

## Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*

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**Abstract.** Vocalizing by natural-living harbour seals has been considered to be rare, limited primarily to aerial threats. A few studies on captive harbour seals, however, indicated that this species produced a wider variety of aerial vocalizations than was previously thought. The objective of this study was to determine whether adult male harbour seals in the wild vocalized under water during the breeding season and whether there was any variation in vocalizations between individuals. Underwater vocalizations of 10 males were tape-recorded at Point Lobos State Reserve, California during the spring and summer of 1991. Females did not vocalize except on land when they threatened other seals. Observational data was taken to identify the vocalizing seal and to determine whether other seals in the vicinity showed any reactions to the vocalizations. Five vocalization types were identified and analysed: grunt, groan, creak, bubbly growl and roar. There were significant differences between males with regard to the frequency measurements of the roars as well as to their entire acoustic displays but there was little intra-individual variation. It is suggested that underwater vocalizations are used in male–male competition and/or as reproductive advertisement displays to attract females.

Until recently, harbour seals, *Phoca vitulina richardsi*, were considered to be one of the least vocal pinnipeds with only aerial grunts, growls and snorts making up their repertoire (Bigg 1981). There were some indications that this was not an accurate perception when a few captive animals were recorded producing various vocalizations, primarily in air. To our knowledge, Schevill et al. (1963) made the first underwater recordings of a captive male harbour seal, *Phoca vitulina concolor*, which were 'hard to hear and harder to analyze'. Their recordings, however, were made in January, which is outside of the breeding season. Another interesting study on captive harbour seals examined vocal mimicry (Ralls et al. 1985). One male seal named 'Hoover' produced a wide variety of aerial vocalizations including mimicry of human words, with the greatest amount of vocalizing occurring during the reproductive season. These data, plus additional studies, as well as anecdotal evidence (see Hanggi 1992 for a review), raised questions about how such vocalizing related to the breeding behaviour of this species.

Harbour seals breed along the eastern Pacific coast from Mexico to the Gulf of Alaska and have

an extended pupping season due to clinal variation (Riedman 1990). They congregate in mixed sex and age groups in areas ranging from sandy beaches to offshore rocky outcroppings. Females may stay in oestrus for up to 9 weeks and males appear to be in breeding condition for up to 9 months (Bigg 1981). Riedman (1990) states that harbour seals are somewhat polygynous with dominant males mating with more than one female. However, the mating behaviour of this species has not been well documented and there have been only a few reported observations of aquatic mating (see Bigg 1981 for a review). During the breeding season, male harbour seals interact with varying degrees of aggression with other males and perform elaborate visual aquatic displays of fore- and hindflipper slapping of the water surface and lobtailing. Sullivan (1981) believes that such displaying is related to reproductive behaviour but he does not report any breeding activities after such displays nor does he discuss the possibility of vocal displays.

In many pinniped species, vocalizations play an important role in coordinating social and sexual behaviour. Mothers and their offspring are able to

recognize each other through their vocalizations, which can be crucial in maintaining contact in a breeding system where there are numerous conspecifics present such as on crowded rookeries (see Hanggi 1992 for a review). Recognition of individuals is not restricted to mothers and pups for many of the pinnipeds. Threat calls of adult male elephant seals, *Mirounga angustirostris*, show individual differences (Shiple et al. 1981) as well as geographical differences (Le Boeuf & Peterson 1969). E. B. Hanggi, E. C. Spada, R. J. Schusterman & C. Carello (unpublished data) found large inter-individual variation in the barks of territorial adult male California and Galapagos sea lions, *Zalophus californianus*, suggesting that males could recognize other males on a breeding rookery. Male subantarctic fur seals, *Arctocephalus tropicalis*, appear capable of discriminating the vocalizations of neighbours from strangers (Roux & Jouventin 1987) and Stirling (1971) suggests the same for the South Australian fur seal, *Arctocephalus forsteri*. Male Weddell seals, *Leptonychotes weddelli*, have a larger, more complex repertoire than females which they appear to use in underwater territorial displays during the breeding season (Thomas & Kuechle 1982). The harp seal, *Phoca groenlandica*, maintains underwater territories and is also very vocal, with 15 vocalizations in its repertoire (Mohl et al. 1975). Studies examining the relationship between frequency of vocalization and seasonal reproductive behaviour of both captive and natural living pinnipeds include the ringed seal, *Phoca hispida* (Stirling 1973), bearded seal, *Erignathus barbatus* (Burns 1981), harp seal (Terhune & Ronald 1976), walrus, *Odobenus rosmarus* (Ray & Watkins 1975), California sea lion (Schusterman & Dawson 1968; Schusterman 1978) and spotted seal, *Phoca largha* (Gailey-Phipps 1984). These vocalizations are thought to be used to attract females and/or establish dominance or territories among males.

