

UNDERWATER VOCALIZATIONS AND VOCAL ACTIVITY
OF CAPTIVE HARP SEALS
(*Pagophilus groenlandicus*)

CENTRE FOR NEWFOUNDLAND STUDIES

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Underwater Vocalizations and Vocal Activity of Captive Harp Seals

(Pagophilus groenlandicus)

By

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Abstract

Pinnipeds are ecologically and socially diverse, attributes that are reflected in their systems of communication. The purpose of this investigation was to document the vocal repertoire and annual cycle of vocal activity in the harp seal, a species that communicates mainly underwater, but whose social and communicative systems are poorly known.

The study's main objectives were to describe the vocal repertoire of captive harp seals through a complete annual cycle and to document annual, seasonal and diel trends in vocal activity. Plasma testosterone in males before, during and after the breeding season were also analyzed to document relationships of testosterone concentration to vocal activity.

The repertoire comprised 18 vocal classes, eight of which have not been described previously. Vocal activity varied seasonally and with time of day. Calls of low frequency (≤ 3 kHz) and with few harmonics (≤ 3) were predominantly used outside the breeding season, and calls of high frequency and with a high number of harmonics predominated in the breeding season.

Levels of plasma testosterone were investigated in four captive harp seals of different ages. Concentrations varied from a minimum of ca. 0.01 ng/ml in April and May to a maximum of 9.4 ng/ml in March. Peaks in concentration occurred at the time when testes are largest in mature wild males, which is several weeks before wild females enter oestrus. Also, peaks in concentration were correlated with high rates of vocalisation. Peak levels of testosterone were lowest in the young and socially subordinate seals.

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List of Abbreviations and Symbols Used

B	breeding season
dB	decibel
h	hour
HV	high vocalizations
Hz	hertz
kg	kilogram
kHz	kilohertz
l	liter
LV	low vocalizations
m	meters
msec	milliseconds
NB	non-breeding
ng/ml	nanograms per milliliter
NV	no vocalizations
sd	standard deviation
sec	seconds

Chapter 1: Introduction

Pinnipeds are good models for studies on signal structure and variation, and on the relationships of signal structure to communicative behaviour (Miller, 1991). These animals have diverse social systems, including large breeding concentrations on ice or land, aquatic and terrestrial mating, territoriality and dominance hierarchies (Le Boeuf, 1991). The group is also diverse ecologically and geographically, so comparative intra- and interspecific studies are possible (Miller, 1991). Many species of pinnipeds can be observed in great detail at close range in the wild and in captivity, and they employ many communicative patterns that are easy to describe. Studies of captive animals have the additional advantages of enabling observations on individuals over long periods and at close range (Miller, 1991). Studies of captive animals are particularly advantageous for most phocids, because much of their social and communicative activity takes place underwater (Rogers et al., 1996).

The harp seal (*Pagophilus groenlandicus*) is a phocid whose social and communicative behaviour are poorly documented and understood (Merdsøy et al., 1978; Ronald and Healey, 1981; King, 1983; Lavigne and Kovacs, 1988; Sergeant, 1991). For example, all studies of harp seal vocalizations have been conducted during the breeding season, yet harp seals are gregarious throughout the year (Lavigne and Kovacs, 1988). Hence it is likely that harp seals are vocally active throughout their annual cycle, and not just during the breeding season as Ronald and Healey (1981) supposed. Furthermore, because harp seals are seasonal breeders, it is likely that vocal activity is related to seasonally varying physiological processes, including the testicular cycle (Miller et al., 1998).

The harp seal is a gregarious migratory phocid of the northern Atlantic Ocean and adjacent Arctic. Three populations (corresponding to whelping areas) are recognized: Jan Mayen; White Sea; and Newfoundland and Labrador, including the Gulf of St. Lawrence (Sergeant, 1991). Seals from the three populations have similar migratory patterns. In the fall seals start to migrate south from the Arctic. They feed intensively during migration and before breeding (Sergeant, 1973, 1991; King, 1983; Lavigne and Kovacs, 1988) then, in late January, females congregate on the pack ice to give birth from late February to mid March. Actual pupping dates vary from population to population; in the White Sea it occurs in February and March, while in the Jan Mayen Sea it is slightly later. Pups are born between 20 February and 10 March in the Gulf of St. Lawrence, and slightly later in Newfoundland. Pups are nursed for approximately 12 days; mating occurs shortly thereafter (Kovacs, 1987; Sergeant, 1991). Mating occurs in water and rarely on ice (Popov, 1966; Merdsoy, et al., 1978; Sergeant, 1991). Young females mate first during the breeding season, followed by parturient females (Popov, 1966). Each male is believed to mate with one or more females (King, 1983). Harp seals are almost certainly polygynous (Sergeant, 1991), although mechanisms of competition among males and the nature of the mating system are not known (Bonner, 1990; Merdsoy et al., 1978). When the breeding season is over seals start moving northward to moulting areas, and in April and May haul out on the pack ice in aggregations to undergo their annual moult. After moulting, they migrate northward to feeding grounds (Lavigne and Kovacs, 1988). The three populations of harp seals do not differ morphologically, but there is little interchange among them (Sergeant, 1973, 1991; King,

1983; Lavigne and Kovacs, 1988). The sexes are similar in size and pelage. Body length averages 1.9 m for adult males and 1.8 m for females, and body mass averages 135 kg for males and 120 kg for females. Pups are about 0.9 m long at birth (King, 1983) and weigh about 11.8 kg; body mass increases to 23 kg within 4-5 days of birth (Ronald and Healey, 1981). Harp seals feed on at least 62 different species of organisms, mainly capelin (*Mallotus villosus*), Arctic cod (*Boreogadus saida*), herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*) and redfish (*Sebastes species*) (Lawson et al., 1995).

