

Structure, complexity, and organization of vocalizations in harp seal (*Phoca groenlandica*) pups

Edward H. Miller¹ and Alana V. Murray²

¹ Biology Department, Memorial University, St. John's, Newfoundland, A1B 3X9 Canada

² Zoology Department, University of Alberta, Edmonton, Alberta, T6G 2E9 Canada

Summary

Pup harp seals (*Phoca groenlandica*) vocalize frequently in air during the approx. 2-week-long relationship with their mothers. Airborne vocalizations of harp seal pups were recorded in the Gulf of St. Lawrence, Canada. Recordings were analyzed to provide baseline descriptions of acoustic structure, complexity, and organization. Vocalizations were characterized by harmonic structure, frequency modulation, and broadband noise.

Vocalizations of harp seal pups were variable in duration (range, 156-2046 msec), but averaged longer (approx. 760 msec) than in most phocid seals. The vocalizations were similar to those of other phocids in glottal pulse rate (up to 940 Hz). Harp seals differed greatly from other pinniped species in having very complex pup vocalizations, with up to 15 abrupt shifts in character within single calls (e.g.: from tonality to broadband noise). Calls showed strong organization: transitions did not occur at random. Both call duration and position within a call affected acoustic attributes. Supralaryngeal filtering (including vocal-tract resonance) and separate sound sources may have occurred, though evidence is only suggestive. The high complexity and organization of harp seal pup calls seem functionally unnecessary in light of the species' simple and brief mother-pup bond. Possibly these vocal qualities are epiphenomena of development towards the complex system of adult underwater communication, rather than being of detailed communicative significance only between mothers and pups.

Key words: Harp seal, *Phoca groenlandica*, bioacoustics, vocalization, communication

Introduction

Knowledge of signal structure is essential for understanding a species' communication system. Such knowledge can provide insights into mechanisms of signal production and control. It is necessary for inferring adaptations of signals to physical and social environments, and for phylogenetic studies. Signal structure and variation are important to numerous facets of communication, in-

cluding message content, contextual variation, development, cultural change, and individuality (Green, 1975; Smith, 1977). Acoustic structure and variation are especially important in communication in mammals, whose social complexity, intelligence, and extensive use of short-range graded signals interact to produce communication systems of great richness and complexity (Kiley, 1972; Green, 1975; Marler, 1976; Klingholz and Meynhardt, 1979; Eisenberg, 1981;

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Harcourt *et al.*, 1993; Macedonia and Evans, 1993).

Pinnipeds are good models for comparative research on signal structure and variation, and on the relationships of signal structure to the behavior of communicating (Miller, 1991). The group comprises 34 species distributed around the world, from tropical to polar areas (Ridgway and Harrison, 1981a, b; King, 1983). Their social systems are correspondingly diverse, including large dense breeding concentrations on ice or land, dispersed parturient females attended by males, aquatic and terrestrial territoriality, dominance hierarchies, etc. (Stirling, 1983; Boness, 1991; Le Boeuf, 1991). In addition to their diversity in ecology and mating systems, pinnipeds display a host of physiological and behavioral strategies for growth, development, and maternal care (Bowen, 1991). Some contrasts can be illustrated with the hooded seal (*Cystophora cristata*), walrus (*Odobenus rosmarus*) and Galapagos fur seal (*Arctocephalus galapagoensis*) (Fay, 1982; Bowen *et al.*, 1985; Trillmich, 1987, 1990; Perry and Stenson, 1992). Female hooded seals give birth solitarily on floating ice, then attend their pups continuously and nurse them frequently until they are weaned at only 4 days of age. Female walrus give birth in large dense aggregations on floating ice, associate with their calves continuously, and travel and feed with their calves until weaning, which may not occur until the calves are 3 years old. Galapagos fur seal females routinely care for their pups until they are 2 years old, yet spend much time separated from them due to the females' need to feed offshore; some females nurse and care for their "pups" until they are 4 or 5 years old, i.e. when they may be as large as their mothers (see also Higgins and Gass, 1993). Such profound species differences are probably reflected in communication be-

tween mothers and pups, raising questions such as: Over what distances does communication occur? In what circumstances does communication take place? How much ambient environmental noise from biological and non-biological sources is there? What information is made available through signaling? How is contextual information used in communication? To answer such questions, good baseline descriptions of signal structure are needed. The purpose of our study was to provide a baseline description of structure, complexity, and organization of acoustic signals by harp seal (*Phoca groenlandica*) pups.

Knowledge of the ecological and social setting of the relationship between mothers and pups is important for understanding communication between them. The following summary is based on work by Stewart (1983), Kovacs (1987), Lavigne and Kovacs (1988) and Lydersen and Kovacs (1993). Females give birth in large aggregations on floating sea ice near Jan Mayen, in the White Sea, in the northwestern Atlantic Ocean off Newfoundland and Labrador, and near the Magdalen Islands in the Gulf of St. Lawrence. Females are separated from one other during parturition, and remain so throughout the approximately 2-week-long lactation period. In common with other pinniped species, female harp seals engage in extensive olfactory investigation of the pup's face immediately after birth, and subsequently nose (presumably smelling) the pup frequently to confirm its identity (e.g.: during reunions). Females remain with their pups continuously for the first few days after birth, then spend much time (up to 85%) away from them in the water, to dive and feed. They usually remain within hearing range of their pups, however, and make frequent visual checks of them. Pups vocalize frequently to solicit nursing, while nursing, or while fol-

lowing the mother. Unlike many pinniped species, harp seal females vocalize very little towards their pups. Breeding harp seals are exposed to few airborne sounds from other species and to very little environmental noise generally. Under water, harp seals employ a great variety of sounds (Møhl *et al.*, 1975; Watkins and Schevill, 1979; Terhune, 1994). In summary, harp seals have a relatively brief and functionally simple bond between mother and pup, with correspondingly simple requirements for airborne vocal signaling. Therefore, the species should be a good model for investigating acoustic signal "morphology" in a simple system, establishing baselines both for focused research on communication between harp seal females and pups, and for comparative studies. Superficial analyses of airborne sounds by harp seals are provided by Terhune and Ronald (1970) and Miller (1991). Underwater sounds are described by Møhl *et al.* (1975), Watkins and Schevill (1979), and Terhune (1994). General studies on the species' underwater acoustic communication are Schevill *et al.* (1963), Terhune and Ronald (1976), Terhune, Stewart and Ronald (1979), Terhune, Terhune and Ronald (1979), Terhune and Ronald (1986), and Terhune *et al.* (1987). In-air and underwater audiograms are in Terhune and Ronald (1970, 1971, 1972), Fobes and Smock (1981), and Fay (1988). On ear anatomy, see Ramprashad *et al.* (1972), Repenning (1972), Møhl and Ronald (1975), and Ramprashad (1975).

Materials and methods

Observations and audio recordings of undisturbed mother and pup harp seals (Fig. 1) were made during field trips to the Gulf of St. Lawrence, Canada, in March of two years (lasting 5 and 13 days, respectively). In one year, a camp was established on the ice with-

in the whelping patch; in the other year, daily trips to the patch were made by helicopter. Seals were recorded from the side or front, over distances of 5-10 m. Sounds were recorded at 19 cm/sec on Scotch 176 tape, with a Nagra IS tape recorder and Sennheiser MKH 816 microphone. Loud vocalizations that saturated the tape were noted at the time of recording, and were excluded from analyses to avoid spurious harmonics on sonagrams (Greenewalt, 1968). Recordings of 12 pups (P1-P12) were made, but quantitative analyses on the two smallest samples (P10 and P11) were not undertaken.

Two sonagrams of each vocalization were prepared on a Kay Elemetrics Sona-Graph 7029A, with analyzing filter bandwidths of 45 and 300 Hz (Kay Elemetrics Co., Pine Brook, New Jersey, U.S.A. 07058). Hereafter these are referred to as narrow- and wide-band sonagrams, respectively. Quotation marks are used for comparable sonagrams produced through digital analyses (*i.e.*, "narrow-" and "wide-band" analyses). The vocalizations extended to > 4 kHz in frequency, but were analyzed over 40-4000 Hz because attributes of interest were revealed clearly on that range. Calls were characterized by a sequence of codes, corresponding to sections of calls separated by abrupt changes (transitions) in attributes of interest. Some transitions were from one harmonic structure to another (e.g.: Fig. 2k, marked by arrow); others were between broadband noise and no noise (e.g.: Fig. 2e, marked by arrows); etc. Several transitions occurred in most calls. Hereafter, we refer to call parts as those portions of a vocalization separated by abrupt transitions (including the start of a call before the first transition, and the end of a call after the last transition). Many parts were brief (e.g.: the central three in Fig. 2d, the third and fourth in 2e). All parts of a 7-part call are marked in Fig. 2h.



