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

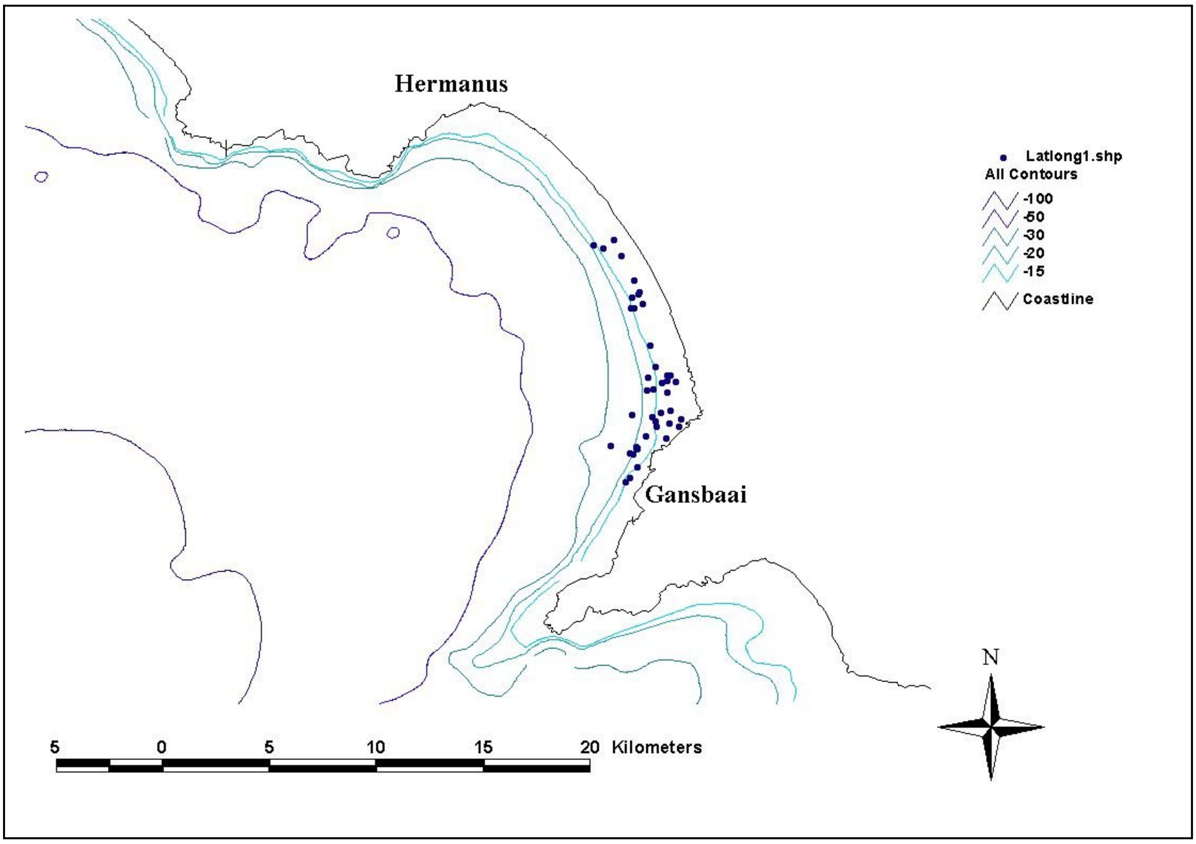

Figure 1.1 Walker Bay and positions of recording locations from the boat, with depth profiles for the bay.