Möhl et al. (1975) provided the first description of the vocal repertoire of the harp seal, based on recordings made during the breeding season. Subsequent studies of breeding animals have revealed that the vocal repertoire is larger and more structurally diverse than originally thought (Terhune, 1994; Miller and Murray, 1995). These field studies were necessarily limited temporally, and they did not include behavioural observations of vocalizing seals. It is important that vocalizations should not be studied as isolated events, but that the social and environmental contexts in which calls are produced must be considered also. The context contributes to the management of interactions and orderliness of relationships between individuals. Consequently, the study of the social and environmental contexts of any communicative process is important for understanding the mechanisms of social behaviour (Smith, 1975). In the same way, analyzing the physiological and anatomical aspects of the calls is important. Therefore, a study that includes ethological and physiological aspects of seal vocalizations is necessary for full understanding of the communicative process. The main objectives of this study were to describe the acoustic

repertoire of captive harp seals and to document annual, seasonal and diel trends in vocal activity. I also assessed changes in vocal activity in relation to changes in levels of plasma testosterone in males before, during and after the breeding season.

Chapter 2: Methods

2.1 Seals and the seal facility

Nine harp seals of different ages and both sexes were studied at the Ocean Sciences Centre at Logy Bay, Newfoundland. Some seals had been born in captivity or had lived at the Center since 1995 ("residents"). Others ("new") were captured as adults in 1995 (Table 2.1). Seals were maintained in two wooden outdoor tanks measuring 12.3 m in diameter and 2.5 m in depth. They were bordered by approximately 190 m² 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. Seals were fed *ad libitum* with herring around mid day; however, diet varied on occasions due to other studies (Lawson et al., 1995).

2.2 Collection of data

Collection of data 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 the breeding dates given by Sergeant (1991).

Data were collected mainly early in the morning and late in the evening, when human disturbance was minimal. Valves to the tanks were closed to reduce background noise during recording sessions.

Table 2.1. Summary information of the captive harp seals at the Ocean Sciences Centre (OSC).

Animal	Name	Age Class	Origin
Male 1	Virgil	Adult	Captured as adult in NF, 1991
Male 2	Elmo	Adult	Captured as adult in NF, 1995
Male 3	Tyler	Adult	Captured as adult near Magdalen Islands, PQ, 1990
Male 4	Mickey	Adult	Captured as adult in NF, 1995
Male 5	Victor	Juvenile	Born at the OSC, 1993
Male 6	Jamie	Juvenile	Born at the OSC, 1994
Female 1	Babette	Adult	Captured as adult near Magdalen Islands, PQ, 1989
Female 2	Chelsea	Adult	Captured as adult in NF, 1995
Female 3	Rhonda	Adult	Captured as adult in NF, 1995
Female 4	Bridget	Adult	Captured as adult in NF, 1995

Sound recordings and behavioural observations were carried out simultaneously. Objectives during observation sessions were to obtain: (1) airborne and underwater recordings throughout one complete annual cycle; (2) sound samples representative of the vocal repertoire; and (3) behavioural and contextual information associated with vocalizations, including the identity of calling animals.

During the 1996 breeding season, seals were allocated to the tanks in several ways to determine sexual differences in vocalizations and to assess influences of group composition on vocal activity (Table 2.2):

- Treatment 1: One adult male with all females
- Treatment 2: One adult female with all males
- Treatment 3: All males
- Treatment 4: All seals

In 1997 it was not possible to repeat this design due to conflict with other studies.

2.3 Data analysis

Most statistical analyses were done using SPSS Release 6.1.2 (Norusis, 1992). Circular statistics were performed with Oriana Version 1.0 (Kovach, 1994). The probability level accepted for a significant difference was $\alpha = 0.05$.

⁶⁰ **Table 2.2.** Summary of group composition in tanks during observations in 1996.

Animals in Tank 1	Hours of observation	Animals in Tank 2	Hours of observation	Dates
F4, M1, M2, M5, M6	26.0	F1, F2, F3, M3, M4	20.0	2 – 23 February
M1, M2, M3, M5, M6	25.0	F1, F2, F3, F4, M4	30.0	23 – 28 February
M1, M3, M4, M5, M6	22.5	F1, F2, F3, F4, M2	35.0	28 February to 5 March
F2, F3, M1, M4	12.6	F1, F4, M2, M3, M5, M6	10.4	6 - 8 March
F1, F2, F3, F4	65.0	M1, M2, M3, M4, M5, M6	73.6	8 - 12 March
F1, F2, F3, F4, M3	5.5	M1, M2, M4, M5, M6	9.5	13 - 14 March
F1, F2, F3, 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, F2, F3, F4, M1	17.0	M2, M3, M4, M5, M6	10.5	23 – 27 March
F1, F2, F3, F4, M1, M2, M3, M4, M5, M6	36.0			27 - 31 March

Note: F1-F4 refers to female 1, female 2, etc; and M1-M6 refers to male 1, male 2, etc.

Chapter 3: Underwater and aerial vocalizations of captive harp seals

3.1 Introduction

Communicative systems of great richness and complexity occur in mammals, especially those species exhibiting a complex social organization and that use many short-range signals (Miller and Murray, 1995). Animals rely on different sensory channels for communication. The importance of different channels (e.g. vocal, visual or olfactory) depends on a species' physiological and sensory attributes, habitat characteristics, transmission distance, and social system (Krebs and Davies, 1993). Communication involves signals that are often complex and variable. Variability in signals is shaped by learning, personal histories, bonds between individuals, and other social, ecological and genetic factors (Miller, 1991).

Pinnipeds emit a great variety of sounds in air and water. For example, otariids use a diverse range of airborne vocalizations throughout the year in such contexts as territoriality by breeding males, location and maintenance of contact between mothers and pups, and social play (Schusterman and Dawson, 1968). In contrast, the ringed seal (*Pusa hispida*) is silent for most of the year, and has only a small repertoire of underwater sounds in the breeding season (Stirling, 1973; Kunnasranta et al., 1996). About half the phocids mainly employ underwater vocalizations; aerial vocalizations predominate in grey seals (*Halichoerus grypus*), elephant seals (*Mirounga angustirostris*), hooded seals (*Cystophora cristata*) and monk (*Monachus*) seals (Bartholomew and Collias, 1962;

Miller and Job, 1992; Ballard and Kovacs, 1995). Documentation of the underwater vocal repertoire and understanding of vocal communication in phocids are fragmentary, with almost all knowledge based on loud discrete vocalizations used in the breeding season (Schusterman et al., 1970; Stirling, 1973; Møhl et al., 1975; Terhune and Ronald, 1986; Rogers et al., 1996). Essentially nothing is known about non-breeding vocalizations or short-range vocalizations, which must be important in underwater social interactions of most species.