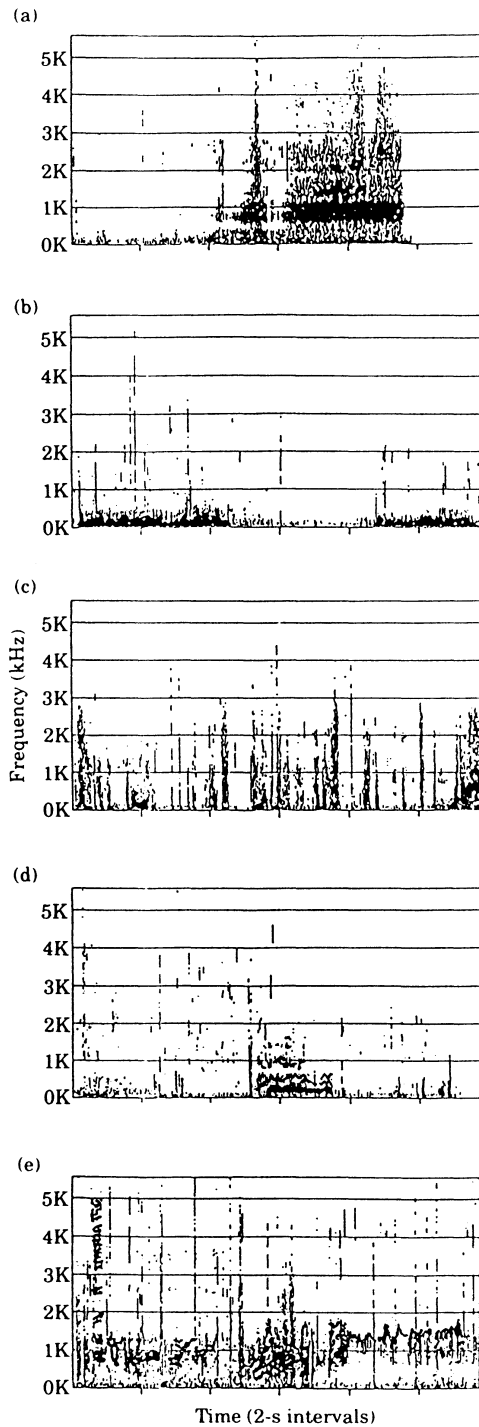
The surprising vocal ability of captive male harbour seals, along with this species' known breeding behaviour, led to the hypothesis that males in the wild produce vocalizations under water which, in conjunction with visual aquatic displays, might be used in male-male competition and/or as reproductive advertisements to attract females. In a previous paper, we gave initial results showing that natural-living male harbour seals do produce underwater vocalizations during

the breeding season (Hanggi & Schusterman 1992). In this paper, we document the basic vocal repertoire of these seals and demonstrate that there are individual differences in vocalizations and in vocal displays between male harbour seals.