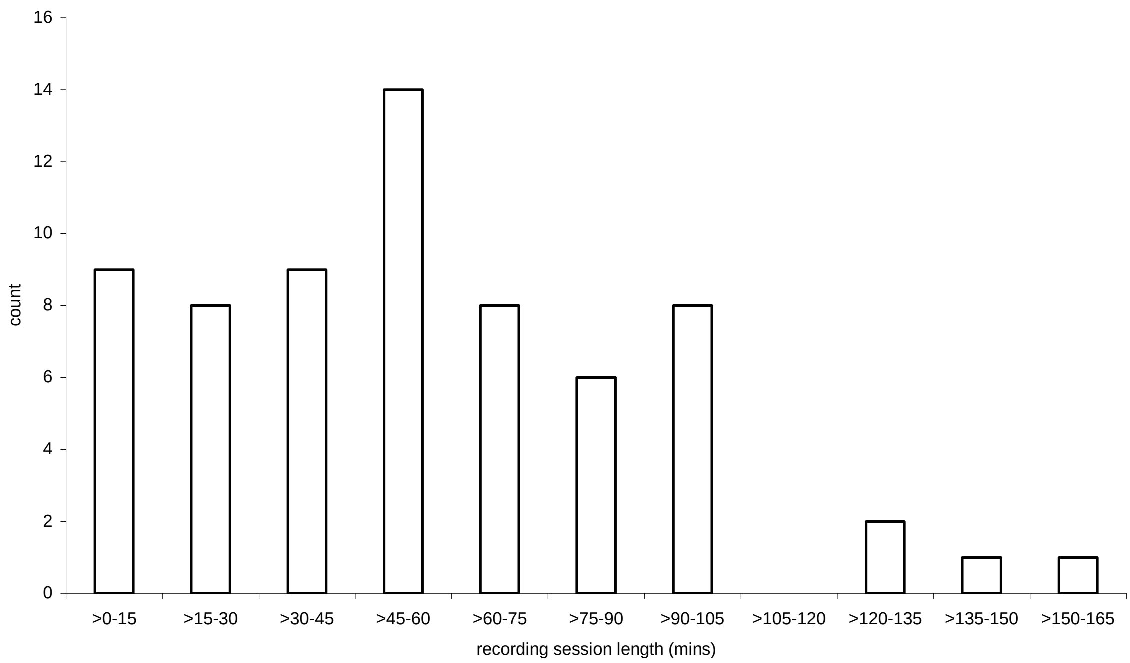

Figure 1.2 Distribution of recording sessions of varying lengths (N=66), ranging between 4 and 150.5 minutes (bin size 15 minutes).

