Bioacoustics: The International Journal of Animal Sound and its Recording
Publication details, including instructions for authors and subscription information:
http://www.tandfonline.com/loi/tbio20

STRUCTURAL CHARACTERISTICS OF PULSED CALLS OF LONG-FINNED PILOT WHALES GLOBICEPHALA MELAS

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Available online: 13 Apr 2012

Bioacoustics
The International Journal of Animal Sound and its Recording, 2009, Vol. 19, pp. 67–92

STRUCTURAL CHARACTERISTICS OF PULSED CALLS OF LONG-FINNED PILOT WHALES *GLOBICEPHALA MELAS*

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ABSTRACT

The pulsed calls of Long-finned Pilot Whales *Globicephala melas* have received little study, and their structure and function remain unclear. We examined the pulsed calls of Pilot Whales off Nova Scotia by taking multiple measures of 419 spectrograms from recordings made over a span of eight years. The results offer a quantitative description of pulsed call structure necessary for subsequent analysis of signal functionality and social relevance. Pilot Whale pulsed calls were found to be physically complex, with multiple, independently modulated components that are likely rich in information and difficult for eavesdroppers to imitate. The production of such structurally complicated signals suggests they play an important role in Pilot Whale communication. The pulsed calls appear to form two main call types: those with a maximum visible sideband above 18 kHz and those with a maximum visible sideband below 15 kHz. However, there is no indication of further discrete categories despite a large amount of variation between calls within those two broad categories. The high variation in call structures may indicate communicative plasticity, allowing the whales to communicate state, such as level of arousal, and to compensate for variable background noise levels. The structural similarity of Pilot Whale and Killer Whale *Orcinus orca* pulsed calls raises the question of whether the distantly related whale species, with a shared but rare social structure, have evolved similar call structures to solve similar communication challenges.

Keywords: *Globicephala melas*, Long-finned Pilot Whales, pulsed calls, vocalizations, communication

INTRODUCTION

Quantifying the acoustic signals of a species is a necessary precursor for the investigation of their use and function. The underwater sounds of many cetacean species are generally classified into three main sound classes: clicks, tonal signals (or whistles), and pulsed calls (e.g. Lilly & Miller 1961; Ford 1989). Clicks are rapid and often repetitive bursts of short, broadband sounds, primarily used for echolocation (Kellogg

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et al. 1953; Au *et al.* 2003). Whistles, which are continuous tonal sounds with few or no harmonics, are thought to be used as contact calls between individuals (see Sayigh *et al.* 2007), and may facilitate cohesion of the group during foraging or travel (Ford 1989; Weilgart & Whitehead 1990). Pulsed calls are rapidly produced broadband sound pulses, with distinct tonal properties caused by high pulse-repetition rates (PRR) that often shift abruptly (Schevill & Watkins 1966; Ford 1989). The PRR is reflected in the intervals between the sidebands (SBI) and is usually modulated over the duration of a call (Watkins 1967; Ford 1989).

Many odontocetes produce pulsed calls, including Belugas *Delphinapterus leucas* (Karlsen *et al.* 2002), Narwhals *Monodon monoceros* (Ford & Fisher 1978), False Killer Whales *Pseudorca crassidens* (Murray *et al.* 1998) and Killer Whales *Orcinus orca* (Ford & Fisher 1983). The most thoroughly described are those of "resident" type Killer Whales off British Columbia (Ford 1987, 1989). Killer Whale pulsed calls are often composed of both an upper frequency component (UFC) and a lower frequency component (LFC) (Miller & Bain 2000) (see Figure 1). The LFC consists of rapidly produced broadband pulses that overlap to produce the equivalent of sine wave tones (Yurk 2005). The LFC is equivalent to the "pulse" part of the call. The LFC can often be further divided into elements (parts of the call separated by abrupt shifts in the PRR) and segments (parts of the call separated from each other by a time gap) (Figure 1). The UFC, on the other hand, is a narrow band signal that can have true harmonic bands. It is equivalent to a whistle, produced concurrently with an LFC (Yurk 2005). Simultaneous LFC and UFCs are likely an example of biphonation, the production of two independent fundamental

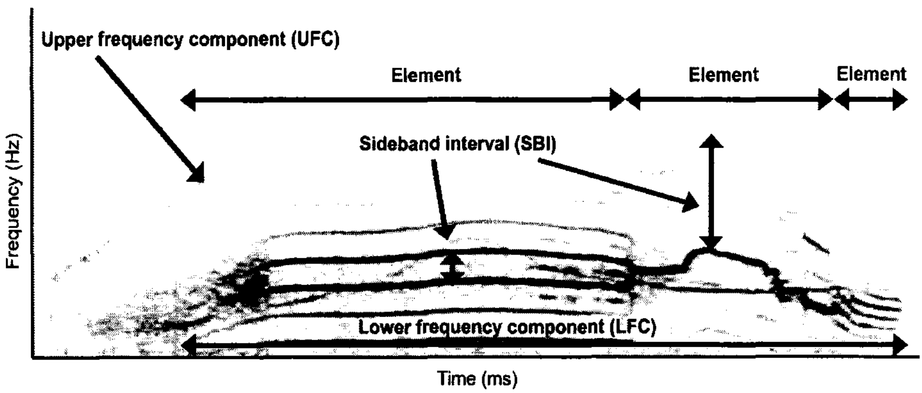

Figure 1. Spectrographic example of a Long-finned Pilot Whale pulsed call. Calls may consist of two components, an upper frequency component (UFC) that is a narrow-band tone, and a lower frequency component (LFC) that is a broadband pulse. The pulse repetition rate (PRR) is reflected by the sideband interval (SBI). Elements are distinguished by abrupt shifts in the PRR.

frequencies in a call spectrum (Brown & Cannito 1995). The source of biphonation in odontocetes has been suggested to be the result of air being pushed across the two MLDB complexes (tissues located above the superior bony nares) at the same time (Cranford 2000).

Cetacean vocal signals are often categorizable into discrete call types, as is observed with Killer Whale pulsed calls (Ford 1987; Filatova *et al.* 2007), Sperm Whale *Physeter macrocephalus* codas (Weilgart & Whitehead 1997) and possibly Bottlenose Dolphin *Tursiops truncatus* signature whistles (Sayigh *et al.* 2007; but see McCowan & Reiss 2001). Call types may be favoured in species with the need for honest signalling when identifying individuals or groups, as discrete calls are likely more difficult for a non-member to imitate (McGregor 2005). However, this may not always be the case, and calls can instead be graded along a continuum. For example, the calls of adult male beluga whales in Svalbard, Norway are highly graded and cannot be reliably divided into categories (Karlsen *et al.* 2002). Similarly, the whistles of Pilot Whales appear to form a graded continuum between seven basic types (Taruski 1979). These graded calls may allow one signal to have multiple functions. A graded call may, for instance, communicate arousal level or behavioural state (Taruski 1979; Bain 1986; Murray *et al.*1998).

Long-finned Pilot Whales *Globicephala melas* are extremely vocal, using a combination of clicks, whistles and pulsed calls to communicate and interact with their environment (Taruski 1979; Weilgart & Whitehead 1990). Preliminary descriptions of their vocal repertoire were offered by Busnel and Dziedzic (1966) and Busnel *et al.* (1971). Detailed and large-scale studies of their whistles undertaken by Taruski (1979) and, more recently, by Weilgart and Whitehead (1990), provided a more in-depth study of whistle usage in various contexts. Pilot Whale whistle structure, in the context of species specificity, has also been examined by several authors, including Steiner (1981) and Rendell *et al.* (1999). However, a thorough description of Pilot Whale pulsed calls had never been attempted to date.

