Aquatic Mammals 2003, **29.2,** 278–288

Repetition patterns within harp seal (*Pagophilus groenlandicus*) underwater calls

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Abstract

Rhythmically repeated calls used during vocal communication have important implications for the extent to which pinnipeds successfully transmit information over long distances and during times of high levels of background noise. Harp seals (*Pagophilus groenlandicus*) have a large vocal repertoire and many of their underwater vocalizations consist of multiple elements. Between-call and within-call variability of element and interval durations for the thirteen multiple-element call types were very consistent. These elements are repeated regularly in predictable patterns. Three distinct patterns were identified with respect to the timing of call intervals: all intervals <1 s (short-short pattern), all intervals >1 s (long-long pattern) and intervals alternating between <1 s and >1 s (short-long pattern). Harp seal multiple-element calls are rhythmically repeated and elements of the calls occur at highly predictable intervals. Rhythmical repetition would likely enhance the probability of a call being detected and could serve to identify the species of the caller.

Key words: harp seal, vocalization, multiple-element, repetition, pattern, rhythm, anti-masking, *Pagophilus*.

Introduction

Harp seals (*Pagophilus groenlandicus*) form large groups for the purposes of whelping, breeding, and molting (Lavigne & Kovacs, 1988; Sergeant, 1991). Northwestern Atlantic seals of the Gulf Herd population migrate south by late September from their summer feeding grounds off the coasts of Greenland and northern Labrador, to winter breeding grounds in the Gulf of St. Lawrence (Sergeant, 1991). When the seals arrive at their winter breeding grounds they must be able to find suitable ice, as well as each other (Terhune & Ronald, 1986).

Sound is the only means for long distance communication under water. Seals are able to hear under water with a maximum sensitivity between 2 kHz and 30 kHz, although the overall hearing range is from 0.1 to 64 kHz (Terhune & Ronald, 1972; Terhune, 1991). Harp seals possess a large vocal repertoire. Some of the calls are short single sounds, while others consist of regularly repeated elements (Møhl *et al*., 1975).

Masking is a phenomenon that occurs when noise interferes with the ability of an animal (seal) to detect a sound even when the signal is above the animal's absolute hearing threshold (Richardson, 1995). Masking of harp seal calls could occur when a high level of background noise, abiotic or biological, is encountered (Hawkins & Myrberg, 1983; Terhune & Ronald, 1986; Richardson, 1995).

Vocalizations of harp seals are thought to serve a social communicative function and could be used to assist with herd formation through distant communication, as well as for courtship through close range communication (Terhune & Ronald, 1976, 1986). An increase in the calling rates in mid-March is associated with the onset of courtship and mating (Terhune & Ronald, 1976). This dual function of the calls could present a conflict where louder and more distinct long-range calls are emitted at the same time as quieter short-range calls, causing a masking effect. Within the herd, calling rates often are so high that it is not easy to distinguish individual vocalizations and the seals must compete with conspecific sounds to be heard (Terhune & Ronald, 1976, 1986).

An element is considered to be a single distinct sound having a clearly distinguishable beginning and end. Multiple element calls consist of more than one discrete sound. Distinctive characteristics of underwater vocalizations, such as repetition of call elements, would allow calls to 'slice through' background noise and avoid being masked (Watkins & Schevill, 1979). A rapid sequence of brief sounds is more detectable against background noise than a single brief sound (Richardson, 1995).

Seals that repeat short duration calls at regular rates enhance the probability of communicating with distant conspecifics in both masked and unmasked situations (Turnbull & Terhune, 1993).

Turnbull & Terhune (1993) demonstrated that regular pulse repetition enhances acoustical detection thresholds for harbour seals (*Phoca vitulina*). Terhune *et al*. (1994) found that Weddell seals (*Leptonychotes weddellii*) increase the number of elements in multiple-element underwater calls as a response to conspecific masking. Analyses of recordings taken at a Weddell seal breeding site found that overlapped calls were longer due to the addition of elements, than were similar calls emitted without interruption. Harp seals increase the number of elements of most multiple-element calls when the number of calls per min increases (Serrano & Terhune, 2001).

In windy conditions, which cause increased background noise levels, king penguins (*Aptenodytes patagonicus*) lengthen the duration of their vocalizations by repeating the same call many times. By increasing repetition of information during times of high level background noise, the birds could increase the probability of communicating during short time windows when the noise level drops (Lengagne *et al*., 1999).

Harp seal calls can be classified into distinctive types, a number of which include multiple-element calls (types 3, 6, 9, 10, 11, 12, 14 and 15) characterized by Møhl *et al*. (1975) and types 24 and 25 described by Serrano (2001). Within an individual multiple-element call, the timing, frequency and duration of each element appears to be quite consistent. This consistency within calls, as well as between calls, suggests that the seals produce rhythmically repeated vocalization patterns. The purpose of this study was to investigate the apparent rhythms that occur in harp seal multiple-element calls and determine if the element and interval durations, and frequencies within a call, are consistent throughout the call.