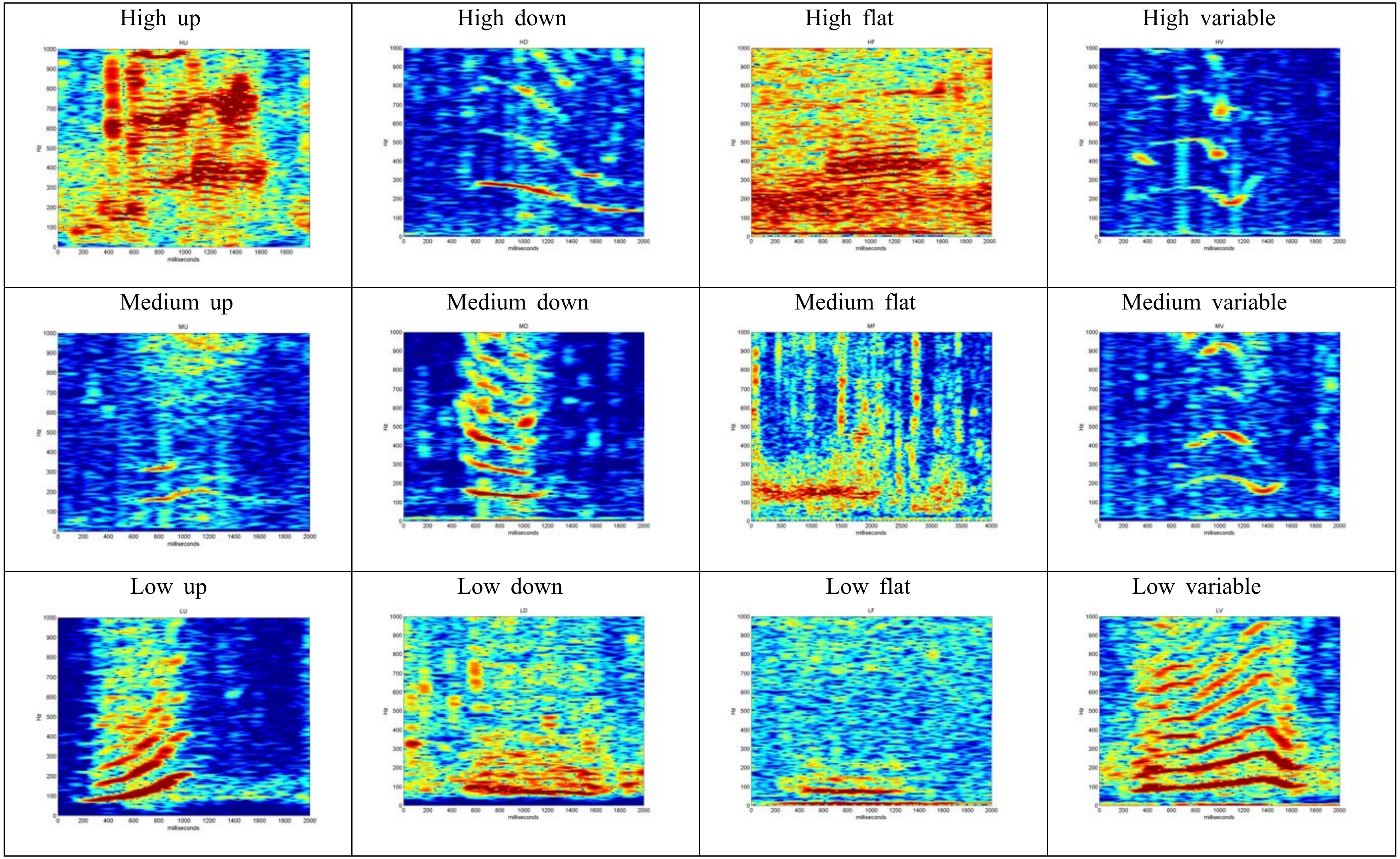

Figure1.3 Twelve tonal or mixed tonal and pulsive calls, classified by acoustic contour (*up*, *down*, *flat* and *variable*), and starting frequency (*low*=55 Hz–<110 Hz, *medium*=110 Hz–220 Hz, and *high*=220 Hz–<440 Hz). Y-axis for each spectrogram frequency range 0–1000 Hz.

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.

