CHAPTER TWO

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

1. Introduction

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

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

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

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

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

2. Materials and method

Between June and November, 1999, underwater recordings were made in Walker Bay, South Africa (*fig. 2.1*) during daylight hours, from a 6m semi-rigid inflatable boat, in the presence of southern right whales.

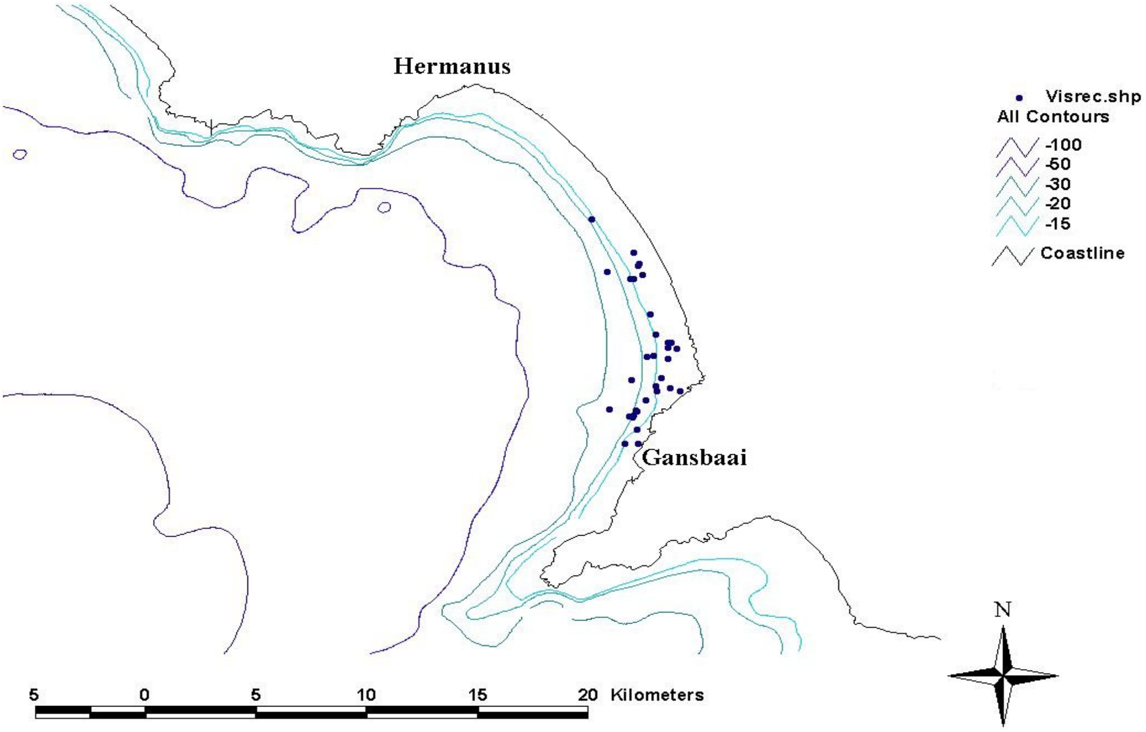

Figure 2.1 Positions (dots) from which simultaneous acoustic recordings and visual observations of whales were made from a semi-rigid inflatable boat with an elevated viewing platform in Walker Bay, South Africa, between June and November, 1999. All sampling points fell within the zone with a maximum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

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

2.1 Data collection

Acoustic recordings

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

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

Visual observations

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

2.2 Data analysis

Continuous recording sessions

In order to determine the number of whales present during any single continuous recording session, it was first necessary to include only those periods where there was an overlap of visual observation and acoustic recording, excluding non-overlapping data from both categories. Rates of sound production were determined both directly from the number of recorded calls per unit time, irrespective of the number of whales sighted from the boat (overall call rate, or OCR), and also in relation to the number of whales sighted (call rate per whale, or CPW). Acoustic recordings and visual observations were made between 23rd June, 1999 and 20th November, 1999, on 19 days (3 in June, 5 in July, 2 in September, 4 in October and 5 in November). After discarding non-synchronous data, 59 continuous recording sessions, covering 47 hours and 21 minutes, remained.

Counts of whales sighted from the boat

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

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

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

$$\text{Average \#whales} = \sum (\text{whale\_minutes\_i..whale\_minutes\_n}) / \sum (\text{duration\_i..duration\_n}) \qquad (1)$$

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

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

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

Generalized linear model

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

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

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

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

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

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

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

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

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

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

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

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

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

Call rates per whale in the presence of increasing whale numbers

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

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

3. Results

3.1 Generalised Linear Model

Factors contributing to the observed variation in call density

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

Effect of month

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

Effect of wind

Compared to conditions of no wind, and adjusted for month and number of whales, the predicted number of calls with a NE wind was 31% of that with no wind (p=0.2, ns); the predicted number of calls with a SW wind was 23% of that with no wind (p = 0.1, ns); the predicted number of calls with a SE wind was 18% of that with no wind (p = 0.05); the predicted number of calls with a NW wind was 16% of that with no wind (p = 0.2, ns) (*fig. 2.3*).

