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.
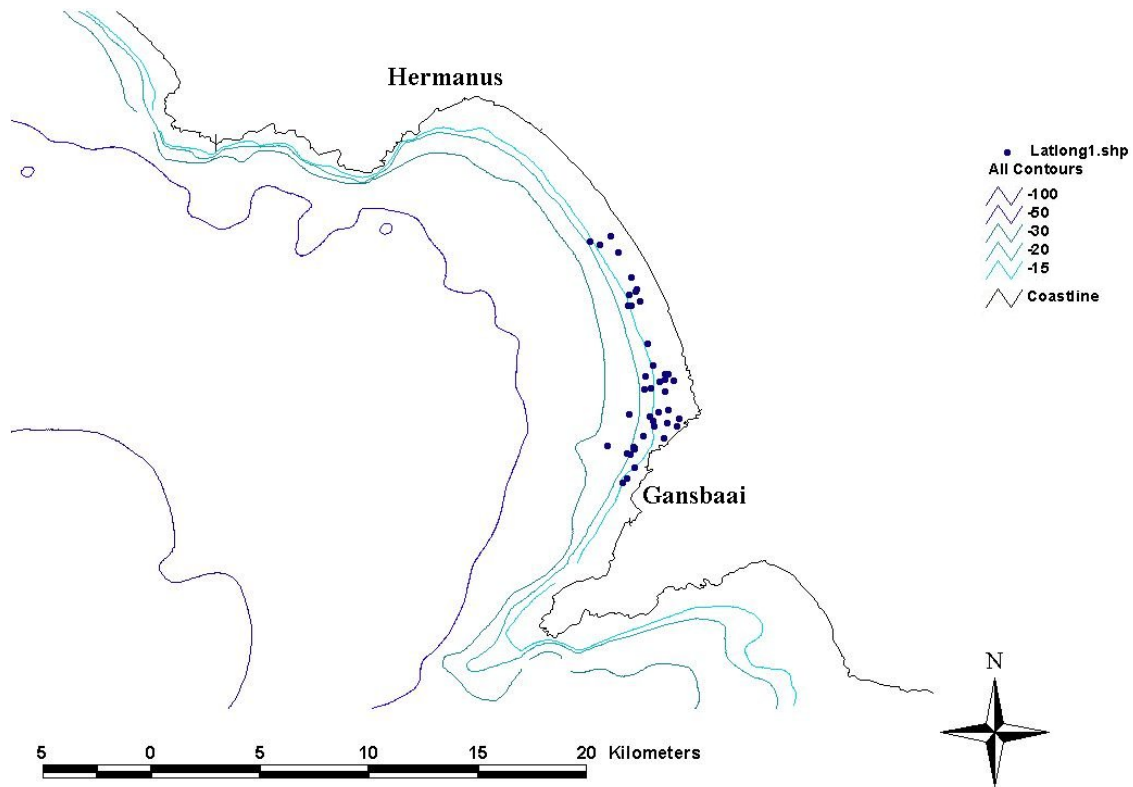
Figure 4.1 Positions from which right whales calls were recorded in Walker Bay, South Africa, between June and November, 1999.
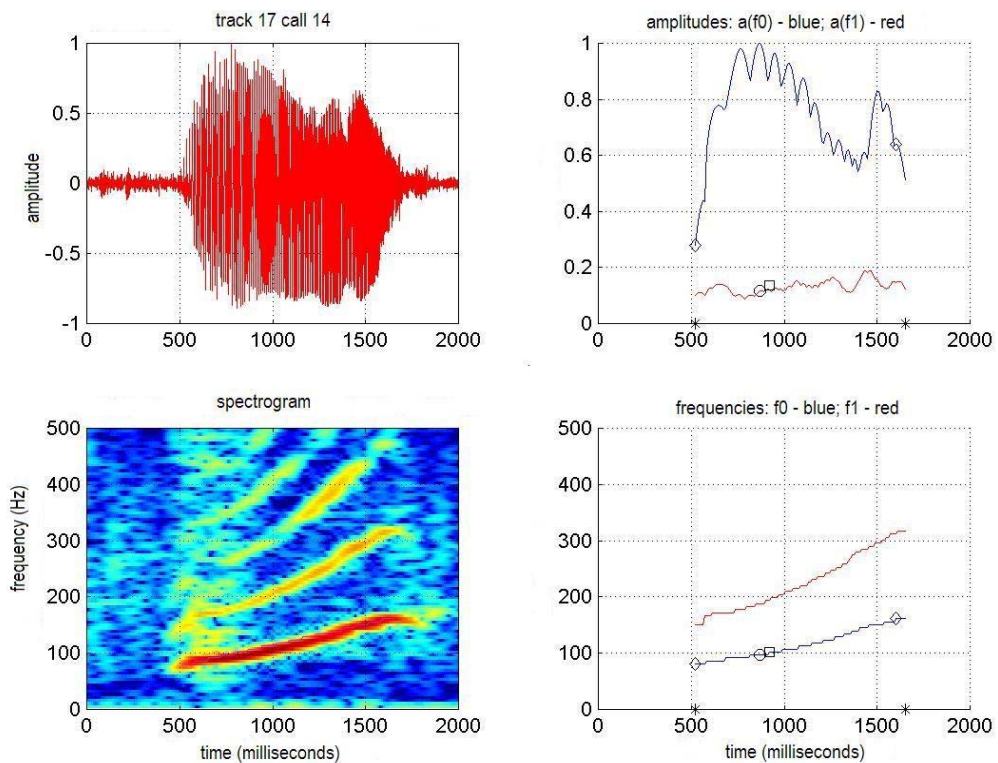

Figure 4.2 Amplitude (top right) and frequency (bottom right) measurements from a spectrogram (bottom left) of an *up* call (raw signal top left). Amplitude and frequency modulations of the fundamental, a(f0), f0, and first harmonic, a(f1), f1, in blue and red respectively. Call region between diamonds; 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