## METHODS

We tape-recorded underwater vocalizations and made observations of harbour seals at Moss Cove, Point Lobos State Reserve, California for 3 days a week (6–10 h/day) during the 1991 breeding season, which occurs during the months of May–July. Moss Cove is an approximately 183 × 91 m cove with rocky outcroppings and cliffs on either side of a pebble beach. Harbour seals hauled out primarily on about 10 rocks separated from the shoreline in the southern part of the cove with the closest rock approximately 1.5 m from land. Five of these rocks and the rocky shoreline formed a circular border around a small area of water which we called the arena. The arena varied in depth from approximately 1 to 4.6 m with an uneven substrate. On the north shore of the cove and in another adjacent cove to the south there were also harbour seals but these seals were not part of the group we observed. The maximum number of seals in our area was approximately 55 and included animals of all age classes and both sexes. A total of six newborns survived the season. Because the only marine mammals in this area were harbour seals we are confident that our recordings were from this species.

We suspended a hydrophone into the centre of the arena by attaching it to a 6.1-m long PVC pipe that floated at the water surface and was attached to the rocks on shore. The hydrophone was part of a RS301A Acoustic Listening System (made by Acoustics Systems Inc., Goleta, California) and tape-recordings were made using a Sony TC-D5M stereo tape-recorder, system frequency response 0.03 kHz to 17 kHz ± 3 dB. We made underwater recordings on one channel and used the other channel for narration. We began recording when we heard the first vocalization by means of headphones or when a seal entered the arena and behaved in a manner that suggested it would start vocalizing. Such behaviour included floating, submerging then surfacing and looking around, followed by swimming slowly in and out of the area. At other times, two male seals would interact aggressively by rolling over each other, biting and



clasping then separating and one or both would perform some visual displaying (fore- or hind-flipper slapping, lobtailing; Sullivan 1981). We left the tape-recorder on until the seal either stopped vocalizing for several minutes or left the arena. This was defined as a vocalizing bout. We also made recordings when no seals were in the water as a baseline for background noise. We did, on occasion, see submerged seals, visual displaying at the water surface and interactions farther away from our study site but were unable to pick up any vocalizations. This does not imply that the seals were not vocalizing, more likely, some of these animals may have been out of acoustic range. At times, noise levels from wave action were high, which may have blocked transmission.

In the arena, we were able to identify the vocalizing seal for all bouts recorded by observing which seals were present, which seals were at the surface or under water at the time of the vocalization, and the synchronicity of submerging and vocalizing. Individuals were recognizable by the pattern of their pelage and by scars. All vocalizations were produced under water with the exception of aerial threats between animals hauled out on the rocks. On most days the vocalizing seal was visible enough while it was submerged so that the body orientation could be determined.

For standardization and to assist in comparisons, we made sonograms of vocalizations of 10 adult male harbour seals as 10-s samples over a frequency range of 0–5 kHz, using 256 points per frame. We also examined sonograms on a 0–10 kHz scale to determine whether there were any sounds above 5 kHz. All vocalizations were below 5 kHz so we used this value as the maximum frequency because this range allowed for more precise measurements. This analysis was done on a Macintosh IIfx computer using the MacRecorder program (11 kHz sample rate, anti-aliasing filter, non-compressed recording). Counting each vocalization as a separate unit, we analysed a total of 1882 vocalizations. The physical parameters measured were duration and frequency, and the general pattern of the

Figure 1. Vocalization types produced by adult male harbour seals. (a) Roar, (b) bubbly growl, (c) a series of 14 grunts, (d) groan and (e) creak. Note the long durations of the roar, bubbly growl and creak and the short durations of the grunts.

vocalization as well as presence or absence of tonality was noted. Onomatopoeic names were given to aid in classifying each sound. Tonal calls showed harmonic structure and were probably produced in the larynx, whereas non-tonal calls were non-harmonic and may have been made by muscle contractions of the pharyngeal region (Gailey-Phipps 1984).