Here we present the results of fine-scale spectrographic analysis of pulsed calls from a study of Long-finned Pilot Whale pulsed calls off Cape Breton Island, Nova Scotia. We investigate the presence or absence of discrete call types within their repertoire, and discuss the similarities between Pilot Whale and Killer Whale pulsed calls.

METHODS

Recordings and acoustic analysis

Pilot Whale vocalization recordings used in this analysis were made by a number of different observers in Bay St. Lawrence (47°02′N, 60°29′W) and Pleasant Bay (46° 50′N, 60° 47′W), along the north-west coast of Cape Breton Island, Nova Scotia, Canada from 1998-2000 and 2005. Opportunistic surveys were conducted through July and August from the whale-watch vessel *Northern Gannet* in Bay St. Lawrence (1998-2000), and from *Double Hookup* in Pleasant Bay (2005). There were three scheduled trips daily out of Bay St. Lawrence, each 2.5-3 hours long. In Pleasant Bay, there were five scheduled trips daily, each 1.5-2 hours long. All scheduled trips were taken, unless the Beaufort sea state was greater than 5-6 or too few people signed-up for the trip. The number of scientific observers on the whale-watching vessels was either one or two, depending on the year.

At the start of an encounter, the boat engine was turned off, and an omnidirectional Vemco VHLF hydrophone (10Hz-20kHz) was lowered over the side of the boat to a depth of 10-15m. The recording systems varied over the years, but mostly consisted of a Sony TCM 5000 eV analog cassette-tape recorder (1998-2000) or a Sony PCM-2800 digital audio track recorder (2005). The frequency responses of these recording systems were between 20 Hz and 20 kHz. Date and time were recorded using a microphone before the hydrophone was lowered into the water, and start and stop times of recordings were also noted. The hydrophone was lifted from the water at the end of an encounter. A total of 274 encounters included recordings, resulting in approximately 65 hours of recorded vocalizations.

Vocalization recordings from cassette tapes (1998-2000) were played back and digitized at a sampling rate of 44.1 kHz, with a 16-bit sample size, using the spectrographic software program CoolEdit Pro (ver. 2.0). Recordings for all years (1998-2000, 2005) were then displayed graphically on spectrograms and inspected for the presence of pulsed calls by listening to the recordings while visually monitoring the spectrograms. Only calls with suitable signal to noise levels and well-defined contours were used in the analysis. Pulsed calls were extracted and measured using the acoustics software Raven Pro (ver. 1.3). The spectrograms were produced using 1024 point Fast-Fourier Transformations (FFT) and a Hamming window for each analyzed time series. Resulting spectrograms had a time resolution of two milliseconds and a frequency resolution of 61 Hz. For each call, between 17 and 43 frequency, duration and count (e.g. number of elements) variables were measured (mean = 22.5 variables) depending on the complexity of the call. The measured variables are described in Table 1. The two primary goals in choosing which time and frequency variables to measure from the spectrograms were: (1) to choose measures that would represent the LFC and UFC contours as effectively as possible, and (2) to remain consistent with measurements made by studies on Killer Whale pulsed calls (Ford 1987; Miller & Bain 2000). The fundamental frequency was found for each pulsed call using a power spectrum analysis. The frequency at which the signal contained the

TABLE 1

Description of the variables measured for each Pilot Whale pulsed call.

Variable	Description	Units
NUM_ELEMENTS	Number of parts delineated by abrupt shifts in the pulse repetition rate	
NUM_SEGMENTS	Number of parts separated by empty space	
NUM_INFL_PTS	Number of abrupt frequency modulations along the fundamental frequency	
UFC_Y_N	Presence or absence of an upper frequency component (biphonation)	
UFC_INFL_PTS	Number of abrupt frequency modulations along the UFC	
UFC_ST_FREQ	Start frequency point of the UFC	Hz
UFC_END_FREQ	End frequency point of the UFC	Hz
UFC_DUR	Total duration of the UFC	sec
TC_SBI_ST	Sideband interval at the beginning of a pulsed call (from the FF to the next band)	Hz
TC_SBI_END	Sideband interval at the end of a pulsed call	Hz
SBI_#_ST	Sideband interval at the beginning of each part of a pulsed call	Hz
SBI_#_MID	Sideband interval in the middle of each part of a pulsed call	Hz
SBI_#_END	Sideband interval at the end of each part of a pulsed call	Hz
TC_DURATION	Total duration of the pulsed call, including the UFC	sec
PART_#_DUR	Total duration of each separate part of a pulsed call	sec
SPACE_DUR	Total duration of the empty space between two segments	sec
TC_HIGH_FREQ	Frequency of maximum visible sideband of a pulsed call	Hz
TC_LOW_FREQ	Frequency of minimum visible sideband of a pulsed call	Hz
TC_DELT_FREQ	Change in frequency of a pulsed call from the lowest visible sideband to the highest	Hz
TC_ST_FREQ	Start frequency point of a pulsed call on the fundamental frequency	Hz
TC_END_FREQ	End frequency point of a pulsed call on the fundamental frequency	Hz
FF	Fundamental frequency of the pulsed call (from power spectrum analysis)	Hz

highest energy was considered the fundamental frequency (Watkins 1967). Power spectra were produced with 32 768 point FFT, with a 3Hz frequency resolution and a time resolution of 429ms.

Statistical analysis

Pulsed call description

Descriptive statistics were calculated for the measured parameters. A principal components analysis (PCA) using a correlation matrix of the measured variables was then used to further elucidate which parameters appear to contribute most to pulsed call variability. The matrix was rotated using Varimax rotation, which attempts to minimize the variance of squared loadings for each factor and improves interpretability of the factors (Jolliffe 2002). The PCA was initially run both with and without rotation. However, the pattern of loadings is simplified after Varimax rotation and the results were more informative. Thus, only the results from the Varimax rotation will be included here. Any variables with many missing data points were excluded from the PCA (for example, any measurements specific to the 2nd parts of the more complex calls or the duration of the UFC for biphonic calls). The Kaiser criterion was used to select the number of components (linear combinations of the original variables) to keep in the analysis, which excludes all principal components with an eigenvalue less then one (Jolliffe 2002). Thus, any component that explained less variance than an original variable in the correlation matrix was excluded.

Killer Whale pulsed call measurement ranges from various published sources (Schevill & Watkins 1966; Hoelzel & Osborne 1986; Ford 1987) were collected to compare Killer Whale pulsed calls with those of Pilot Whales. Pilot Whale and Killer Whale pulsed calls are aurally very similar, the two species have overlapping ranges (Reeves *et al.* 2002) and both exhibit natal group philopatry (Bigg *et al.* 1990a; Amos *et al.* 1993a, 1993b). It is more difficult to compare Pilot Whale pulsed calls with those from other species within the Orcininae and Globicephalinae subfamilies, mainly due to a lack of available information as well as major differences in call structure and methodology across studies.

Call types

Two automatic classification methods were applied to the measurement data to determine the presence or absence of discrete call types within the Pilot Whale pulsed call repertoire. The first was a k-means cluster analysis (20 iterations). k-means clustering divides a set of values into a selected number of groups (k) by maximizing between-group variation relative to within-group variation. It iterates through the data until transferring individuals between groups does not increase between-group variation (Everitt *et al.* 2001). However, the main disadvantage of k-means clustering is the partially arbitrary selection of k. To increase the probability of finding clustering that was meaningful, the test was run several times (from $2 \geq k \leq 10$) and the results were compared. k-means clustering was carried out using SYSTAT (ver. 12).