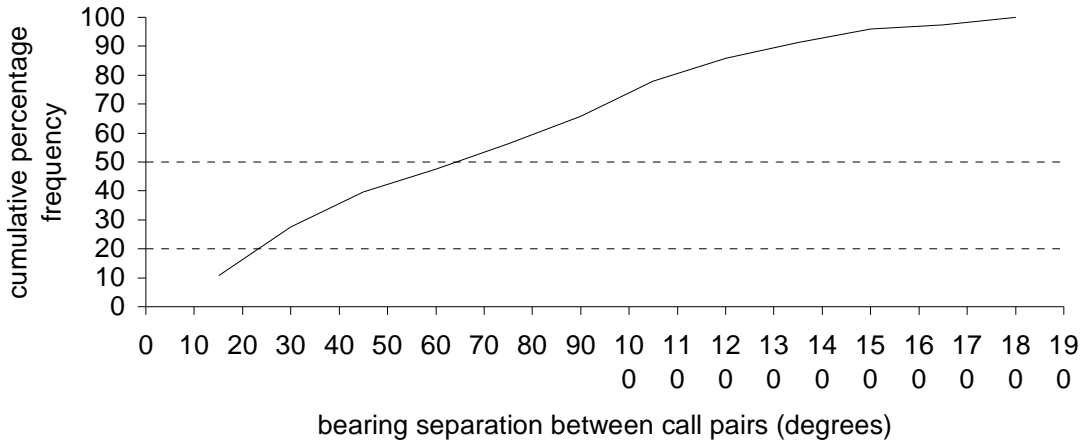
Figure 4.3 Distribution of separations in degrees between distant call pairs: 80% of call separations are greater than 20°, and 50% are greater than 60°.
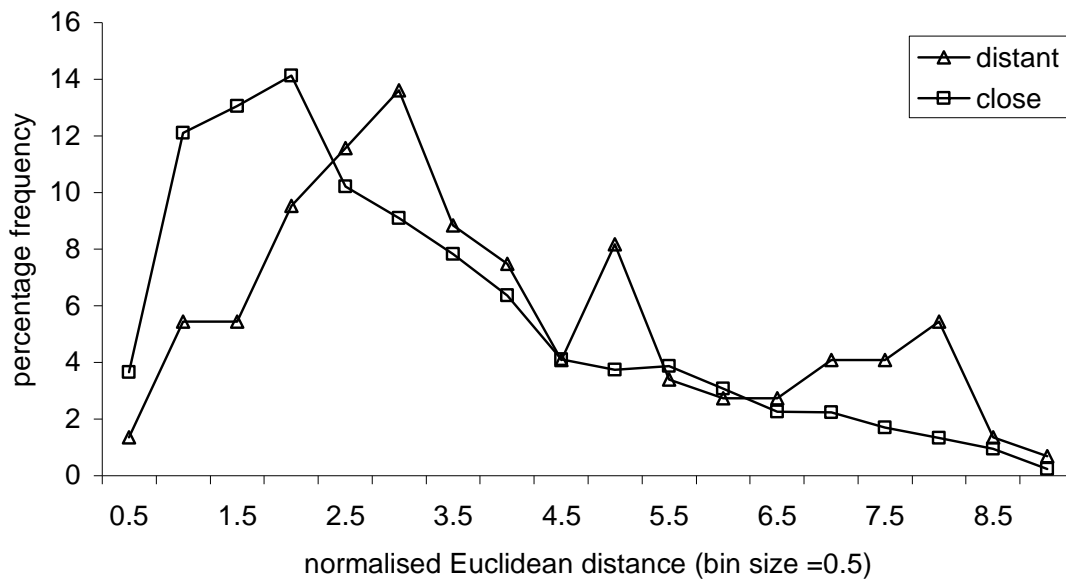

Figure 4.4 Frequency distribution of Euclidean distances between 'close' and distant call pairs.
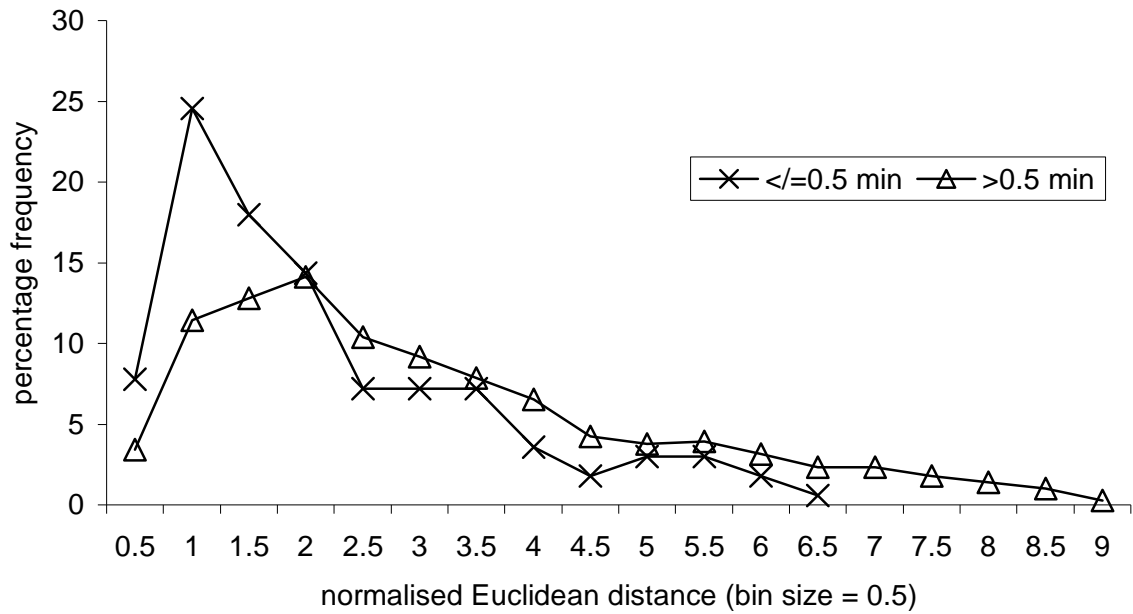
Figure 4.5 Percentage frequency distribution of Euclidean distances for call pairs (excluding distant pairs) separated by up to 0.5 minutes, and in excess of 0.5 minutes.