Studies on captive pinnipeds can contribute greatly to our understanding of the vocal repertoire and vocal communication (Rogers et al., 1996). Captives can be observed or manipulated experimentally, observed at close range for long periods, and have subtle vocalizations and other behaviour observed and recorded. Findings from captive studies can be used to augment information from field studies, provide insights into social functions of vocalizations, and suggest new lines of inquiry for field investigations.

Underwater sounds are important in social communication of most phocids because they are the sole means of long-distance communication and are more effective than optical or tactile communication over short distances. Phocids possess a wide variety of underwater vocalizations, which have been thought to be produced only during the breeding season (Schusterman et al., 1970; Stirling, 1973; Møhl et al., 1975; Ronald and Healey, 1981; Terhune and Ronald, 1986; Rogers et al., 1996;). The repertoire of the harp seal is particularly distinctive because of the wide structural variety of its phonations

(Watkins and Schevill, 1979). Møhl et al. (1975) recorded 16 different kinds of underwater calls for the species, plus one aerial call. Terhune (1994) recognized three additional kinds of calls, and reported geographic variation in vocalizations. Miller and Murray (1995) described a new call used by females, and complex and highly graded vocalizations used by pups.

Functions of vocalizations in harp seals are not well known, but because calls contrast with environmental ambient noise they seem well suited for long-distance advertisement of various kinds (Watkins and Schevill, 1979), for example to promote herd formation or attract mates (Terhune and Ronald, 1986). Harp seals can hear airborne sounds between 1 kHz and 32 kHz in frequency, produced with an intensity of 33 to 42 dB/0.0002 dyn/cm² (Terhune and Ronald, 1971). Under water, they can detect sounds from 76 Hz to 100 kHz, and hear best over the frequency range 2 - 23 kHz (Terhune and Ronald, 1972). Under quiet conditions, a harp seal sound might be detectable by another seal at a distance of 2 km, and a vocalizing herd has been detected with hydrophones at 30 - 60 km (Terhune and Ronald, 1986).

The purposes of this study were to document the acoustic repertoire of captive harp seals, and to determine seasonal trends in vocal activity and the use of different kinds of calls.

3.2 Methods

Audio recordings of underwater and aerial vocalizations of harp seals were made from January 1996 to May 1997. Most recordings were made in the breeding seasons of 1996 and 1997. Recordings were made for 3-4 hr in mornings (0530 - 0930 h) and 5-6 hr in evenings (1700 - 2300 h or 1800-2400 h). Some recordings were made at mid day when there was no human disturbance. Sampling times, other than mid day, were chosen because of low human disturbance and because harp seals are considered to be most active then (Terhune and Ronald, 1976). Outside the breeding season, recordings were made twice a week when possible, generally once each morning and evening. Aerial recordings were made opportunistically.

During recording sessions, behavioural observations were dictated into a tape recorder. Each time a vocalization was recorded, seals at the water surface were identified and descriptions of observable interactions were made. The location of each seal (in or out of the tank) was noted at the beginning of each recording session and movements between tank and decking during observation sessions were also noted.

Recording equipment consisted of: a Sony stereo tape recorder model TC-D5PROII, with a recording response of 40-14,000 Hz (± 3 dB); an omnidirectional hydrophone with a recording response of 6 to 40,000 Hz at 4 dB with an external power supply (Marine Mammal Research Unit, Hut B-3, Room # 13, Fisheries Centre, University of British Columbia, Vancouver, B.C. V6T 1Z4, Canada); and a Prologue unidirectional microphone, model 14H-LC with a recording response of 40 to 13,000 Hz

at 3 dB (Short Brothers Inc., 22 Hart Avenue, Evanston, Illinois 602023696, U.S.A.).

Underwater sounds were analyzed with CSL 4300 (Kay Elemetrics Co., Pine Brook, New Jersey, U.S.A. 07058). Calls were digitized with a 10-bit A/D converter at a sampling rate of 20 kHz. Measurements on duration, interval between calls (for vocalizations produced as doublets), and various attributes of frequency, modulation, and harmonic structure were made (measurements were taken approximately at the middle of the call), as detailed below. Power spectra were computed by Fast Fourier Transformation using 1024 points per analysis, no smoothing, no pre-emphasis and a Blackman window. When background noise was high, a high-pass variable cut off criteria, or band-pass Blackman filter was used (depending on the recording). Measurements were taken using an analyzing-filter bandwidth of 46 Hz, giving measurements accurate to ± 41 Hz and ± 220 msec. To develop a classification that is repeatable, I familiarized myself with vocal structures by repeatedly listening to the calls while watching the real-time display. To be classified as a distinctive call, the following characteristics were necessary: heard from more than one individual; less variability within than between call types; stereotyped; and objectively identifiable.

3. 3 Results

I identified nine call types (eight underwater, one aerial) that have not been described previously for the species (Fig. 3.1). These are described below; numbers used follow from call types 1-19 as recognized by Møhl et al. (1975) and Terhune (1994).

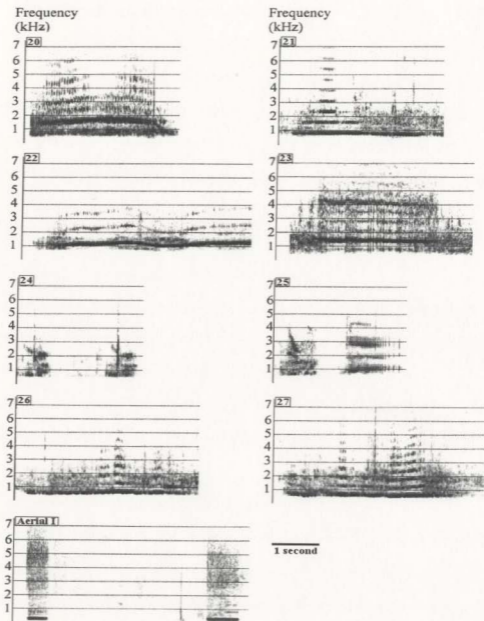


Figure 3.1. Sonograms of call types observed in this study that have not been described previously. Number of call types are in boxes.