The second method was hierarchical average linkage clustering using Mahalanobis distances and was performed using the computer package SOCPROG (Whitehead 2009). Hierarchical average linkage is a clustering technique that groups calls with high indices of similarity into common branches of a tree (Johnson 1967). It has been shown to be a successful clustering method for classifying Bottlenose Dolphin whistles (Janik 1999). Clustering was stopped using maximum modularity (Q), which indicates the number of clusters at which similarity is maximized within clusters and minimized between them (Newman 2006). The cophenetic correlation coefficient (CCC) was calculated to determine whether the clusters give an accurate representation of the relationships between the calls. A CCC greater than 0.8 is generally considered acceptable (Bridge 1993). The CCC for a hierarchical cluster tree is the linear correlation coefficient between the cophenetic distances obtained from the tree and the original distances (or dissimilarities) used to construct the tree (Atchley & Bryant 1975). Thus, it is a measure of how faithfully the tree represents the dissimilarities among observations.

RESULTS

Properties of Pilot Whale pulsed calls

From the 65hrs of Pilot Whale recordings, a total of 419 pulsed calls were isolated and measured, spanning 94 encounters over 4 different years (Figure 2). The number of elements, parts of the call separated by abrupt shifts in the PRR, in a pulsed call ranged from 1 to 6, with an average of approximately 2 per call (see Figure 3, Table 2). The majority of calls had relatively few parts, with 47% composed of only 1 element and 93% being completely unsegmented. Segmented calls are composed of two of more sections, separated from each other by a time gap. Of the 7% of calls that were segmented, 93% had 2 segments, and only 7% had 3 segments. Segments of calls were separated by an average of 0.089sec of silence. Approximately 20% of all calls contained a UFC. The UFC measurements coincided with the uppermost values of published Pilot Whale whistle data from recordings off Newfoundland (Table 3) (Rendell *et al.* 1999). However, the UFCs were generally higher frequency and had more inflection points than the published whistle values (Table 3).

Approximately half of the calls measured contained between 1-2 inflection points, and 41% had 3 inflection points or more (max = 18) (see Figure 4, Table 2). The duration of a pulsed call ranged from short chirps (0.172sec) to drawn out squeals (2.173sec). However, duration had the lowest coefficient of variation of all variables measured, indicating that Pilot Whale pulsed calls are more stereotyped in length than any other characteristic measured. The

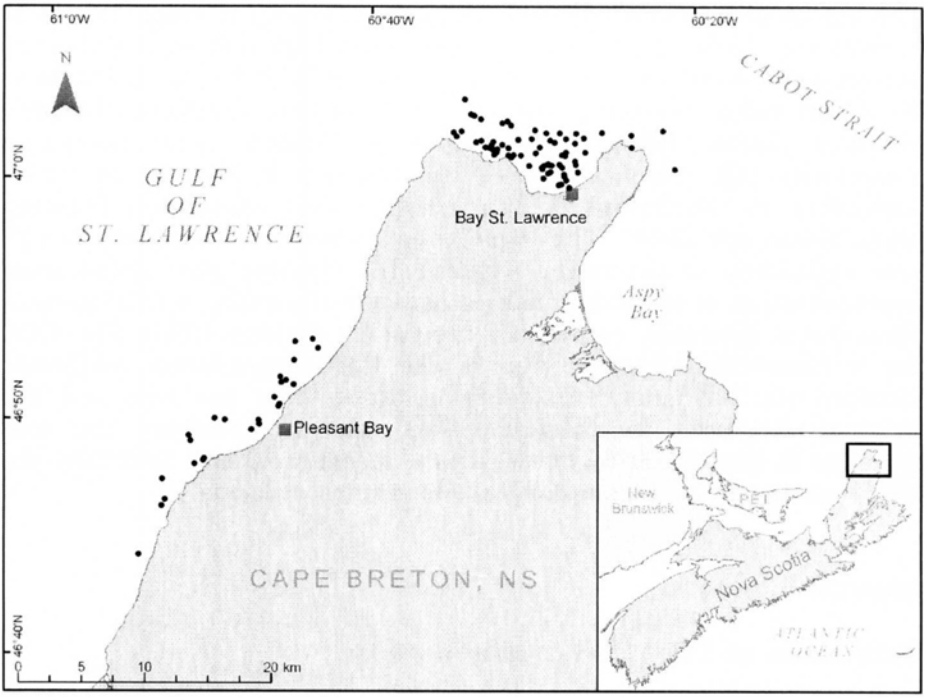

Figure 2. Map of the northwest tip of Cape Breton Island, Nova Scotia, Canada where the two field sites are located. The position of each Pilot Whale encounter from which pulsed calls were extracted is plotted (n = 94). Inset map shows Nova Scotia and surrounding maritime provinces.

first element of LFCs ranged in fundamental frequency from 0.81 to 9.4 kHz. Sidebands were visible from as low as 140 Hz to above the 20 kHz limit of the spectrograms, and had an average interval of 1.4 kHz at the beginning of a call and 1.5 kHz at the end of a call. The maximum PRR observed was 5500 pulses/sec. Pulse repetition rate, duration of each element in a call, and the duration of silence between each segment varied the most between calls (see Table 2).

The measured characteristics of Pilot Whale pulsed calls were similar to those published for Killer Whales, although Killer Whales seem to have slightly shorter LFCs, slightly longer UFCs, a narrower range of pulse repetition rates and marginally lower UFC and LFC frequencies (Table 4). There do not appear to be sufficient differences between these values to distinguish Pilot Whale pulsed calls reliably from those of Killer Whales when, for instance, categorizing calls from sources such as autonomous recordings. However, further analyses, such as a discriminant function analysis using comparable Killer Whale and Pilot Whale data, are needed before dismissing this possibility.

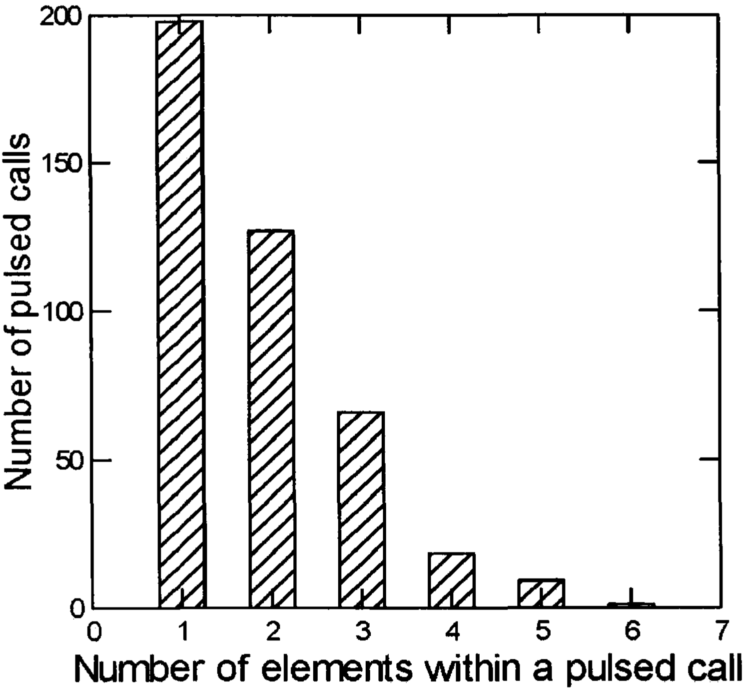

Figure 3. Number of elements per Pilot Whale pulsed call (n = 419).