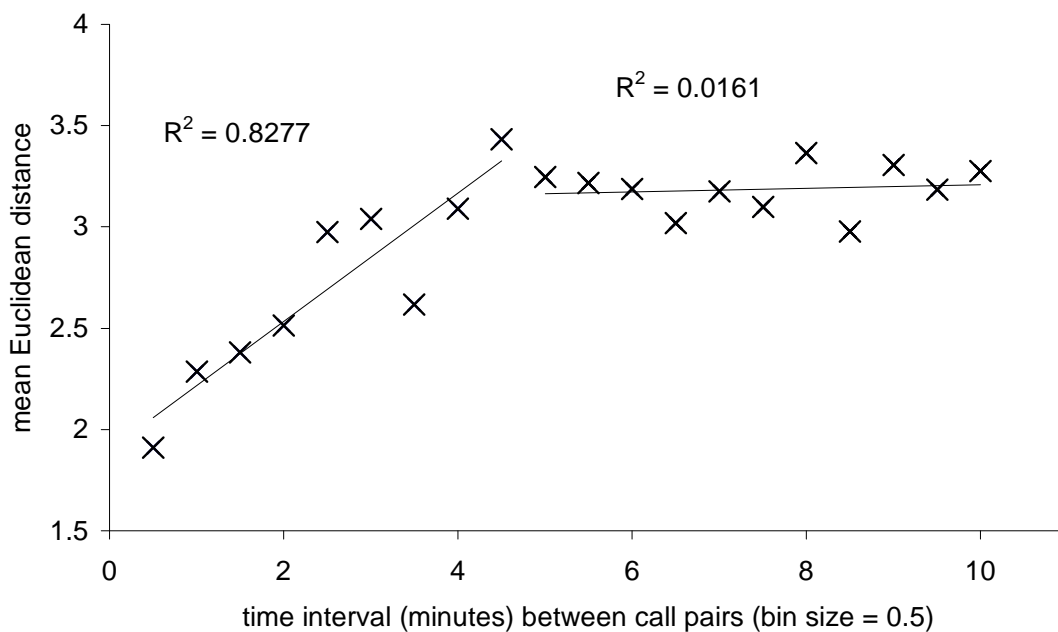

Figure 4.6 Mean Euclidean distances for call pairs (excluding distant pairs) with increasing time intervals between calls. Note the strong positive correlation up to around 4.5 minutes, after which Euclidean distances appear to stabilise, with no further correlation.

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..

	DISTANT			CLOSE					
Track	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.
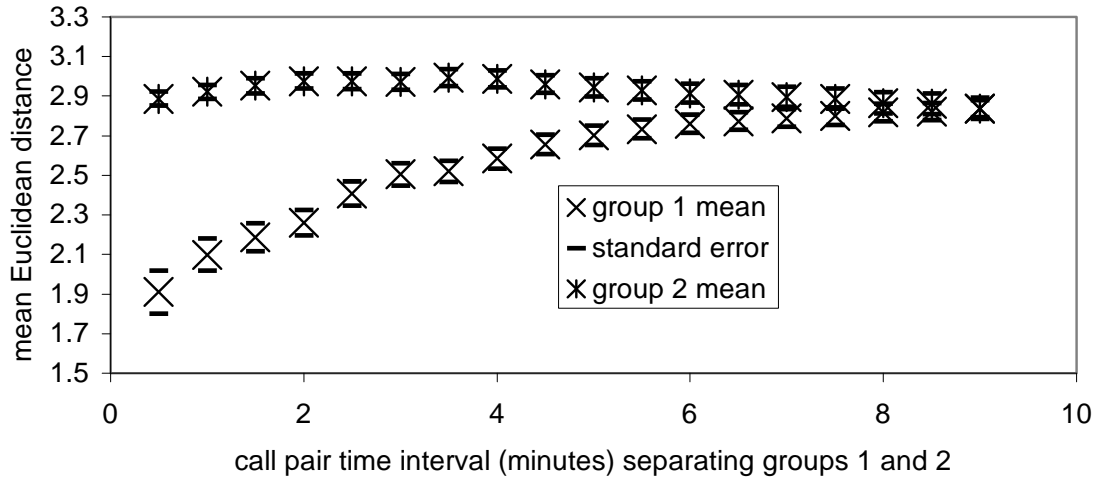
Figure 4.7 Mean Euclidean distances between call pairs, for group 1 and for group 2. Groups are separated by a defined but increasing time interval (*x*-axis), with group 1 call pairs separated by time intervals up to (*x*), and group 2 call pairs separated by time intervals exceeding (*x*).
