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How vocal are harp seals (*Pagophilus groenlandicus*)? A captive study of seasonal and diel patterns

A. Serrano[1,2] and E. H. Miller[1]

[1]*Biology Department and Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF, Canada A1B 3X9*
[2]*Department of Biology, University of New Brunswick, P.O. Box 5050, Saint John, NB, Canada E2L 4L5*

Abstract

The purpose of this study was to document the annual cycle of underwater vocal activity in captive harp seals (*Pagophilus groenlandicus*). This species is vocally active on ice and under water during the breeding season. Vocal behaviour in the non-breeding season is unknown, but the species is highly gregarious throughout the year so we predicted vocal activity year-round. Ten harp seals of both sexes and various ages were studied in large outdoor tanks with flow-through ambient seawater from January 1996 to May 1997. The study was conducted in Newfoundland, within the species' natural range, so vocal activity should be representative of that in the wild. Vocal activity varied seasonally and with time of day. Rates of underwater vocalization increased in February and peaked in March (the breeding period) and were higher at night than during the day. This study showed that captive groups of harp seals are vocally active throughout the year. Field recordings outside the breeding period are needed to extend these findings and to determine the social functions of vocalizations in feeding, migration, and other contexts.

Key words: harp seals; *Pagophilus groenlandicus*, diel activity; vocalizations; seasonality.

Introduction

Seasonal changes in the environment induce adaptive variations in animal behaviour (Boyd, 1991). Some aspects of annual cycles of pinnipeds have been well studied (e.g. migration, parturition, mating), but seasonal and diel vocal activity has been documented only in isolated studies. Male Weddell seals (*Leptonychotes weddellii*) are vocal when establishing and defending underwater territories, and show increased calling rates at this time (Morrice *et al*., 1994). Seasonal and diel variations in vocal activity of pinnipeds in the high Arctic was documented by Stirling *et al*. (1983), who proposed that the decline in vocalization rates might be due to fewer social interactions. Annual and diel variations in underwater vocalizations of Weddell seals were studied by Green & Burton (1988), who found high vocal activity at night. Male elephant seals (*Mirounga angustirostris*) are most vocal after sunset and least active at mid day, a pattern that reflects ambient temperature (Shipley & Strecker, 1986). Crabeater (*Lobodon carcinophagus*) and leopard (*Hydrurga leptonyx*) seals are most vocal in evenings and early mornings (Thomas & DeMaster, 1982). Grey seals (*Halichoerus grypus*) are most vocal at nights (Chwedeñczuk & Frysz, 1983). Harp seals (*Pagophilus groenlandicus*) are more vocal at night than morning or early afternoon (Terhune & Ronald, 1976). Scattered evidence suggests low daytime vocal activity, but details and causes that determine diel patterns are poorly documented and understood (Terhune and Ronald, 1976; Watkins & Schevill, 1979).

The harp seal is one of the most intensively studied pinnipeds in the world (Ronald & Healey, 1981; Ronald & Dougan, 1982; Lavigne & Kovacs, 1988; Sergeant, 1991). Harp seals have been exploited for commercial purposes for more than a century (Ryan, 1994), and numerous studies have been conducted on its annual cycle, feeding, reproduction, growth, and many other topics. However, little is known about the species' social structure or communication because it is highly migratory and breeds on and in association with pack ice. Several studies on behaviour of females and pups have been made, but only scattered information exists for underwater behaviour or social interactions among adults (Merdsoy *et al*., 1978; Lavigne & Kovacs, 1988). Numerous accounts of vocalizations during the breeding period have been published. Schevill *et al*. (1963) first reported underwater vocalizations from the species (a captive female), and Møhl *et al*. (1975) provided a detailed account of underwater

Table 1. Composition of harp seal groups and hours of behavioral observations during 1996[1].

Seals in tank 1	Hours of observation	Seals in tank 2	Hours of observation	Dates
F4, M1, M2, M5, M6	26.0	F1 to F3, M3, M4	20.0	2–23 February
M1 to M3, M5, M6	25.0	F1 to F4, M4	30.0	23–28 February
M1, M3 to M6	22.5	F1 to F4, M2	35.0	28 February–5 March
F2, F3, M1, M4	12.6	F1, F4, M2, M3, M5, M6	10.4	6–8 March
F1 to F4	65.0	M1 to M6	73.6	8–12 March
F1 to F4, M3	5.5	M1, M2, M4 to M6	9.5	13–14 March
F1 to F4, M3, M4	14.5	M1, M2, M5, M6	8.0	14–15 March
F1, F3, M3, M4	19.5	F2, F4, M1, M5, M6	25.5	15–21 March
F1, F3, M3, M4	7.0	F2, F4, M1, M2, M5, M6	9.0	21–23 March
F1 to F3, F4, M1	17.0	M2 to M6	10.5	23–27 March
F1 to F4, M1 to M6	36.0	None		27–31 March