Principal components analysis

The PCA produced five principal components with eigenvalues less than one that together explained approximately 70% of the total variance observed (Figure 5, Table 5). This is within the desired range of 70-90% (Jolliffe 2002). The first component of the Varimax-rotated display represents the first and middle SBIs of the first element of a call. The second component represents the frequency of the highest visible sideband of a call. The third component encompasses the measurements of the fundamental frequency of a pulsed call. The fourth component relates to the more general structural characteristics of a call, namely the number of elements, segments and inflection points. Finally, the fifth component represents the duration, presence or absence of a UFC, and the final SBI (see Table 6). From the scores plots (see Figure 6), the clearest delineation appears to be between calls with very high frequency maximum visible sidebands and those with lower frequency maximum visible sidebands. Approximately 70% of all calls measured had a highest visible sideband at or above 18 kHz, while most of the remaining 30% had maximum visible sidebands at or below 15 kHz (Figure 7). There do not appear to be any other substantial groupings of calls based on the PCA scores plots.

TABLE 2

Descriptive statistics of Pilot Whale pulsed calls.

Variable	N	Min	Max	Median	Mean	SE	SD	CV
Total call								
Duration (sec)	419	0.172	2.173	0.761	0.791	0.014	0.277	0.35
Number of elements	419	1	6	2	1.8	0.0	1.0	0.55
Number of segments	419	0	3	0	0.1	0.0	0.5	3.70
Number of inflection points	419	0	18	2	2.8	0.1	2.4	0.85
Minimum frequency (Hz)	419	140	3459	1289	1279	26	525	0.41
Maximum frequency (Hz)	419	3970	20000	12110	13176	236	4834	0.37
Delta frequency (Hz)	419	1774	19797	10706	11897	238	4866	0.41
Start frequency (Hz)	419	490	9238	2510	2739	69	1411	0.52
End frequency (Hz)	419	814	10720	2703	2985	70	1427	0.48
Fundamental frequency (Hz)	419	814	9368	2782	2937	55	1122	0.38
Sideband interval, start (Hz)	419	67	5506	1260	1396	45	915	0.66
Sideband interval, end (Hz)	419	84	4749	1349	1496	35	711	0.48
Part 1								
Duration (sec)	419	0.023	1.441	0.344	0.416	0.015	0.316	0.76
SBI start (Hz)	419	67	5506	1260	1396	45	915	0.66
SBI middle (Hz)	419	67	5188	1221	1407	44	904	0.64
SBI end (Hz)	419	67	5188	1281	1399	40	826	0.59
Part 2								
Duration (sec)	221	0.040	1.626	0.470	0.483	0.022	0.322	0.67
SBI start (Hz)	221	68	5295	1750	1927	61	908	0.47
SBI middle (Hz)	221	68	4959	1835	2016	66	986	0.49
SBI end (Hz)	221	68	4791	1946	2020	66	983	0.49
Duration of silence (sec)	29	0.01	0.43	0.05	0.09	0.02	0.09	0.98

Part 3								
Duration (sec)	94	0.030	1.080	0.220	0.284	0.023	0.226	0.79
SBI start (Hz)	94	71	4203	1540	1804	93	902	0.50
SBI middle (Hz)	94	71	4959	1481	1826	105	1016	0.56
SBI end (Hz)	94	71	4248	1412	1776	96	933	0.53
Duration of silence (sec)	2	0.03	0.09	0.06	0.06	0.03	0.04	0.72
Part 4								
Duration (sec)	28	0.034	0.585	0.123	0.225	0.038	0.199	0.88
SBI start (Hz)	28	68	4925	1718	1971	221	1170	0.59
SBI middle (Hz)	28	136	4791	1839	1964	206	1089	0.55
SBI end (Hz)	28	136	4203	1596	1856	187	988	0.53
Part 5								
Duration (sec)	10	0.090	0.821	0.101	0.225	0.080	0.254	1.13
SBI start (Hz)	10	84	3687	1481	1454	306	969	0.67
SBI middle (Hz)	10	84	4112	1482	1478	351	1110	0.75
SBI end (Hz)	10	84	4041	1297	1449	352	1114	0.77
Part 6								
Duration (sec)	1	0.316	0.316	0.316	0.316	–	–	1
SBI start (Hz)	1	1205	1205	1205	1205	–	–	1
SBI middle (Hz)	1	1064	1064	1064	1064	–	–	1
SBI end (Hz)	1	1418	1418	1418	1418	–	–	1

TABLE 3

A comparison of mean Pilot Whale pulsed call UFC measurements with published Pilot Whale mean whistle values (1 SD).

Variable	*G. melas* UFC	N	*G. melas* whistle (Rendell *et al.* 1999)	N
Duration (s)	0.60 (0.40)	85	0.62 (0.38)	384
Start frequency (Hz)	7598 (2029)	85	4180 (2110)	384
End frequency (Hz)	7019 (3369)	85	4280 (2270)	384
No. of inflection points	2.15 (2.02)	85	0.39 (0.80)	384

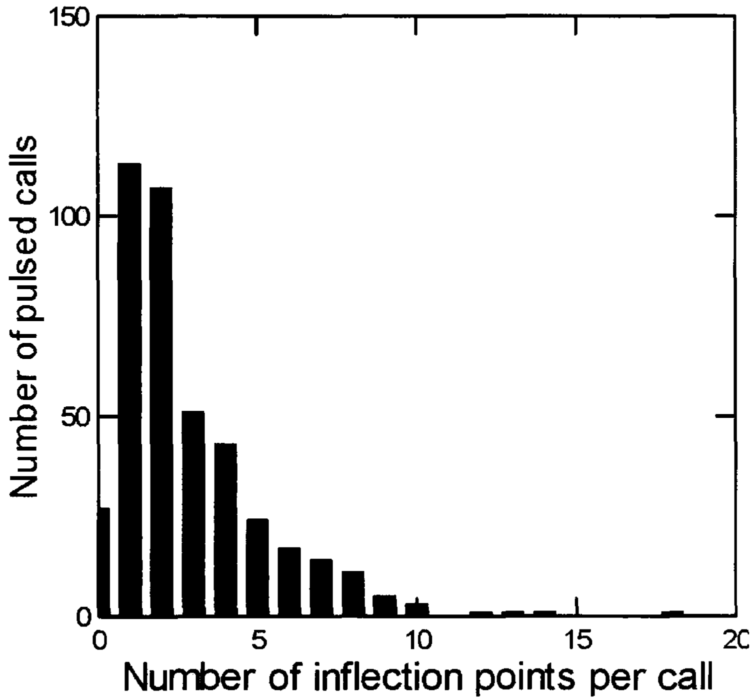

Figure 4. Number of inflection points per Pilot Whale pulsed call (n = 419).

K-means cluster analysis

The *k*-means cluster analysis was repeated 9 times (using numbers of clusters from $2 \geq k \leq 10$). Clusters were plotted as grouping factors on the PCA scores plots in order to visualize any potential call groupings. The patterns observed were not substantially different across the *k* values, and indicated the presence of two broad call types (those with maximum visible sidebands above 18 kHz and those below 15 kHz) (see Figures 7 and 8). However, there were no clear delineations

TABLE 4

A comparison of Pilot Whale and Killer Whale pulsed call characteristics. The overlap reflects the percentage of the ranges that are common to both the Pilot Whale and the Killer Whale pulsed call measurements.