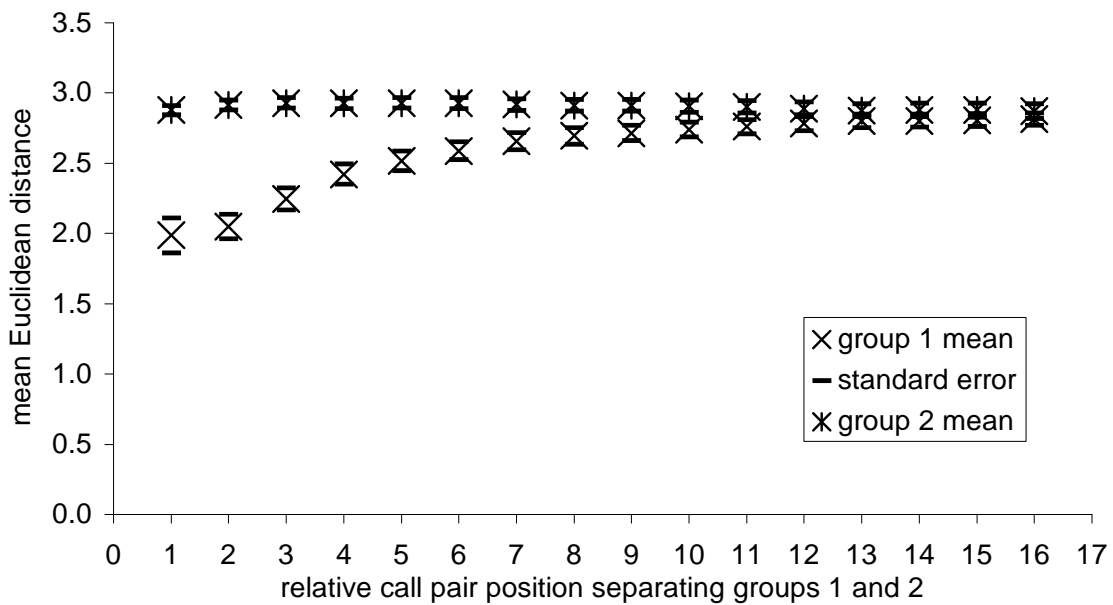

Figure 4.8 Mean Euclidean distances between call pairs, for group 1 and for group 2. Groups are separated by a defined position of one call in a pair, relative to the other call in the pair (1=adjacent). This defining position increases iteratively (*x*-axis), with group 1 call pairs positioned relative 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
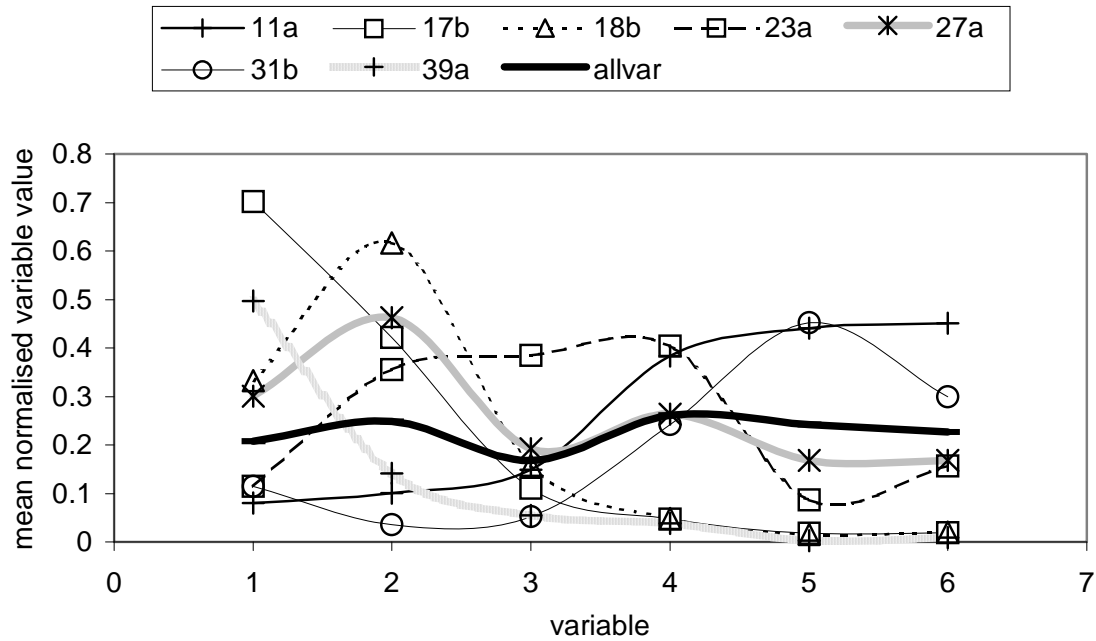
Figure 4.9 Mean normalised WT-derived variable values for seven selected pairs of *up* calls. Each pair is close in time, bearing and Euclidean distance, and is drawn from a different recording session, and so potentially represents one of seven different whales (the two calls from each pair produced 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.