Underwater call type 20 (N= 94; Figs. 3.1, 3.2).

General description and usage: Intermediate in duration and fundamental frequency; fundamental frequency increases slowly over call then declines near the end; quasi-rhythmic modulation of the fundamental occurs; harmonically rich in at least part of the call. Males were observed to utter this call; it is not known if females did. The call was used mainly by animals interacting at close range during the breeding season of 1996 and non-breeding season of 1997.

Mean duration (N=43): 1.59 sec (sd = 0.986).

Mean fundamental frequency (N=43): 702 Hz (sd = 79.2).

Mean maximal frequency (corresponding to highest harmonic; N=43): 6710 Hz (sd=713).

Harmonic structure: Some harmonics present in all calls; up to 10 harmonics in high-amplitude portions of call, reaching approximately 7 kHz.

Modulations: Quasi-rhythmic frequency modulation (at approximately 30 Hz) over much of the call; amplitude modulation present but irregular; high-amplitude parts of call typically harmonically rich.

Underwater call type 21 (N= 79; Figs. 3.1, 3.3).

General description and usage: Rich in harmonic structure near beginning of the call, with energy concentrated in the fundamental and first two harmonics. Males and females uttered this call mainly during the breeding season when interacting at close range.

Mean duration (N= 36): 1.35 sec (sd = 0.428).

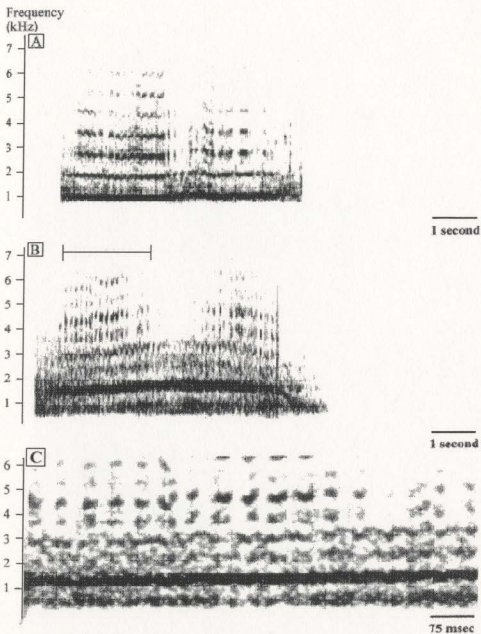


Figure 3.2 Sonograms of call type 20. A and B calls from different seals. C segment of call marked in part B, on different temporal and frequency scales.

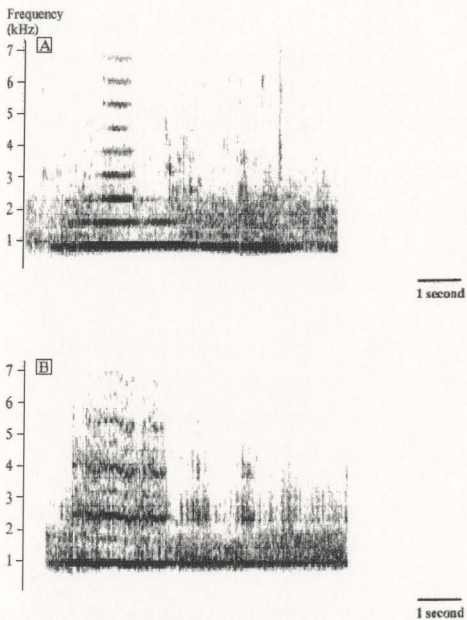


Figure 3.3. Sonograms of call type 21. Calls from different seals.

Mean fundamental frequency (N= 36): 680 Hz (sd = 86.3).

Mean maximal frequency (corresponding to highest harmonic; N=36): 5980 Hz (sd = 933).

Harmonic structure: Rich in harmonic structure; up to 10 harmonics present.

Modulations: Slightly modulated over all the call.

Underwater call type 22 (N= 84; Figs. 3.1, 3.4).

General description and usage: Intermediate in duration and fundamental frequency; fundamental plus two harmonics and slow rhythmic modulations characterize this call. This call was used commonly during breeding and non-breeding seasons by males and females.

Mean duration (N=35): 2.19 sec (sd = 0.977).

Mean fundamental frequency (N=35): 849 Hz (sd = 217.6).

Mean maximal frequency (corresponding to highest harmonic; N=35): 3410 Hz (sd = 1222).

Harmonic structure: fundamental frequency plus two harmonics.

Modulations: Slow rhythmic modulation occurred throughout call, a rate of 3 Hz and rapid modulations.

Underwater call type 23 (N= 32; Figs. 3.1, 3.5).

General description and usage: Characterized by at least nine harmonics throughout the call, with energy concentrated in first and fifth harmonics; quasi-rhythmic modulations of fundamental. Recorded infrequently both breeding and non-breeding seasons.

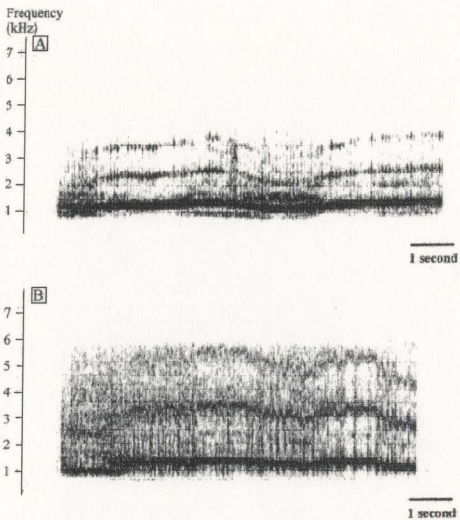


Figure 3.4. Sonograms of call type 22. Calls from different seals.