Variable	Pilot Whales	N	Killer Whales	N	% overlap
LFC frequency range	0.8–9 kHz	419	1–6 kHz (Ford 1987)	3600	61%
Duration LFC	0.2–2.2 sec	419	0.5–1.5 sec (Ford 1987)	3600	50%
Pulse repetition rate	67–5506 pulses/sec	419	250–2000 pulses/sec (Ford 1987)	3600	32%
UFC frequency range	2.6–16 kHz	419	2–12 kHz (Hoelzel & Osborne 1986)	19	67%
Duration UFC	0.1–1.5 sec	419	0.5–2.5 sec (Schevill & Watkins 1966)		42%

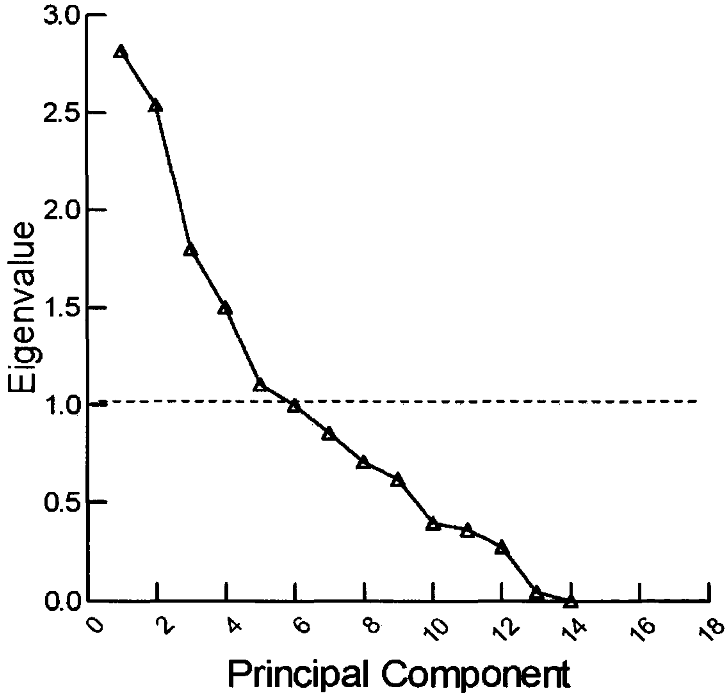

Figure 5. Plot of eigenvalues of the principal components. Most of the variance in the pulsed call data is contained in the first five principal components.

TABLE 5

Eigenvalues and percentage of total variance explained (with and without Varimax rotation) of the 5 principal components of Pilot Whale pulsed calls.

		% of total variance explained	
Principal Components	Eigenvalue	without rotation	with Varimax rotation
1	2.82	20.12	15.77
2	2.54	18.14	15.00
3	1.80	12.86	15.64
4	1.50	10.72	14.09
5	1.11	7.89	9.23
Cumulative		69.73	69.73

of call types in any scores plots that did not include the maximum visible sideband, and there was never any indication of tight clusters, indicating multiple distinct call types.

Hierarchical cluster analysis

The average linkage cluster analysis was stopped at a Mahalanobis distance of 7.9, with Q = 0.003 (Figure 9). As can be seen in Figure 10, this produces a dendrogram with a single main branch, representing one universal cluster. The CCC was 0.84, indicating that the clustering was successful at representing the differences between the calls (Bridge 1993). The clustering was repeated with single and complete linkages, however both techniques resulted in CCCs that were less robust than with average linkage (0.79 and 0.59 respectively). The low modularity of the best clustering, which itself contained all the calls, appears to indicate that there are no discrete pulsed call types for Pilot Whales in this study. This hypothesis is further supported by the results observed from both the PCA scores plots and the *k*-means cluster analysis, which indicate that there are no clear call types except for an apparent dichotomy based on the maximum frequency of the highest visible sideband.

DISCUSSION

The structural complexity of pulsed calls

The results of this study show that the pulsed calls of Long-finned Pilot Whales are structurally complex. Although few calls were segmented, more than half contained two or more elements caused by

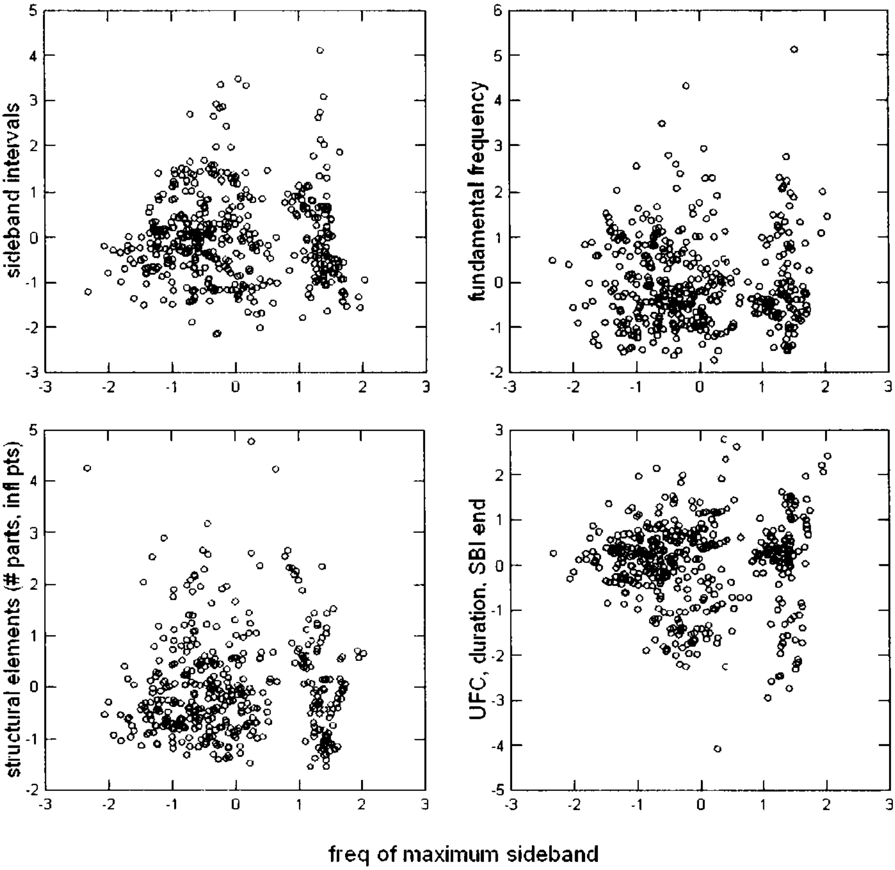

Figure 6. Scores plots of component 2 (frequency of the maximum visible sideband) with (a) component 1 (sideband intervals of the first element), (b) component 3 (fundamental frequency parameters), (c) component 4 (structural elements: number of parts and inflection points), and (d) component 5 (presence or absence of a UFC, duration and final SBI of the call) of the PCA. Only scores plots with component 2 showed any grouping pattern. Consequently, other scores plots are not shown.

modulated pulse repetition rates over the course of the call. There was a wide variety of call structures, varying from relatively simple (e.g. one element, zero inflection points) to very complex (e.g. 6 elements, 3 segments, or 18 inflection points) (Figure 11). Roughly 20% had simultaneous, independently modulated UFCs, equivalent to complex high frequency tonal calls. There appear to be several dimensions and many "degrees of freedom" within which animals can modulate these signals.

After data reduction through PCA, pulsed calls still required a minimum of five main structural components to be described

TABLE 6

Loadings (correlations between variables and components) of the Varimax rotated PCA on the spectrographic pulsed call variables. High loadings (greater than 0.5) are bolded. Variables which are highly loaded on the same component are strongly related.