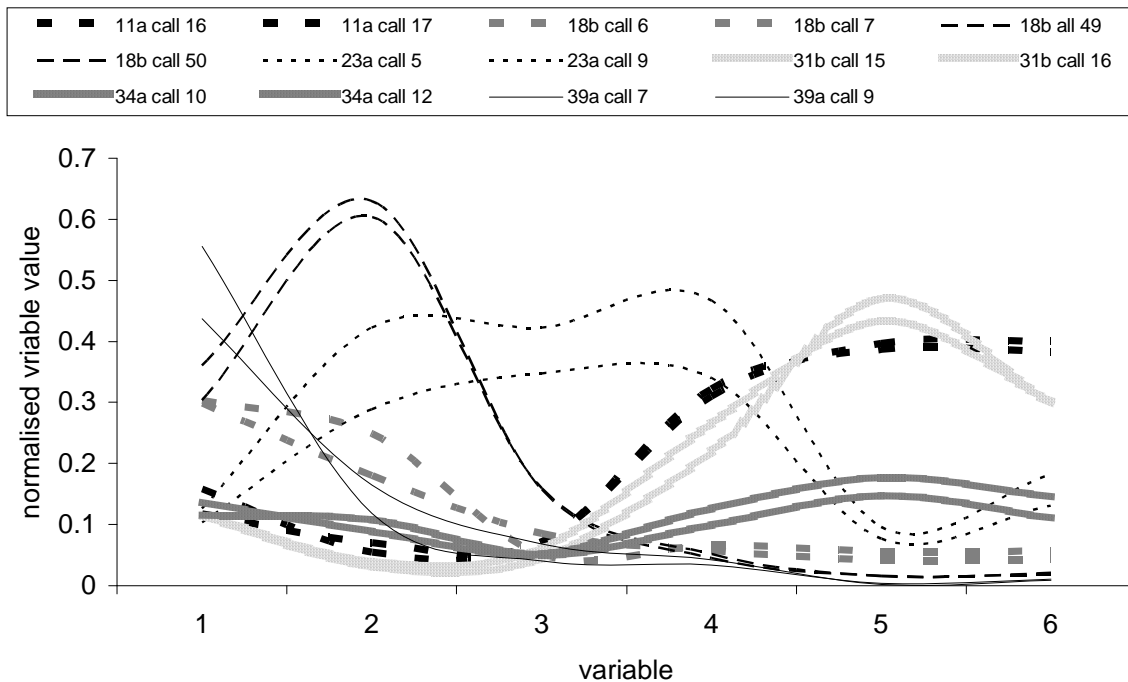
Figure 4.10 Normalised WT-derived variable values for selected pairs of *up* calls close in time, bearing and Euclidean distance, shown above as similar pairs of lines, each representing one call, and each pair potentially representing two calls from a single animal. Note the similarity between pairs.
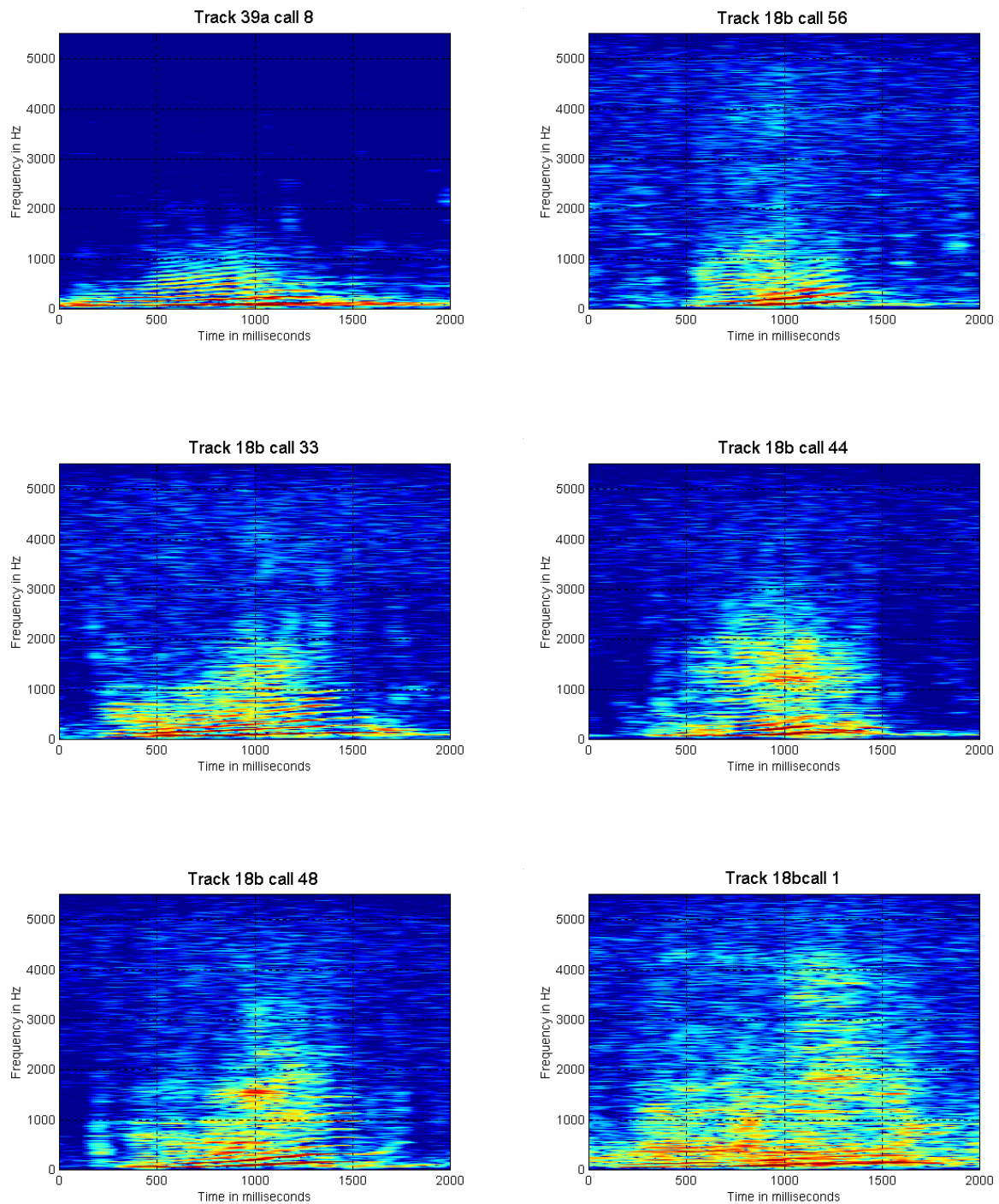
Figure 4.11 Spectrograms of *up* calls displaying high levels of energy (yellow and red), clearly associated with vocalisations, into increasingly higher bandwidths. Upper left: energy to 1000 Hz; upper right: energy to 1300 Hz, with some energy right up to 4800 Hz; middle left: main energy to 2500 Hz; 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.