We ran a chi-squared contingency table analysis (using Statview 512+ on a Macintosh IIfx) to determine whether there were significant differences between individuals in terms of the number of different vocalization types produced by each male. Only one seal vocalized at any given time and all seals behaved similarly while vocalizing. For example, males typically positioned themselves ventral side up while roaring, then surfaced and looked around, and then submerged again to continue vocalizing. The entire vocal display of each seal was used in this analysis to avoid contextual biases. We also performed a one-factor ANOVA test on 20 roars from each of five males to determine whether individual differences could be found by examining one vocalization type. The parameters measured for the roar were duration, and the minimum, maximum and mean frequency of the fundamental. We used the roar vocalization because it was loud, persistent, produced by all males recorded and often repeated, which indicates that it is important in self-advertisement (Gailey-Phipps 1984).

## RESULTS

### Description of Vocalizations

All underwater vocalizations recorded were produced by males. Refer to Hanggi & Schusterman (1992) for a complete description of the behaviour patterns associated with the acoustic displays. Females were not heard vocalizing except when threatening other seals on the rocks. Aerial threats were made by both sexes but will not be discussed here. Five distinct vocalization types were produced by most of the seals: the grunt (689 of 1882, 36.6%), the roar (484 of 1882, 25.7%), the bubbly growl (409 of 1882, 21.7%), the groan (190 of 1882, 10.1%) and the creak (110 of 1882, 5.8%). Although grunts were produced more often than any other vocalization, they are short vocalizations (see Fig. 1c), whereas roars and bubbly growls are long and intense, so in terms of time and energy spent on each of

these vocalization types the roar may be the predominant vocalization.

### Roar

The roar was one of the primary vocalizations used by male harbour seals (Fig. 1a). Roars were given alone or right after bubbly growls and often occurred in succession. They varied in tonal quality and occasionally showed some harmonics. The mean duration of this vocalization for five males was 4.2 s, with a minimum duration of 1.8 s and a maximum of 10.9 s. The minimum frequency of the fundamental had a mean of 283 Hz, with a range of 25–650 Hz. The maximum frequency of the fundamental had a mean of 810 Hz, with a range of 438–1550 Hz. The overall mean frequency was 547 Hz, ranging from 313 to 1100 Hz. This vocalization had less intense bands at intervals up to 3000 Hz and part of the roar sometimes extended beyond 4000 Hz. Frequency range typically increased as the roar progressed. In general, the beginning of the roar sounds breathy and then becomes harsh and louder with a raspy quality. To the human ear it sounds like an animal roaring while releasing air through the mouth.

### Bubbly growl

This vocalization often preceded the roar and was produced by all males recorded. The quality was normally non-tonal but for one animal there was some tonal variation. The duration ranged from 1 s to more than 8 s and this vocalization was very low in frequency (less than 100–250 Hz with no part of the vocalization extending above 400 Hz; see Fig. 1b). To the human listener it sounds as if the seal is blowing a large stream of bubbles and, in fact, when water conditions were good, bubbles could be seen rising to the surface during this vocalization.

### Grunt

This category includes an assortment of very short vocalizations ranging from 0.1 to 0.5 s. Grunts could be given singularly but were generally produced in a series. The frequency range began at approximately 100 Hz and could peak above 4000 Hz. The aural sounds include 'waap', 'rurrh', 'wahwap', 'hhuh' and a pulsed growl. Some of these had a tonal quality showing numerous harmonics when the time axis was extended.