Number of whales

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

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

Relative frequencies of call types

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

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

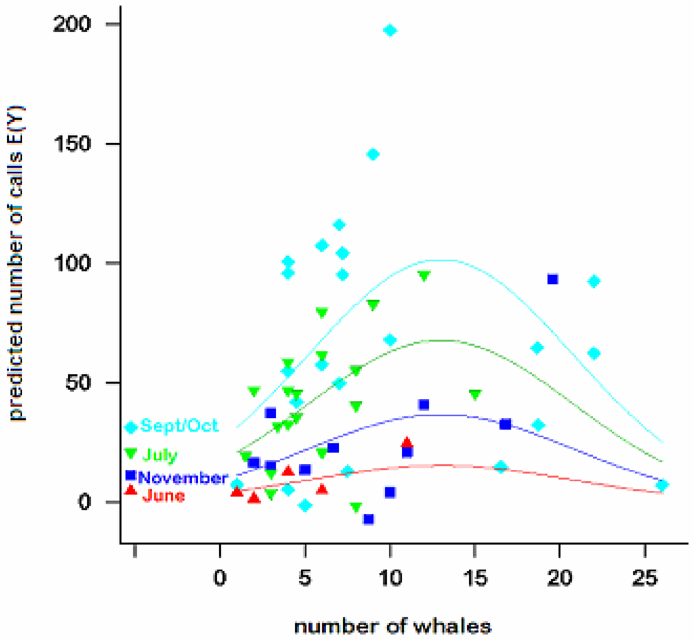

Figure 2.2 The effect of month on predicted number of calls E(Y), compared to June and incorporating information about the other independent variables, wind direction and number of whales (June: red; July: green; September/October: light blue; November: dark blue).

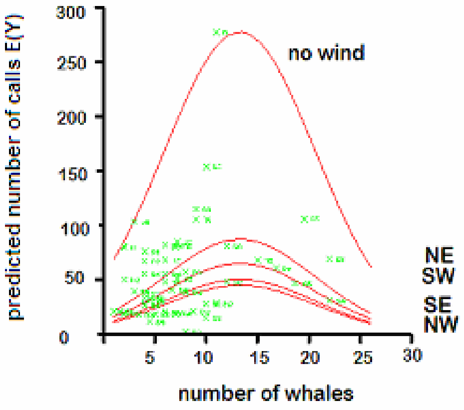

Figure 2.3. The effect of wind direction on predicted number of calls E(Y), compared to no wind and incorporating information about the other independent variables, month and number of whales.

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

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

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

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

The impact of various aggregation sizes

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

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

The impact of various call types

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

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

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

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

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

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

In other words, the relative production of various call types could potentially deliver information about the local whale density (*fig. 2.7, 2.8*). In general lower numbers of whales were most likely to produce *low up* calls more often than *medium down* and *high down* calls (*fig. 2.6*), although because of low numbers of calls in some expected call frequency categories when analyzing all thirteen call types, the chi-squared analysis was not performed, as it was with onset frequency- and acoustic contour-defined calls (*fig. 2.7, 2.8*). Calls defined by onset frequency alone followed patterns that were easier to interpret than those of calls defined by acoustic contour alone. Similar levels of *low*, *medium* and *high* calls were recorded for smaller gatherings of whales (*fig. 2.7*). When whales were present in higher numbers, the call profile was likely to include lower levels of *high down* calls and elevated levels of *medium down* calls (*fig. 2.6*). High whale numbers would also indicate wide separations in the high levels of prolific *medium* calls, intermediate levels of *low* calls and depressed levels of *high* calls (*fig. 2.7*).

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

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

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

The same two peaks in a generally declining call rate per whale for *low up* calls, were manifest for *low* calls when grouped by onset frequency (*high*, *medium* and *low*, *fig. 2.13*), and for *up* calls, when grouped by acoustic contour (*up, down, flat* and *variable*, *fig. 2.14*). All other call types (*medium* and *high*, for onset frequency, *fig. 2.13*, and *down*, *flat* and *variable*, for acoustic contour, *fig. 2.14*) showed a consistent decline, with the same marginal increase in gunshot calling rates per whale at highest whale numbers.