[1]F1–F4 refer to females 1 through 4; M1–M6 refers to males 1 through 6.

calls. Airborne calls were described by Terhune & Ronald (1976), Miller (1991), and Miller & Murray (1995). Almost all published analyses to date are from the breeding period. Møhl *et al.* (1975) commented that the species was relatively silent in captivity, though they noted five kinds of calls when two unacquainted females were housed together.

Harp seals are highly social throughout the year, undertaking long-distance migrations in herds, and feeding in groups on the Arctic summering grounds. It seems extremely likely that such social activities require vocal communication all year around. To test this hypothesis, we monitored underwater vocal activity before, during, and after the breeding season in a colony of captive seals.

Materials and Methods

Study animals and facility

Ten harp seals of different ages and both sexes were studied at the Ocean Sciences Centre (Memorial University of Newfoundland) at Logy Bay, Newfoundland (47°38′N 52°40′W). Some seals were born in captivity or lived at the Centre since 1990 ('residents'). Others ('new') were captured as adults in 1995. Moulton *et al.* (1999) provided further information on these animals. Seals were maintained in two wooden outdoor tanks, each measuring 12.3 m in diameter and 2.5 m in depth. The tanks were bordered by approximately 190 m^2 of wooden decking to which the seals had free access. The tanks were supplied with fresh seawater pumped from Logy Bay and were drained and cleaned at least weekly. The seals were usually fed twice a day, around 1000h and 1500h.

Equipment and data collection

Data collection started on 12 January 1996 and ended on 30 May 1997. For purposes of analysis, data were classified as 'breeding season' (19 February–31 March) and 'non-breeding season' (1 April–18 February) based on dates in Sergeant (1991). Underwater vocalizations usually were recorded twice per week outside the breeding season, and in the breeding seasons of 1996 and 1997. Recordings were made for 3–4 h in mornings (0530–0930h) and 5–6 h in evenings (1700–2300h or 1800–2400h). These sampling times were chosen because of low human disturbance and because harp seals are considered to be most active then (Terhune & Ronald, 1976). Some recordings were made at midday if there was no human disturbance. Aerial recordings were made opportunistically and not included in these analyses.

Data on underwater calling rates were summarized as half-hour and daily means and classified as being in the non-breeding or breeding season. Data also were classified by time of day: morning (0100 to 1100h), mid-day (1200 to 1600h), or evening (1700 to 2400h).

During the 1996 breeding season, seals were placed in the tanks in several combinations to investigate sexual differences in vocalizations and influences of group composition on vocal activity (Table 1): Treatment 1 (T1), one adult male with all four females; T2, one adult female with all adult males; T3, all six males only; T4, all four females only; and T5, all seals combined. It was not possible to repeat this design in 1997 due to conflicts with other studies. However, having all adult females and adult males in the same tank for most 1997 recording sessions was possible.

Recording equipment consisted of: a Sony stereo cassette recorder model TC-D5PROII, with a recording response of 0.04–14.0 kHz ($\pm$ 3 dB) and an omnidirectional hydrophone (built by Marine Mammal Research Unit, University of British

Table 2. Relationship between rate of underwater vocalization to group composition in harp seals during 1996.

Group composition	Number underwater vocalizations/hour[2]
All females*	1.0 ± 0.34 (6)
All males†	4.3 ± 1.81 (7)
One female plus all males	6.3 ± 1.05 (7)
One male plus all females	7.8 ± 3.03 (7)
All females plus all males	12.8 ± 2.32 (19)

*$P=0.016$ [one-way ANOVA among group types; 'all females' differed significantly from 'all females plus males' by Scheffé's test ($P=0.049$)].
†Mean rate of underwater vocalization ± S.D., hours recorded in parentheses.

Columbia) with a recording response of 0.006 to 40.0 kHz (at 4 dB down).

Data processing and analysis
A third of the samples was selected randomly to eliminate the autocorrelation component introduced by sequential sampling (Kovach, 1994). Remaining samples were classified by rate of underwater vocalizations: NV, no vocalizations (0 per hour); LV, low rate (1–11 per hour); or HV, high rate (12–84 per hour). Mean time of day and circular standard deviations were calculated and summarized according to year and season for all call categories (Kovach, 1994).