Materials and Methods

Recording equipment and data collection

Digital Audio Tape (DAT) recordings of harp seal underwater calls in the Gulf of St. Lawrence, Canada, were obtained during the breeding season (February–March; Sergeant, 1991). Recordings were made near the Magdalen Islands during three different years; 3–4 March 1993, 28 February–15 March 1999, and 7–9 March 2000 ($n=15$ recordings, each at a different site).

The recordings were made on ice floes occupied by harp seals (no other species were observed near these locations) during daylight. Recording sessions varied from 1 to 5 h. The sex and age of the vocalizing seals could not be determined, but it is known that both mature females and males are vocally active (Serrano, 2001). Thousands of seals were observed on the ice at the times of the recordings, but it was not possible to determine the number of vocalizing seals under water or their proximity to the hydrophone.

The hydrophones were placed 10–20 m away from the nearest seals and were lowered 5–10 m below the ice through breathing holes. For the 1993 and 1999 recordings, a Brüel and Kjær 8100 hydrophone, a Brüel and Kjær 2635 charge preamplifier, and a Sony DAT recorder (model TCD-D3 or TCD-D100) were used. The frequency response of the system was ±1 dB from 0.02 to 22 kHz. In 2000, recordings were made with a Vemco VHLF hydrophone and a Sony DAT recorder (model TDC-D100), with a combined frequency response of ±4 dB from 0.02 to 20 kHz.

Data analysis

A sound spectrum analyzer, GRAM (Version 6.0.9), was used for analyzing the calls made on the tapes and measuring the call features (timing and frequency). After a preliminary examination of the tapes, it was determined that eight call types (3, 6, 9, 10, 11, 12, 14, and 15; Møhl *et al*., 1975) were the most frequently occurring multiple-element calls. Two of these call types (6 and 14) were further divided.

Call type 6, the chirps (Møhl *et al*., 1975), were divided into two distinct types. A mid-frequency (<3.0 kHz) chirp generally made up of three or four longer elements was designated as call type 6.1, or 'low chirp'. A higher frequency chirp (4.0–6.0 kHz), usually consisting of more than ten rapidly repeated short elements, was referred to as call type 6.2, or 'high chirp'.

Call type 14, the grunts, were divided into five distinct types. Type 14.1 consists of short, paired, low frequency (<1.0 kHz) broadband elements, occurring with generally greater than ten elements per call. The interval duration within pairs was slightly less than the duration between pairs, with all interval durations less than 1000 msec. Call type 14.2 is generally greater than ten elements, unpaired and made up of short narrowband elements usually 0.7–0.9 kHz, (reaching frequencies up to 1.7 kHz). Mid frequency (<3.0 kHz) broadband 'grunts' or 'groans', sometimes occurring in pairs, were designated as call type 14.3. Type 14.4 and 14.5 are calls in which the elements shift frequency from beginning to the end. Both calls are low in frequency (<1.0 kHz). Type 14.5 differs from 14.4 by a distinctive and very short broadband constant frequency segment occurring at the start of the call.

Thirteen different call types were considered in this study. To avoid potentially analyzing a large

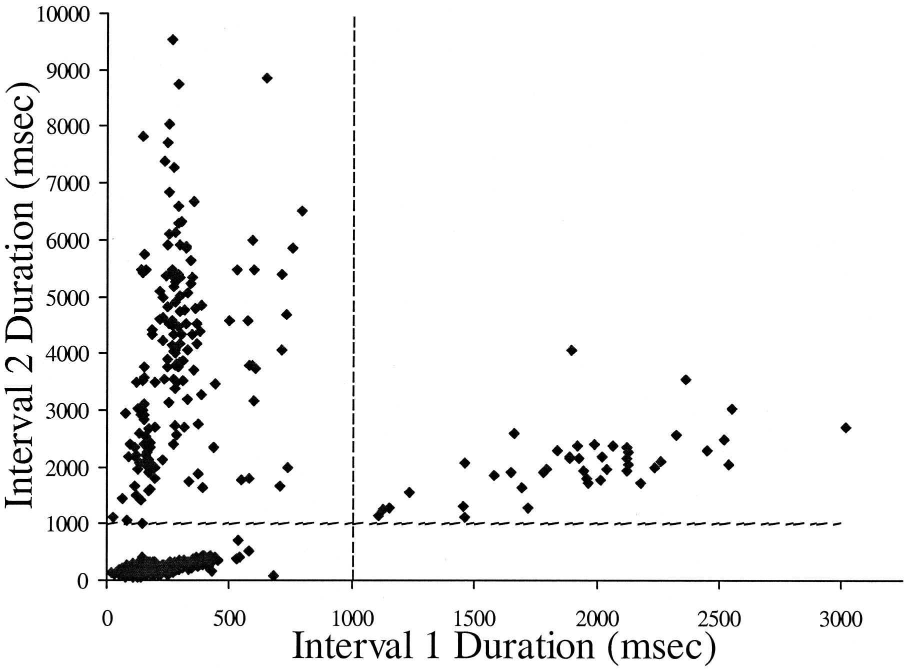

Figure 1. Interval 1 duration versus interval 2 duration of harp seal underwater multiple-element calls. Three distinct call patterns based on interval durations are shown: Pattern 1 (short–short)=lower left, $n=974$; Pattern 2 (long–long)=right side, $n=43$; Pattern 3 (short–long)=upper left, $n=161$.

number of calls from a single seal, the upper limit of 15 samples of each call type per recording location was examined from any one location (each recording). Recordings from 15 locations were analyzed. For each location, the first 15 calls of each of the 13 call types that were not masked by background noise were selected for analysis.