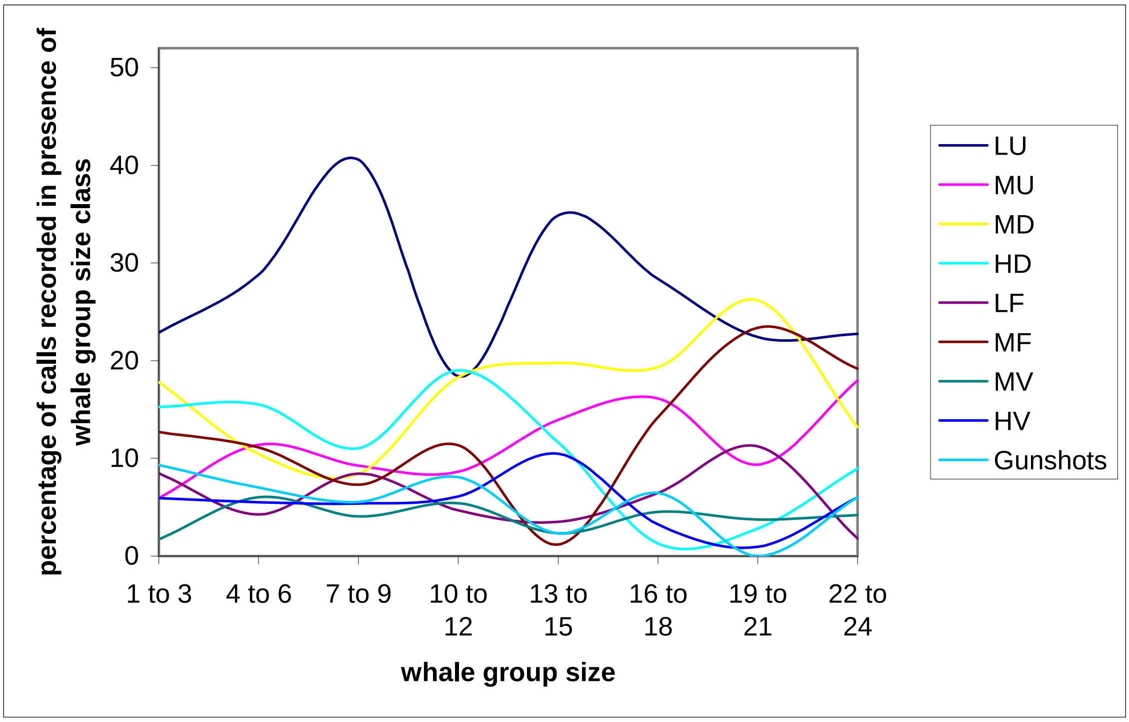

Figure 2.4. Relative call compositions of the most abundant calls recorded in the presence of a range of whale numbers (9 call types for which distribution differed significantly from a random distribution, Pearson's chi-squared test, p=>0.00001). After meeting LU calls at 20% in presence of 10 to 12 whales, MD calls increase and HD calls decrease their relative proportions of call totals in the presence of greater numbers of whales.

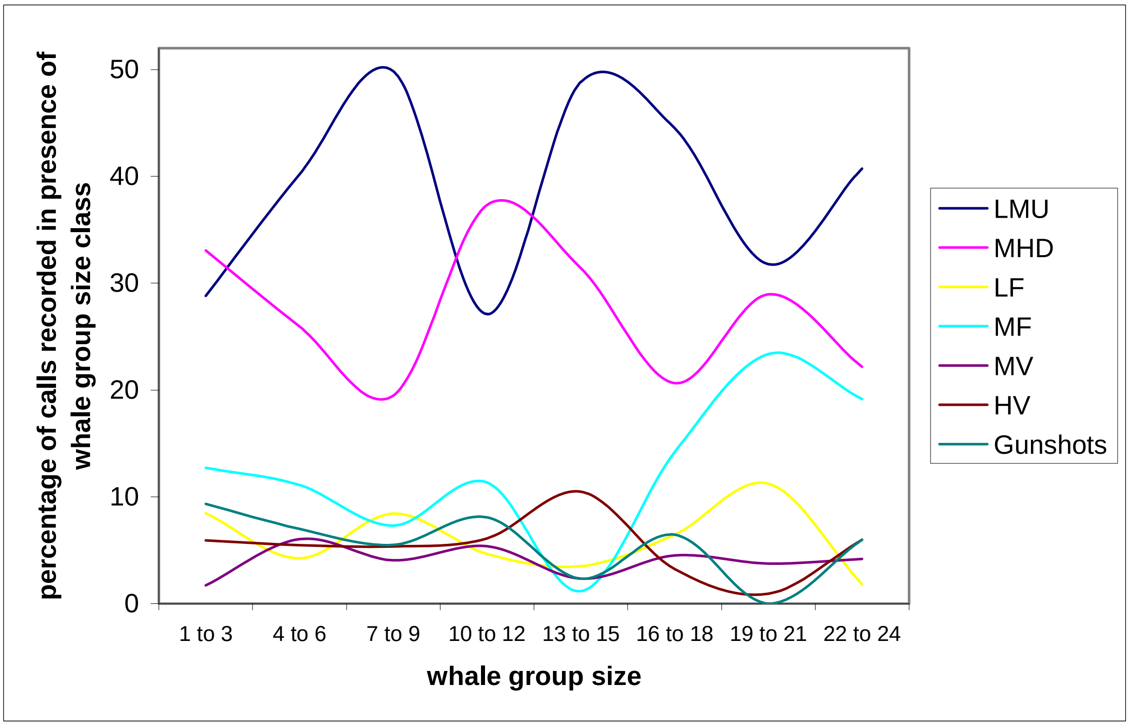

Figure 2.5. Relative call compositions of the call data from figure 2.4 (above), with [LU and MU] amalgamated as LMU, and [MD and HD], as MHD. In the presence of 10 to 12 whales, MHD calls are more abundant than LMU calls. Both dominate throughout. Note dramatic rise in MF calls in presence of high numbers of whales. Gunshots are most abundant in presence of low whale numbers.