Table I. Total number of vocalization types per male harbour seal

Seal		Grunt	Groan	Creak	Bubbly growl	Roar
Streak Ear	<i>N</i>	48	2	1	70	134
	%	18.8	0.8	0.4	27.4	52.6
Tan Male	<i>N</i>	32	4	1	42	64
	%	22.4	2.8	0.7	29.4	44.7
Grizzly	<i>N</i>	120	10	19	39	47
	%	51.0	4.3	8.1	16.6	20.0
Dark Cap	<i>N</i>	93	11	12	37	31
	%	50.5	6.0	6.5	20.1	16.9
Light Belly	<i>N</i>	83	21	24	48	40
	%	38.4	9.7	11.1	22.2	18.5
Brown Head	<i>N</i>	91	9	0	46	82
	%	39.9	3.9	0.0	20.2	36.0
Tear Drop	<i>N</i>	31	15	5	11	4
	%	47.0	22.7	7.6	16.7	6.0
Lip Bump	<i>N</i>	23	8	4	13	18
	%	34.8	12.1	6.1	19.7	27.3
Rdl	<i>N</i>	77	96	42	76	49
	%	22.6	28.2	12.4	22.4	14.4
Chin Groove	<i>N</i>	91	14	2	27	15
	%	61.1	9.4	1.3	18.1	10.1

Figure 1c shows a variety of these vocalizations produced by one individual.

#### Groan

This category comprised vocalizations that were similar to grunts but were longer in duration and sounded like moaning and tonal groaning to the human listener. The duration ranged from 1 to 5.5 s with a mean of 1.7 s. The frequencies ranged from less than 100 Hz to approximately 1500 Hz. An example of this less common vocalization is shown in Fig. 1d.

#### Creak

Figure 1e depicts examples of the creak vocalization. This vocalization was tonal, showing harmonics ranging in frequency from approximately 700 to 2000 Hz and sometimes extending beyond 4000 Hz. The duration ranged from 0.5 to 6 s and the longer creaks fluctuated in frequency as they progressed. To the human ear, creaks sound as if a rusty hinged door is being opened.

#### Individual Variation of Vocalizations

##### Variation based on vocalization types

There were significant differences in the usage of vocalization types between male harbour seals

(Table I;  $\chi^2=512.183$ ,  $df=36$ ,  $P=0.0001$ , contingency coefficient=0.463, Cramer's  $V=0.261$ ). A chi-squared contingency table analysis showed significant differences ( $\alpha \leq 0.025$ ) between the vocalizations of 40 of 45 pairings of seals. Of these pairings, only Streak Ear-Tan Male, Grizzly-Dark Cap, Light Belly-Dark Cap, Dark Cap-Lip Bump, and Light Belly-Lip Bump did not differ significantly in their use of vocalization types. This indicates that, at least to the human listener, individuals can be identified by their overall acoustic display. For example, Streak Ear's primary vocalization was the roar (52.6% of his total vocalizations) with grunts making up only 18.8%. Grizzly, on the other hand, produced many more grunts (51.1%) and fewer roars (20.0%).

##### Individual variation based on a specific vocalization

To determine whether there was any variation between male harbour seals based on a specific vocalization type, we measured roars of five males for the following parameters: duration, and the minimum, maximum and mean frequency of the fundamental (Table II). A one-factor ANOVA and a Fisher's paired least significant difference test showed that there were significant differences (95% significance level) between all of the males

Table II. Values of parameters measured for five adult male harbour seals

Seal		Duration (s)	Frequency (Hz)		
			Minimum	Maximum	Mean
Streak Ear	Mean	4.3	620.0	1372.5	996.3
	SD	1.6	25.1	105.7	58.1
Tan Male	Mean	4.1	245.5	510.5	378.0
	SD	0.9	15.1	28.8	18.5
Grizzly	Mean	5.6	248.1	842.3	545.2
	SD	2.0	46.2	99.7	55.3
Dark Cap	Mean	4.2	226.3	584.4	405.3
	SD	2.4	25.0	53.9	35.1
Brown Head	Mean	3.5	51.3	707.5	379.4
	SD	1.2	12.8	40.6	17.8