A Watson's F-test (Watson & Williams, 1956) was used to test the null hypothesis that the mean time of day (for NV, LV, and HV) were equal across years and seasons. This model was used because time of day was included as a predictor variable (Watson & Williams, 1956). We used F-statistics to compare the lengths of the mean vectors for each sample; the results in F-statistics are the same as Fisher's variance-ratio statistic that is commonly used in linear statistics, including analysis of variance (Kovach, 1994). Most statistical analyses were done using SPSS Release 6.1.2. Circular statistics were performed with Oriana Version 1.0 (Kovach, 1994). The probability level of accepted for a significance difference was $\alpha=0.05$.

Results

Rates of underwater vocalizing were highest in sexually mixed groups and lowest in groups of only females or only males. However, only T3 (all males; mean=4.3 vocalizations/hour) and T4 (all females; mean=1.0 vocalizations significantly) (Table 2). The rate of underwater vocalization was not significantly associated with group size (Table 3).

Table 3. Relationship between the rate of underwater vocalizations and harp seal group size during 1996.

Group size*	Number underwater Vocalizations/hour†
4	9.6 ± 3.12 (7)
5	11.3 ± 1.74 (6)
6	7.9 ± 1.96 (7)
10	11.1 ± 0.42 (19)

*$P=0.656$ (one-way ANOVA among group sizes).
†Mean rate of vocalization ± S.D., number in parentheses is hours of recording.

In 1996, the rate of underwater vocalizations increased in late January, varied but remained high in February, and peaked in early March. The highest rate was 43/hour (6 March) and the lowest was 0/hour (29 February; 8 April). Rate of underwater vocalization declined slightly in the middle of March, but increased again at the end of March. The highest rate in the non-breeding season was 13/hour (22 January) and on 22 April and 6 May none were heard. Rate of vocalization was significantly lower in the non-breeding (one-way ANOVA; $P=0.048$): the highest weekly mean rate of vocalizations was 11.8 and the lowest was 7.5. During the non-breeding season the highest weekly mean rate of vocalizations was 6.9 and the lowest was 0 (Fig. 1).

A similar pattern was present in 1997. Vocal activity started to increase by the end of January, the rate varied, but remained high in February, and activity peaked in mid March. The maximum hourly rate of vocalization for the 1997 breeding season was 21 (13 March) and the minimum was 0 (19 February). During the non-breeding season the highest hourly rate was 10 (2 February) and the minimum was 0 (14 January; 14, 15, and 22 April; 15 and 16 May). During the breeding season, the maximal hourly mean rate of vocalization per week was 12.8 and the lowest was 2.4. During the non-breeding season, the maximal hourly mean rate of vocalization per week was 6.7 and the minimum was 0 (Fig. 1). As in 1996, in 1997 the rate of vocalization was significantly higher during the breeding season (one-way ANOVA; $P=0.016$).

Rate of underwater vocalizations did not differ significantly between morning and evening samples in 1996 or 1997 (one-way ANOVA; $P=0.39$) (Fig. 2). Highest hourly rates of evening calling were 21.7 and 19.6 (breeding) and lowest were 0 (non-breeding) in 1996 and 1997, respectively. Highest hourly rates of morning calling were 11.7 and 15.7 (breeding) and 1.5 and 0 (non-breeding) in 1996 and 1997, respectively.