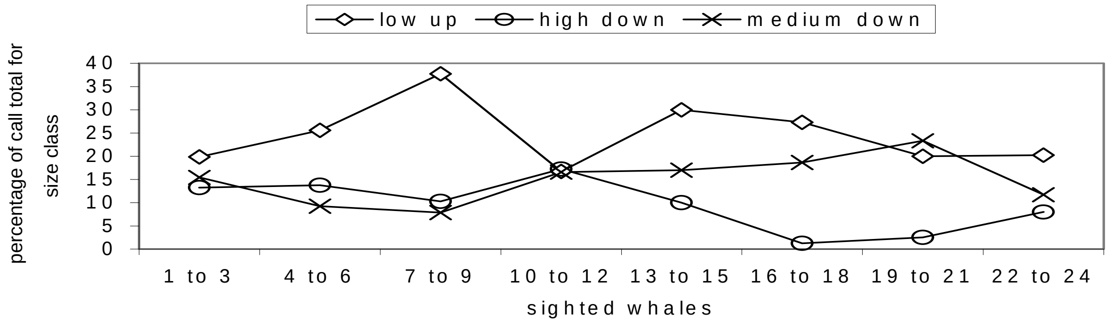

Figure 2.6 Relative contributions to the call total within size class, for the whole season, of three of thirteen call types, bounded by both acoustic contour and onset frequency (*low up*, *medium down* and *high down*). These call types exert the greatest influence on variation in the relative proportions of calls in the presence of differing whale aggregation sizes..

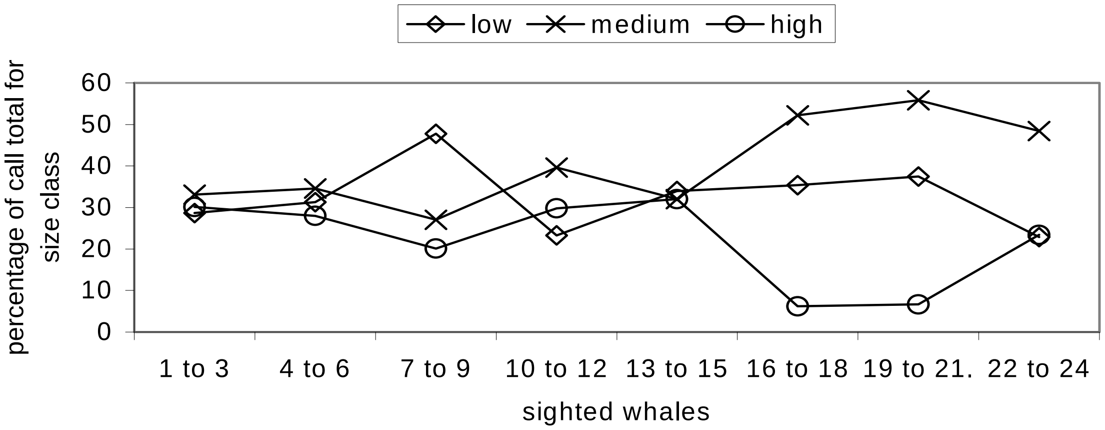

Figure 2.7 Relative contributions of call types exerting the greatest influence on variation in the relative proportions of call types in the presence of differing whale aggregation sizes, to the call total within size class, for the whole season. Call types defined by onset frequency alone (*low*, *medium* and *high*).

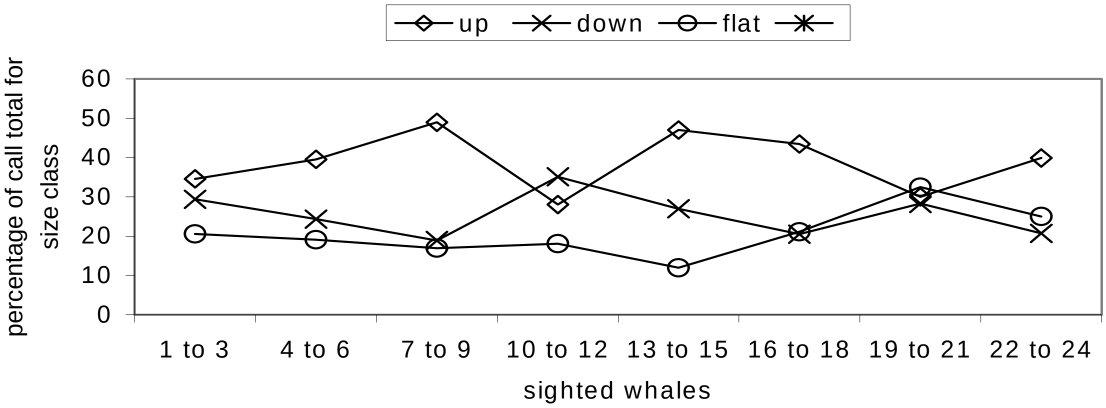

Figure 2.8 Relative contributions of call types exerting the greatest influence on variation in the relative proportions of calls in the presence of differing whale aggregation size, to the call total within size class, for the whole season. Call types defined by acoustic contour alone (*up*, *down*, *flat*).