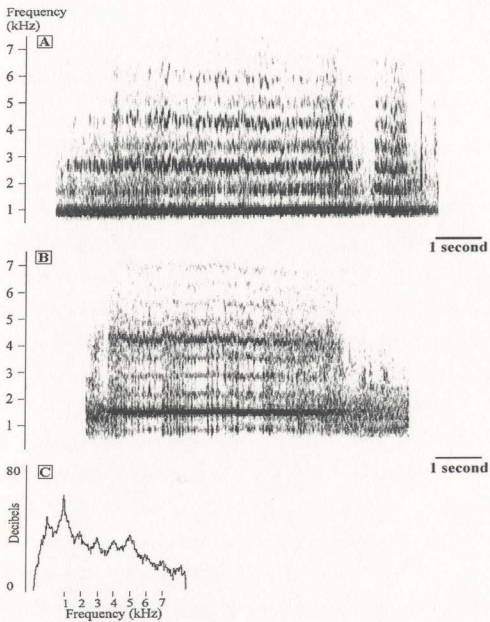


Figure 3.5. Sonograms of call type 23. A and B - Calls from different seals; C - Power spectrum B.

Mean duration (N=19): 2.16 sec (sd = 0.463).

Mean fundamental frequency (N=19): 827Hz (sd = 238.5).

Mean maximal frequency (corresponding to highest harmonic; N=19): 6420 Hz (sd = 579).

Harmonic structure: Very rich in harmonics (nine or more).

Modulations: Modulated at about 45 Hz.

Underwater call type 24 (N= 134; Figs. 3.1, 3.6).

General description and usage: Call always produced as doublet; duration of first and second calls are 0.46 sec (sd=0.472) and 0.48 sec (sd=0.516) respectively, with an interval between them of 0.58 sec (sd=0.616); each part has distinctive formant at beginning, plosive sound in middle, and constant-frequency portion at end. This call was used mainly in short-range interactions between males and females in breeding season, and sometimes in short-range interactions between males.

Mean duration (N=50): 1.53 sec (sd = 1.133).

Mean fundamental frequency (N=50): 603 Hz (sd = 106.2), 2nd part: 627 Hz (sd = 90.2).

Mean maximal frequency (corresponding to highest harmonic; N=50): 6570 Hz (sd = 969), 2nd part: 6960 kHz (sd = 700).

Harmonic structure: Some harmonics present in both parts, up to eight in first and up to 10 in second.

Modulations: None.

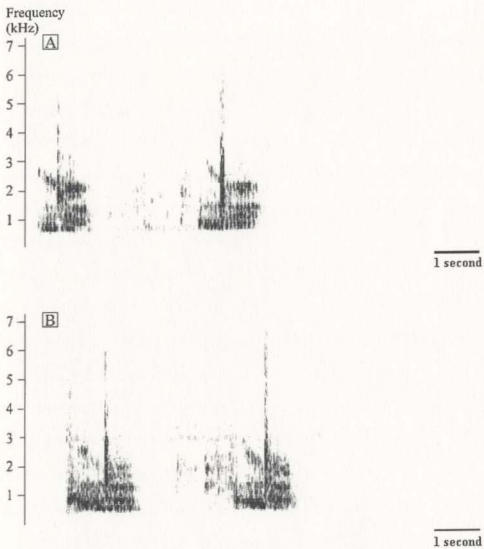


Figure 3.6. Sonograms of call type 24. Calls from different seals.

Underwater call type 25 (N= 67; Figs. 3.1, 3.7).

General description and usage: Always produced as doublet: first part with mean duration of 0.38 sec (sd=0.169); first part begins with formant which ends about halfway through the first part. The second part is a series of pulses, beginning at a rate of approximately 110 Hz and decelerating rapidly. The second part averaged 1.04 sec (sd=0.515) in duration. The interval between parts was 0.298 sec (sd=0.201). Call used during close interactions between animals, mainly in breeding season; uttered by males and females.

Mean duration (N=34): 1.83 sec (sd = 0.848).

Mean fundamental frequency (N=34): 587 Hz (sd = 50.7), 2nd part: 788 Hz (sd = 137.2).

Mean maximal frequency (corresponding to highest harmonic; N=34): 3387 Hz (sd = 1147), 2nd part: 5842 Hz (sd = 874).

Harmonic structure: Three harmonics in the first part and up to four in the second part.

Modulations: Second part modulated at 28 Hz (beginning) and 8 Hz (end).

Underwater call type 26 (N= 50; Figs. 3.1, 3.8).

General description and usage: Intermediate in duration and low in fundamental frequency; rich in harmonics and with one or two discrete segments in middle of call; recorded in 1996 only. Used mainly during breeding season in short-range interactions between males and females.

Mean duration (N=23): 1.67 sec (sd = 0.479).

Mean fundamental frequency (N=23): 624 Hz (sd = 61.02).

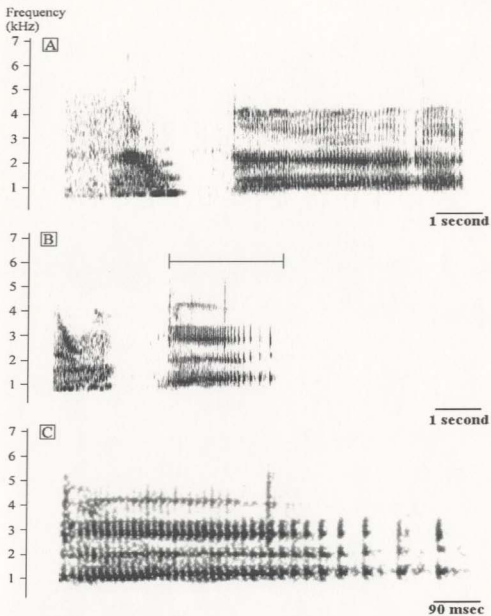
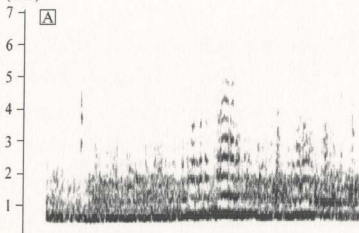


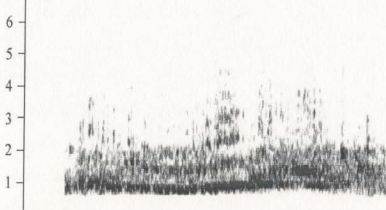
Figure 3.7. Sonograms of call type 25. A and B calls from different seals; C segment of call marked in part B, on different temporal scales.