Figure 1. a, top. Typical dispersion within aggregation of breeding harp seals (Gulf of St. Lawrence). Most seals shown are adult females with pups. b, bottom. Pup harp seal resting beside hole through which its mother regularly entered and exited the water.

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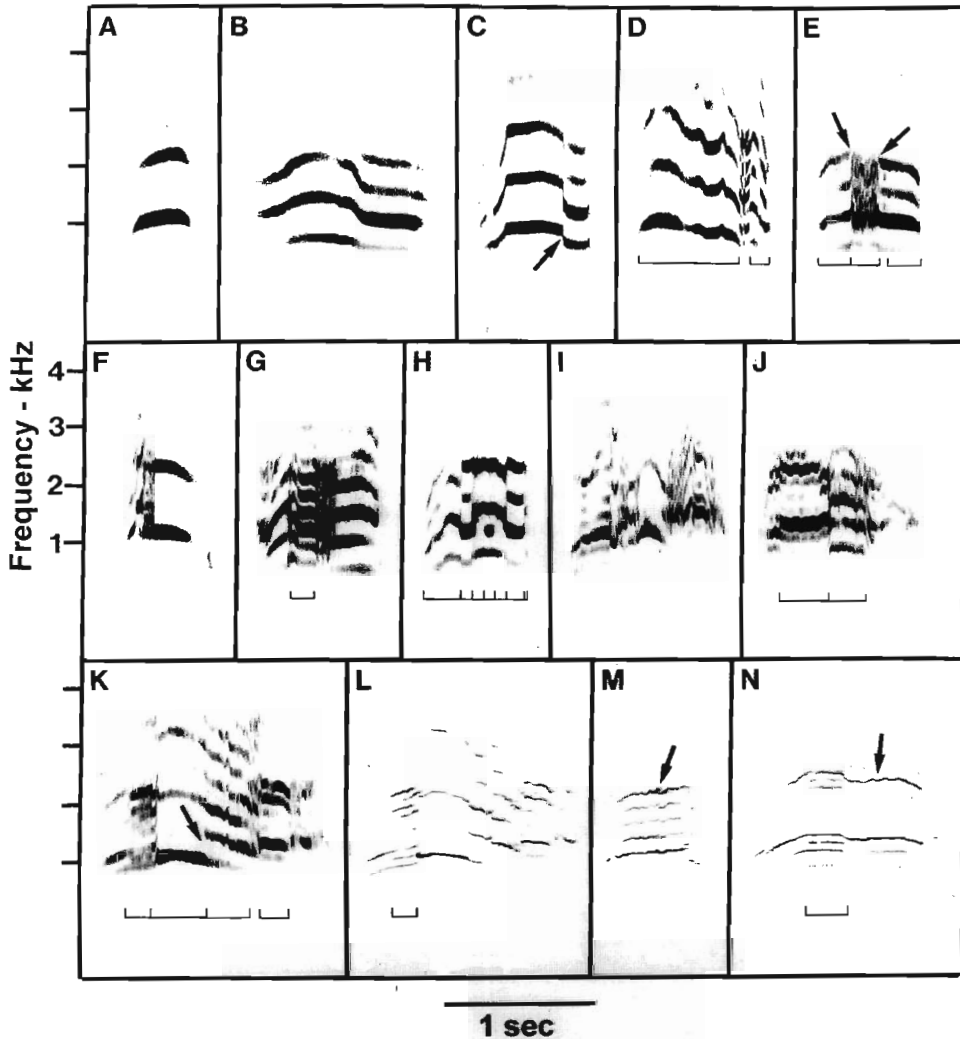


Figure 2. Sonograms representing structural variation and complexity, and illustrating attribute codes. a -- Simple 1-part call with low spectral richness (SR = 1). b. Longer one-part call, also with SR = 1. Note that most energy is in the second harmonic, especially towards the end of the call. c. Two-part call with SR = 1. Note the sharp drop in frequency in the transition between the two parts (marked with arrow); the frequency shift near the beginning of the call was not sharp enough to be considered as a transition. d. Five-part call. The first and final parts are underlined (the central three parts were brief so are not distinguished here). Part 1 has rhythmic FM. e. Five-part call with broad-band noise as the second part; parts 1, 2 (broad-band noise), and 5 are underlined (parts 3 and 4 were brief so are not distinguished here). f, g Two successive calls by P8. A part with SR = 3 is underlined in (g); the final part of (g) has SR = 2. h. Seven-part call; all parts are underlined. i, j. Two successive calls by P1. The first marked part in j shows SR = 3 and rhythmic FM (underlined), apparent as closely spaced sidebands in narrow-band sonogram (l). In k, parts with SR = 1, 2, and 3 occur after the pulsed part (all are marked). The transition between SR = 1 and SR = 2 is marked by an arrow. m. Narrow-band sonogram of call with rhythmic FM (marked with arrow). n. Narrow-band sonogram of call with pulsing (underlined) and rhythmic FM (marked with arrow).

Some calls were analyzed in detail with CSL 4300 (Kay Elemetrics Co., etc.; see above). They were digitized with a 10-bit A/D converter at 20 kHz, for the frequency range 0-10 kHz. Analyzing details for sonagrams are given in the legends to Figures 2-6. Power spectra were computed by FFT using 1024 points per analysis bin, no smoothing, no pre-emphasis, and a Blackman window.

To characterize the entire call, number of call parts and frequency trends at each call's start and end (judged by eye) were used: flat ($\pm 45^\circ$); rising ($< -45^\circ$ relative to the horizontal, for the start, and $> 45^\circ$ relative to the horizontal, for the end) or falling (as for rising, but in reverse). Durations of calls and call parts were measured in msec. Call parts were characterized further in the following ways (Fig. 2):

Spectral richness (SR)

This attribute was easy and reliable to code within calls. It reflected both harmonic "richness" and fundamental frequency, because low-frequency calls had more closely spaced harmonic bands than did higher-frequency calls. Assigned codes were 0, 1, 2, or 3. In practice, it was easiest to assign SR = 3 and then assign other codes on that basis. For SR = 3, harmonic bands (as displayed on wide-band sonagrams) were immediately adjacent (or nearly so), as in Figure 2g (marked part), 2j (first marked part), and 2k (last marked part). When harmonic bands were separated by a space about the width of a harmonic band they were coded as SR = 2, as in Figure 2e (first and last marked parts), 2j (second marked part), and 2k (third marked part). SR = 1 was assigned when there was greater separation between harmonic bands, as in Figure 2a, b, c (before arrow), d (first marked part) and k (second marked part). Different SR codes were assigned to successive call parts that had the

same harmonic relationships. For example, in Figure 2c a transition was noted between SR = 1 (before arrow) to SR = 2 (after arrow), even though harmonic relationships did not change throughout the call. Similarly, in Figure 2d, the first part (marked) had SR = 1, whereas the last part (marked) -- with the same harmonic relationships -- had SR = 2. Code SR = 0 applied to situations when broadband noise was so intense that SR could not be assessed (e.g.: Fig. 2e, second part).

Broadband noise

Noise often occurred without obscuring harmonic structure (e.g.: Fig. 2j, second marked part) Noise was coded as absent (0) or present (1).

Pulsing

This attribute was expressed as fine, closely spaced vertical lines on wide-band sonagrams and as extra harmonics on narrow-band sonagrams [e.g.: Fig. 2k (first marked part), 2l (marked part), and 2n (marked part); Watkins, 1967]. It was coded as absent (0) or present (1). Note that narrow-band sonagrams were used to confirm whether this attribute was present, but were not used in assigning SR codes. We do not consider this attribute to represent glottal pulsing.

Rhythmic frequency modulation (FM)

The term "rhythmic" is used loosely. FM was scored if a call part had approximately rhythmic modulation of the carrier frequency. FM was coded as absent (0) or present (1): see Figure 2j (first marked part), 2m and 2n (both marked by arrow).