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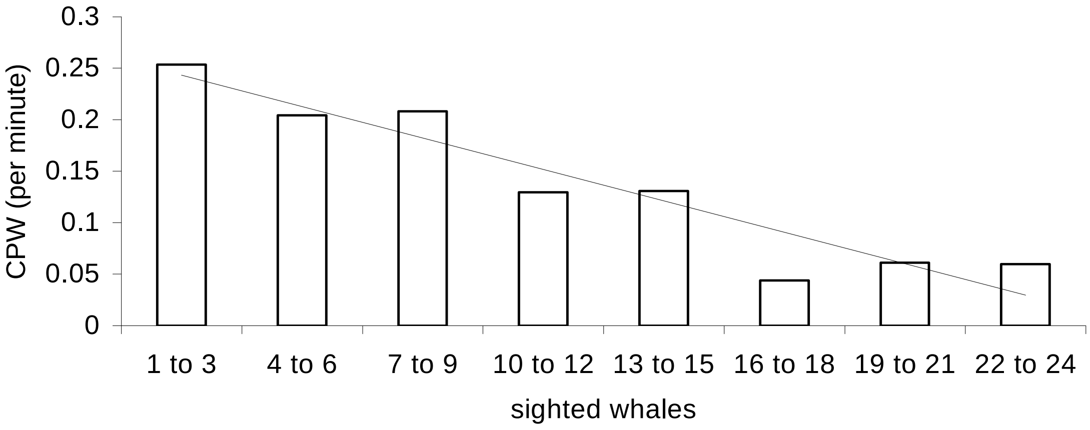

Figure 2.9 CPW with increasing numbers of whales, for all calls, over the whole season.

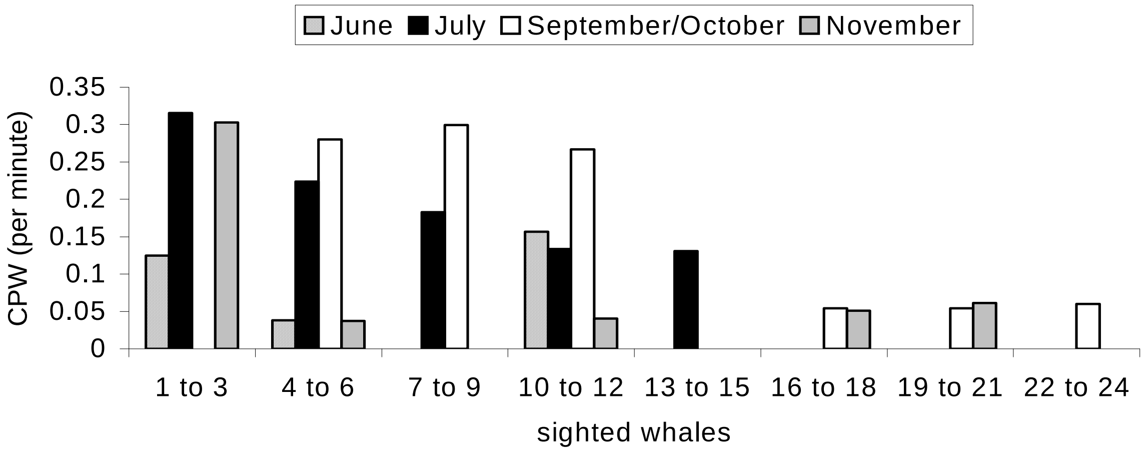

Figure 2.10 CPW with increasing numbers of whales, for all calls, viewed monthly.