For each multiple-element call examined, the following features were noted:

(1) Call type.

(2) Total number of elements in the call.

(3) Element duration (msec) of each element in the call, up to the first ten elements of the call. Measures from only the first ten elements per call were made for practical purposes related to the time available for data analysis, and because the majority of calls contained ten elements or less.

(4) Interval (inter-element) duration (msec) of each interval in the call, up to the first nine intervals of the call.

(5) Frequency (Hz) of elements in the call. For constant frequency calls (types 3, 10, 14.2, 14.3 and 15), the mid-frequency of each element in the call was measured. For frequency-shifting calls (types 6.1, 6.2, 9, 11, 12, 14.4 and 14.5), the start and end frequencies of each element were measured.

For initial analysis of the data, histograms, and scatter plots of element and interval durations of calls were produced using the entire data set. These charts were examined to identify distinct patterns, with respect to timing, present within the multiple-element calls. Three distinct patterns of interval duration were identified. In Figure 1, the patterns are shown by plotting interval 1 durations against interval 2 durations; however, the three patterns do extend throughout the entire call (Table 1).

Means and standard deviations of element and interval durations within the calls of each of the three patterns were calculated, and ANOVA tests were run to determine the consistency of measures within each pattern. The sample sizes for each of the call types present in patterns 1, 2 and 3 were identified and where appropriate the 13 multiple-element call types were further divided into call sub-types based on the three patterns of interval duration. Means and standard deviations of element and interval durations for each of these call sub-types were calculated in order to examine consistency within call sub-types. For the analysis of consistency of within-call frequency values, the frequency data were converted into octaves; $\log_2$ (Hz). The octave levels were analyzed by using ANOVA

Table 1. Mean, standard deviation (in brackets), and coefficient of variance (CV) of element and interval durations (msec) of three patterns of harp seal underwater multiple-element calls. Number of specific elements and intervals of the call are also given (*n*).

Element durations				Interval durations			
Category	Mean	CV	*n*	Category	Mean (msec)	CV	*n*
Pattern 1							
Element 1	105 (65.7)	0.63	974	Interval 1	214 (81.6)	0.38	974
Element 2	109 (65.6)	0.60	974	Interval 2	220 (67.2)	0.31	974
Element 3	108 (63.1)	0.58	974	Interval 3	204 (72.0)	0.35	974
Element 4	107 (62.4)	0.58	974	Interval 4	218 (60.3)	0.28	629
Element 5	118 (61.6)	0.52	629	Interval 5	193 (67.3)	0.35	540
Element 6	113 (60.0)	0.53	540	Interval 6	215 (55.2)	0.26	443
Element 7	107 (55.0)	0.51	443	Interval 7	184 (63.1)	0.34	361
Element 8	102 (51.6)	0.51	361	Interval 8	212 (48.7)	0.23	268
Element 9	99 (50.3)	0.51	268	Interval 9	177 (57.1)	0.32	236
Element 10	97 (46.3)	0.48	236				
Pattern 2							
Element 1	318 (90.0)	0.28	43	Interval 1	1938 (405.3)	0.21	43
Element 2	323 (106.4)	0.33	43	Interval 2	2080 (576.5)	0.28	43
Element 3	312 (92.7)	0.30	43	Interval 3	2096 (627.6)	0.30	43
Element 4	316 (94.2)	0.30	43	Interval 4	2199 (397.2)	0.18	10
Element 5	270 (92.4)	0.34	10				
Pattern 3							
Element 1	134 (68.3)	0.51	161	Interval 1	282 (155)	0.55	161
Element 2	146 (72.7)	0.50	161	Interval 2	3931 (1734)	0.44	161
Element 3	133 (64.8)	0.49	161	Interval 3	297 (262)	0.88	161
Element 4	147 (73.2)	0.50	161	Interval 4	4099 (1555)	0.38	98
Element 5	130 (69.1)	0.53	98	Interval 5	263 (141)	0.54	95
Element 6	148 (73.4)	0.50	95	Interval 6	4213 (1557)	0.37	37
Element 7	146 (63.9)	0.44	37	Interval 7	281 (149)	0.53	37
Element 8	142 (69.2)	0.47	37	Interval 8	4546 (1850)	0.41	12
Element 9	125 (49.7)	0.40	12	Interval 9	276 (135)	0.49	11
Element 10	136 (69.8)	0.51	11				

and descriptive statistics (mean and standard deviation) in order to determine similarities of frequency within each call sub-type.