The statistical software SAS-PC and BIOM (Rohlf, 1992) were used for conventional univariate statistical analyses (Rohlf and Sokal, 1981; Sokal and Rohlf, 1981). Sample sizes were based on recordings from 10 of

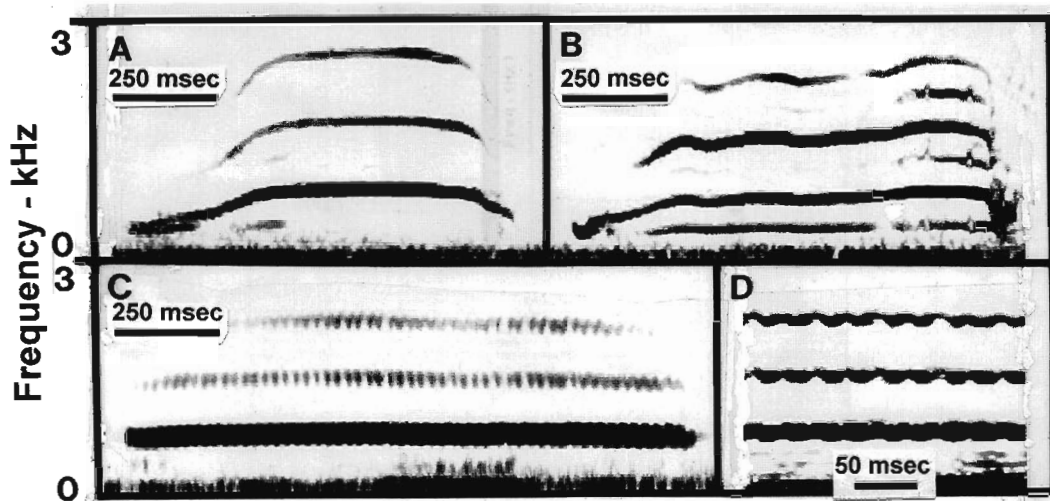


Figure 3. Sonograms of calls by adult female harp seals (analysis corresponding to 57-Hz analyzing filter bandwidth). a, b. Successive calls by mother in water, directed towards its pup about 3 m away on the ice surface. c. Call by adult female in threat directed towards another female 2 m away on the ice surface. Note the nearly constant carrier frequency (approx. 730 Hz in the centre of the call). d. Portion of (c), shown on different time scale to illustrate the rhythmic modulation in amplitude and frequency. The modulations occurred at a rate of approx. 35-40 Hz.

the 12 pups recorded. For some analyses, only the six pups with large sample sizes were used. We followed two approaches to document trends: (a) across individual pup samples; and (b) across pup means. Reaching statistical significance for the latter was difficult because of the small number of pups and because of high variation among pup samples due to individual differences, contextual variation, etc.

Results

General observations

Females occasionally vocalized spontaneously or in response to their pups' calls, or when leading their pups over the ice surface (Figs. 3a, b). Females uttered a long, loud harsh call in agonistic circumstances, as when threatening other females, foreign pups, or humans (Fig. 3c, d). No other kinds of female vocalizations were observed. Harp seal pups called much more frequently and

loudly than did females, and in more circumstances. The simplest use of loud calling by pups was when they solicited nursing from their absent mothers. Pups (particularly young ones) then often uttered a loud vocalization every few seconds for several minutes, while remaining at one location. Examples of the time course of spontaneous calling by pups are shown in Figure 7. Absent mothers usually responded promptly (within a few minutes) by hauling out and approaching their pups. However, some pups (even young pups) vocalized for more than 30 min without their mothers appearing. Old pups sometimes called around or even into holes in the ice through which their mothers had exited, or through which their mothers usually returned. Once hauled out, females typically approached and nosed their pups (often pups moved towards their approaching mothers), then led them some distance before nursing. In common with other pinnipeds, female harp seals

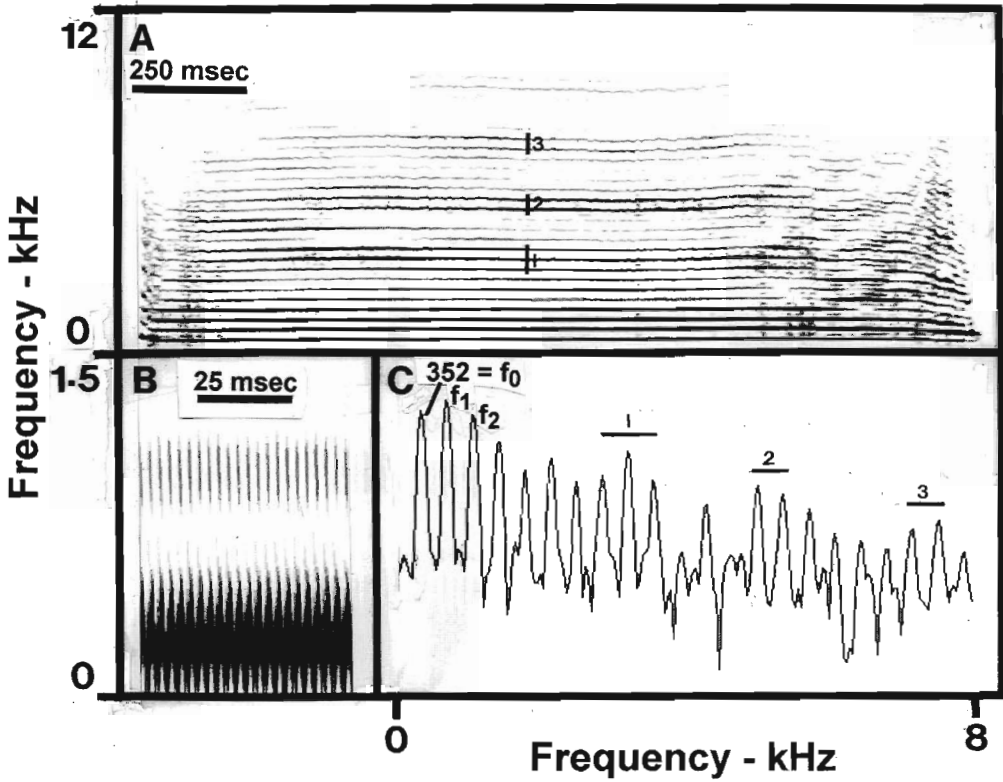


Figure 4. Analyses of a Weddell seal (*Leptonychotes weddellii*2f) pup vocalization. a -- "Narrow-band" sonagram [analysis corresponding to 57-Hz analyzing filter bandwidth (afb)]. The lowest band represents the glottal pulse rate (at approx. 350 Hz). Note the resonant zones with high energy [three zones are marked; see also (c)]. b. "Wide-band" sonagram of central portion of the same vocalization (879-Hz afb). This analysis reveals the simple pattern of glottal pulsing. c. Power spectrum of central 100 msec of (a), shown over 0-8000 Hz. Note the simple harmonic series and the regions of resonance [marked as in (a)].

repeated ly led, nursed, led then nursed again, and so on, for the early parts of nursing bouts (or even for entire bouts), with distances of 25-30 m being covered.

Pups commonly vocalized as they followed their mothers in such situations, or when their mothers were frightened by humans or human activity (e.g.: ships or aircraft). Pups often vocalized softly while beginning to nurse or during nursing. Some excerpts from field notes can serve as specific examples (M = mother; P = pup; F = other female): "P lying 4-5 m from hole in ice. P increasing-

ly restless, but silent and remaining where it's been lying. Over several min, M appears few times in hole, looks silently towards P. Finally M hauls out and moves to P, and nursing begins. Only then does P vocalize, with several soft calls."

"M hauls out and silently approaches P. M stops approx. 1 m away. P looks at M, moves towards M, then begins to suckle. P silent throughout entire interaction."

"M approx. 1 m ahead of P, leading it. P follows silently. M stops and threatens

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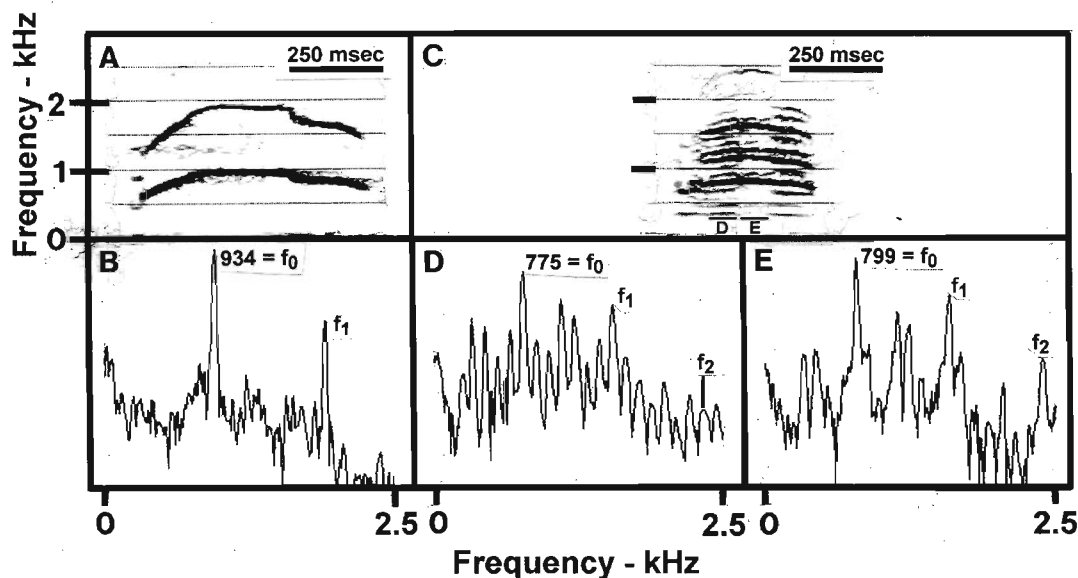


