.31	11.69	11.18
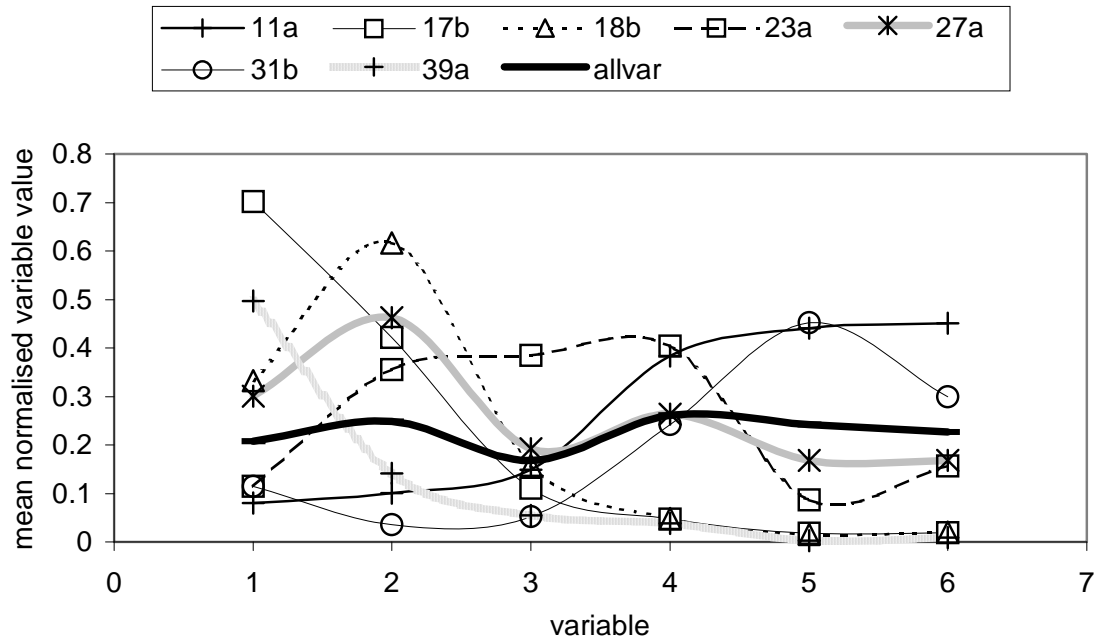
Figure 4.9 Mean normalised WT-derived variable values for seven selected pairs of *up* calls. Each pair is close in time, bearing and Euclidean distance, and is drawn from a different recording session, and so potentially represents one of seven different whales (the two calls from each pair produced by one whale). Variable values for the whole dataset are represented by the solid, heavy black line without symbols. Variation from the overall mean is greatest around variables 1 and 2 (lower frequencies) and 4, 5 and 6 (higher frequencies) and most stable for variable 3.
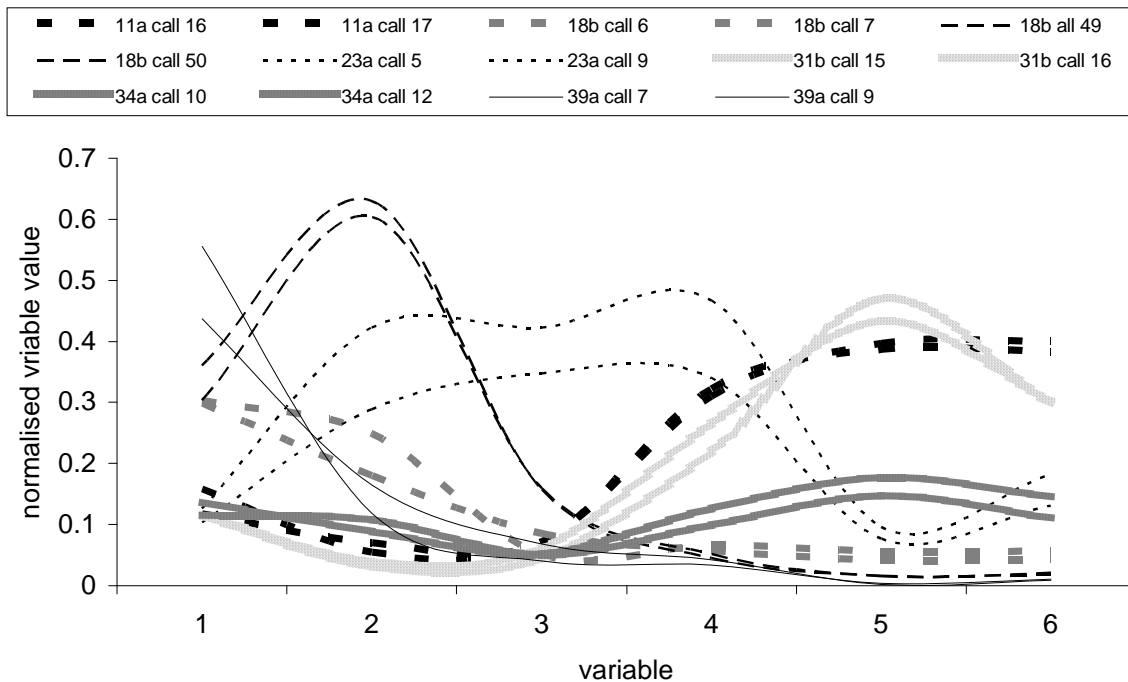
Figure 4.10 Normalised WT-derived variable values for selected pairs of *up* calls close in time, bearing and Euclidean distance, shown above as similar pairs of lines, each representing one call, and each pair potentially representing two calls from a single animal. Note the similarity between pairs.