To enable measures of within call consistency, each value (element, interval or frequency) was transformed to a proportion of the second measure for each of the categories. The second element and interval durations were chosen because visual inspection of the data indicated that the first element and interval values were frequently shorter than subsequent values. The standardized data were used to determine within-call consistency for individual calls.

This transformation gives a measure of the temporal stability within calls. That is, if the second element was shorter or longer than average (for that pattern), would the other elements in that call be of the same length or of variable length? If the element and interval durations are consistent within each call, the coefficients of variation would be expected to be very small.

Results

In total, 1178 multiple element calls were examined in this study. Up to the first 15 clear calls of each call type from any one recording were chosen for analysis. For most call types, the calls analyzed from each site were spaced-out along the recording because many were uncommon or had a low signal to noise ratio, which prohibited obtaining accurate measurements. Initial analysis of the data using several element and interval duration scatter plots and histograms revealed three distinct call patterns. These patterns became apparent when interval durations were compared (Fig. 1). Table 1 shows the stability of the three basic patterns. Mean element and interval durations seem to be

Table 2. Number of each harp seal underwater multiple-element call sub-types within Patterns 1, 2 and 3.

Call type	Pattern 1	Pattern 2	Pattern 3
3	162		
6.1	3	27	8
6.2	96		1
9	67		
10	30		9
11	82	1	44
12	14		
14.1	32		1
14.2	82		
14.3	170	15	98
14.4	57		
14.5	36		
15	143		
Total	974	43	161

consistent throughout the calls for each of the patterns, but the standard deviations from these means were found to be high. Some of the 13 call types exhibited more than one of the three interval patterns identified (Table 2, Fig. 2).

The most common pattern, Pattern 1 (the 'short-short' calls), consisted of 974 calls in which all interval durations were shorter than 1000 msec (Table 1). This pattern occurred in 82.6% of the calls analyzed and was exhibited by all 13 call types (Table 2). Calls of sub-type 14.1, Pattern 1, showed a tendency for elements of the call to occur in pairs with short intervals separated by slightly longer intervals, and all interval durations less than 1000 msec.

Pattern 2 (the 'long-long' calls) consisted of 43 calls in which all interval durations were longer than 1000 msec (Table 1). This pattern occurred in 3.7% of the calls analyzed and was exhibited in call types 6.1, 11 and 14.3 (Table 2). It should be noted that call type 11 does not commonly occur as a long-long call, as only one of the 127 type 11 calls examined displayed Pattern 2 timing (Table 2).

Calls in which the first interval and all odd numbered intervals are less than 1000 msec, and all even numbered intervals are longer than 1000 msec, are Pattern 3 calls (the 'short-long' calls; Fig. 1, Table 1). This interval pattern results in the characteristic 'double-grunt' or paired element calls in which the first two elements are produced quickly and followed by a relatively long pause, which is again followed by another pair of elements occurring quickly. Pattern 3 occurred in 161 (13.7%) of the calls. The majority of the calls with this pattern were type 14.3 calls, while the pattern also occurred in call types 6.1, 10 and 11. Call types 6.2 and 14.1 each had only one instance of a short-long call (Table 2).

Of the 1178 calls analyzed, only three of the multiple-element calls did not fall into any of the three call patterns identified. These calls were actually 'long–short' calls, very similar to the 'short–long' calls of Pattern 3. They began with a single element followed by a longer interval and then followed the paired element timing of Pattern 3. When the first element of these calls was left-out, the call essentially became a Pattern 3 (a short–long) call. These calls could have been pattern 3 calls in which the first element was left-out or not recorded. As these long–short calls are very few in number, and because it was highly unlikely that they were the result of a new pattern, but rather a consequence of a disrupted Pattern 3 call, they were not considered in this study.

Element durations were consistent for the three patterns; all mean element durations were less than 400 msec. Element durations of calls in Patterns 1 and 3 were typically about 100 msec long, while Pattern 2 consisted of slightly longer element durations around 300 msec (Table 1). In both Pattern 1 and 2, calls with longer element durations tended to have longer interval durations (Table 3). The majority of Pattern 1 and Pattern 3 calls had a greater number of elements than Pattern 2 calls, with the latter usually consisting of only four elements (Table 1).

ANOVA tests were used to check the consistency of element and interval durations for calls of each of the three patterns. A significant difference between the means of the element durations ($F_{9,\ 6363}=4.42$, $P<0.001$) was found when all Pattern 1 calls were analyzed. However, when the Pattern 1 calls were examined separately in groups according to the number of elements the calls contained, (calls with only four elements, calls with only five elements, etc., to calls with ten or more elements) no significant differences were found among mean element durations. For example, when all Pattern 1 calls having only four elements were analyzed, the ANOVA produced an F-statistic of $F_{3,1360}=0.40$ and $P=0.750$. The mean interval durations for Pattern 1 calls were also found to be significantly different ($F_{8,5387}=22.99$, $P=0.001$), when all Pattern 1 calls were analyzed. When the calls were analyzed in groups according to the number of elements present, no significant differences were found for calls having only four, five, seven, or nine elements; however, calls having six, eight or ten elements did show significant differences between the mean interval durations. This may be attributed to the tendency for elements of some calls to be paired (for example, call type 14.1).