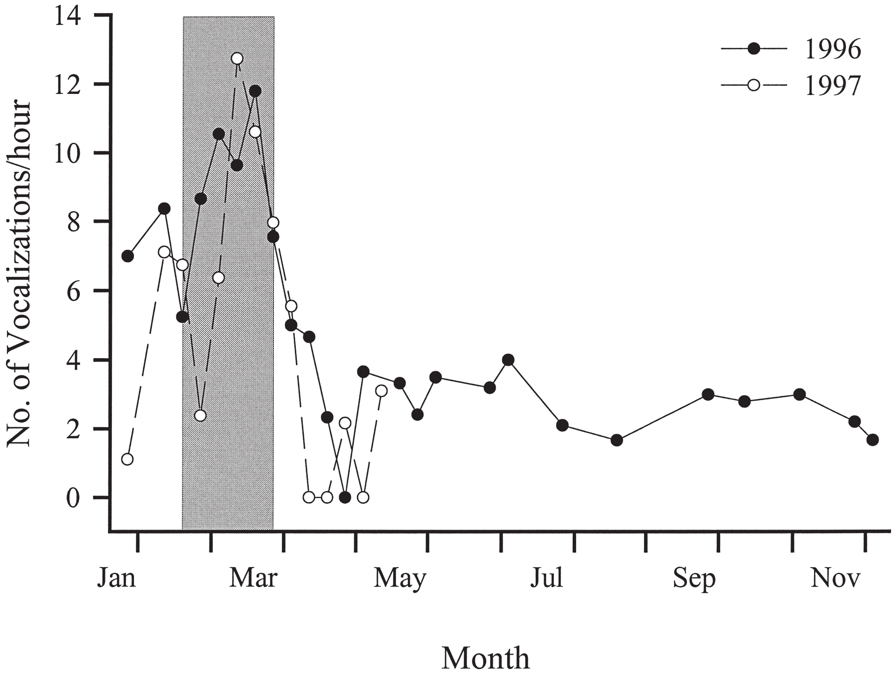

Figure 1. Seasonal variation in calling rates of harp seals, based on weekly means. Shaded area indicates breeding season.

Vocal activity peaked at different times of the day in the non-breeding and breeding seasons of 1996 and 1997 (Table 4). NV differed significantly between years in both seasons. Mean time of day for NV was in early morning during the non-breeding season and in evening or late at night in both years. Mean time of day for LV differed significantly between years. Mean time of day for LV was morning in the non-breeding seasons of both years and the breeding season of 1996, but at night in the breeding season of 1997. Mean time of day of HV did not differ significantly between the non-breeding seasons of 1996 and 1997, but differed significantly between the breeding seasons of 1996 and 1997.

Discussion

The increase in vocal activity in February and the peak in March are consistent with the timing of reproduction in the wild (Terhune & Ronald, 1976; Lavigne & Kovacs, 1988, Sergeant, 1991) and with high vocal activity in mid March in the Gulf of St. Lawrence (Terhune & Ronald, 1976).

The function of repetitive calling during the breeding season is to distinguish the signaler from the background noise (Watkins and Schevill, 1979; Terhune and Ronald, 1986). This is particularly important because all acoustic signals are masked by environmental noise (Brenowitz, 1986). High calling rates, when vocalizations are intended for short-range communication, might mask the calls of other seals (Watkins and Schevill, 1979; Terhune and Ronald, 1986). In other words, to reduce ambiguity a signaler must increase the stereotypic nature of the signals, and as a consequence the amount of information that the signal conveys is increased (Krebs and Davies, 1993). Calls produced at high rates function better for long-range communication, signaling an individual's location. Other characteristics of communication sounds function better over short distances e.g., signaling gender, individual identity, hierarchical status, or signaler intentions (Watkins and Schevill, 1979; Terhune and Ronald, 1986).

Vocal activity of these captive harp seals declined in late March and early April in both 1996 and 1997. At this same time, moult begins in the wild northwestern Atlantic (Sergeant, 1991). Møhl *et al.* (1975) made underwater recordings in the vicinity of moulting herds, but detected no underwater sounds attributable to harp seals. The low vocal activity at this season presumably reflects the few social interactions that occur at this time and the small percentage of time spent by seals in the water (Møhl *et al.*, 1975; Moulton *et al.*, 1999). The low