Figure 4.11 Spectrograms of *up* calls displaying high levels of energy (yellow and red), clearly associated with vocalisations, into increasingly higher bandwidths. Upper left: energy to 1000 Hz; upper right: energy to 1300 Hz, with some energy right up to 4800 Hz; middle left: main energy to 2500 Hz; middle right: energy to 3000 Hz; bottom left: energy to 3500 Hz; bottom right: energy to 4500 Hz.

The possibility of mimicry

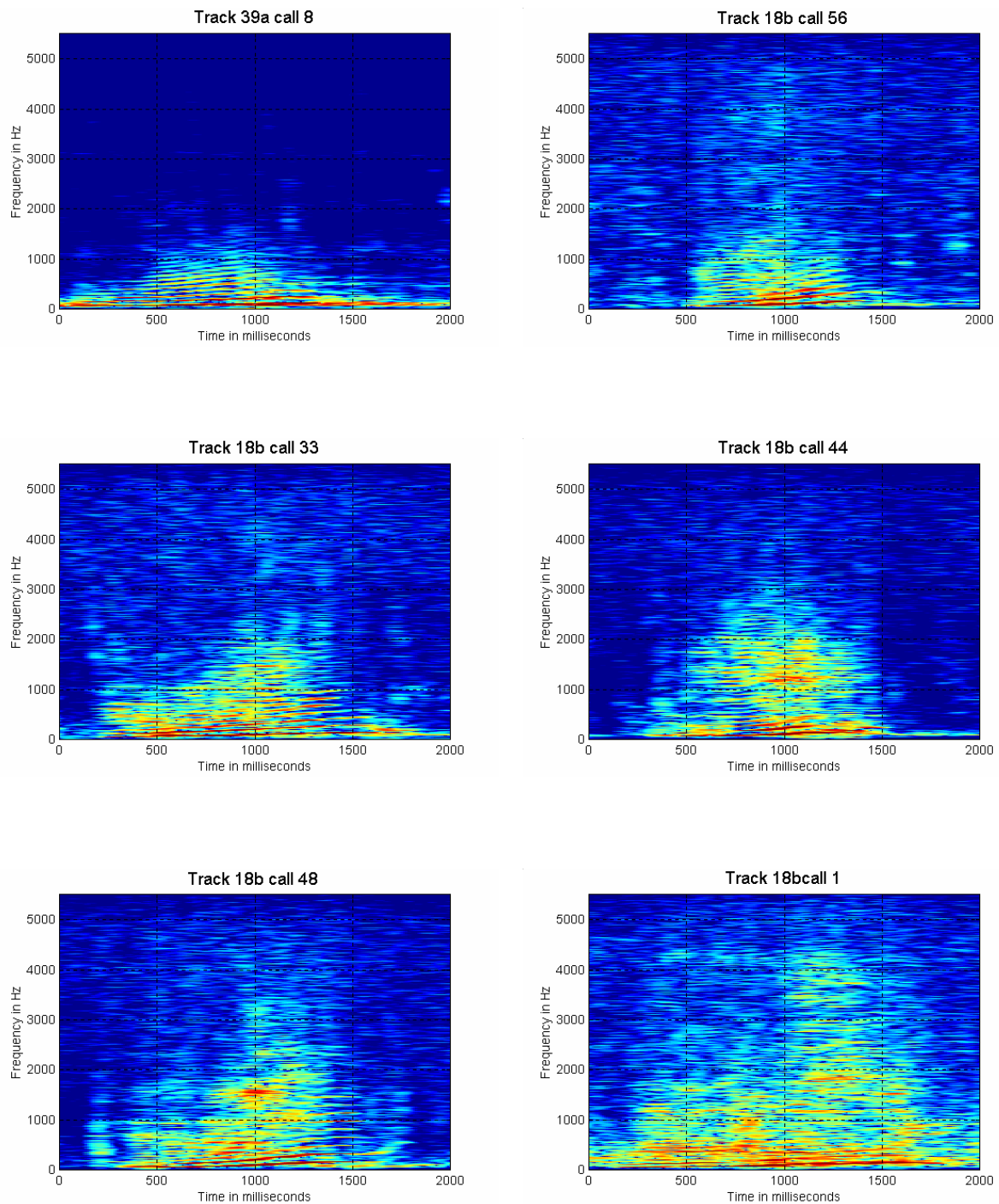When selecting groups of calls close together in time and bearing, and examining their similarity in structure using Euclidean distances, in most cases good matches were obtained, lending support to individual identification based on vocal characteristics as a viable concept. The confounding factor in this comparison, the mixed nature of the 'close' group of call pairs, dictated that these matching call pairs were arbitrarily pre-selected from a pool of call pairs containing pairs both from two neighbouring whales and from one whale, and there was no objective way of telling these two call pair types apart. Given the nature of the data, call pairs close in time and physical location but separated by large Euclidean distances in no way detracted from the instances of good matches, but confined them to illustration and anecdote, rather than the more compelling evidence of the other analyses.