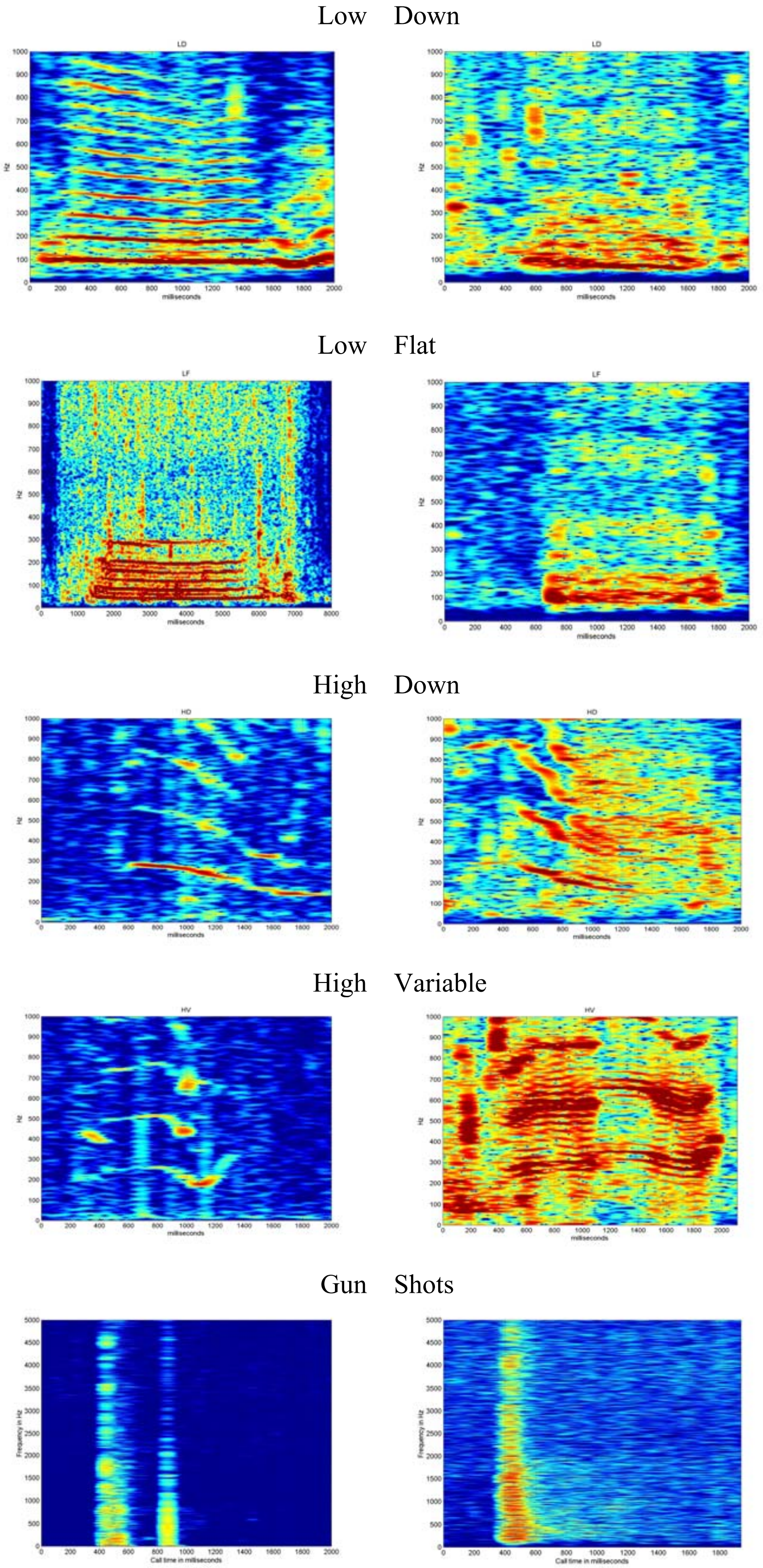

Figure 1.4 Paired calls (right and left); top three with similar starting frequencies and general acoustic contours, but with highly contrasting sound qualities: more tonal on the left, more pulsive on the right; various observed combinations of these qualities suggested a tonal/pulsive continuum (Y-axis 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

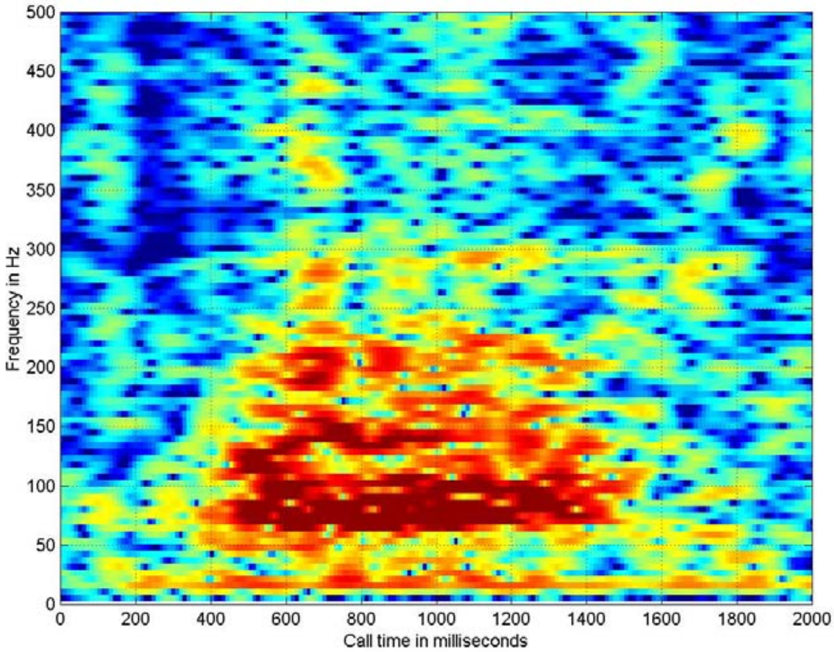

Figure 1.5 Low frequency growl around 70 Hz. Note element near 20 Hz, possibly associated with the growl, starting just before it, and continuing after it (cf. *fig. 1.6*)

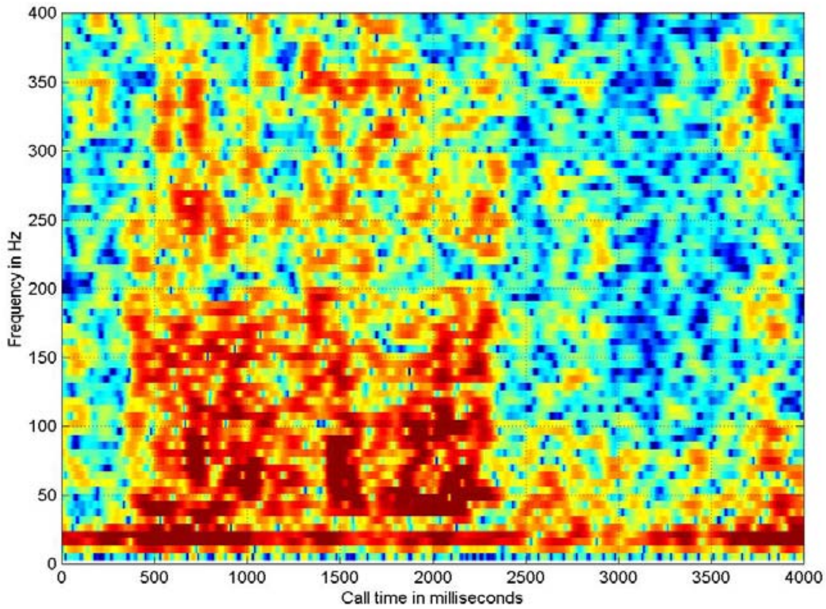

Figure 1.6 Low call with a growl-like quality, and a peak frequency shifting from 22 Hz, where it overlaps with ambient noise in that frequency range, through 65 Hz, and to 86 Hz, dropping again to 43 Hz. Ongoing low-frequency noise is independent of growl (cf. *fig. 1.5* above).