for most of the parameters. The parameter with the least amount of inter-individual variation was duration, with only three of 10 pairings showing a significant difference between individuals and, therefore, was not considered a reliable measure. Both the minimum and maximum frequency measurements proved to be very reliable, nine of 10 pairings and 10 of 10 pairings showing significance, respectively. The mean frequency was also useful with eight of 10 pairings showing significance. There were no significant intra-individual differences in the frequency measurements ( $\alpha > 0.05$ , Mann-Whitney *U*-test). For two of the five seals, however, there was intra-individual variation in vocalization duration and thus this parameter was, once again, not reliable. Examples of two roars from five different males are given in Fig. 2. As can be seen, frequencies of the fundamentals were very different between males, for example, the mean frequency was 996 Hz for Streak Ear and 379 Hz for Brown Head.

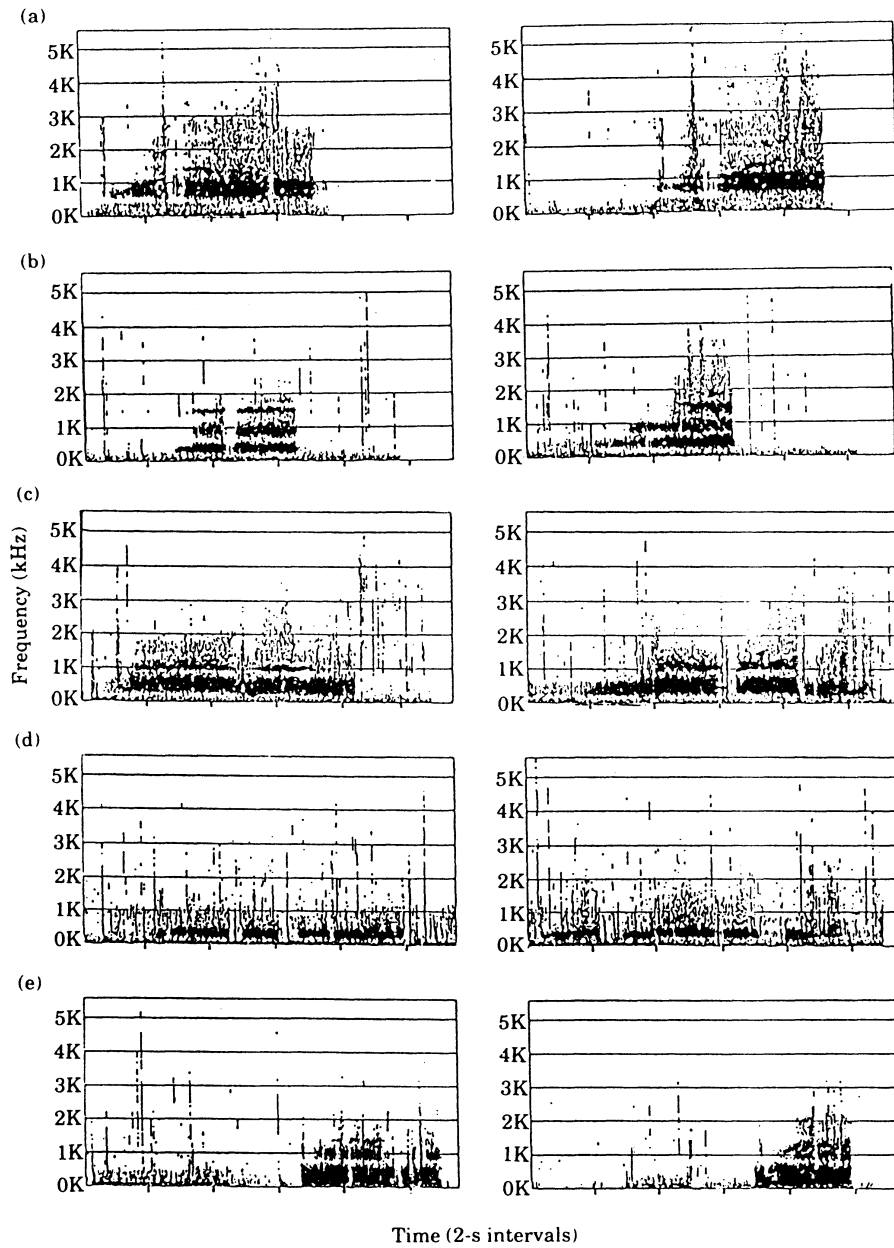
## DISCUSSION

We report two major findings. For the first time, we have evidence that male harbour seals in the wild are vocal under water during the breeding season. Second, we show significant differences in underwater vocalizations between individual males.