Figure 5. Analyses of two vocalizations from a harp seal pup (P5). a. Sonagram of first call [analysis corresponding to 114-Hz analyzing filter bandwidth (afb)]. "Wide-band" analyses barely resolved glottal pulsing, because it was at such a high frequency (approx. 940 Hz in the centre of the call). b. Power spectrum of central 200 msec of (a), revealing harmonically related peaks at approx. 934 and approx. 1868 Hz. c. Sonagram of second vocalization (114-Hz afb): The fundamental frequency of vibration is represented by the lowest dark line, which reaches a maximum of approx. 800 Hz, in the middle of the call. Marked portions are analyzed further in (d) and (e). d. Power spectrum of 75 msec of first portion of (c), showing the fundamental frequency (f_0) at approx. 775 Hz and its first two harmonic overtones (f_1 , f_2), plus many harmonically unrelated energy peaks. e. Power spectrum of the central 100 msec of (c), showing f_0 , f_1 and f_2 , plus some harmonically unrelated energy peaks.

(posturally and vocally) F that surfaces next to M; P vocalizes loudly in immediate response. M repeats threat to F, and P again calls at once then hastens to M's face, and initiates naso-nasal greeting."

"M silently approaches sleeping P. P awakens, looks at M and vocalizes, then starts to approach M. M moves approx. 5 m away, then lies broadside and presents belly to P. P calls 12 more times in the approx. 50 sec it takes to reach M and start suckling."

"M and P in water (through hole) together. M out of sight often, and P dives occasionally for brief periods. M and P haul out together. Nursing starts immediately, approx. 1 m from the hole. Both animals silent."

"M and P are asleep, separated by approx. 1 m. M shifts uneasily at my approach, approx. 10 m away. Without lifting head, and unable to see me, P immediately vocalizes softly several times."

Characteristics of calls and call parts

The detailed structure of harp seal pup vocalizations can be introduced by considering call structure in another phocid species, the Weddell seal (*Leptonychotes weddellii*) (Fig. 4). Pups of this species have simple calls consisting of long trains of glottal pulses. When analyzed for high resolution in the frequency domain, sonagrams appear as equally spaced horizontal lines with the lowest one representing the glottal pulse repetition rate (approx. 350 Hz), and the oth-

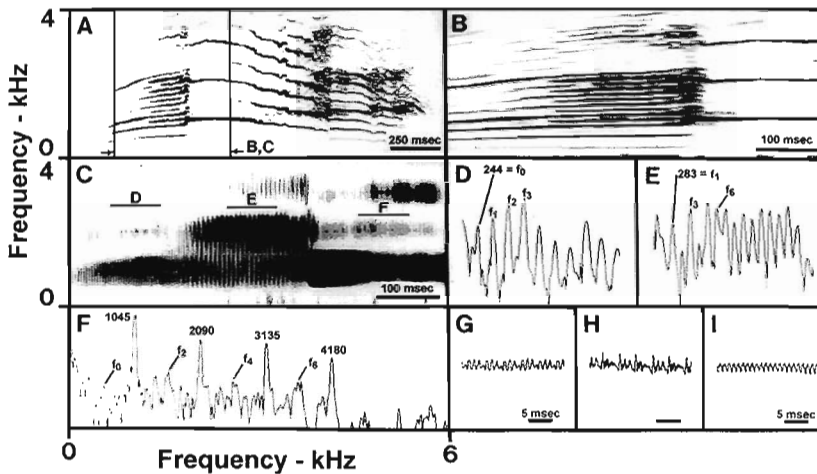


Figure 6. Analysis of pulsing in harp seal pup (P1) vocalization. a. Sonagram of entire call [analysis corresponding to 28-Hz analyzing filter bandwidth (afb)]. The segment shown in parts (b) and (c) is marked. b. "Narrow-band" sonagram of 600-msec portion marked in (a) (28 Hz afb). c. "Wide-band" sonagram of portion marked in (a) (439 Hz afb). Note the moderately fast pulses at the start, the slow (double) pulses in the middle (pulsed at a rate of approx. 138 Hz), and the fast pulses at the end. The portions analyzed in (d), (e) and (f) are marked. d, e, f -- Power spectra of 80-msec samples marked in (c), shown over 0-2500 Hz [parts (d) and (e)], or 0-6000 Hz [(f)]. The frequency values for some energy peaks are marked (see text). g, h, i -- Waveforms in the three parts marked in (c).

ers at integral multiples of that (see Watkins, 1967). The number and strength of higher-frequency lines result from several factors, such as the relative durations of pulses and intervals between pulses (Watkins, 1967). Several broad bands of high energy reflect resonances.

Harp seals differ in several ways. First, most analyses do not resolve pulses because the pulse repetition rate is very high. A simple call of P5, for example, had a maximum pulse repetition rate of approx. 930 Hz (Figs. 5a, b). Second, most calls in this species are spectrally complex, likely because of separate sound sources or supralaryngeal filtering, resulting in pulsing, broadband noise, etc. (Hauser, 1992). Furthermore, rapid transitions between these features occur in most calls (Fig. 2). A second call from P5 had a complex spectrum possibly due to separate sound sources (Fig. 5c-e). In this call, the maximum pulse repetition rate

was approx. 800 Hz, with a strong harmonic at approx. 1600 Hz, and a weaker one at approx. 2400 Hz. Other frequency components were harmonically unrelated to the glottal pulse rate, as seen clearly in the call's initial portion. There, many frequency components were separated from one another by approx. 110 Hz.

Pulsing exemplifies the acoustic complexity of harp seal pup calls. It was present in many wide-band sonagrams, with corresponding closely spaced lines on narrow-band sonagrams. More detailed "narrow-band" sonagrams are shown in Figure 6a and b; and a "wide-band" sonagram is shown in Figure 6c. The different pulse rates in the three sections are apparent in Figure 6c (at approx. 240, approx. 140 and approx. 525 Hz, respectively). These different rates are clear in power spectra, with energy peaks for the fundamental at approx. 240 and approx. 525 Hz in the first and third portions (Fig. 6d, f).

For the middle portion, the first peak above low-frequency background noise was approx. 280 Hz; presumably this was the second harmonic (Fig. 6e). In addition to differing in pulse rate, the three sections also differed in waveform (Fig. 6g, h, i). Pulses in the middle appeared to be compound (double?), and complexity of waveform followed the sequence middle > start > end. Again, supralaryngeal filtering or separate sound sources may account for these structures.

Call duration varied over an order of magnitude (156-2046 msec; Table 1). Calls of different pups averaged 430-1177 msec long, with a grand mean (mean of pup means) of 760 msec. Variation in call duration was moderate, with Coefficients of Variation (CVs) of 17-32% over the ten pups, i.e. a substantially lower range than most published estimates for temporal measurements on pinniped vocalizations (see Miller 1991: Fig. 4.10).

The number of parts per call varied greatly within and across pups (Table 1). All pups uttered some 1-part calls and some with > 3 parts. The range was 1-16 parts per call, with large differences across pups. Data for P6 and P7 illustrate extremes of this variation: most (90%) of P6's calls had only 1-2 parts, with a maximum of 4; while most (> 95%) of P7's calls had > 2 parts (up to 16) (Fig. 8). Despite large variation overall, the number of parts per call averaged only 1.5-6.4 across pups, with a grand mean of 4.0. CVs were higher for number of call parts than for call duration, being 39-60% across pups.

Call parts varied greatly in duration, ranging from 6-1242 msec, and with CVs of 58-110% (Table 1; measurement error on brief call parts had no effect on overall trends). The high variation was due in part to the lumping of measurements from different

positions in calls, since a part's position influenced its duration (see next section).

Call duration and the number of parts per call were significantly positively correlated for each pup except P1, though variation was high (Spearman's r_s ; $p < 0.005$ for pups P2-P10; Fig. 9).

Rhythmic FM was present in many parts of calls (20% of P3's call parts and 60% of P6's; other pups were intermediate; Table 2). Noise occurred in 0-28% of call parts in different pups, and pulsing in 0-13%; combined, noise and pulsing were present in 1-30% of call parts in different pups. Harmonics typically were present in call parts, and only 0-14% of call parts in different pups exhibited a fundamental with no harmonics (grand mean across pups, 6%).