Variables	Principal Components 1	2	3	4	5
NUM_ELEMENTS	-0.033	0.176	-0.143	**0.809**	0.027
NUM_SEGMENTS	-0.118	-0.034	-0.079	**0.558**	0.055
NUM_INFL_PTS	0.205	0.031	0.021	**0.762**	0.047
UFC_Y_N	-0.193	0.144	-0.044	-0.036	**-0.769**
TC_SBI_ST	**0.947**	0.043	0.083	0.001	0.147
TC_SBI_END	0.102	0.274	0.217	0.272	**0.579**
TC_DURATION	0.01	0.156	0.124	**0.501**	**-0.524**
TC_HIGH_FREQ	0.048	**0.980**	0.012	0.076	-0.037
TC_LOW_FREQ	0.362	-0.081	**0.548**	-0.082	-0.008
TC_DELT_FREQ	0.008	**0.983**	-0.047	0.085	-0.036
TC_ST_FREQ	0.378	-0.054	**0.638**	-0.274	0.005
TC_END_FREQ	-0.243	0.072	**0.810**	-0.008	0.2
SBI_1_MID	**0.933**	0.048	0.048	0.055	0.14
FF	0.032	0.006	**0.850**	0.029	-0.017

reasonably. The pulse repetition rate at the beginning and middle of the first element were strongly related to each other, but not to any other variables. As abrupt shifts in the PRR delineate different elements, it is not surprising that multiple measurements of the sideband interval within one element are strongly associated. The final SBI of the call, on the other hand, is not at all associated with the SBIs from the first element, reflecting modulation of the PRR from the start to the end of a call. The frequency of the highest visible sideband and the range of frequencies within a call were highly associated, but showed little relationship with any other variable. All of the frequency variables measured to describe the LFC contour (namely start and end frequency, lowest frequency and fundamental frequency) were moderately related to each other, but not much to any of the other variables. The general structural elements of a call (the number of elements, segments and inflection points) were related to each other and somewhat related to the duration of a call. It appears that calls with a higher number of elements are likely to be more segmented, have more inflection points and be longer than those with fewer elements. Finally, the presence or absence of a UFC was most related to the duration of a call and the final SBI of a call, such that calls with a UFC appear to be longer, with smaller final SBIs than those without a UFC.

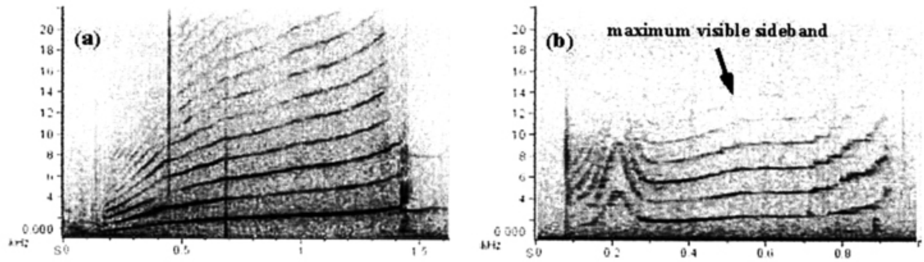

Figure 7. Examples of (a) a pulsed call with a maximum visible sideband above 18 kHz, and (b) a pulsed call with a maximum visible sideband below 15kHz.

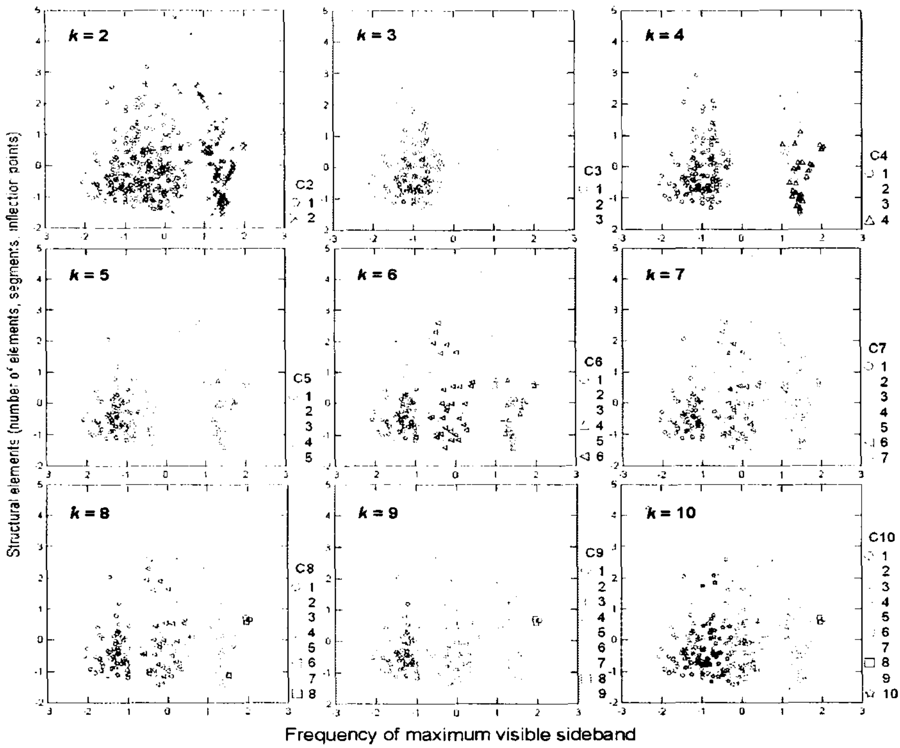

Figure 8. *K*-means cluster analysis groupings (with number of clusters from $2 \geq k \leq 10$) shown as the grouping variable for the PCA scores plots of component 2 (frequency of maximum sideband) and component 4 (structural elements). Aside from the plots shown, there was no clear delineation of call types.

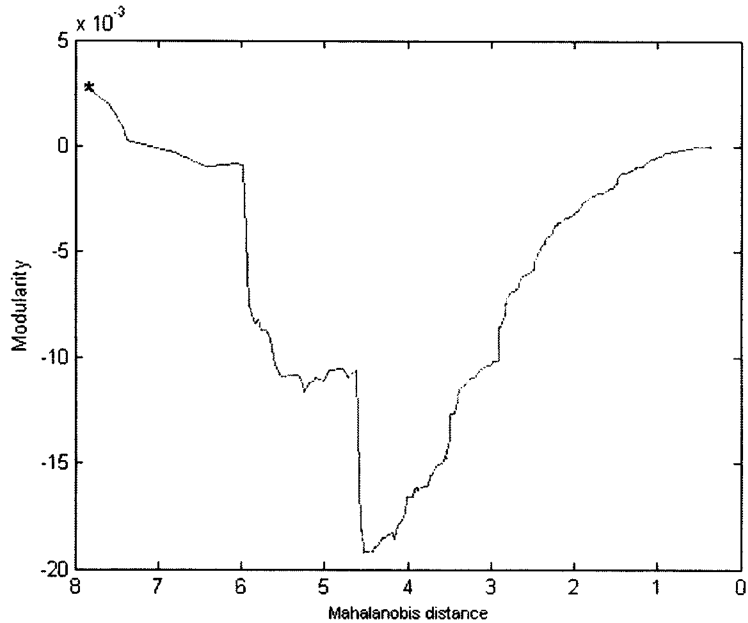

Figure 9. Modularity graph for the hierarchical cluster analysis of pulsed call similarity. Maximum modularity (Q) = 0.003 as indicated by the asterisk.