For pattern 2 calls, ANOVA results indicate that there were no significant differences between mean

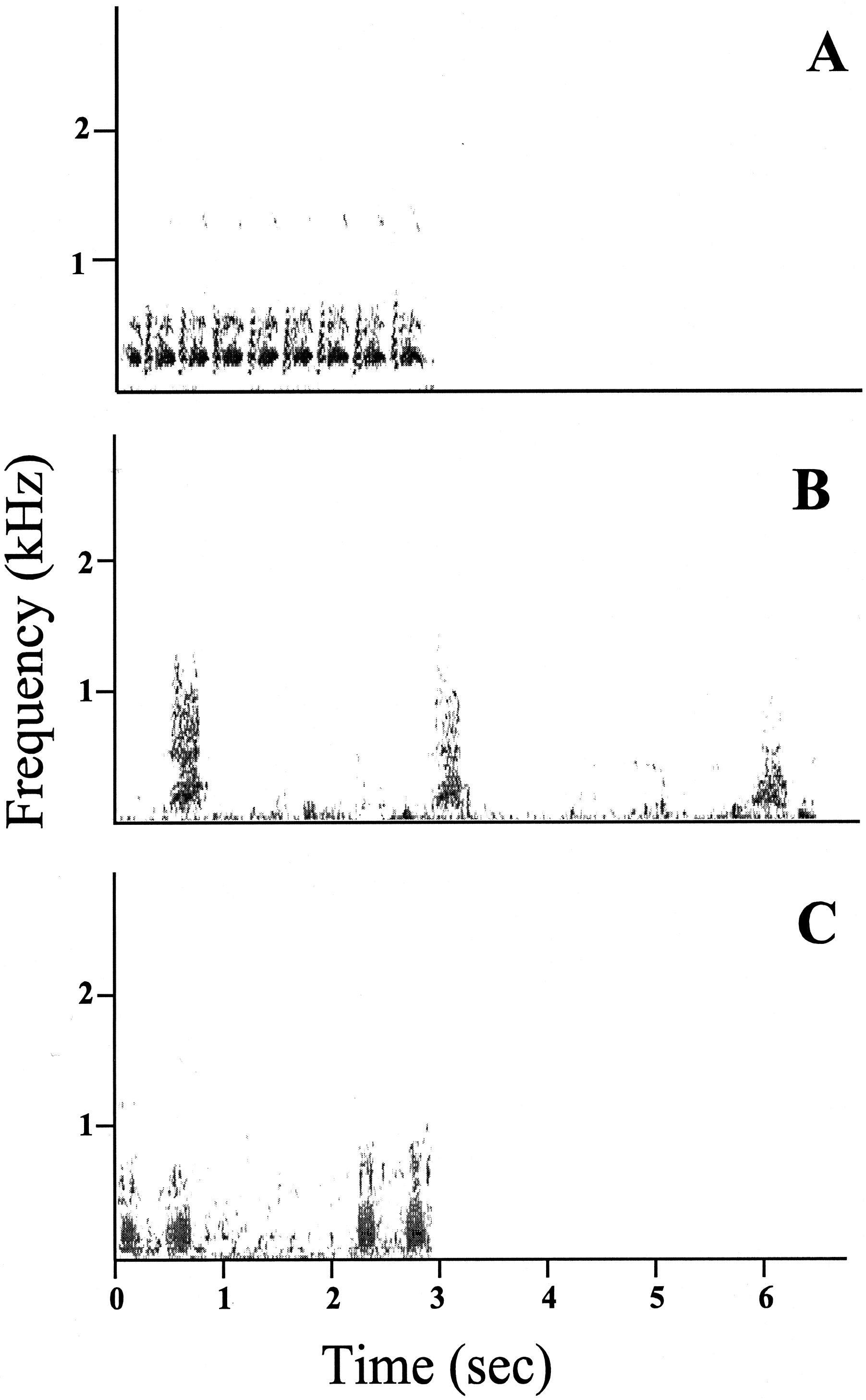

Figure 2. Harp seal underwater call type 14.3, displays all three interval timing patterns; A=Pattern 1, B=Pattern 2, C=Pattern 3.

Table 3. Mean (first number given) and standard deviation (in brackets) for all element (Ele) and interval (Int) durations in msec present in the calls of each harp seal underwater multiple-element call sub-type of Patterns 1, 2 and 3. For Pattern 3 calls the mean and standard deviation of even intervals (IntE) and odd intervals (IntO) are indicated.