Relationships of acoustic characteristics to number of parts and to part position

Variables and attributes were influenced strongly by the number of parts in a call and by position within a call. One simple trend was for the first and last parts of calls to begin with constant or increasing frequency (95-100% in different pups), and to end with constant or decreasing frequency (93-100%). Another trend was for 1-part calls to be much longer than the first part of 2-part calls, whose first part in turn was longer than the first part of calls with > 2 parts (Table 3a). One-part calls usually had rhythmic FM (Table 3b) and little noise or pulsing, whereas FM was less common and noise/pulsing were more common in other circumstances (e.g.: noise/pulsing were present in 31% of middle parts of calls with > 2 parts; Table 3c). Finally, there was less broadband noise and lower spectral richness in 1- than in 2- and > 2-part calls (Table 4).

Table 1. Descriptive statistics for call variables

| Pup number (N calls) | Call duration (msec) | No. parts per call | Part duration (msec) |
|-------------------------|-------------------------|-------------------------|-------------------------|
| P 1 (131) | 921±24 (29.8) | 4.5±.18 (45.8) | 203±8 (97.1) |
| P 2 (74) | 628±23 (31.5) | 3.2±.22 (59.1) | 196±10 (77.5) |
| P 3 (91) | 523±13 (23.7) | 2.4±.15 (59.6) | 215±12 (80.9) |
| P 4 (49) | 1177 ±38 (22.6) | 6.3±.39 (43.3) | 187±12 (109.7) |
| P 5 (60) | 430 ±17 (30.6) | 1.5 ±.11 (56.8) | 293±18 (57.6) |
| P 6 (43) | 612±18 (19.3) | 1.7±.11 (42.4) | 365 ±28 (64.8) |
| P 7 (101) | 975±25 (25.8) | 6.4 ±.26 (40.8) | 153 ±5 (89.4) |
| P 8 (164) | 688±9 (16.8) | 4.4±.14 (40.7) | 156±5 (93.3) |
| P 9 (80) | 823±22 (23.9) | 5.1±.22 (38.6) | 162±7 (89.3) |
| P12 (72) | 828±30 (30.7) | 4.5±.32 (60.3) | 182±11 (107.4) |
| Overall ranges | 156-2046 | 1-16 | 6-1242 |
| Grand means | 760±72 | 4.0±.55 | 193±29 |

1) Cell entries for pups are Mean ± SE (CV). Maxima and minima for variables and CVs are in **bold type**.

2) For N (No. of parts per call), see the first column of Table 2.

3) Means of the 10 pup means.

Table 2. Data summary for attributes of call parts

| Pup number (N call parts) | FM | Noise/ pulsing | Spectral richness | | | |
|------------------------------|-------------|-------------------|-------------------|-------------|-------------|-------------|
| | | | 0 | 1 | 2 | 3 |
| P 1 (594) | 49.8 | 27.5 | 8.9 | 23.7 | 32.8 | 34.5 |
| P 2 (236) | 24.6 | 25.8 | 0.9 | 74.6 | 23.7 | 0.9 |
| P 3 (221) | 19.5 | 18.1 | 3.6 | 69.2 | 15.4 | 11.8 |
| P 4 (308) | 58.4 | 17.5 | 6.5 | 54.6 | 25.3 | 13.6 |
| P 5 (88) | 50.0 | 3.4 | 0.0 | 83.0 | 14.8 | 2.3 |
| P 6 (72) | 59.7 | 1.4 | 8.3 | 87.5 | 4.2 | 0.0 |
| P 7 (642) | 52.0 | 30.2 | 8.6 | 41.6 | 35.1 | 14.8 |
| P 8 (723) | 40.1 | 27.6 | 13.6 | 42.7 | 24.5 | 19.2 |
| P 9 (404) | 57.9 | 27.3 | 4.0 | 45.5 | 32.7 | 17.8 |
| P12 (327) | 58.4 | 26.0 | 9.5 | 58.1 | 22.3 | 10.1 |
| Means | 47.0 | 20.5 | 6.4 | 58.0 | 23.1 | 12.5 |

Table entries are proportions for each pup (in per cent). Maxima and minima across pups are in **bold type**.

Vocalizations in harp seal pups

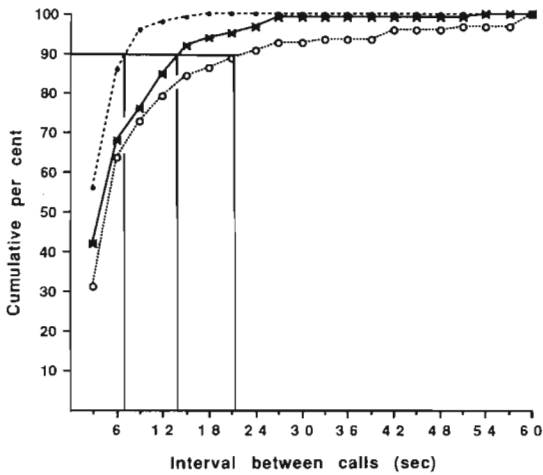


Figure 7. Intervals between successive calls within long calling bouts of lone pup harp seals. Cumulative frequency distributions are shown for three pups ($N=100$ calls per pup); 90% points (marked) were approx. 6 to approx. 20 sec.

Influences of part position within > 2-part calls were examined in more detail for the six pups with largest sample sizes. An example of data breakdown is given in Table 5, for P9. That pup's vocalizations tended towards more rhythmic FM in 3-5- part calls than in > 5-part calls. The trend towards more FM in middle parts of 3-5- part calls was present in all 18 comparisons (6 pups \times 3 positions); eight were statistically significant ($p < 0.05$). No other trends emerged, and only one other comparison (for spectral richness) was statistically significant for a single pup.

The strong relationships of FM and part duration to part position led us to explore their relationships further, using data on middle parts of calls with > 2 parts. Trends were consistent across pups: parts with FM were longer than parts without FM; and parts were briefer in multi-part calls (Table 6; Fig. 10). Trends were evaluated by Kendall's Coefficient of Concordance (W), based on ranks of part durations for each of the six

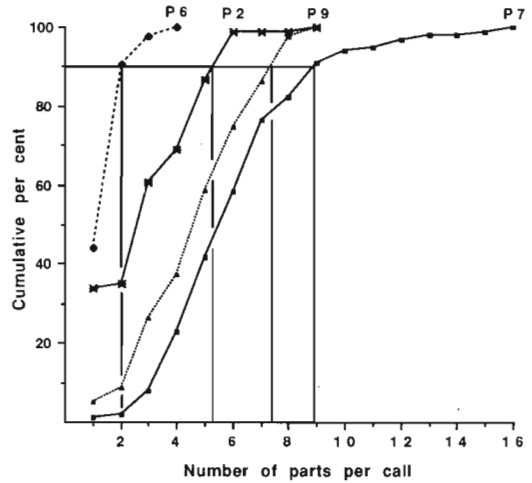


Figure 8. Frequency distribution of the number of parts per call. Cumulative frequency distributions are shown for four pups; 90% points (marked) were approx. 2 to approx. 9 parts.

pups: for FM present, $W = 0.66$, $p < 0.005$; for FM absent, $W = 0.47$, $p < 0.025$.

In summary, acoustic variables were influenced both by part position and number of parts in a call. Strong position effects occurred within calls, so calls were not merely random assemblages of their constituent parts. Overlain on this clear pattern was one with multi-part calls differing strongly from calls with fewer parts, rather than just being extended versions of them.

Correlations and sequential associations among acoustic characteristics

There was great variation across pups in the patterns of association among attributes, and no interpretable trends were detected either within or across pups, through multi-dimensional scaling of each pup's call parts. Furthermore, estimates of association among attributes were low [Cramér's V ranged from 0.17 ($N = 404$) to 0.40 ($N = 231$) across pups]. For these reasons, further association analyses were not carried out.

Table 3. Relationships of acoustic variables and attributes to part position within calls¹

| A. Part duration in msec (Mean±SE) | | | |
|---|--------|--------|--------|
| Part position: | | | |
| No. parts ² | Start | Middle | End |
| 1 | 575±25 | -- | -- |
| 2 | 338±75 | -- | 324±62 |
| > 2 | 158±34 | 158±13 | 184±12 |

| B. Presence of rhythmic FM in per cent | | | |
|---|-------|--------|------|
| Part position: | | | |
| No. parts ² | Start | Middle | End |
| 1 | 76.1 | -- | -- |
| 2 | 38.1 | -- | 59.7 |
| > 2 | 37.6 | 42.6 | 42.3 |

| C. Presence of noise and pulsing in per cent | | | |
|---|-------|--------|------|
| Part position: | | | |
| No. parts ² | Start | Middle | End |
| 1 | 0.9 | -- | -- |
| 2 | 16.9 | -- | 4.9 |
| > 2 | 10.1 | 31.4 | 11.4 |

¹ Table entries are grand means of the 10 pup means.² Sample sizes are: 1 - 149; 2 - 86; and > 2 - 630.