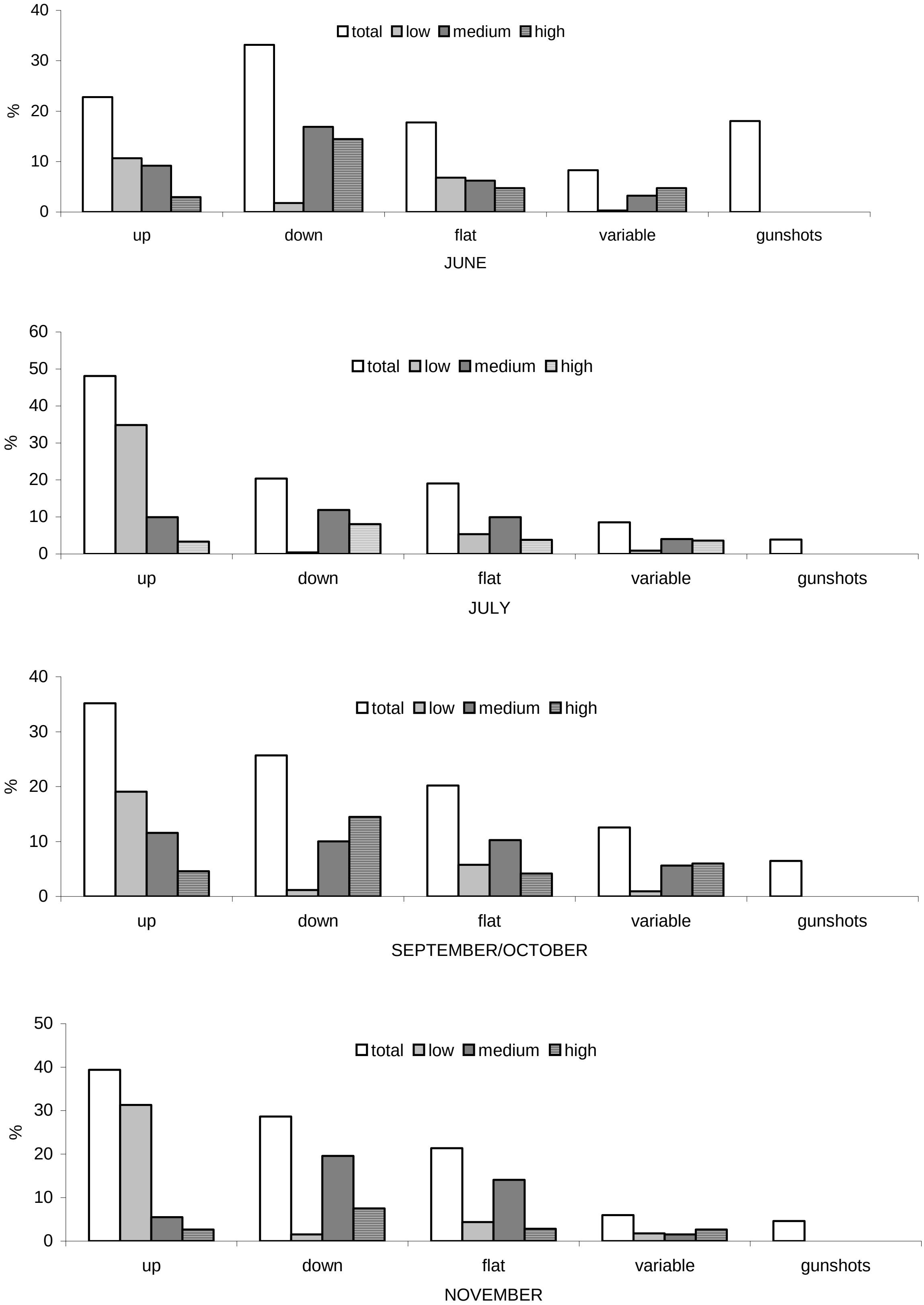

Figure 1.7 Proportional contributions of call types within each month group.