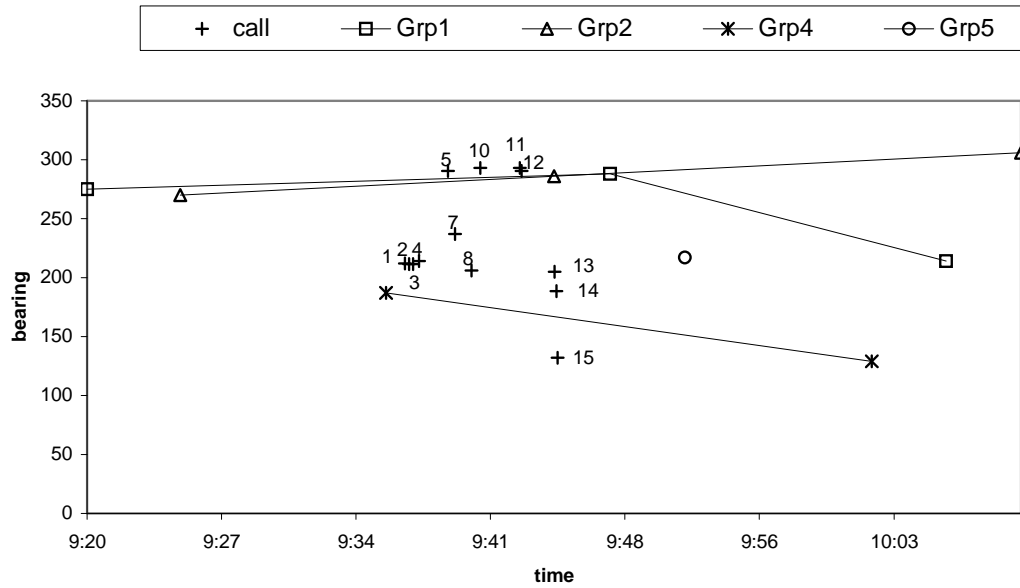
Figure 4.12a Track 27a. Selected calls close in time and bearing, are numbered for comparison with the multidimensional scaling plot of the same calls, below. Lines joining whale group sighting symbols refer to the inferred positions of groups of whales sighted from the boat during recordings, when submerged.
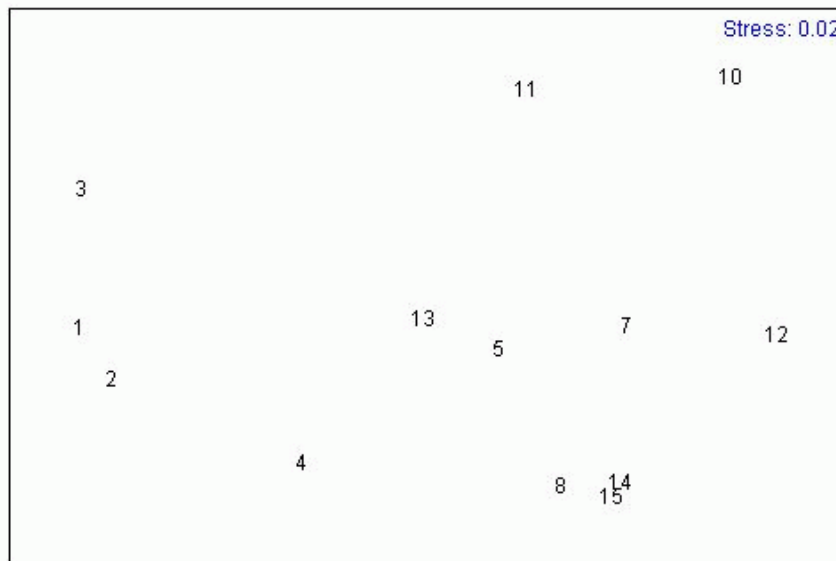

Figure 4.12b Multidimensional scaling plot of selected calls numbered above, from track 27a. Six WT-derived variables were entered for each call, standardised and transformed. The plot represents the normalised Euclidean distance between calls. Calls (1, 2, 3 and 4) group together loosely on the left 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.