Combinations of acoustic attributes can be considered to yield different "kinds" of call parts. For example, (FM + low spectral richness + no noise) is one kind of part; (no FM + low spectral richness + no noise) is another; etc. Viewed in this way, 20 kinds of parts were noted, with a distinctly skewed distribution. One kind [(spectral richness = 1; FM present; no noise) = (coded 110)] accounted for nearly 25% of parts; (coded 210) was second, at about 16%; and so on (Fig. 11). The rarest combinations were (coded 001) and (coded 000). A few combinations with low (=

0) spectral richness did not occur, although they were logically possible (coded 002; all combinations beginning with 01). Clearly, attributes did not combine at random within call parts.

To explore sequential effects, we examined transitions between attributes of middle parts in calls with > 3 parts (4-part calls have one transition between middle parts; 5-part calls have two transitions; etc.). Six pups had adequate sample sizes (N = 130-328 middle transitions per pup) for this analysis, which examined transitions between: (a) spectral richness (codes 1, 2 and 3 only, because of small sample sizes for code 0); (b) rhythmic FM; and (c) noise (excluding pulsing, because of small sample sizes). Results disclosed pronounced non-random sequencing in transitions between attribute states, for several pups. In spectral richness, calls of P1 and P7 showed non-random sequencing, though trends differed between the pups (Table 7). Rhythmic FM showed a significant excess of transitions between like states (*i.e.*, FM-FM; no FM-no FM), for two pups. In contrast, noise showed significantly more transitions than expected between unlike states (*i.e.*, noise-no noise), in both P7 and P8. In conclusion, non-random sequencing of acoustic attributes is expressed commonly in the calls of harp seal pups.

Discussion and conclusions

Comparative remarks on general acoustic structure

In simple quantitative features, vocalizations of harp seal pups are similar to those in other pinniped species. Glottal pulse rate in harp seal pups is approx. 140-940 Hz (see Figs. 5 and 6). Estimates for pups of other species are up to approx. 110 Hz in the Hawaiian monk seal (*Monachus schauinslandi*), and 350-450 Hz in the harbor seal (*Phoca*

Vocalizations in harp seal pups

Table 4. Relationship of spectral richness to part position within a call¹

| No. parts | Spectral richness | | | |
|-------------------|-------------------|-------------|------|------|
| | 0 | 1 | 2 | 3 |
| 1 | 0.0 | 97.5 | 2.5 | 0.0 |
| 2 (first part) | 8.3 | 66.3 | 23.7 | 1.7 |
| 2 (last part) | 6.7 | 81.4 | 8.6 | 3.3 |
| >2 (first part) | 22.9 | 50.4 | 14.3 | 12.4 |
| > 2 (middle part) | 1.0 | 43.9 | 35.1 | 20.0 |
| >2 (last part) | 11.5 | 60.7 | 19.2 | 8.7 |

¹ Table entries are grand means of the 10 pup means, for per cent occurrence in call parts of the different classes of spectral richness. Maximum values within rows are in **bold type**.

Table 5. Data structure for analysis of number of call parts on variables and attributes. Data are for pup P9 (N = 80 calls)

| Variable or attribute | Position of part within call: | | | | | |
|----------------------------|-------------------------------|-------------|-----------|-----------|-------------|-------------|
| | Start | | Middle | | End | |
| | 3-5 parts | > 5 parts | 3-5 parts | > 5 parts | 3-5 parts | > 5 parts |
| Spectral richness | | | | | | |
| 0 | 7.5 | 18.2 | 0.0 | 18.2 | 2.5 | 9.1 |
| 1 | 55.0 | 51.5 | 39.8 | 44.2 | 47.5 | 48.5 |
| 2 | 32.5 | 27.3 | 33.7 | 33.3 | 32.5 | 24.2 |
| 3 | 5.0 | 3.0 | 26.5 | 20.6 | 17.5 | 18.2 |
| Rhythmic FM ¹ | | | | | | |
| 0 | 12.5 | 39.4 | 43.4 | 56.4 | 20.0 | 42.4 |
| 1 | 87.5 | 60.6 | 56.6 | 43.6 | 80.0 | 57.6 |
| Noise | | | | | | |
| 0 | 97.5 | 87.9 | 56.6 | 59.4 | 97.5 | 97.0 |
| 1 | 2.5 | 12.1 | 14.5 | 22.4 | 2.5 | 3.0 |
| Pulsing | | | | | | |
| | 0.0 | 0.0 | 28.9 | 18.2 | 0.0 | 0.0 |
| Part duration ² | | | | | | |
| | 224±24 | 133±14 | 205±20 | 125±8 | 144±14 | 115±15 |

¹ Each of the blocks of data in **bold type** shows significant heterogeneity (P < 0.05; 2 test).

² Cell entries are Mean±SE.

Table 6. Relationships among part duration (table entries¹), part position, number of parts (for calls with > 2 parts), and rhythmic FM in middle parts of a call (pooled data for six pups)

| | Part position: | | | | | |
|--------------------------------|-------------------|-------------------|-------------------|------------------|-------------------|-------------------|
| | Start | | Middle | | End | |
| | 3-5 parts | > 5 parts | 3-5 parts | > 5 parts | 3-5 parts | > 5 parts |
| FM = 0 | 102±11 67-138 | 82±8 56-112 | 130±13 81-164 | 81±2 71-88 | 99±8 73-118 | 79±8 57-110 |
| FM = 1 | 295±30 173-392 | 212±31 121-300 | 277±14 243-320 | 174±9 150-212 | 291±29 162-348 | 185±15 132-231 |
| Mean, FM : 0/1 ² | 3.2 | 2.7 | 2.2 | 2.2 | 3.0 | 2.5 |

¹ Cell entries show call durations as: grand means of the six pup means (Mean±SE) (above); and range of individual pup means (below). Data are in msec.

² Mean of [(duration of parts with FM:0)/(duration of parts with FM:1)] across the six pups. Note that the values are the means across pups, so were not derived from values in the table.

Table 7. Examples of significant transitions between attributes of middle elements, for calls with > 3 parts¹

| A. Tonality ² | Following part: | | | | | | |
|-----------------------------|-----------------|-----------|-----------|------------|------------|-----------|---|
| | P1 (N=179) | | | P4 (N=160) | | | |
| | 1 | 2 | 3 | 1 | 2 | 3 | |
| Preceding part | 1 | 10 | 28 | 2 | 45 | 42 | 9 |
| | 2 | 22 | 30 | 14 | 35 | 7 | 4 |
| | 3 | 10 | 13 | 50 | 8 | 5 | 5 |
| B. Rhythmic FM ³ | P1 (N=190) | | | P7 (N=328) | | | |
| | | 0 | 1 | 0 | 1 | | |
| Preceding part | 0 | 66 | 35 | 76 | 58 | | |
| | 1 | 36 | 53 | 73 | 121 | | |
| C. Noise ⁴ | P7 (N=306) | | | P8 (N=206) | | | |
| | | 0 | 1 | 0 | 1 | | |
| Preceding part | 0 | 105 | 93 | 80 | 53 | | |
| | 1 | 96 | 12 | 63 | 10 | | |

¹ Table entries show large positive and negative deviations from expected values.

² G (with Williams' correction) and p estimates are: for P1, 62.5 and < 0.001; for P4, 16.6 and < 0.005.

³ G (with Yates' correction) and p estimates are: for P1, 10.9 and < 0.001; for P7, 10.9 and < 0.001.

⁴ G (with Yates' correction) and p estimates are: for P7, 62.5 and < 0.001; for P8, 16.6 and < 0.001.