In at least two instances calls which grouped closely in Euclidean distance and time were widely separated physically (*figs. 4.12a,b, 4.13a,b*), and so could not have come from the same individual. Inspection of both example discrete Daubechies WTs, and the FFT spectrograms above (lower graphs, *figs. 4.14, 4.15*) showed that these pairs of calls were structurally similar. One possible explanation is that of mimicry. If mimicry does occur, this would further confuse attempts to detect individually identifiable vocalisations using indirect methods of analysis, as in this study.

Figure 4.12a Track 27a. Selected calls close in time and bearing, are numbered for comparison with the multidimensional scaling plot of the same calls, below. Lines joining whale group sighting symbols refer to the inferred positions of groups of whales sighted from the boat during recordings, when submerged.

Figure 4.12b Multidimensional scaling plot of selected calls numbered above, from track 27a. Six WT-derived variables were entered for each call, standardised and transformed. The plot represents the normalised Euclidean distance between calls. Calls (1, 2, 3 and 4) group together loosely on the left hand side of the plot, and (10, 11 and 12) group loosely on the right hand side, the two groups matching their physical separation. (8 and 14) group tightly with 15, which cannot come from the same animal. The similarity of call 15 to 14, coming immediately after it, is suggestive of mimicry.
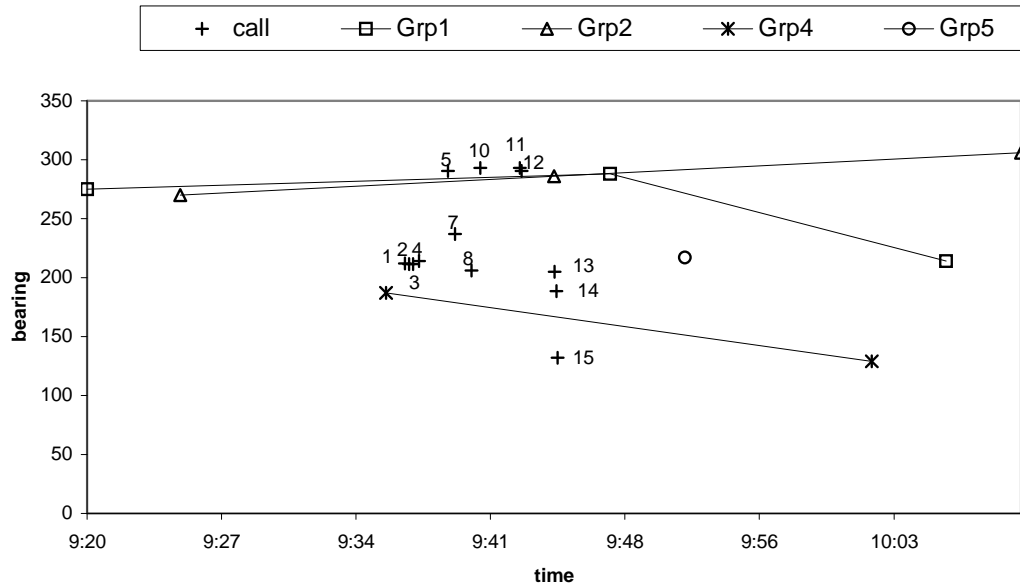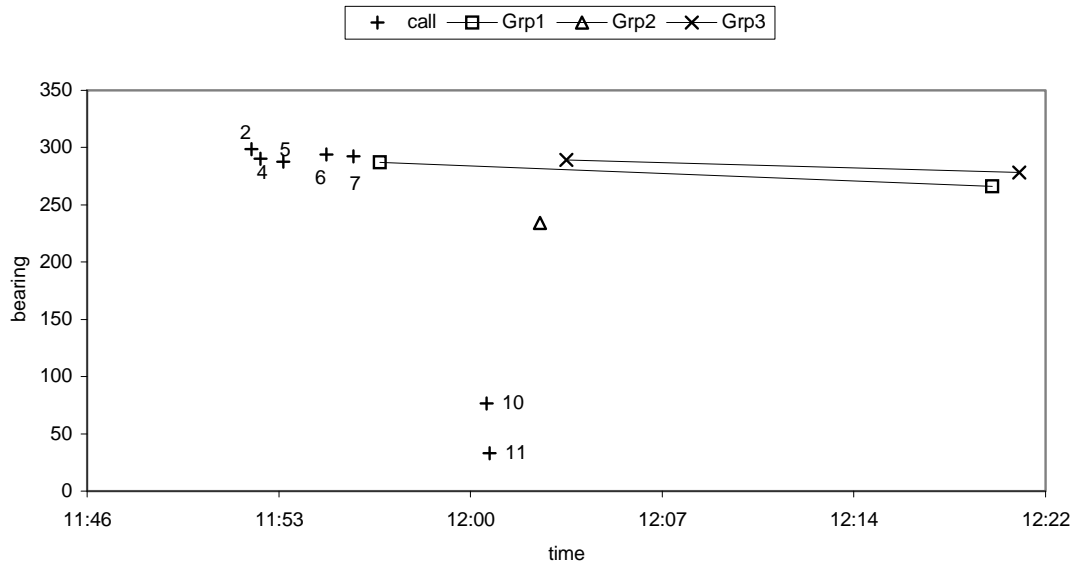
Figure 4.13a Track 30b. Selected calls close in time and bearing, are numbered for comparison with the multidimensional scaling plot of the same calls, below. Lines joining whale group sighting symbols refer to the inferred positions of groups of whales sighted from the boat during recordings, when submerged.
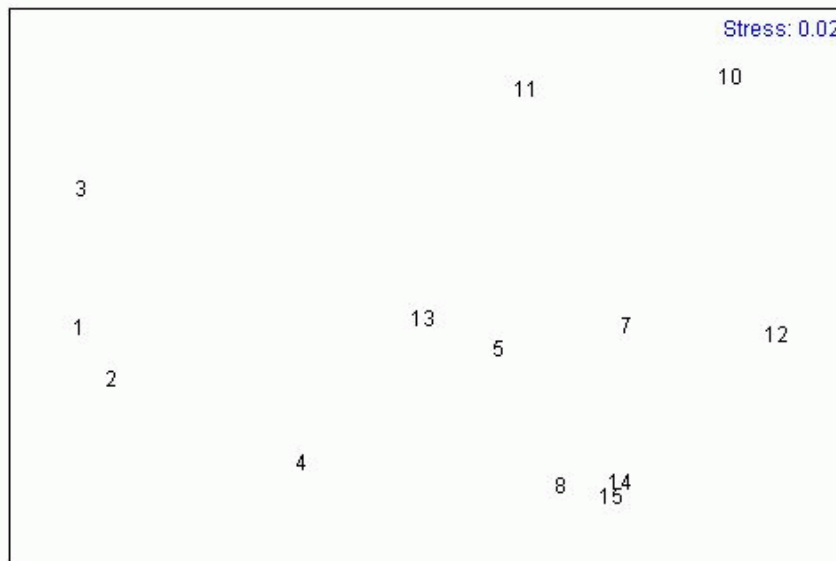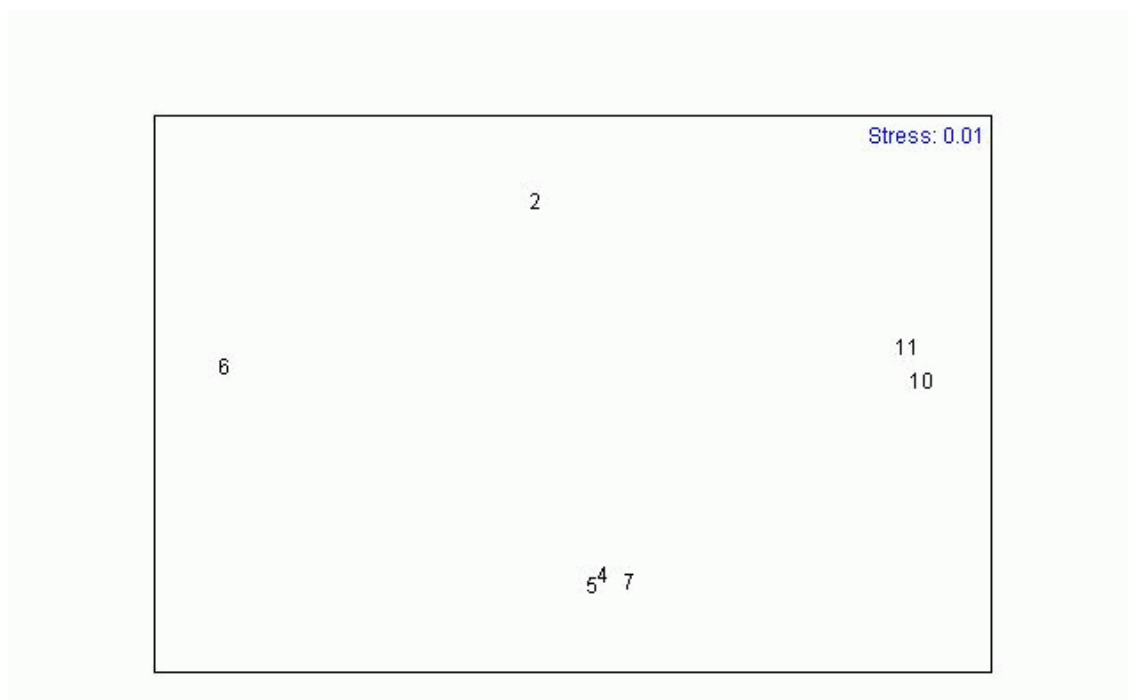