of the intercall intervals on the y 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

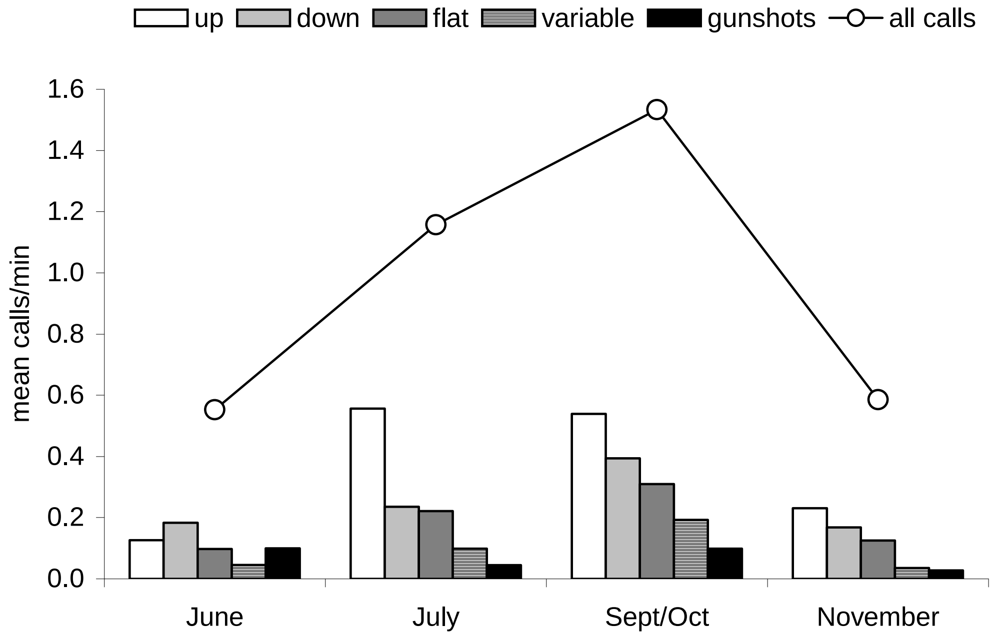

Figure 1.8 Mean overall call rate (all calls), and call rates for tonal calls (*up*, *down*, *flat* and *variable*) and gunshots, calculated for each monthly period.

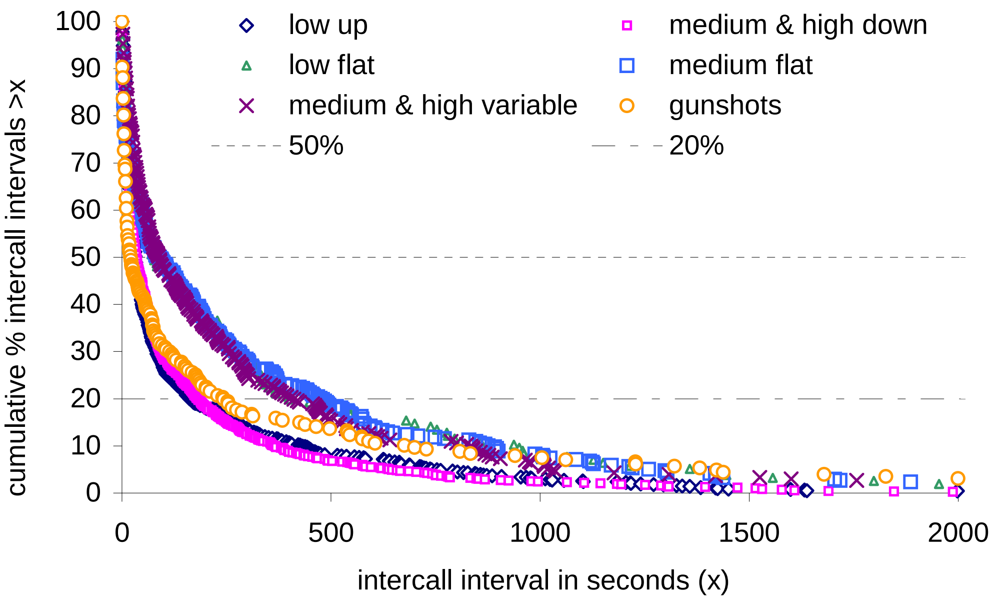

Figure 1.9 Cumulative percentage intercall interval distribution for the most prevalent call types, as defined by starting frequency and acoustic contour, and for gunshots.