Vocalizations in harp seal pups

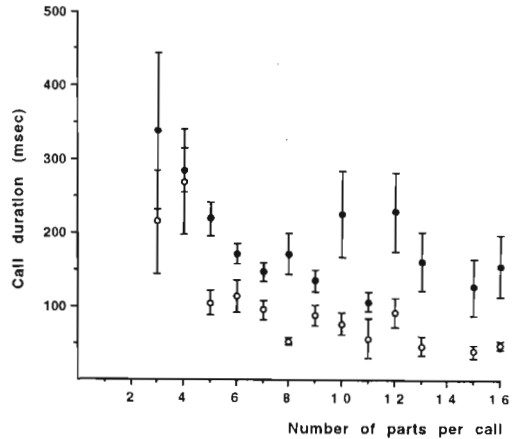
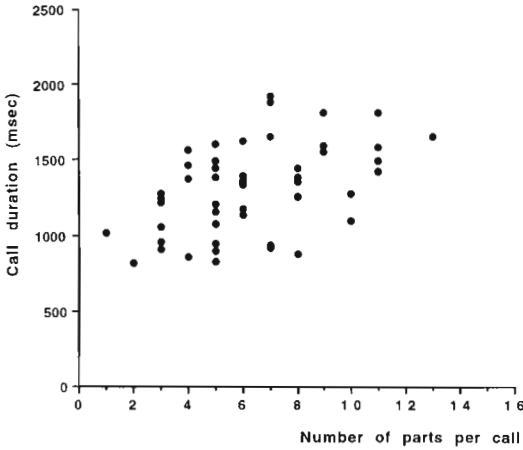
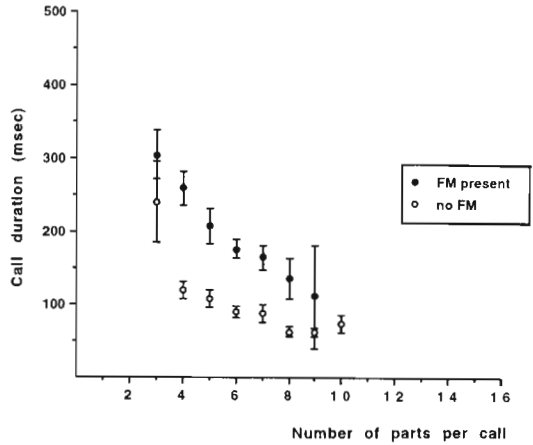
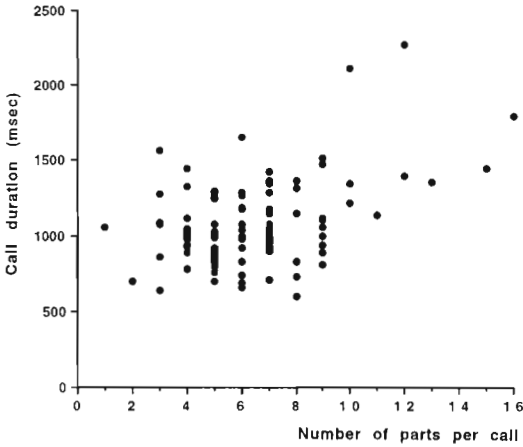


Figure 9. Relationship of call duration to number of parts in a call. Samples for two pups are shown; note the great variation within each.

Figure 10. Relationship of part duration to number of parts per call and to the presence of rhythmic FM. Samples for two pups are shown.

vitulina) and Weddell seal (Hamilton, 1980; Renouf, 1984; Job, 1992; Miller and Job, 1992; Fig. 4, this paper). In the much larger northern elephant seal (*Mirounga angustirostris*), glottal pulse rate of pups is very high and can exceed 1 kHz (Bartholomew and Collias, 1962; Insley, 1989, 1992; see also Rasa, 1971). Thus, harp seal pup vocalizations can have a high glottal pulse rate, but higher rates occur in at least one other phocid species. Overall, there is no simple inverse relationship of

glottal pulse rate to body size across species [Peters (1987) reported a similar finding for Felidae].

Harp seal pup vocalizations also are not remarkable in duration, although they may be longer than most reported for phocids (approx. 760 msec; range 156-2046). Estimates for other species are (in msec): harbor seal, approx. 440; northern elephant seal, 467; and Hawaiian monk seal, 665 (Hamilton, 1980;

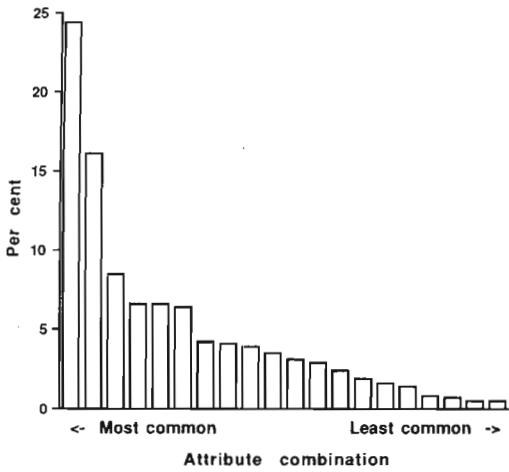


Figure 11. Frequency distribution of attribute combinations in call parts. The commonest combination was for SR = 1, FM = 1, and Noise = 0 (110), accounting for nearly 25% of all observed combinations. In descending order, the others are: 210, 310, 101, 100; 200, 311, 211, 102, 300, 201, 301, 111, 112, 302, 312, 202, 212, 001, and 000.

Insley, 1989, 1992; Job, 1992). Some calls of Weddell seal pups are nearly 2 sec long (Thomas, 1979; Fig. 4, this paper).

Calls of young walrus, fur seals and sea lions differ from those of phocid pups both structurally and functionally. When communicating with the mother, walrus calves use sounds ranging from soft monosyllabic "barks" over short distances, to loud repeated polysyllabic barks, mainly over longer distances (Kibal'chich and Lisitsyna, 1979; Miller, 1985, 1991, Kastelein *et al.*, this volume, Verboom and Kastelein, this volume). Vocalizations of otariid pups exhibit a similar range of structural variation, with loud stereotyped calls used mainly to communicate with the mother over long distances (Trillmich, 1981). Frequency characteristics of calls by young walrus and otariids have not been reported on in detail. Judging from published sonagrams, barks of walrus calves have a glottal pulse rate of approx.

200-500 Hz (Miller, 1985). Based on harmonic intervals it seems to be approx. 200-300 Hz in the northern fur seal (*Callorhinus ursinus*) [Insley, 1989; Kastelein *et al.*, 1995; see also Lisitsyna (1973, 1988) and Takemura *et al.* (1983)]. Polysyllabic barks of walrus commonly are > 1 sec in total length, though single constituent barks within them are very brief (Miller, 1985: Fig. 4; Miller, 1991: Fig. 4.14); isolated barks usually are < 1 sec long (Miller, 1985: Fig. 6). In the northern fur seal, pup calls average 891 msec long; in the Steller sea lion (*Eumetopias jubatus*) they average approx. 1100 msec (Lisitsyna, 1980, 1981; Insley, 1989). Published sonagrams of pup calls for other otariid species suggest similar durations (Peterson and Bartholomew, 1969; Stirling, 1972; Brown, 1974; Trillmich and Majluf, 1981; Trillmich, 1981; Roux and Jouvantin, 1987). In summary, vocalizations by walrus calves and otariid pups are similar to those of phocid pups in glottal pulse rate, but otariid pup calls are up to twice as long.

The complexity of harp seal pup calls sets the species apart from other pinnipeds. Several call "parts" can be recognized in other species, but they are fewer in number and seem to be less differentiated structurally than in the harp seal. In his study, Insley (1992) noted that northern elephant seal "pup and female calls often alternated between tonal and harsh call components", resulting in 1-2 parts (maximum: 5) per call [Insley, 1989; also see sonagrams in Bartholomew and Collias (1962: Figs. 1, 2)]. A few internal transitions occur in some calls of Hawaiian monk seal pups (Job, 1992: Figs. 8, 9). Other published sonagrams of phocid pup vocalizations reveal no transitions, although complex transitions certainly occur commonly in other circumstances, e.g.: by weaned northern elephant seals and by captive adult harbor seals seemingly mimicking human speech (Rasa, 1971; Ralls *et al.*, 1985).

In contrast to most phocids, some internal transitions occur regularly in the brief barks of walrus calves (Miller, 1985: Figs. 4, 6). Calls of *Arctocephalus* pups are complex and frequently have several distinctive parts set apart by sudden transitions, as in harp seals. Good sonagrams illustrating this feature are in Trillmich (1981: Fig. 5) and Roux and Jouvantin (1987: Fig. 6) (see also Brown, 1974: Fig. 5). Northern fur seal pups reportedly begin their calls with a staccato series and end with a tonal part (Insley, 1989, 1992), although this is not apparent in the sonagrams in Lisitsyna (1973, 1981, 1988) or Takemura *et al.* (1983). Calls by sea lion pups appear to be simpler than in fur seals, with no (or few) internal transitions: see Peterson and Bartholomew [1969: Figs. 11, 12; their Fig. 9 seems aberrant]; Stirling (1972: Fig. 2), Lisitsyna (1980: Fig. 2; 1981: Fig. 10) and Trillmich (1981: Fig. 6). Overall then, vocalizations of harp seal pups are more complex than those described for pups of other pinniped species, as characterized by the number of transitions or parts in them. Before presenting possible explanations of this high complexity, we treat two other dimensions of complexity: formants and syntactical organization.