Frequency
(kHz)



1 second

B



1 second

Figure 3.8. Sonograms of call type 26. Calls from different seals.

Mean maximal frequency (corresponding to highest harmonic; N=23): 6630 Hz
(sd = 423).

Harmonic structure: Most of the call with few harmonics and discrete segments with up to 11 harmonics present.

Modulations: Pulsed, especially in middle of call.

Underwater call type 27 (N= 64; Figs. 3.1, 3.9).

General description and usage: Intermediate in duration and high in fundamental frequency; has six harmonics, and modulations that result in several discrete segments. Recorded only in 1996; used mainly during breeding season in short-range interactions between males and females.

Mean duration (N=24): 1.78 sec (sd = 0.540).

Mean fundamental frequency (N=24): 866 Hz (sd = 82.8).

Mean maximal frequency (corresponding to highest harmonic; N=24): 6600 Hz (sd=461).

Harmonic structure: Up to 11 harmonics.

Modulations: Few frequency modulations in middle portion of calls. Each modulated segment has a duration of 0.02 sec and is modulated at 4 Hz.

Aerial call type I (N= 38; Figs. 3.1, 3.10).

General description and usage: This vocalization is emitted as series of doublets; the calls averaging 0.50 sec and 0.78 sec long, respectively, with interval of 3.55 sec between. This call had fairly flat fundamental, few harmonics, and was very broadband because of noise.

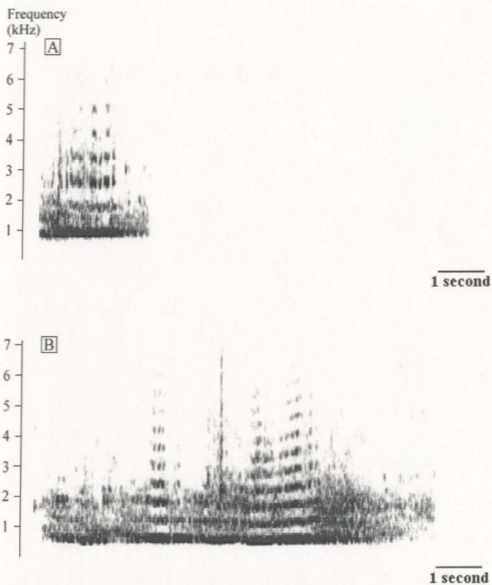


Figure 3.9. Sonograms of call type 27. Calls from different seals.

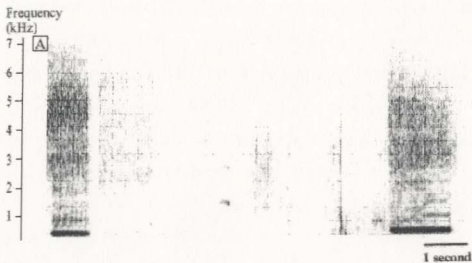


Figure 3.10. Aerial call type I. A call from male 3; B call from male 2.

Only adult males uttered this call; the subordinate male with lowest levels of testosterone and the two juveniles never uttered this call. The call was produced with mouth closed and nostrils opened, with contractions moving up the throat and the neck. Males used this call in confrontational situations with other adult males, swimming in circles at the surface of the tank while vocalizing (as though patrolling the tank), and occasionally leaping clear of the water. Males also used this call to attract females when females were out of the tank: they swam vocalizing towards the female, sometimes leaping clear of the water, as though to attract the female's attention.

Mean duration (N=23): 4.87 sec (sd = 0.623).

Mean fundamental frequency (N=23): 206 Hz (sd = 0.01).

Broadband noise extends up to (N=23): 7.711 kHz (sd= 0.641).

Table 3.1 shows seasonal trends in the relative incidence of call types and the identity of the caller.

3.4 Discussion

The vocal repertoire observed in this study included eight underwater and one aerial call types that have not been described previously, plus eight other underwater call types. Considering the limited scope of this study, it seems clear that the vocal repertoire of this species is considerably larger and more structurally diverse than previously thought. Vocalizations of harp seals have been studied extensively based on field samples (Møhl et al., 1975; Watkins and Schevill, 1979; Terhune and Ronald, 1986; Terhune,

Table 3.1. Seasonal trends in the relative incidence of call types.

Call type	Non-breeding	Breeding	Caller identity
1996			
13	54.5	27.1	Adult male and females
1	30.4	17.5	Adult male and females
7	5.9	1.6	Adult males
21	3.9	5.9	Adult male and females
23	1.1	2.9	Adult male and females
2	0.7	5.7	Adult males
14	0.7	3.6	Adult male and females
27	0.7	9.1	Adult male and females
3	0.3	0.1	Unknown
20	0.3	1.0	Adult males
22	0.3	10.0	Adult male and females
26	0.3	7.3	Adult male and females
15	0.0	0.0	Adult males
18	0.0	4.1	Adult male and females
24	0.0	2.5	Adult male and females
25	0.0	0.8	Adult male and females
N	12.0	15.0	
1997			
18	21.9	6.2	Adult male and females
13	20.4	14.4	Adult male and females
20	14.7	7.4	Adult males
14	11.4	11.6	Adult male and females
1	10.4	11.9	Adult male and females
2	7.6	2.8	Adult males
21	4.2	2.7	Adult male and females
25	2.8	7.4	Adult male and females
7	2.3	0.5	Adult males
22	1.9	1.4	Adult male and females
15	0.9	13.8	Adult males
24	0.4	15.7	Adult male and females
23	0.4	1.0	Adult male and females
26	0.0	2.4	Unknown
27	0.0	0.0	Adult male and females
3	0.0	0.0	Adult male and females
N	13.0	14.0	

1994; Miller and Murray, 1995), but data reported here are the first to include vocalizations outside the breeding season; it seems likely that further field studies in diverse circumstances (e.g. migration, feeding) would reveal even more kinds of vocalizations.