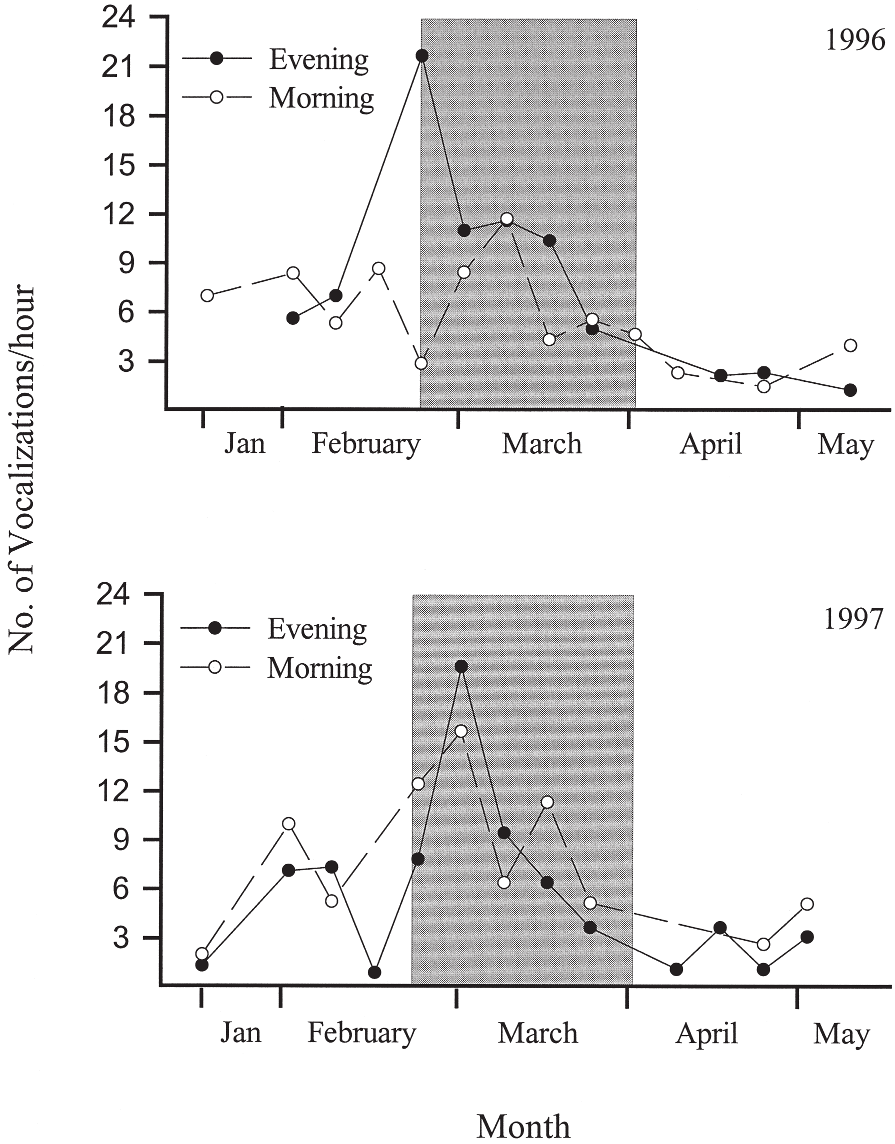

Figure 2. Monthly variation in calling rates of harp seals in mornings and evenings, during 1996 (top) and 1997 (bottom) based on weekly means. Shaded area indicates breeding season.

vocal rate could also relfect the desire to remain quiet during a vulnerable time or to save acoustic energy for more activities like mating.

Contrary to Terhune & Ronald (1976), vocalization rates did not differ significantly between day or night in our study. Mean time for HV was at night for the 1996 breeding season, but during the day for the 1997 breeding season. A similar trend was apparent for LV. Only the mean time for NV occurred at night in both years. Differences between our results and those of Terhune & Ronald (1976) could be due to: (1) fewer recordings, shorter sampling period, and consideration of only high-frequency vocalizations by the latter authors, or (2) effects of captivity on vocal activity in our study (Martin & Bateson, 1994).

In the breeding seasons of 1996 and 1997, high-frequency vocalizations with many harmonics were used more commonly than low-frequency calls with few harmonics. This pattern was reversed in the

Table 4. Relationship between harp seal vocal activity and time of day and reproductive season.

Reproductive season	Underwater vocalization category	Time of day ± 1 SD	
		1996	1997
Non-breeding	NV*	11 ± 0.98 (21)	7 ± 0.37 (25)
	LV*	11 ± 0.16 (49)	8 ± 0.15 (26)
	HV	8 ± 0.82 (3)	8 ± 0.63 (10)
Breeding	NV†	23 ± 0.37 (22)	18 ± 0.45 (34)
	LV‡	2 ± 0.42 (49)	21 ± 0.23 (47)
	HV*	22 ± 0.92 (36)	10 ± 0.41 (37)

Number in parentheses is hours of recordings.
*P<0.001 (Watson's F-test comparing years).
†P=0.030 (Watson's F-test comparing years).
‡P=0.050 (Watson's F-test comparing years).

non-breeding seasons of both years. Vocalizations that predominated in the breeding season can be easily distinguished at close range in the noisy breeding-season underwater environment (Møhl *et al*., 1975; Watkins & Schevill, 1979; Terhune & Ronald,1986). The structurally complex vocalization types used during the breeding season probably are adapted to contrast with ambient noise (Watkins & Schevill, 1979), and also could convey rich information at close range because frequency attenuation and environmental degradation are minimal over short distances (Møhl *et al*., 1975). Seals probably have need for more varied types of sounds (i.e., more information content) during more social periods.

Harp seals were vocally active around the year and in various seasonal settings. To understand social structure and vocal behaviour in this species, field recordings from outside the breeding season are needed. Main activities in that period are migration, local movements, and pursuit of aggregated (and sometimes highly mobile) prey, all of which require coordinated activity, at least partly mediated by vocalizations.

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