Call type	Pattern 1		Pattern 2		Pattern 3	
3	Ele	113 (33.0)				
	Int	190 (55.6)				
6.1	Ele	101 (68.9)	Ele	330 (63.5)	Ele	105 (62.6)
	Int	335 (163.1)	Int	195 (562.9)	IntE	279 (591.0)
					IntO	2553 (811.0)
6.2	Ele	70 (169.6)				
	Int	31 (70.5)				
9	Ele	123 (42.8)				
	Int	252 (77.1)				
10	Ele	150 (41.0)			Ele	172 (29.9)
	Int	226 (45.6)			IntE	271 (70.7)
					IntO	4116 (1088.0)
11	Ele	47 (16.1)			Ele	60 (35.2)
	Int	194 (59.7)			IntE	162 (73.5)
					IntO	2637 (932.2)
12	Ele	75 (21.1)				
	Int	160 (28.7)				
14.1	Ele	215 (37.7)				
	Int	173 (54.1)				
14.2	Ele	84 (24.0)				
	Int	255 (53.6)				
14.3	Ele	156 (54.9)	Ele	303 (119.4)	Ele	172 (54.7)
	Int	208 (65.2)	Int	2165 (516.2)	IntE	315 (155.7)
					IntO	4536 (1522.0)
14.4	Ele	119 (47.4)				
	Int	257 (58.2)				
14.5	Ele	258 (73.2)				
	Int	243 (106.9)				
15	Ele	48 (24.4)				
	Int	160 (28.7)				

duration of the elements ($F_{4,177}=0.65$, $P=0.631$), or mean duration of the intervals ($F_{3,135}=1.04$, $P=0.378$). Pattern 3 calls also showed no significant differences between mean element durations ($F_{9,924}=1.07$, $P=0.385$), mean odd-numbered interval durations ($F_{4,460}=0.47$, $P=0.760$), or mean even-numbered interval durations ($F_{2,293}=0.60$, $P=0.551$).

For all three patterns, there appeared to be more variation in the timing of elements occurring at the beginning and end of the calls than during the middle of the calls. In many cases, the first element was cut short. Typically, for longer calls with many elements, the last few elements tended to be shorter than the rest of the elements (as can be seen for Pattern 1 calls; Table 1).

The interval duration patterns for each call sub-type were examined (Table 3). Again, the standard deviations of element and interval durations appeared to be high. The high standard deviations resulted in large coefficient of variance (CV) values. For each of the call sub-types, data were standardized by converting values as a proportion of the second measure for each of the categories (element, interval or frequency). The standardized data showed consistent mean durations for the element and intervals, while standard deviations generally remained large, as can be seen with call sub-type 9, Pattern 1 (Table 4). Generally, the CV value decreased (or remained about the same) when the data were standardized (Table 4). For call sub-type 3, Pattern 1, and the one long-long call of sub-type 11, Pattern 2, standardizing the data increased the CV value.

The frequencies of the calls were more consistent than the timing and had smaller CV values. The standardized data showed similar results and the majority of the call sub-types gave proportional mean values of 1.00 for frequency (when rounded), with very small CV values. Table 4 represents the analyses from a single call type.

Table 4. Mean, standard deviation (in brackets), and coefficient of variance values (CV), of element (msec), interval (msec) and frequency ($\log_2$ (Hz)) of the beginning (StartFreq) and the end (EndFreq) of the elements, for the first five successive elements of the type 9 (Frequency–Shift Keying call; Møhl *et al.*, 1975) harp seal underwater multiple-element call. The data were also standardized relative to the value of the second element, interval or frequency. Standardized mean, standard deviation (in brackets), and coefficient of variance values (CV_{STAND}) are given. The sample size (*n*) refers to the number of calls analyzed.

Category	Mean (SD)	CV	Standardized	CV_{STAND})	*n*
Element 1	127 (47.0)	0.37	0.97 (0.184)	0.19	67
Element 2	132 (44.5)	0.34	1.00	—	67
Element 3	129 (42.5)	0.33	1.01 (0.172)	0.17	67
Element 4	131 (41.4)	0.32	0.96 (0.222)	0.23	67
Element 5	122 (41.4)	0.34	1.00 (0.192)	0.19	44
Interval 1	276 (93.0)	0.34	1.08 (0.225)	0.21	67
Interval 2	254 (77.1)	0.30	1.00	—	67
Interval 3	254 (81.3)	0.32	1.00 (0.196)	0.20	67
Interval 4	243 (68.6)	0.28	0.95 (0.104)	0.16	67
Interval 5	241 (56.5)	0.23	1.00 (0.129)	0.11	44
StartFreq 1	9.2 (0.41)	0.04	0.98 (0.163)	0.17	67
StartFreq 2	9.2 (0.38)	0.04	1.00	—	67
StartFreq 3	9.2 (0.39)	0.04	1.00 (0.019)	0.02	67
StartFreq 4	9.2 (0.43)	0.05	1.00 (0.014)	0.01	67
StartFreq 5	9.2 (0.42)	0.05	1.00 (0.015)	0.01	44
EndFreq 1	8.4 (0.44)	0.05	0.98 (0.163)	0.17	67
EndFreq 2	8.4 (0.44)	0.05	1.00	—	67
EndFreq 3	8.3 (0.46)	0.06	1.00 (0.025)	0.02	67
EndFreq 4	8.4 (0.47)	0.06	1.00 (0.030)	0.03	67
EndFreq 5	8.4 (0.48)	0.06	1.00 (0.025)	0.03	44