The new vocalizations described above differed in several ways from those described by Møhl et al. (1975) and Terhune (1994). First, calls were relatively brief, with an average duration of 1.75 sec (except calls 22 and 23, that typically were > 2 sec long). Calls described by Møhl et al. (1975) and Terhune (1994) characteristically lasted less than 1 sec and they did not report longer calls.

Second, mean fundamental frequency differed among some calls with an average of 677 Hz. Call type 22 and 23 were the most different, with an average of 838 Hz. The vocal repertoire described previously is constituted of calls with a fundamental frequencies approximately of 400-500 Hz.

Third, the vocalizations described in my study generally are more harmonically rich than calls described previously. Five (call types 20, 21, 23, 26 and 27) of eight calls were characterized by having eight or more harmonics. Consequently, these vocalizations showed higher frequencies (up to 7.5 kHz) than previously described call types. Call types 22 and 25 differed from the rest of the vocalizations. Call types 22 and 25 had a mean maximum frequency of 3.4 kHz, compared with a mean maximum frequency of 7.7 kHz for other call types.

Most of the calls observed had prominent frequency modulations, a characteristic shared with many of the calls described by Møhl et al. (1975) and with calls 17 and 18 described by Terhune (1994). Call types 24 and 25 have one formant at the beginning of the call, ending about halfway through the call. Formant structures are also present in some of the calls described previously.

Harp seals from the Jan Mayen Sea and the Gulf of St. Lawrence differed in their vocal repertoires (herd vocal repertoires included distinctive call types not present in the other herd). Suggesting that geographical differences occur among these two populations (Terhune, 1994). Vocalizations described in the present study also differed from previously described samples, possibly because some seals from Newfoundland were studied, which have not been recorded previously. If the three populations rarely mix (Sergeant, 1973), it is possible that some of the call types observed also reflect geographical variations. Geographic variation is known for Weddell seals (*Leptonychotes weddellii*; Morrice et al., 1994), bearded seals (*Erignathus barbatus*; Cleator et al., 1989), and other marine mammals.

Almost all call types observed (except call types 22 and 23) in this study were associated with short-range interactions involving males; animals that not were interacting were never observed to call. The extensive use of vocalizations in short-range interactions suggests that long-range advertisement serving for herd formation and courtship may be secondary or minor (Møhl et al., 1975; Watkins and Schevill, 1979; Terhune and Ronald, 1986). Clearly, those call types used mainly in the breeding season

may serve in courtship, but they may function equally for managing social interactions among males. These calls have physical characteristics of calls used at close range by harp seals during the breeding season (Watkins and Schevill, 1979). Merdsoy et al. (1978) observed that males threatened other males underwater with vocalizations associated with air bubbles streaming from their nares. If this type of vocalization is the one I described as aerial call type I, it supports the interpretation that this call is used in threats between males. It is unlikely that every call type in a vocal repertoire has a special communicative function distinct from all others (Hailman and Ficken, 1996). However, call types share characteristics that reflect general principles of organization in a communicative system. The understanding of these principles of organization is important for inferring communicative adaptations (Hailman and Ficken, 1996).

The incidence of call types differed between 1996 and 1997. In contrast, Terhune and Ronald (1986) reported no differences between years in the vocal repertoire of harp seals in the Gulf of St. Lawrence. The observed differences between 1996 and 1997 in my study likely reflect differing environmental circumstances. For example, call type 15 (described by Møhl et al., 1975) was used only in 1997. Most (80%) of occurrences of this call were when seals hauled out through a ice hole (in 1996 no ice formed in the tanks), as one of the males tried to control access to the hole. Similar behaviour has been reported for hooded seals (*Cystophora cristata*; Ballard and Kovacs, 1995).

Some questions about mammalian behaviour can be answered only by comparisons across taxa that have convergent attributes. To make comparisons, it is necessary to recognize phylogenetic relationships. The closest living species to the harp seal is the ribbon seal (*Histiophoca fasciata*), and the second closest is the hooded seal; the bearded seal is considered as the least derived member of the phocine seals (Watkins and Ray, 1977; Perry et al., 1995).

Ribbon seals are predominantly solitary animals distributed throughout the Bering Sea and the western North Pacific Ocean (Burns, 1981). Two kinds of underwater calls have been reported (Watkins and Ray, 1977). Hooded seals emit eight different call types, although the repertoire is suspected to be more varied (Ballard and Kovacs, 1995). Calls of hooded seals are mainly aerial and are produced by both males and females; underwater calls are suspected to be produced only by males (Terhune and Ronald, 1976; Ballard and Kovacs, 1995). Harp seals are distributed in the northern Atlantic. They are highly gregarious and use at least 27 underwater calls and two aerial calls. Bearded seals are distributed throughout the Arctic and tend to be solitary (Burns, 1981). Bearded seals produce six different types of vocalizations, mainly by adult males during the breeding season (Cleator et al., 1989). Characteristically, harp and hood calls are harmonically and structurally rich, and calls are brief. In contrast, ribbon and bearded seal calls are narrow in bandwidth, frequency-modulated (Watkins and Ray, 1977; Cleator et al., 1989), and (in bearded seals) very long (33 sec or more; Cleator et al., 1989). Only one call of ribbon seals and no calls of bearded seals are harmonically rich. As well, modulations in ribbon

and bearded seals are elaborate, but are extremely simple in harps and hoods.

Gregarious polygynous pinnipeds typically have a more developed repertoire than species that are solitary and monogamous (Cleator et al. 1989). In a polygynous system, interactions between individuals are more complex and varied, so calls needed to be used and varied accordingly. Differences in the vocal repertoire between these species might support this idea. Bearded and ribbon seals are solitary animals, therefore they do not need a complex repertoire. Contrary, harps and hoods are polygynous and gregarious, thus the interactions between individuals are more varied and complex. Probably vocalizations diversify in parallel with diversification of displays from a monogamous system to a polygynous system.