Figure 4.13b Multidimensional scaling plot of selected calls numbered above, from track 30b. Six WT-derived variables were entered for each call, standardised and transformed. The plot represents the normalised Euclidean distance between calls. Calls (4, 5 and 7) may be from one animal; calls (6) and (2) each come from separate individuals. Calls (10) and (11), though tightly clustered, can not be from the same animal, which suggests mimicry in (11) of (10).
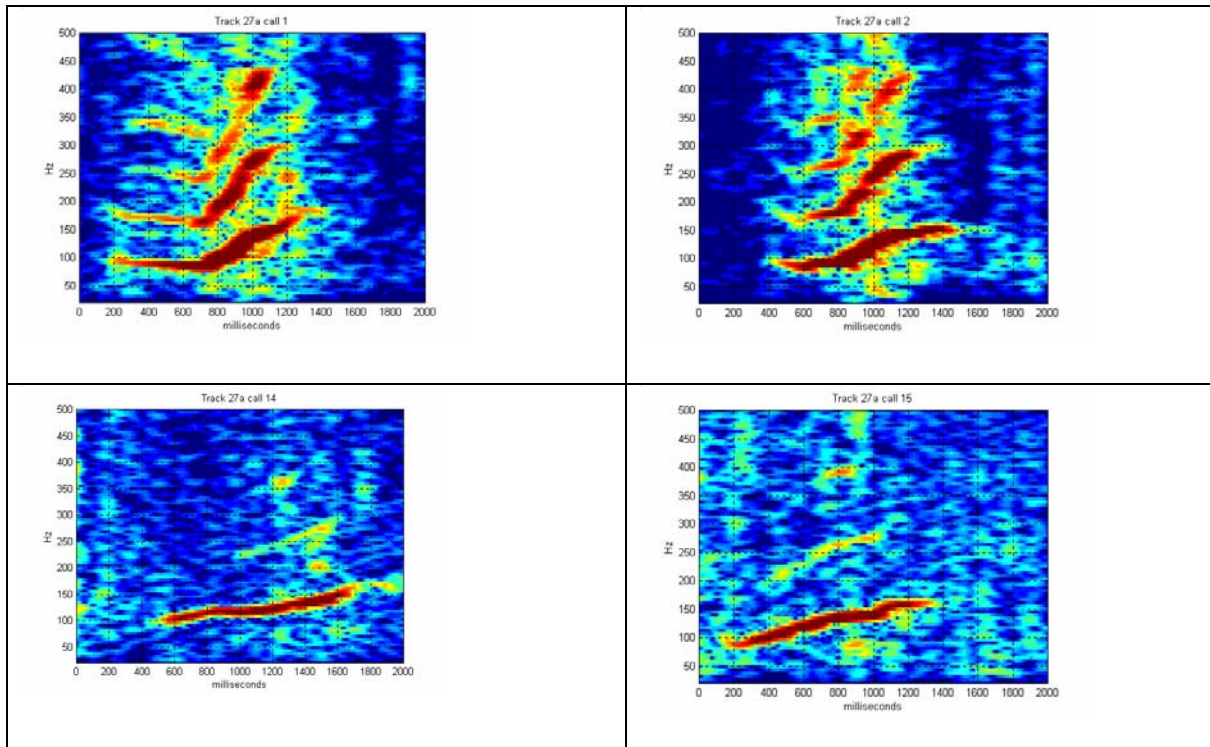
Figure 4.14 Spectrograms of Track 27a call pairs (1 and 2), and (14 and 15). Sampling rate: 10 125 samples per second, FFT size 2048, overlap 0.95. The upper call pair has similar calls close in time, bearing and Euclidean distance [9:37:00, 212°; 9:37:14, 211°] The lower pair, contrastingly, are close in time and Euclidean distance but widely separated in bearing [9:45:09, 188°; 9:45:11, 132°], perhaps representing mimicry.
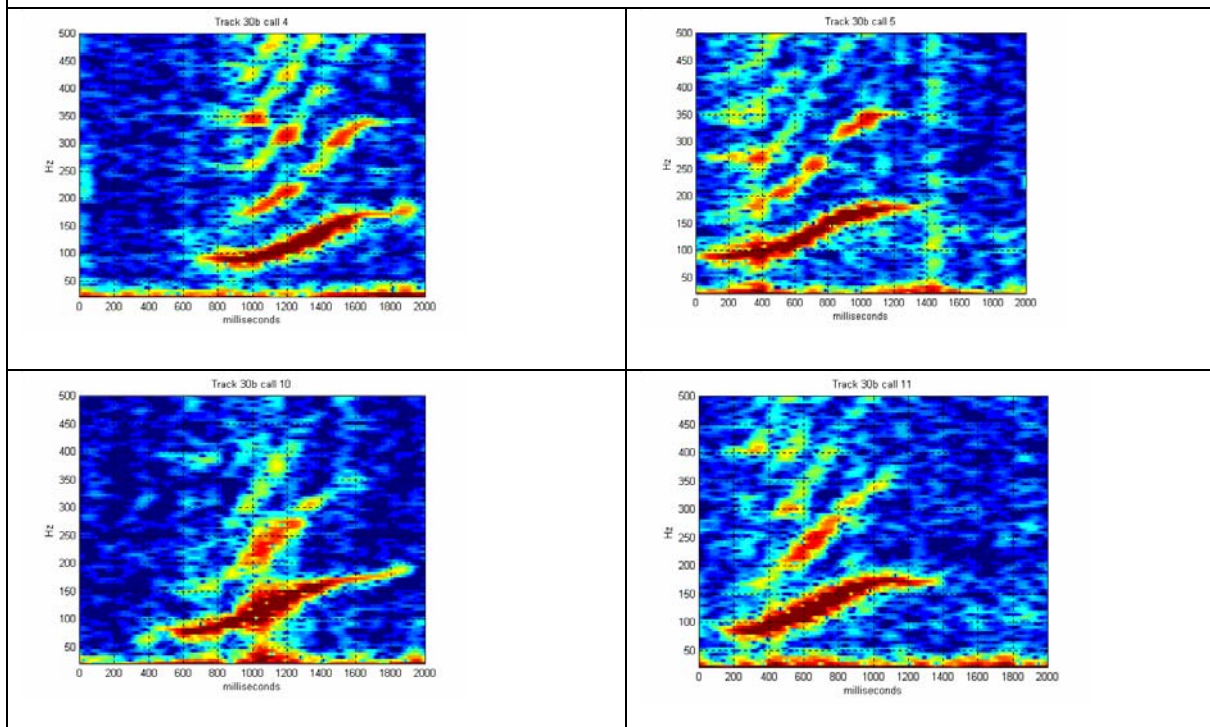
Figure 4.15 Spectrograms of Track 30b call pairs (4 and 5), and (10 and 11). Sampling rate: 10 125 samples per second, FFT size 2048, overlap 0.95.The upper call pair has similar calls close in time, bearing and Euclidean distance [11:52:30, 294°; 11:53:22, 292°]. The lower pair, contrastingly, are close in time and Euclidean distance but widely separated in bearing [12:01:00, 77°; 12:01:07, 33°], perhaps representing mimicry.