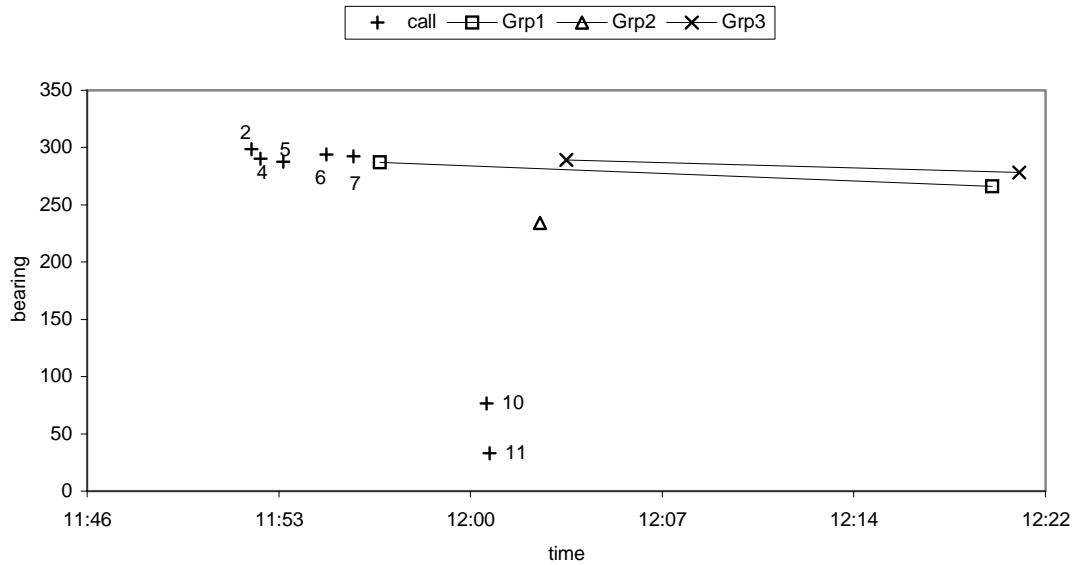
Figure 4.13a Track 30b. Selected calls close in time and bearing, are numbered for comparison with the multidimensional scaling plot of the same calls, below. Lines joining whale group sighting symbols refer to the inferred positions of groups of whales sighted from the boat during recordings, when submerged.
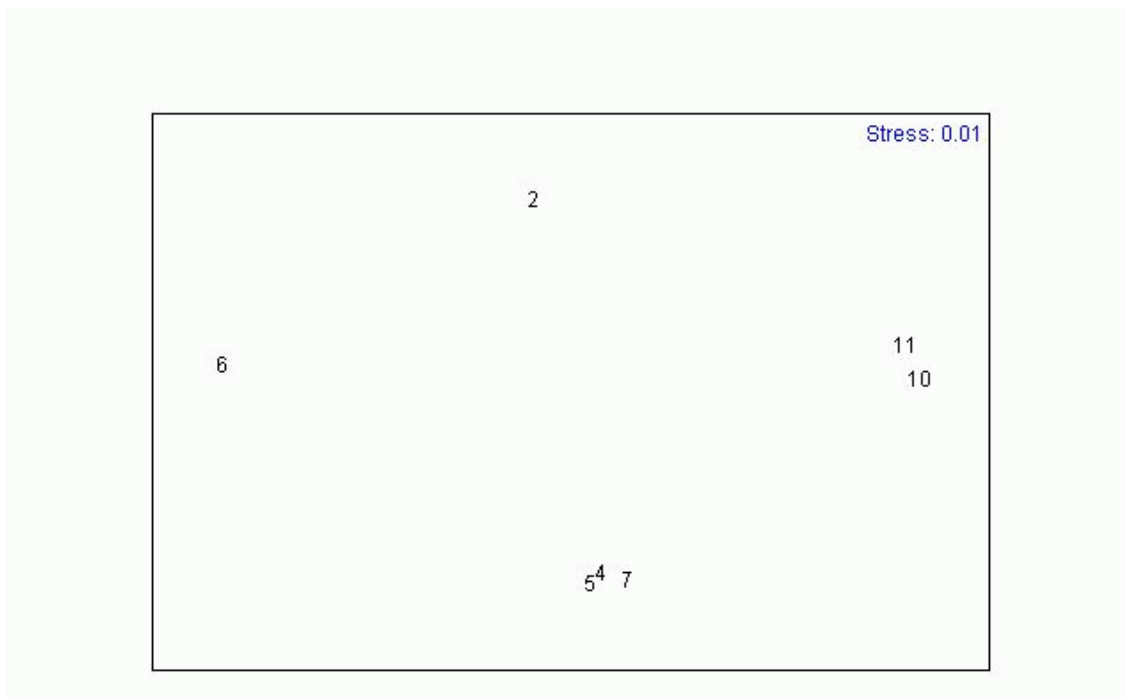

Figure 4.13b Multidimensional scaling plot of selected calls numbered above, from track 30b. Six WT-derived variables were entered for each call, standardised and transformed. The plot represents the normalised Euclidean distance between calls. Calls (4, 5 and 7) may be from one animal; calls (6) and (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).