Formants and syntactical organization

Formants are parts of the frequency spectrum that are reinforced by resonant properties of the vocal tract (Cherry, 1978; Pierce, 1983; Lieberman, 1984). The most suitable kinds of sounds for formants are produced glottally and have a low fundamental frequency and broad frequency range; in combination these provide a relatively complete coverage of the whole frequency range within which resonances may occur (Andrew, 1963). Formants can enrich a species' communication system greatly, but little attention has been paid to their presence or signif-

icance in pinniped vocalizations to date (see Insley, 1992). Because of the low glottal pulse rate and broad frequency range, formants are common in many calls of pup harp seals (e.g.: Figs. 2, 5, 6). Formants occur also in pups of the Weddell seal (Fig. 4) and Hawaiian monk seal (Miller and Job, 1992). They are present in the adult harp seal underwater "grunt" vocalization (Møhl *et al.*, 1975: Figs. 376a and 378), in various non-mimic and mimic airborne vocalizations of captive harbor seals (Ralls *et al.*, 1985: Figs. 2, 4, 5), in airborne walrus vocalizations (Miller and Boness, 1983; Miller, 1985), and in many airborne otariid calls (references provided elsewhere in this paper). Most formants appear simply as bands of resonance (e.g.: Figs. 2, 4, 5 and 6), but others are clearly modulated and are more similar to formants in humans (e.g.: Ralls *et al.*, 1985: Figs. 4, 5; Peterson and Bartholomew, 1969: Fig. 5). Formants thus occur widely in pinniped calls (mainly airborne ones). Separate sound sources (e.g.: vibration of the velum) and other types of supralaryngeal filtering than resonance may occur in harp seal pups, and may account for many complex spectral features (see Hauser, 1992).

Various forms of non-random structure in the calls of harp seal pups were detected, such as where certain acoustic properties (like rhythmic FM) predominate in calls, the relationship of call length (number of parts) to the incidence of properties like FM, the extent to which different properties occur with one another, and sequential dependencies among properties. The non-random organization of harp seal pup vocalizations merits the term "syntax" (defined simply as "any system of rules that allows us to predict sequences of signals": Snowdon, 1982). More specifically, a distinction between "lexical" and "phonological" syntax can be

recognized (Marler, 1977a), with the latter term applying to the different facets of acoustic organization summarized above.

Some aspects of phonological syntax are widespread in pinnipeds and other mammals, like the tendency for vocalizations to begin with rising frequency and to end with falling frequency (Hauser and Fowler, 1992). Such a widespread trend may simply reflect increasing air pressure at the beginning of a vocalization, and declining air pressure at the end (R.A. Kastelein, pers. comm.). Other patterns we detected for harp seal pups have no counterparts known to us, though obviously their general acoustic properties are widespread [e.g.: broadband noise, rhythmic FM, complex pulsing, and spectral richness; see Marler (1977a) and Morton (1982)]. Sequential syntactical organization is striking in the stereotyped long-distance vocalizations of pup fur seals (e.g.: Trillmich, 1981; Insley, 1989, 1992) but is not apparent in published sonagrams of the less structured calls of other pup phocids or sea lions. However, most published analyses for the latter groups are not detailed or extensive enough to reveal syntactical patterns within vocalizations.

One aspect of phonological syntax stressed by Marler (1977a) is "compounding", when "complex sound sequences ... are compounds of different sounds, some of which [when] uttered separately have a different function." Similarly, Hailman *et al.* (1985) recognized some recombinant properties of bird vocalizations, like recombinability of different element types and ability to generate novel combinations. Both Marler (1977a) and Hailman *et al.* (1985) dealt with discrete temporally separated elements, rather than portions of physically continuous sounds such as were analyzed herein. Also, information on functions of the different types of

call parts is lacking. Even so, most of the structural properties those authors discussed apply well to our observations (parenthetically, we note that their approaches seem eminently well suited for analyzing the complex underwater vocalizations of harp seals and antarctic phocids).

Why are harp seal pup vocalizations so complex and variable?

Harp seal pup vocalizations intergrade extensively between simple soft calls that predominate over short distances and louder more complex calls that predominate over longer distances: there are no classes into which calls can be placed easily. As for otariids, all that can be stated is "extreme forms ... are given under clearly different circumstances" (Trillmich, 1981). In *Arctocephalus*, each of the "extreme forms" varies little across repetitions, although the calls are structurally complex (Trillmich, 1981). In the harp seal, great structural variation occurs even across successive calls by a single pup. Marler (1976) suggested that such structural variation in calls is unlikely to represent "disorderly, erratic variation resulting from a loose relationship between vocal morphology and the physiological determinants of other ongoing behaviors" [see also Marler and Tenaza (1977)]. Instead, structural variation likely carries important though subtle information of an affective or symbolic kind (e.g.: Kiley, 1972; Green, 1975; Marler, 1977b; Maier, 1982).

Can the preceding generalization apply to harp seals? In long and complex social relationships like those between mother and pup Galapagos fur seals and Steller sea lions, many kinds of communication occur in many different circumstances, and major developmental changes in the offspring (over years!) must be integrated into the fabric of signaling. The mother-pup relation-

ship in harp seals lasts only about 1-10% as long as in various otariid species, is behaviorally simple, and faces very simple challenges, e.g.: mothers do not travel far from their pups; their separations are brief; pups remain in one place, and breeding density is low compared with otariids and elephant seals (Stewart, 1983; Kovacs, 1987; Lavigne and Kovacs, 1988). Thus, the amount of socially useful information in harp seal pup calls is unlikely to be reflected simply by acoustic structure (e.g.: it is hard to imagine that there are more kinds of affective information that must be transmitted from pup to mother in this species than in otariids). Indeed, even pup harp seals that are playing alone on the ice surface are "vocal ... growling and 'mumbling' almost continually" (Kovacs, 1987; see also Terhune *et al.*, 1994). Acoustic complexity and variation in pup calls of this species may be epiphenomena of a developing vocal system that eventually become manifest in highly complex adult underwater communication (Møhl *et al.*, 1975; Thomas 1979; Watkins and Schevill, 1979; see also Terhune *et al.*, 1994). Developmental parallels occur in "subsong" or "plastic song" of young songbirds, before they develop their final adult song, and "babbling" of human infants (Marler, 1977a, Marler and Peters, 1982). To test this possibility for seals, two questions can be asked: (a) how is contextual information used in vocal communication?; and (b) are there sex differences in vocal development? Comparative studies on acoustic structure and variation of pup calls in other species (especially phocids) would be illuminating, as certain kinds of social bonds (e.g.: mother-offspring) are particularly important for understanding affiliative communication (Marler, 1976; Eisenberg, 1981; Harcourt *et al.*, 1993), and species differ greatly in this regard: the hooded seal, for example, has an extremely brief mother-pup bond and a low diversity

of underwater calls; most antarctic seals have fairly brief mother-pup bonds, but complex underwater repertoires like the harp seal; etc.

Suggestions for future research

Acoustic structure of airborne vocalizations of pinnipeds is astonishingly poorly known, considering how easy it is to study many species and record large samples of vocalizations (Watkins and Wartzok, 1985; Miller and Job, 1992; Asselin *et al.*, 1993). To our knowledge, even sonagrams of pup calls in the context of the mother-pup bond are lacking for most species. In the Phocidae, analyses for only six of the 18 species have been published: the Hawaiian monk seal, harp seal and northern elephant seal have been studied reasonably well; while acoustic structure of pup vocalizations in the harbor seal, Weddell seal and Grey seal (*Halichoerus grypus*) has been described only meagerly (review in Miller and Job, 1992). Broader and more detailed studies on acoustic structure (including syntax, and effects of separate sound sources and of supralaryngeal filtering), on vocal development, and on the behavior of signaling in young pinnipeds are needed to place our observations on harp seals in proper perspective.

Finally, better knowledge of anatomy and physiology of sound production in pinnipeds would enhance our understanding of how acoustic signals are structured and how they have evolved. Knowledge of anatomy of the pinniped vocal apparatus largely rests on old studies [for reviews, see Negus (1949), Schneider (1962, 1964) and Piérard (1963, 1969)]. Yet vocal anatomy is undescribed for most pinniped species, and there are many remarkable special structures that likely function to produce or modify sounds: e.g. air sacs in the ribbon seal (*Phoca fasciata*), expansible trachea and soft palate in the

Ross seal (*Ommatophoca rossi*), and pharyngeal diverticula in the walrus (Fay, 1960; Abe *et al.*, 1977; Ray, 1981). Even for understanding how acoustic structure, complexity and variability are produced in conventional ways (as in the harp seal), basic research on anatomy and physiology of the pinniped vocal tract would be invaluable (e.g.: Coutinho *et al.*, 1974; Hartley and Suthers, 1988; Shipley *et al.*, 1991; Hauser *et al.*, 1993; West and Larson, 1993).

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