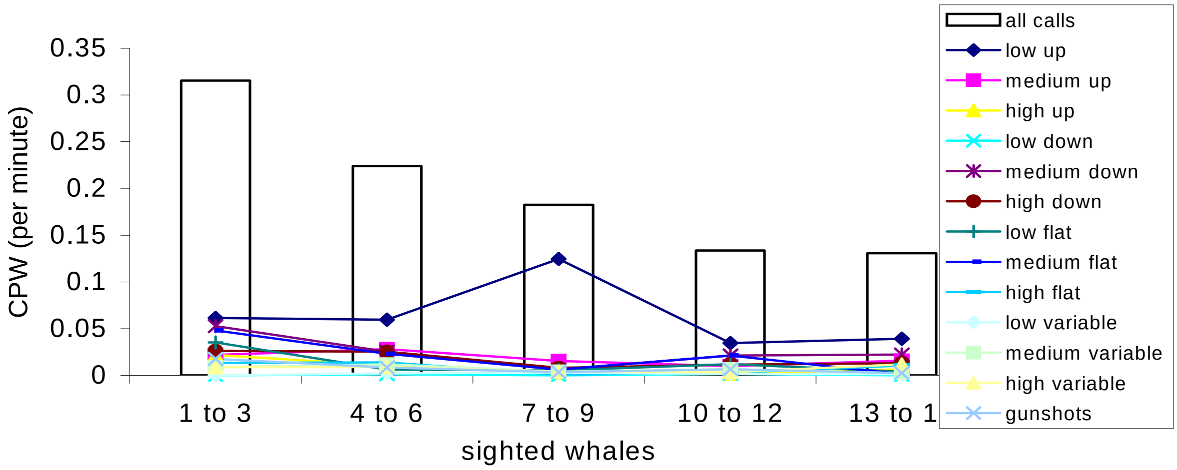

Figure 2.11. July CPW with increasing numbers of whales, for all calls and 13 call types.

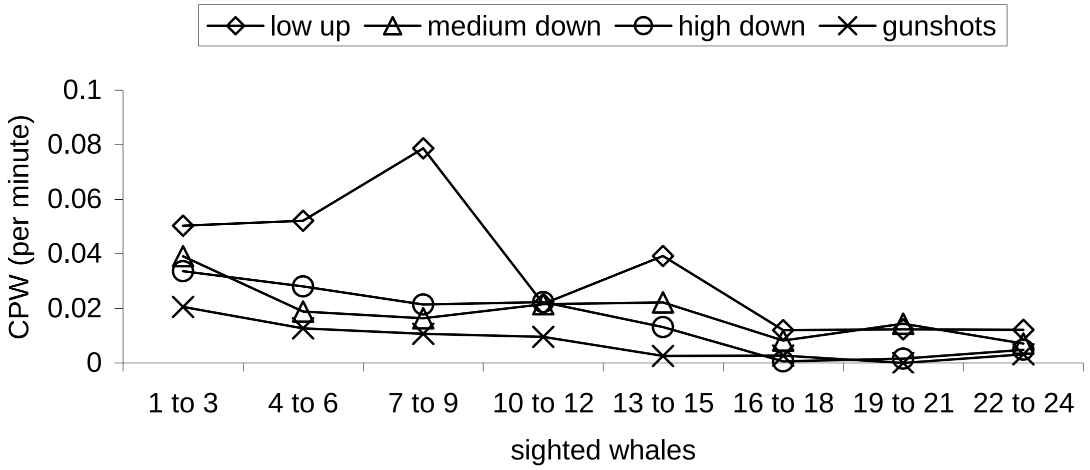

Figure 2.12 CRW of three call types responsible for the greatest variation in relative proportions of call types for different whale aggregation sizes, and of gunshots, over the whole season. Call types other than gunshots are defined by starting frequency and call shape (*low up*, *medium down* and *high down*).

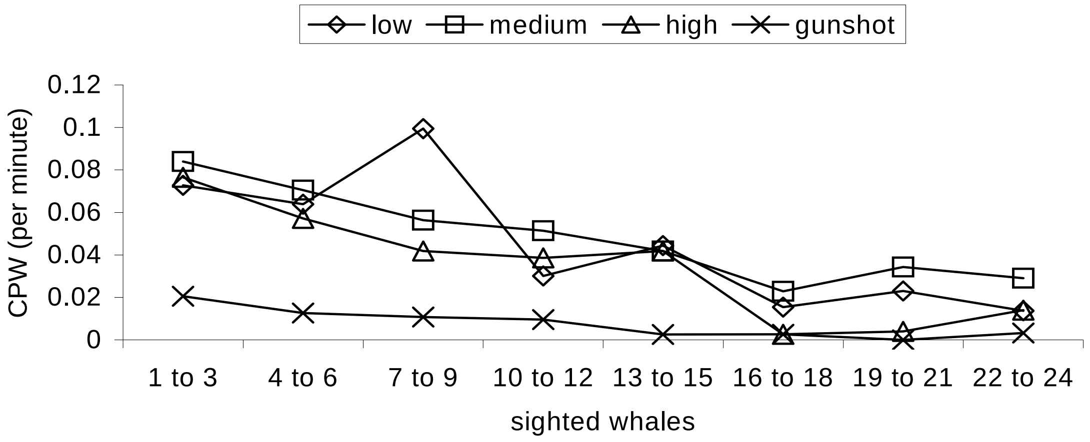

Figure 2.13 CPW with increasing numbers of whales for calls defined by onset frequency (*low*, *medium* and *high*), and for gunshots, over the whole season.