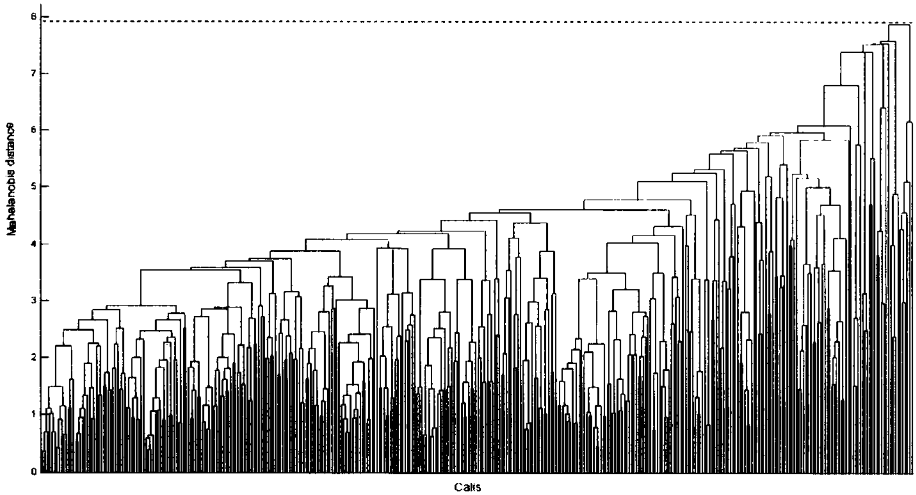

Figure 10. Hierarchical average linkage dendrogram of measured pulsed calls. Clustering was stopped by maximum modularity at the dashed line (Mahalanobis distance = 7.9).

Pilot Whales produce a range of sounds, from structurally simple whistles (Taruski 1979) to the very complex calls described here, with several structural components that can be independently modulated. It has been suggested that such complex vocalizations evolved to serve multiple functions (Bradbury & Vehrencamp 1998) and may transmit several pieces of information at the same time (Hebets & Papaj 2005). For Pilot Whales, the presence of biphonic and monophonic pulsed calls within the same population suggests a possible communicative function of the UFC. Miller (2006) demonstrated that source levels differ across types of Northeast Pacific resident Killer Whale vocal signals. He found that their vocal repertoire could be partitioned into "long-range" pulsed calls with overlapping high frequency components (equivalent to UFCs), and "short-range" sounds including whistles and pulsed calls without a UFC (Miller 2006). If Pilot Whale calls containing UFCs do function in longer-range transmission, they may have inter-group functions such as mate attraction (Ford 1991, Yurk *et al.* 2002) or spatial competition (Miller & Bain 2000), or intra-group functions such as maintaining the cohesion of the group while foraging (Ford 1989; Weilgart & Whitehead 1990). The presence of two independently modulated components within a call could allow senders to convey multiple types of information, including identity, status and condition to potential mates (Hebets & Papaj 2005; Yurk 2005). To our knowledge, source levels and active space (the distance at which another whale can perceive the signal of a conspecific) have not yet been estimated for Pilot Whale calls. However, the use of biphonation in a fifth of their pulsed calls indicates that this may be an important aspect of their communication and should be investigated further.

The non-discrete nature of pulsed calls

All methods of automatic classification indicated that the pulsed calls could not be grouped into multiple discrete call types. However, there was an apparent dichotomy between calls with maximum frequency visible sidebands above 18 kHz and those below 15 kHz. As suggested by Miller (2006), for calls containing a high frequency UFC, it is possible that calls with maximum visible sidebands above 18 kHz allow for relatively longer-range transmission of signals near the surface. Further investigation of the active spaces of both types of calls, as well as their relative intensity levels may further elucidate the functions of such a division in call structures.

Within each broad category, however, there was substantial variation between calls. Graded vocalizations may serve as high information signals, providing fine-grained information on the status, motivation or behavioural context of the sender (Bradbury &

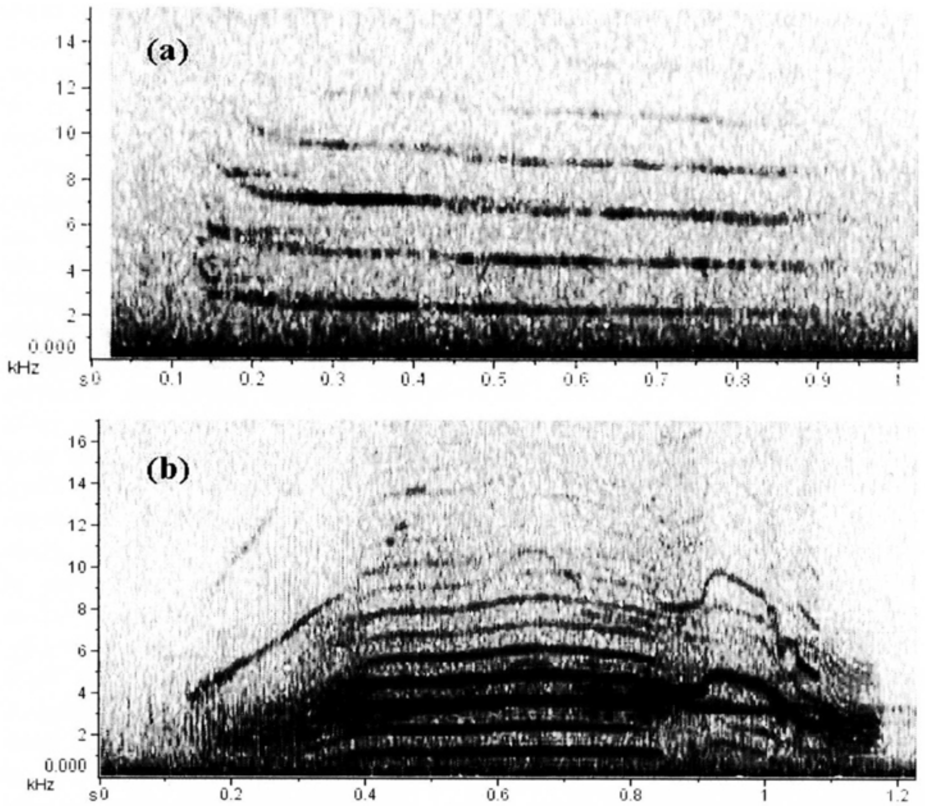

Figure 11. Examples of (a) a simple Pilot Whale pulsed call with a single element and inflection point, and (b) a more complex pulsed call with multiple elements, inflection points and a UFC. Brightness and contrast of spectrograms were modified in Photoshop (CS3).

Vehrencamp 1998; Compton *et al.* 2001). Specific Bottlenose Dolphin whistles show subtle contour variations that generally correspond to individual distinctiveness (McCowan & Reiss 2001) and social familiarity (McCowan *et al.* 1998). False Killer Whales produce a graded repertoire of calls that lie along a continuum and may shift as a function of behavioural state (Murray *et al.* 1998). It is possible that the variation in Pilot Whale pulsed calls observed here may be a consequence of individuals communicating different states or statuses, such as behaviour, arousal or group membership, through modification of subtle characteristics of the calls. The diversity of calls may also reflect a communicative plasticity that facilitates adaptation to a variable environment, allowing effective communication despite interference from background noise, as has been observed in other cetacean species (Au *et al.* 1985; Lesage *et al.* 1999; May-Collado & Wartzok 2008).