4. Discussion

The greatest hurdle in the attempt to characterise the voices of individual whales proved to be the difficulty we experienced in determining bearings to callers in real time, given the available equipment and abundance of whales. Array self-noise and rough weather conditions, leading to poor signal-to-noise ratios, and the unpredictable timing of the calls, made it difficult to capture and process relevant signals from the boat. Once we had found a viable method of post-processing the signals, we were faced with bearings to groups of whales rather than individuals. Given the uncertain group sizes and movement patterns of the whales, there were few opportunities for resolving a computed direction to an individual whale.

Instead we adopted an indirect method, comparing the Euclidean differences between two groups of call pairs, one of which was made up entirely of call pairs from different whales, while the second group contained call pairs from both the same and different whales. While the results of this method were unequivocal in supporting the hypothesized similarity between the *up* calls of an individual whale, it was difficult to move from the general to the particular. Without *a priori* knowledge of the extent of variation within individual repertoires, it was difficult to properly interpret the cluster analysis by finding a threshold of Euclidean distance beyond which two calls were unequivocally from two callers instead of one. The nearest we could get to sets of calls, each from a different whale, was to compare (a) near-simultaneous vocalisations from different directions that were clearly from different groups and (b) vocalisations that were close together in space and time, and that were most likely to be from the same group. Neither grouping was perfect because (a) group sizes were rarely one, (b) groups at different distances on the same bearing could not be distinguished, and (c) there was a possibility of mimicry.

In the light of these ambiguities, the 'balance of evidence' approach was adopted. This included the following conclusions:

1. Distant *up* calls, from different directions but close together in time (that is, clearly from different groups) were more different from each other (that is, had greater Euclidean distances) than 'close' calls (potentially from the same group, and, by extension, potentially from the same individual).

2. The similarity between *up* calls from the 'close' group was greatest when the calls were emitted within 0.5 minutes of each other (and were, therefore, more likely to have come from the same individual), and declined progressively with increasing time interval (when they were increasingly less likely to have come from the same individual, that is increasingly more likely to have come from different whales).

3. Consecutive *up* calls in a sequence (in other words, calls more likely to have come from the same individual) were more similar to each other (and thus closer to the potential 'signature' of one caller)

than each of them was when paired with calls later in the sequence (in which case, call pairs were more likely to have come from different whales).

4. 'Scream'calls from one SAG (and thus, possibly coming from the focal female in that group) were more similar to each other than they were to 'scream' calls from another SAG (where by definition, the calls in each of the call pairs compared, were almost definitely from two different whales (having been recorded several months apart, in July and in October respectively).

Given the possible confounding factors mentioned earlier, the weight of this evidence strongly suggests that individual southern right whales produce individually distinctive vocalisations.