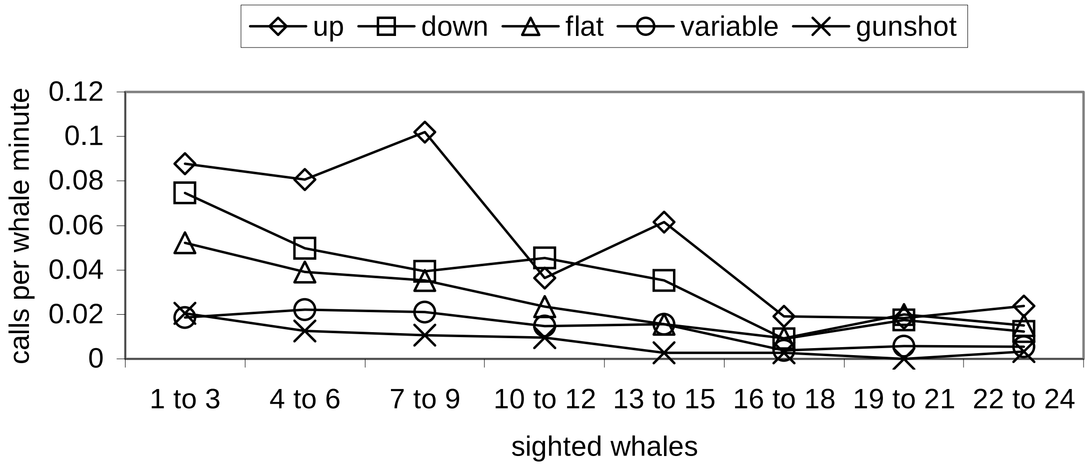

Figure 2.14. CPW with increasing numbers of whales, for calls with four acoustic contours (*up*, *down*, *flat*, *variable*), and for gunshots, over the whole season.

4. Discussion

4.1 Generalised linear model

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

Relationship between OCR, CPW and aggregation size

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

Importantly, the results demonstrated in the inverted parabola in the GLM (*figs.2.2, 2.3*) and modeled in the simulation (*fig. 2.15*) lead to the clear conclusion that, because call rates do not rise linearly with whale numbers, it is not possible to estimate whale numbers from call rates.

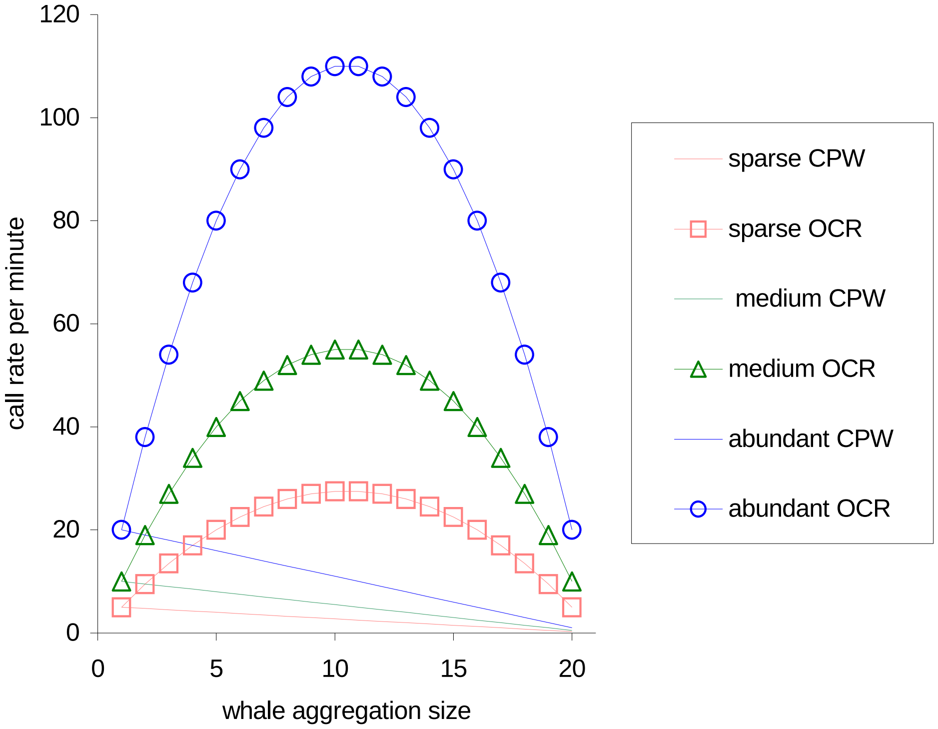

Figure 2.15 Simulated model of CPW and OCR per minute for all whales present, for increasingly large whale aggregations. Hypothetical sparse (red), medium (green) and abundant (blue) rates are modeled.