Table 5 lists the mean frequency values for the call sub-types within each pattern. The standard deviation values are proportionately smaller than those of the interval and element durations. ANOVA tests for call types 6.1 and 14.3 (occurring in all three patterns), and call type 10 (occurring in Patterns 1 and 3) show no significant difference between the mean frequency values for call sub-types within any one call type (with $F_{1,173}=0.42$, $P=0.889$; $F_{9,1411}=0.68$, $P=0.725$; and $F_{9,240}=0.12$, $P=0.351$, respectively). The ANOVA for the starting frequencies of call type 11 (occurring with patterns 1 and 3) did show a significant difference for calls of the two patterns ($F_{9,970}=3.65$, $P=0.001$). The starting frequency was also significantly different within the sub-type 11, Pattern 1 calls ($F_{9,707}=2.12$, $P=0.026$), as well as with sub-type 11, Pattern 3 calls ($F_{9,516}=2.47$, $P=0.009$), indicating that differences in starting frequency were not necessarily linked to the pattern with which the calls were emitted. The ANOVA for ending frequencies of call type 11 showed no significant difference for calls of the two patterns ($F_{9,970}=0.97$, $P=0.460$). The frequency values of the calls (Table 5) appeared to be more consistent than the timing of the elements or intervals, especially within each call type (Table 3).

Discussion

Three distinct patterns of interval duration were identified within harp seal multiple-element calls. The timing of the intervals within calls was used for determining pattern, rather than element duration (which appeared to be quite consistent regardless of the calling pattern). This indicates that interval duration patterns could be important in call identification. Pattern 1 was the most common call pattern, while only a small fraction of calls were produced with the other two patterns (Table 2).

Within the three patterns, other subtle patterns could be present. One such pattern was identified. Call type 14.1 (of Pattern 1) tends to have elements occurring in pairs, but because all interval durations were <1000 msec, they were still considered Pattern 1 calls. The paired element timing within the Pattern 1 calls is much like the Pattern 3 calls, except that the timing of the intervals is shorter both between the paired elements (odd intervals) and between pairs of elements (even intervals). This

Table 5. Mean and standard deviation (in brackets) of frequency ($\log_2$(Hz)) of elements present in each harp seal underwater multiple-element call sub-type. 'Mid' indicates mid-frequency of constant frequency calls, 'Start' and 'End' indicate start and end frequency of frequency-shifting calls.

Call type	Pattern 1		Pattern 2		Pattern 3	
3	Mid	8.94 (0.496)				
6.1	Start	11.45 (0.255)	Start	11.46 (0.225)	Start	11.27 (0.308)
	End	11.48 (0.284)	End	11.48 (0.177)	End	11.32 (0.693)
6.2	Start	12.24 (0.255)				
	End	12.24 (0.255)				
9	Start	9.19 (0.430)				
	End	8.42 (0.468)				
10	Mid	8.88 (0.441)			Mid	8.926 (0.689)
11	Start	10.79 (0.827)			Start	10.33 (0.689)
	End	11.09 (0.641)			End	10.98 (0.0622)
12	Start	9.61 (0.503)				
	End	8.49 (0.606)				
14.1	Mid	8.53 (0.843)				
14.2	Mid	9.32 (0.606)				
14.3	Mid	8.84 (1.052)	Mid	8.70 (0.750)	Mid	8.28 (0.906)
14.4	Start	9.46 (0.332)				
	End	9.46 (0.332)				
14.5	Start	8.75 (0.893)				
	End	8.75 (0.893)				
15	Mid	8.56 (0.776)				

suggests that the paired element timing of Pattern 3 calls is an extended version of the paired timing of some Pattern 1 calls.

The three patterns were consistent for the 13 call types identified with very few outliers. The anomalous calls were likely disrupted pattern 3 calls.

The mean durations of the elements and intervals within each pattern were consistent, while standard deviations appeared high (Table 1). This indicates that there was some variance among element and interval durations within any one pattern. This variance could have been caused by the differences between call types emitted with each pattern and the differences between individual seals. Pattern 1 includes all 13 call types (Table 2), each of which is structurally different than the others. When each call sub-type was examined separately, the large standard deviations still remained, but the means stayed very constant. Analysis of standardized data also showed similar results, although the variance did tend to decrease when the data was converted from absolute to standard values. Variance present within the call sub-types could be attributed to the inconsistency of element durations near the beginning or end of the calls.