Consequently, Pilot Whales may produce call types with multiple variant forms for each type that were not successfully discriminated by the clustering techniques used in this study. Cluster analysis generally has difficulties differentiating call types when there is a natural gradation between categories (Karlsen *et al.* 2002). Resident Killer Whales produce "aberrant" versions of discrete call types that show significant fluctuations in both duration and structural details (Ford 1989) and variable "miscellaneous" pulsed signals that cannot be placed in any clearly defined categories (Ford & Fisher 1983). Such calls are traditionally excluded from further analyses or analyzed separately (Ford & Fisher 1983; Yurk 2005). It is possible that the lack of multiple discrete call types observed in this study is the result of a high number of variable and aberrant calls in the Pilot Whale repertoire that includes discrete categories of calls. No attempt was made to separate the wide spectrum of pulsed sounds that were analyzed into typical or variable (squeaks, squawks) categories before analysis. Whether Pilot Whale pulsed calls could be categorized into more discrete call types when analyzed at a coarser resolution (i.e. by disregarding small variations in frequencies and excluding variable calls) remains to be investigated.

Pilot and Killer Whale pulsed calls: an example of form following function?

Pilot Whale pulsed calls appear to be structurally similar to those of Killer Whales. While Pilot Whales reach a maximum size of 6m and 2320kg (Bloch *et al.* 1993), Killer Whales are obviously larger, reaching a maximum size of 9.8m and 2587kg (Klinowska 1991; Trites & Pauly 1998). Consequently, the slightly higher frequency ranges of Pilot Whale pulsed call variables are not surprising given the general influence of body size on the maximum and minimum frequencies of signals produced by animals (Gerhardt 1994; Matthews *et al.* 1999). What is surprising, however, is the general overlap between the compared structural components of the calls from the two species. The overlap is such that calls captured on autonomous recording devises in areas where the two species are sympatric could not be easily divided accurately based on their pulse repetition rates, LFC frequencies, UFC frequencies or durations.

Taxonomically, both species are members of the Delphinidae family, although the phylogeny of the Delphinidae itself is not well resolved (LeDuc *et al.* 1999). However, recent phylogenetic trees based on cytochrome b sequences place Killer Whales in the subfamily Orcininae and pilot whales in the subfamily Globicephalinae (Figure 12) (LeDuc *et al.* 1999; May-Collado & Agnarsson 2006). Unfortunately, other species within the Orcininae and Globicephalinae families are

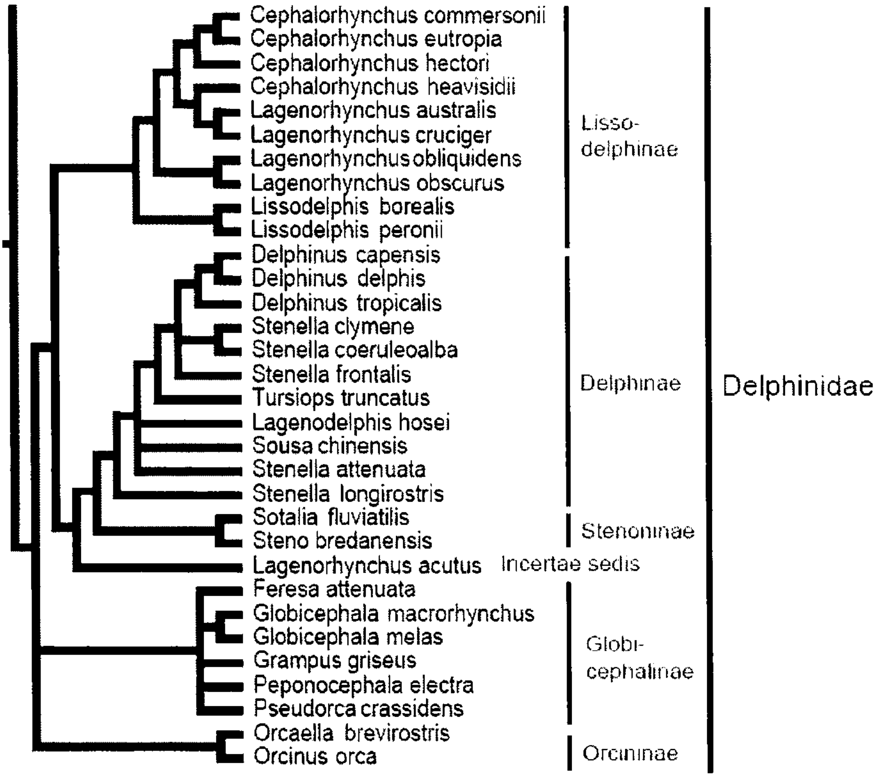

Figure 12. The Delphinidae branch of a recent phylogenetic tree produced by analysis of cytocrome b sequences in a Bayesian framework. Note that Killer Whales *Orcinus orca* are in the Orcininae subfamily, and Long-finned Pilot Whales *Globicephala melas* are in the Globicephalinae subfamily. Reprinted with permission from May-Collado and Agnarsson (2006).

difficult to include in the comparison, mainly due to a lack of available information and differences in call structure and methodology across studies. For instance, false Killer Whale vocalizations appear to be gradually modulated from pulse trains to whistles and have a highly graded structure (Murray *et al.* 1998) that does not allow direct comparison with Pilot Whale pulsed calls. Risso's Dolphins *Grampus griseus* produce a wide variety of sounds, including "barks" and "grunts" that are pulsed tones (Corkeron & Van Parijs 2001) but impossible to compare with Pilot Whale pulsed calls. Melon-headed Whales *Peponocephala electra* appear to produce only whistles and click-bursts (Watkins *et al.* 1997). Interestingly, Irrawaddy Dolphins *Orcaella brevirostris*, the only other species to share the Orcininae subfamily with Killer Whales, produce clicks, whistles and a variety of pulsed calls that do not resemble those of Killer Whales (Van Parijs *et al.* 2000).

The structural similarity of Pilot Whale pulsed calls to those of Killer Whales may reflect the relative importance of signal function on the evolution of delphinid vocalizations. Both Pilot Whales and Killer Whales are matrilineal and exhibit natal group philopatry, an extremely rare social structure where neither male nor female offspring disperse from the natal group (Bigg *et al.* 1990a; Amos *et al.* 1991, 1993a, 1993b). Consequently, the structure of their pulsed calls may be functional for the transmission of short-range group membership information and long-range mate attraction necessary to reduce potential inbreeding costs (Amos *et al.* 1993a; Price 1999; Yurk *et al.* 2002), and promote within-group bonding to maintain and reinforce long-term bonds within a social unit (e.g. Miller *et al.* 2004; Schulz *et al.* 2008). The vocalizations and social organization of resident Killer Whales have been studied extensively for decades (see Ford & Fisher 1978; Bigg *et al.* 1990b), and the course and findings of Killer Whale acoustic research may suggest how to proceed for Pilot Whales. Future work should focus on investigating Pilot Whale pulsed call structure across social and behavioural contexts to further elucidate the possible communicative functions of this complex sound class.

ACKNOWLEDGEMENTS

We would like to thank Andrea Ottensmeyer (1998, 1999, 2000), Tonya Wimmer (1999, 2000), Aimee Ryman (2000), Sara Pullen (2005) and Jessica Mitchell (2005) for making the Pilot Whale recordings used in this study, and the captains and crews of both the *Northern Gannet* (Captain Cox's Whale Watch) and *Double-Hookup* (Captain Mark's Whale and Seal Cruise) for their support while in Cape Breton. We also thank Colleen Barber, Andrew Horn, Marty Leonard, David Logue, Cindy Staicer and an anonymous reviewer for comments on the manuscript, and Jennifer Strang for her assistance with creating the GIS map. The Natural Sciences and Engineering Research Council of Canada (NSERC) provided funding for fieldwork, and L.N. was financially supported by an NSERC graduate scholarship and the Dr. Patrick Lett fund.

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Received 14 January 2009, revised 31 March 2009 and accepted 2 April 2009