Male harbour seals do not appear to hold aquatic territories as do Weddell seals (Thomas & Kuechle 1982) nor do they follow the breeding habits of elephant seals, which have harems of females clustered on land. This species shows little

sexual dimorphism, which is expected from a phocid that breeds in the water (Le Boeuf 1991). The reproductive cycle of female harbour seals makes it possible for one male to mate with more than one female so that slight polygyny is feasible. In such a system, one would expect some degree of male-male competition for access to females (Trivers 1985). Sullivan (1981) contends that male harbour seals use visual aquatic displays to establish breeding privileges through dominance rankings and that they use these behaviour patterns to repel other males and attract females.

Le Boeuf (1991) points out that loud and persistent calls may be necessary in species in which males must attract females. He also states that both visual and auditory displays may serve to indicate a male's fitness because it requires energy and good health to produce prolonged, high-intensity calls or engage in vigorous physical displaying. During the period we observed harbour seals, we never saw females reacting strongly to displaying males and after males finished their vocal displays, they either disappeared or hauled out and rested without any further interactions. Males did, however, interrupt their vocalizing bouts to fight with other males that swam into the area. We believe that males use acoustic displays, in conjunction with visual displays and some degree of fighting, as a form of male-male competition. Following such interactions and displays, males may be able to identify one another based on their vocalizations and thus recognize dominant individuals. The ability of an animal to identify a conspecific through some mechanism that allows recognition from a distance would be highly beneficial. A subordinate could avoid a



**Figure 2.** Examples of the roar vocalization for five adult male harbour seals showing inter- and intra-individual variation. (a) Streak Ear, (b) Tan Male, (c) Grizzly, (d) Dark Cap and (e) Brown Head.

dangerous, physical confrontation with a more dominant individual if it could recognize the dominant animal through some other means,

whether it be visual, acoustical or olfactory. Thus, male-male competition for access to females could be less hazardous. Perhaps females also

assess and recognize males by their acoustic displays and join them at some later time for breeding purposes.

The patterns of behaviour seen during this study are suggestive of a lek system, which is not unheard of in pinnipeds. Male walrus produce bell-like sounds and give visual displays in the water near groups of females hauled out on ice floes (Ray & Watkins 1975). These ritualized displays are believed to attract females. Hooker's sea lions, *Phocartes hookeri*, and California sea lions show signs of intermediate lek systems. It is hypothesized that owing to the wider ranging movements of females, males of these species no longer partake in resource defence, rather, they advertise their traits to females (Boness 1991). The harbour seals in our study exhibited several behaviour patterns that fit the criteria specified by Bradbury (1981) for lek systems. There is no male parental care; no critical resources; males enter and display, both visually and acoustically, in an arena; and females are present during these displays. It is not yet known if females choose displaying males since actual mating was not seen. The purpose of vocal displays, however, is not exclusive to the attraction of females. Male ochre-bellied flycatchers, *Mionectes oleagineus*, use song not only to attract the opposite sex but also in male-male competition on lekking grounds (Westcott 1992).

Future research plans include tracking male and female harbour seals to determine the extent of their movements and their interactions after acoustical and visual displays are performed. By observing both sexes over a prolonged period of time, questions involving dominance, mating behaviour and female choice should be resolved. This will provide a thorough understanding of the function of underwater vocalizations and how they relate to the breeding behaviour of harbour seals.

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