In reaching this conclusion, the WT-based variables proved more powerful in distinguishing individual variation than the FFT-based variables, possibly because the WT analysis addressed the internal energy composition of the call within several bands throughout the signal spectrum, rather than its overall frequency contour over the first two harmonics. In a study of baboon vocalisations the features characterising individuals were found to be mainly filter-related (Rendall, 2003), in that vocal tract filtering effects conferred distinct resonance patterns on calls (Owren et al., 1997). As in this study, barking roe deer were similarly distinguished by the energy in several frequency bands, without reference to the duration and amplitude and frequency modulation of the signal (Reby et al., 1998a). Differing resonance profiles among different whales may have been particularly well detected by the WT-based analysis, because of the advantages in both temporal and frequency resolution conferred by the dynamic processes used in WTs. Whereas spectrograms are calculated using a fixed window size, with a consequent trade-off between time and frequency resolutions (Charif et al., 1995), WTs employ a wavelet scale changing dynamically with signal changes, optimising resolution in both domains.

Another view discounts the feasibility of detecting individual cetaceans vocally, arguing that pressure-induced changes in shape of the vocal tracts of marine mammals as they dive will result in changes in the voices of individual animals. These changes are presumed likely to outweigh the involuntary differences in individual voices due to the differences in their vocal tract structures (Tyack, 1998). This consideration would, however, not be relevant to this study: the mean depth of all sites during recordings was 14.1 metres, and the deepest recording site was 27.5 metres.

Wavelet variables measuring the energy in the lowest and highest frequency components of the call had the greatest effect in discriminating between individuals. The frequency-modulated nature of the call may have facilitated this discrimination, in that the upper and lower ends of the call were more subject to individual variation, while the middle region was covered by most calls. Additionally the higher frequency components would appear in some but not all calls, depending on the extent to which the call was complex or simple. As *up* calls were compared within, and not across, continuous recording sessions, the ambient noise was a constant factor within sessions.

In the spectrogram analysis several measurements were made giving attention mainly to the fundamental (f0) and disregarding the harmonics, because the presence and number of harmonics varied widely between calls. The ratios between the energy of the fundamental and the first harmonic were not effective measures for discriminating between calls from different whales. This may be due to the greater importance of subsequent harmonics, which were not a constant factor in all calls and therefore not measured. The spectrogram harmonics were also a confounding effect in attempting to measure the energy in the fundamental alone. Because the *up* call was frequency-modulated, the fundamental at its higher frequencies could not be separated from the first harmonic.

In the wavelet analysis a simpler approach was used in that energy was measured in frequency bands covering the full spectrum of resolved frequencies. While not tracking specific harmonics changing over time, this method nevertheless reflected additional energy added by any given harmonic within any given frequency band, over the whole signal. A further refinement would be to examine smaller frequency bands.

The importance of small amounts of energy in the higher frequency bands was an interesting result. In a study of manatee vocalisations, which occur, like those in this study, in shallow waters where low frequencies typically attenuate rapidly, the second and third harmonics were more pronounced than the fundamental (Nowacek et al., 2003). The character of many musical instruments is determined largely by their relative harmonic strengths , which create 'timbre' (Campbell & Greated, 1987), and may be perceived independently of the pitch of the fundamental (Marozeau et al., 2003). Individuality in primate vocalizations was encoded in the relative emphasis of the higher harmonics (Masters, 1991). Amongst spotted and spinner dolphins, the presence and relative amplitude of harmonics varied considerably, and were deemed biologically relevant (Lammers et al., 2003). Fallow deer groans were individually distinctive based on the frequency distribution of sound power (Reby et al., 1998b), while red deer stag roars contained fitness-related acoustic cues correlated with age and weight in the resonance frequencies, but not the fundamental (Reby & McComb, 2003). Harmonic content was important in facilitating kin recognition among macaroni penguins, particularly in the absence of a nest as a natural meeting place (Searby et al., 2004).

The role of low frequency components in characterising individual whale voices was not surprising, given the range of onset frequencies detected in various calls. In simultaneous speaker experiments, differences of greater than 2 semitones in the fundamental frequencies of the two voices produced improved perception of one speaker by listeners (Darwin et al., 2003). Baboon listeners were able to discriminate at least at the level of gender, based on the fundamental and first three harmonics (Rendall et al., 2004). Social recognition of individuals amongst lambs (Ligout et al., 2003) and fur seals (Phillips & Stirling, 2000) relied largely on fundamental frequency differences. In a similar way, differences in the onset frequencies of respective whale voices would add to their specificity. Additionally, relative vocal amplitude may be related to physical size or strength, as with cod sounds

(Heike et al., 2004), adding to the acoustic profile of individuals, although the direct inverse relationship between size and vocalisation frequency found in many toothed cetaceans does not always apply amongst great whales (Matthews et al., 1999).

At species level, literature-based research was not found to be as desirable as data-based research (presumably referring to actual recordings) in characterising calls, which were 'not well described' by conventional measurements (Matthews et al., 1999). At the level of the individual, the search for optimal features encoding individuality continues. For southern right whales the relative distribution of acoustic energy across the full frequency range is significant in encoding individual vocal profiles. With such a varied repertoire (*chapter one*), a method relying on features common to several call types, rather than those of any one specific call, should be the long-term goal of future research.