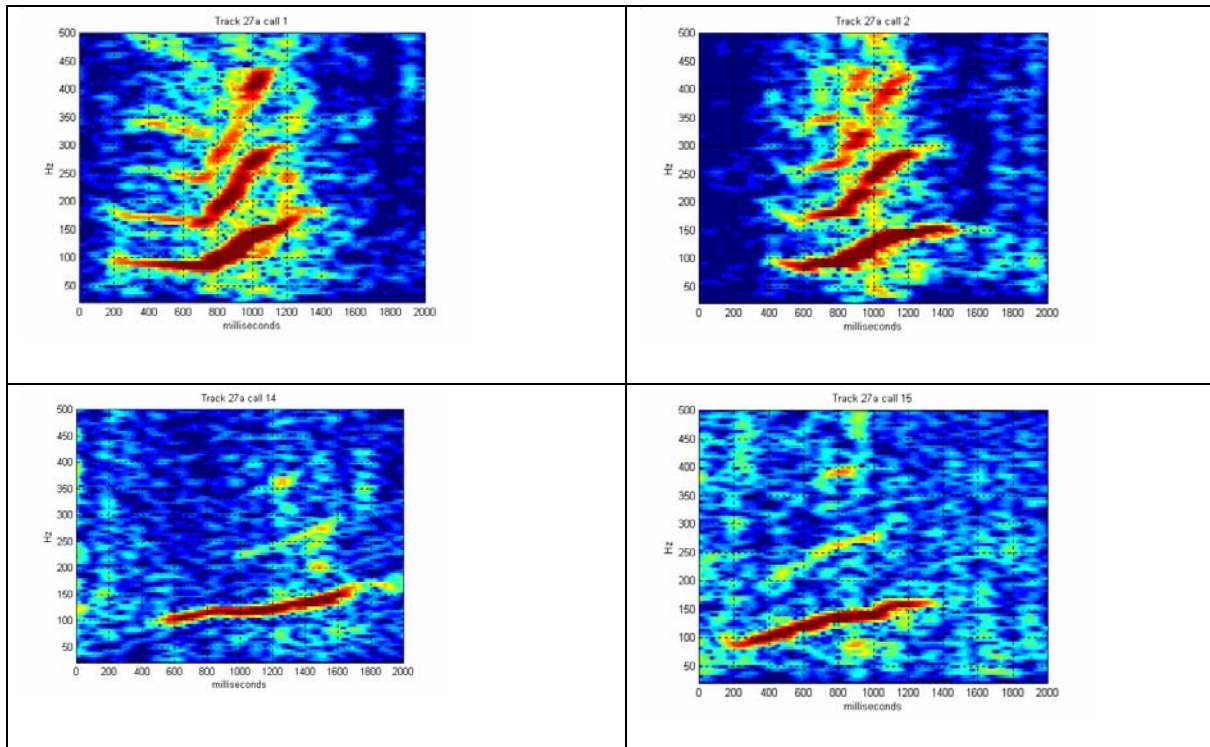
Figure 4.14 Spectrograms of Track 27a call pairs (1 and 2), and (14 and 15). Sampling rate: 10 125 samples per second, FFT size 2048, overlap 0.95. The upper call pair has similar calls close in time, bearing and Euclidean distance [9:37:00, 212°; 9:37:14, 211°] The lower pair, contrastingly, are close in time and Euclidean distance but widely separated in bearing [9:45:09, 188°; 9:45:11, 132°], perhaps representing mimicry.
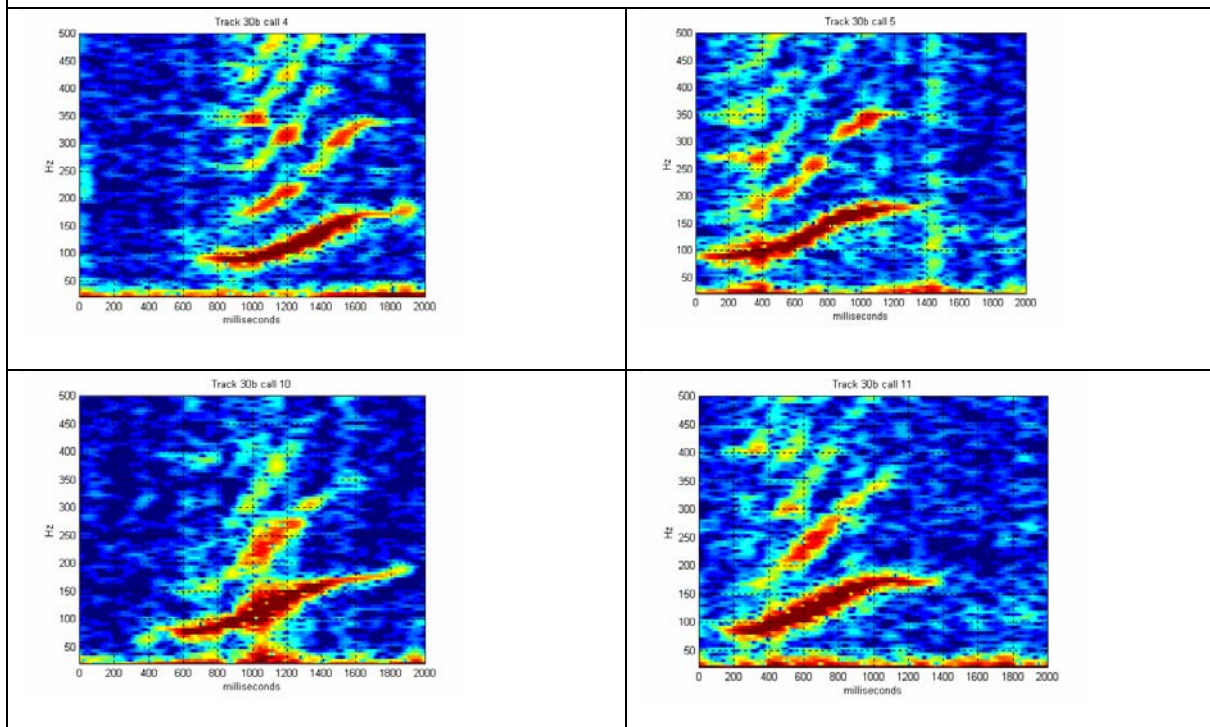

Figure 4.15 Spectrograms of Track 30b call pairs (4 and 5), and (10 and 11). Sampling rate: 10 125 samples per second, FFT size 2048, overlap 0.95.The upper call pair has similar calls close in time, bearing and Euclidean distance [11:52:30, 294°; 11:53:22, 292°]. The lower pair, contrastingly, are close 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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