The frequency of the calls appeared to be very consistent for each of the call sub-types regardless of pattern (Table 5). Small standard deviations demonstrated that calls of different types have a very specific frequency range. ANOVA tests indicate that even though a particular call may occur with various patterns of timing, frequency still remained constant (with the exception of call type 11, which showed variance between means when all calls, as well as when calls of only one specific pattern, were analyzed).

The number of seals that produced the 1178 calls is unknown. Harp seal calling rates of over 75 calls per min are common (Serrano & Terhune, 2001) so with the limit of only 15 calls per type for each location, it is likely that the calls analyzed were recorded from a large number of seals.

The consistency of timing within the harp seal calls is demonstrated clearly by the mean element and interval durations, which were very stable between each of the call types (within the three patterns), as well as within the patterns themselves. The standard deviation measures indicated some variance for element and interval durations. This could be due to use of very precise time measures. The ability of seals to detect a difference of a few milliseconds is likely to be limited, although no studies on this topic have been conducted. The frequency of the calls was very stable with little variation within any one call type. Multiple-element calls emitted by harp seals are rhythmically repeated, with a high predictability in terms of element and interval timing. The three patterns within multiple-element calls can be clearly distinguished from each other. Further studies of seal call predictability are required to determine extent to which rhythmically repeated calls aid in seal communication, and if this phenomenon extends across species.

The presence of rhythmically repeated calls in seal communications has important implications for the extent to which seals can successfully communicate over long distances and during high levels of background noise. Having stereotyped rhythmic patterns in their underwater vocalizations likely confers a number of advantages that would facilitate harp seal communication. In quiet surroundings, the repetition of the call elements likely enhances their detection relative to a single element call. This would potentially increase the detection range of a call by up to 80% (Turnbull & Terhune, 1993). Most ice noises occur as single events and the regular repetition would distinguish multiple element calls from abiotic sources. When other seals are calling or the abiotic noise levels are high, the calls will be more likely to be detected when the elements are repeated in a regular manner. Such calls will be longer and thus, it is less likely that the entire call would be masked by other sounds. If a listener is uncertain about the presence of a faint call, the regular repetition would enable them to confirm its presence by knowing when to expect subsequent elements. By increasing call length through the addition of elements (Serrano & Terhune, 2001) and by producing these elements at regular intervals, harp seals could enhance the probability of call detection by an intended listener. Similarly, King penguins (*Aptenodytes patagonicus*), increase the number of elements in their calls when increasing wind speeds raise the level of background noise (Lengagne *et al.*, 1999).

Call repetition rates can vary with the behavioural situation. The barking rate of an adult male California sea lion (*Zalophus californianus*) increased from 2.1 to 3.0 barks per sec in air and from 1.0 to 1.4 barks per sec under water when the social context changed from nondirectional, self advertisement to chasing or confronting another sea lion (Schusterman, 1977). Some of the variation within the harp seal repetition patterns may be related to the calls being emitted in different behavioural contexts.

Studies of rhythm in bird vocalizations have shown characteristic patterns emerging in songs of different bird species, regardless of whether the songs were developed through independent learning of an individual or through interactions of the individual with other birds. Rhythms present in songs of different species of doves, pigeons, sparrows and shore birds have been statistically demonstrated (Baptista, 1996; Miller, 1996). Generally, variation in the duration of individual notes (elements) and the intervals between the notes (inter-elements) in complex vocalizations are found to provide rhythms characteristic of a species (Baptista, 1996).

Improved species detection should occur if the receiver has only a few patterns to listen for. The three repetition patterns used by harp seals do not likely match those of other seal species in the area. The long trills of bearded seals (*Erignathus barbatus*; Cleator *et al.*, 1989) have duration and frequency shift patterns that are very different from harp seal calls. Some of the underwater calls of hooded seals (*Cystophora cristata*; Ballard & Kovacs, 1995) and ringed seals (*Phoca hispida*; Stirling, 1973) are given in series, but the sound spectrogram patterns in these publications indicate that the patterns are not similar to those of harp seals. For harp seals the waveform, bandwidth, and frequency range of individual call types exhibit considerable variation (Møhl *et al.*, 1975). If the species recognition for harp seals resides in the temporal patterns of the multiple element calls, perhaps the fine structure of the vocalizations is less important. Sounds given using Patterns 1, 2 or 3 would be distinct from random background noise and would match the familiar temporal model. Thus, the three patterns of harp seal calls likely serves to identify the species of the caller, independent of the frequency or waveform of the specific call type.

Acknowledgments

The Natural Sciences and Engineering Research Council of Canada provided the funding for this research. NHK Television of Japan provided logistical support for the field work in 1993. The 1999 and 2000 recordings were made by A. Serrano. A. Bourque, of the Chateau Madelinot, provided in-kind support and hospitality during the field trips. P. Abgrall, P. Rouget, R. Gupta, C. Thompson and reviewers for this journal provided advice on an earlier draft of this manuscript.

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