Mimicry

While the possibility of vocal mimicry in southern right whales confounds the interpretation of vocal traits in individuals, if it exists it cannot be ignored. Many individually distinctive features of mammalian voices are physiologically based and reside in the vocal tract structure; mimicry constitutes an active filtering of the vocal tract to achieve a desired outcome, a feature of human speech, possibly present in some other primate species (Riede & Zuberbuhler, 2003). Male humpback whales adopt novel features introduced by individual singers within a population, into songs sung by all males during the breeding season (Payne et al., 1983). Such vocal mimicry has even occurred between two entirely separate populations (Noad et al., 2000; Noad, 2002) as in the rapid adoption of a new repertoire by humpback whales on the east coast of Australia from a few visitors from the west. Male budgerigars imitate the calls of their female mates (Striedter et al., 2003), and in studies of bird dispersal, song learning was a factor causing male dispersal to be at odds with song divergence (Ellers & Slabbekoorn, 2003).

Dolphin 'signature whistles' identifying one individual are reproduced by another as a form of name-calling (Janik, 2000; Tyack, 2000), possibly evolving because of the unstable acoustic quality of vocalisations subject to the effects of depth, such that recognisable qualities specific to the voices of individuals are not discernible and diverse whistle types are necessitated. Indeed, the 'signature whistle' hypothesis itself has been questioned (McCowan & Reiss, 2001).

The evidence for use of mimicry by southern right whales is not conclusive, but it is important to be alert to the possibility that it exists. The question remains as to the extent to which conscious vocal-tract filtering can mimic the individually distinctive features of mammalian vocalisations. The level at which mimicry operates may be restricted to signal type rather than individually specific acoustic markers. Preliminary results in the present study, comparing *up* calls from different whales, did however suggest a very small proportion of calls possibly employing mimicry within one signal type.

Future research

This study concentrated on *up* calls, because they were believed to be among the commonest southern right whale vocalisations (*chapter one*), produced by all components of the population, including single animals (Clark, 1982), and (as contact calls) likely to contain information about caller identity. The choice of the *up* call to characterise individual vocal profiles was also guided by its stereotypy. Of all southern right whale calls it is the most stable, a useful feature in aiding recognition tasks (Serrano & Terhune, 2002). A stereotyped call allows for highlighting of individual differences, unclouded by random differences in call structure unrelated to vocal apparatus. Nevertheless, on the basis that most SAG calls are probably made by a single animal, the focal female (Kraus & Hatch, 2001; Parks, 2003a; Parks, 2003b; Parks & Tyack, 2005a), such vocalisations could provide an alternate vehicle for investigating individuality in southern right whale vocalisations. Despite the fact that such calls are less stereotyped in nature than *up* calls, they may encode individual identity due to the mammalian non-linear vocal tract features involved in their production, which give them an unpredictable and chaotic character which is 'difficult to ignore' (Fitch et al., 2002). If SAG calls were to serve as target calls for the study of vocal individuality, at least the problem of determining the caller would be less intractable, and the relationship between vocal and other behaviours greatly simplified. Potential drawbacks would be that they may be produced by one sex, and that their nature may be age-related (Parks, 2003b).

Another approach simplifying the connection between call and caller would be to investigate the acoustic properties of aerial voiced blows produced by southern right whales (Clark, 1982) for individual markers. The unambiguous source of these vocalisations would be in their favour, but whether their noisy quality would yield enough individually specific information remains to be seen.

Finally, the option of deploying acoustic recording tags shows some promise, in that it reduces caller ambiguity. It is accompanied by several drawbacks. The cost of tagging is high, and the process somewhat invasive. The tagging of elephant seals produced only nine possible acoustic signatures, obtained during two dives out of a possible fifty, and these were assigned to either the tagged subject or a conspecific (Burgess et al., 1998). Similarly low vocalisation rates were recorded from northern right whales (Parks, 2003a). The inherent disturbance in the procedure may also have accounted for low vocalisation rates, despite the less invasive suction cup attachment used on right whales, and recorded calls were not always from the tag-bearer.

This study strongly suggests that some vocalisations of southern right whales (especially *up* or contact calls) are individually distinctive, are encoded in the relative distribution of energy at a range of frequencies, and are produced by individuals in closely spaced bouts. The use of WTs provided distinctive measures, and this technique holds sufficient promise to warrant further refinement by testing on calls from known callers. Additionally, the more standard use of Fourier transforms should, where possible, include the measurement of acoustic features beyond the first two harmonics, f0 and

f1. A knowledge of the acoustic transmission profiles of relevant study sites will greatly enhance further research into variation in southern right whale vocalisations.

The use of passive acoustics in characterising individual whales holds great promise, and is hindered principally by the inherent ambiguity (for researchers) of caller identity; this may be reduced by using acoustic recording tags or by targeting either the focal females of SAGs, aerial calls, or areas and times of the season where smaller groups of whales are encountered.

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CHAPTER FOUR: INDIVIDUAL VARIATION IN THE CALLS OF SOUTHERN RIGHT WHALES

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