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*

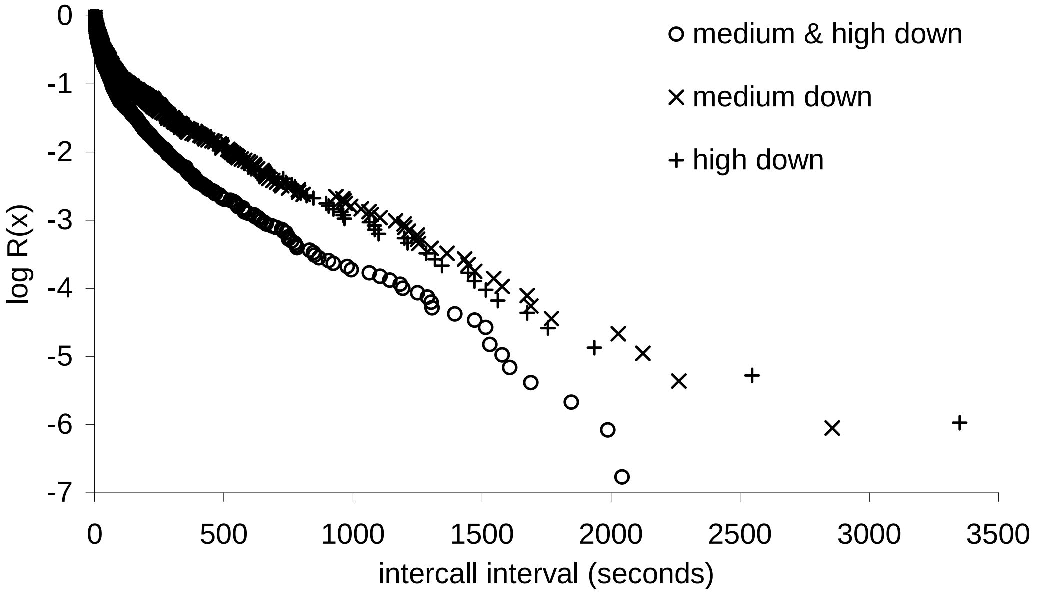

Figure 1.10 Log-survivor function, log R(x), for *medium down* (diagonal crosses), *high down* (upright crosses) and *medium and high down* (circles) intercall intervals. *Medium and high down* intercall intervals are the intervals between both *medium down* and *high down* calls, considered together as one call group.

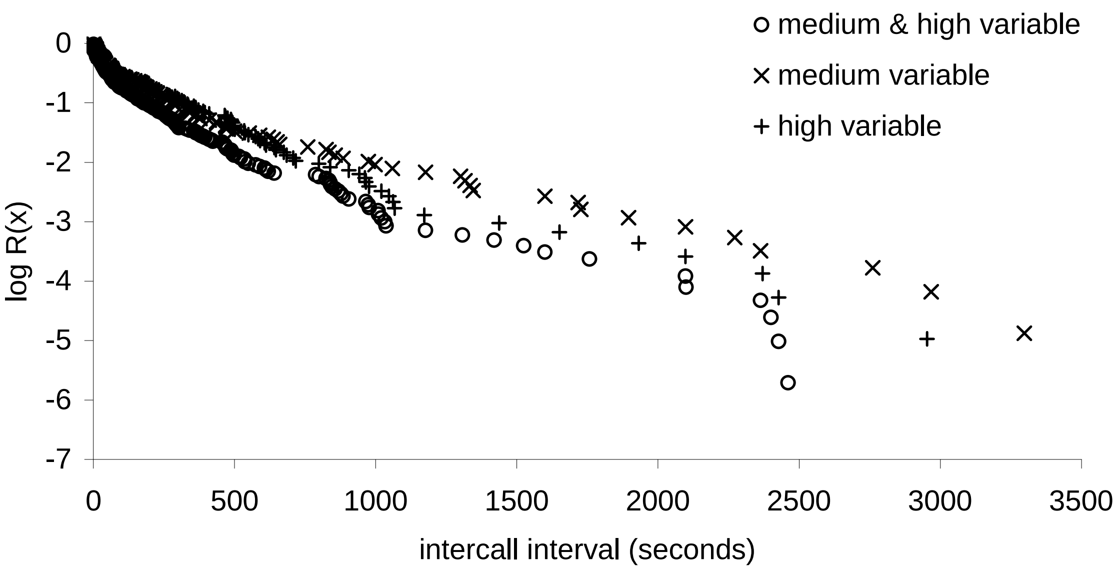

Figure 1.11 Log-survivor function, log R(x), for *medium variable* (diagonal crosses), *high variable* (upright crosses) and *medium and high variable* (circles) intercall intervals. *Medium and high variable* intercall intervals are the intervals between both *medium variable* and *high variable* calls, considered together as one call group.