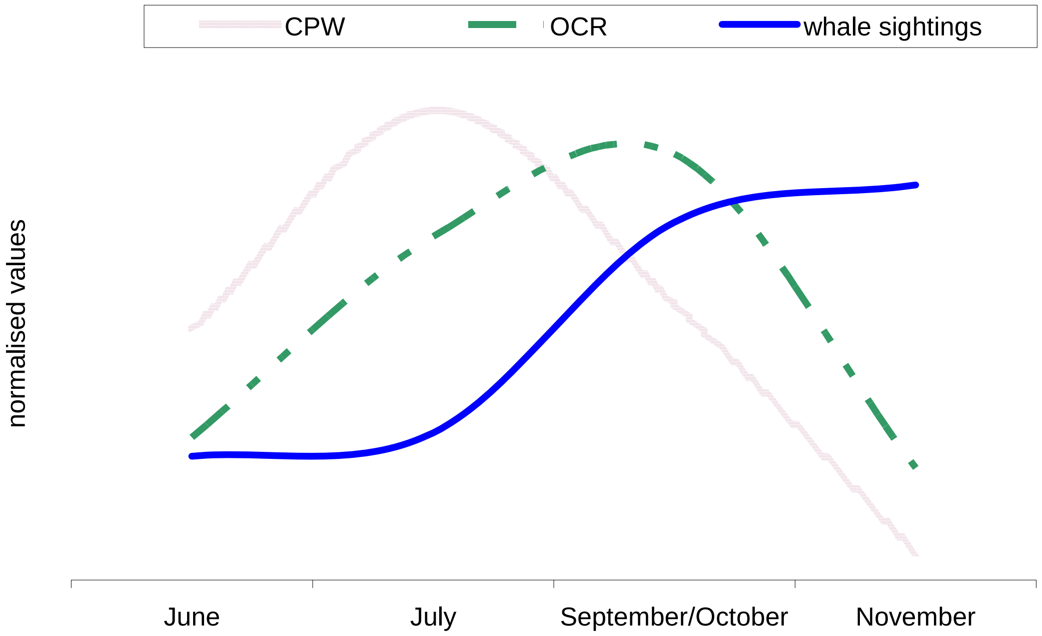

Figure 2.16 OCR, CPW, and whale abundance, for June through November. Observed data are normalised for comparison of trends. CPW clearly peaks in July, with low whale abundance, and is overtaken by OCR in September/October; both fall to their lowest levels with high whale abundance in November. (cf simulation, figure 2.15 above.)

Declining call rates in the presence of large numbers of whales

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

'Eavesdropping'

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

Female harassment avoidance

Low call rates may reflect a deliberate strategy on the part of females, in avoiding harassment, when alone or accompanying a calf. Female southern right whales tend to segregate themselves from other classes, possibly to avoid harassment by males (Elwen & Best, 2004). Humpback whales with calves in Hawaii also chose shallower water than whales without calves, possibly to avoid harassment and injury to calves by sexually active males (Smultea, 1994). In a visually restricted medium such as the underwater ocean environment, acoustic detection is generally the best option for suitors. Under such circumstances there would be a strong selection for the evolution of acoustic detection avoidance strategies. The higher the numbers of males present, the stronger the motivation to remain silent, which may be a factor in the dramatic decline in call density in the presence of high whale numbers. As right whales with calves move out of nursery areas and into regions of the coast such as Walker Bay late in the season (Best et al., 2003), many of the whales present off Gansbaai in October and November may have been cow-calf pairs, accounting partly for their relative silence. Another possibility is that, to avoid detection under such circumstances, acoustic cow-calf interactions would be at a low energy level, such that many of their quieter calls would not have been detected by our hydrophones.

Predator avoidance

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

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

Effects of month

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

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

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

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

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

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

Effects of wind direction

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

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

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

How could the GLM results be used?

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

4.2 The relationship between OCR, CPW and whale numbers

Methods of deriving absolute call rates

There are several methods of analysing calls in time series to derive absolute call rates. The simplest and most direct of these is to calculate a mean call rate by counting the calls produced during each recording session, and dividing the pooled number of calls by the duration of the pooled sessions, using units appropriate to the call density(Serrano & Miller, 2000), or by the product of the duration and the animal numbers (such as whale minutes) to derive individual call rates (Clark, 1982; Clark, 1983). This gives a mean call rate without reference to clustered calls, and rates within and between clusters. The mean number of calls per time-unit has also been used (Cox & Lewis, 1966), as with North Atlantic right whale calls measured in 1-minute samples (Matthews et al., 2001; Parks, 2003a) and humpback dolphin calls per 3-minute sample (van Parijs et al., 2002) to calculate predicted intervals between and within call clusters, where they exist (Matthews et al., 2001). Intercall intervals have also been widely used to characterise call timing, using the log-survivor function (Cox & Lewis, 1966), (*chapter one*). In a study of elephant calling rates, call events, rather than single calls, separated on either side by at least 2 seconds, were counted. Only the densest 30 minute sample from each recording session was used, allowing call event rates to be established without reference to session lengths or long periods of silence, and requiring detailed attention for a dramatically reduced data set (Payne et al., 1998).

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

The relationships between OCR, CPW and numbers of whales

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

Establishing the relationship between numbers of whales and OCR does not require a knowledge of individual call rates. Conversely, estimates of individual call rates do require measurement of OCR, and assume at least a knowledge of the number of whales present in the call origin vicinity; better still, a knowledge of the proportion of silent animals; and ideally, the identity of the caller for each call. Conditions under which this is possible are hard to achieve in studies of non-captive animals, and even more so for cetaceans, with no obvious external sign of vocalisation, so that individual call rates per whale are often approximations rather than precise measurements.

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

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

The relationship between call type and whale numbers

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

Whole season and monthly CPW for various call types

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

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

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

Suggestions for future research

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

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

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