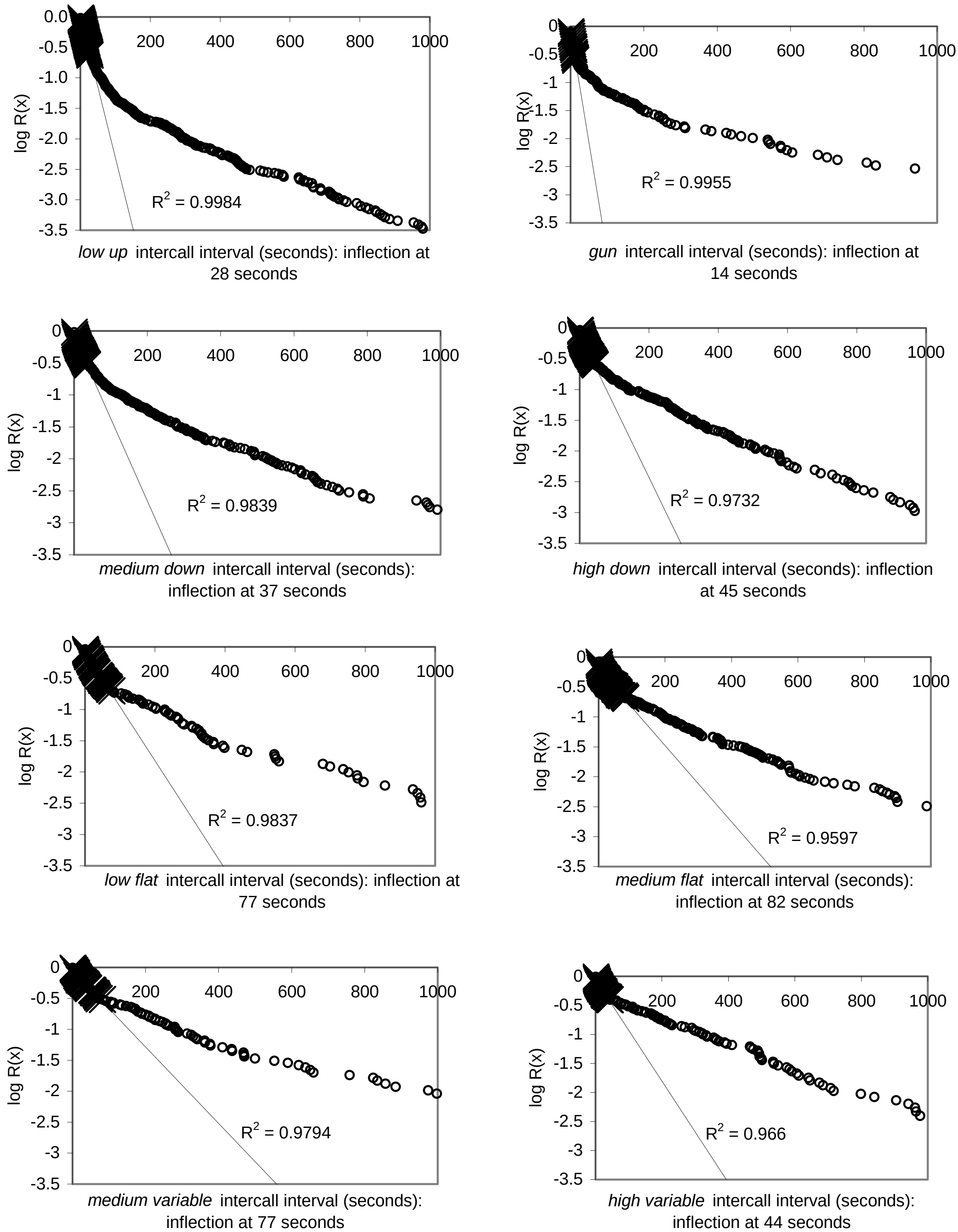

Figure 1.12 Log survivorship function (small circles), log R(x), for intercall intervals for the eight call types most prevalent within their respective acoustic contours. For all figures: X-axis: intercall interval in seconds (left to right, 0 to 1000); Y-axis: log cumulative frequency of (x) (top to 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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