Chapter 4: Seasonal and diel trends in vocal activity

4.1 Introduction

Seasonal changes in the environment induce adaptive variations in animal behaviour (Boyd, 1991). Such changes are particularly notable for species that inhabit regions with marked seasonal cycles. For example, the reproductive cycle of pinnipeds in the high Arctic is controlled by environmental and physiological factors. Consequently, pinnipeds have well defined annual cycles, with accurate timing of different phases of the reproductive cycle (e.g. arrival at reproductive areas, parturition, nursing, mating; Boyd, 1991; Reiter, 1980). Breeding on ice, in particular, has selected for brief synchronized periods of breeding (Stirling, 1975). For instance, the mating period in harp seals is restricted to about 2.5 weeks per year (Sergeant, 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 vocally active when establishing and defending underwater territories, and show increased calling rates at this time (Morrice et al., 1994). Seasonal and diel variation in vocal activity of pinnipeds in the high Arctic was documented by Stirling et al. (1983). Stirling et al. (1983) 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 and Burton (1988), who found high vocal activity at night. Male

elephant seals (*Mirounga angustirostris*) are vocally most active after sunset and least active at mid day, a pattern that reflects ambient temperature (Shiple and Strecker, 1986). Crabeater (*Lobodon carcinophagus*) and leopard (*Hydrurga leptonyx*) seals are vocally most active in evenings and early mornings (Thomas and DeMaster, 1982). Grey seals (*Halichoerus grypus*) are vocally active at nights (Chwedeficzuk and Frysz, 1983). Harp seals are more vocally active at night than morning or early afternoon (Terhune and 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 and Schevill, 1979). Seasonal and diel activities are important in ecological, developmental, and social processes of pinnipeds. Studies of seasonal and diel activities can reveal important and widespread variations in ecological and social processes, and how such variations influence the phylogeny of communication patterns (Miller, 1991).

The objective of this work was to document annual, seasonal and diel trends of vocal activity in captive harp seals.

4.2 Methods

Underwater vocalizations of captive harp seals were recorded at the Ocean Sciences Centre from January 1996 to May 1997. Data on calling rates were summarized as half-hourly and daily means, and were further classified as coming from the non-breeding or breeding season. The non-breeding season was considered to be from 1 April

to 18 February and the breeding season from 19 February to March 31, based on dates given by Sergeant (1991). Data also were classified by time of day: morning (0100 to 1100 h), mid day (1200 to 1600 h) and evening (1700 to 2400 h). Table 4.1 summarizes the number of hours of recording for these periods.

During the 1996 breeding season, seals were placed in the tanks in several ways to assess sexual differences in vocalizations and influences of group composition on vocal activity (Table 2.2).

A third of the observations were selected randomly to eliminate the autocorrelation component introduced by sequential sampling (Kovach, 1994). Resulting data were classified as no vocalizations (NV; 0 calls/hour), low rates of vocalizations (LV; 1-11 calls/hour) and high rates of vocalizations (HV; 12-84 calls/hour). Mean time of day and circular standard deviations were calculated and summarized according to year and season for all response variables (Kovach, 1994).

A Watson's F-test (Watson and Williams, 1956) was used to test the null hypothesis that mean time of day for NV, LV and HV were equal across years and seasons. This model was used because time was included as a predictor variable (Watson and Williams, 1956). F-statistics compare the lengths of the mean vectors for each sample; the results in F-statistics are the same as Fisher's variance-ratio statistic which is commonly used in linear statistics, including analysis of variance (Kovach, 1994).

Table 4.1. Summary of hours of audio recordings.

Year/time of the day	Non-breeding	Breeding	Total
1996			
Morning	48.2	117.5	165.7
Mid day	10.5	14.5	25.0
Evenings	35.3	70.5	105.8
1996 totals	94.0	202.5	296.5
1997			
Morning	50.1	80.5	130.6
Mid day	13.5	18.9	32.4
Evenings	38.5	90.5	129.0
1997 totals	102.1	189.9	292.0
Totals, both years	196.1	392.4	588.5

4.3 Results

Calling rates were highest in sexually mixed groups and lowest in groups of only females or males (Table 4.2). However, rates were not significantly associated with the number of animals in the tank in recording sessions (Table 4.3).

In 1996 the rate of vocalizations increased in late January, varied but remained high in February, and peaked in early March. The highest rate was 43 calls/hour (6 March) and the lowest was 0 calls/hour (29 February, 8 March). Rates of vocalizations declined sharply in the middle of March but increased again at the end of March. The highest rate in the non-breeding season was 13 calls/hour (22 January) and the lowest was 0 calls/hour (22 April, 6 May). The non-breeding season and the breeding season differed significantly in the rate of calling: the highest weekly mean rate of calling in the breeding season was 11.8 calls/hour and the lowest 7.5 calls/hour. During the non-breeding season the highest weekly mean rate of calling was 6.9 calls/hour and the lowest rate was 0 calls/hour (Fig. 4.1).

A similar pattern was present in 1997. Vocal activity started to increase by the end of January, in February the rate varied but remained high, and peaked in mid March. The maximal rate of vocalization for the 1997 breeding season was 21 calls/hour (13 March) and the minimum was 0 calls/hour (19 February). During the non-breeding season the highest rate was 10 calls/hour (2 February) and the minimum was 0 calls/hour (14 January, 14, 15, 22 April, 15,16 May). During the breeding season the maximal weekly mean rate of vocalization was 12.8 calls/hour and the lowest was 2.4 calls/hour. During

Table 4.2. Relationship of rate of vocalizations to group composition in 1996. Mean \pm sd (n) are shown.

Group composition	Rate of vocalizations per seal hour
All females*	1.0 \pm 0.3 (6)
All males*	4.3 \pm 1.81 (7)
One female and all the males	6.3 \pm 1.05 (7)
One male and all the females	7.8 \pm 3.03 (7)
Females and males together	12.8 \pm 2.32 (19)

Note: * denotes groups that were significantly different from the others.

Table 4.3. Relationship of rate of vocalizations to group size in 1996. Mean \pm sd and N are shown.

Group size	Rate of vocalizations per seal hour
Four	9.6 \pm 3.12 (7)
Five	11.3 \pm 1.74 (6)
Six	7.9 \pm 1.96 (7)
Ten	11.1 \pm 0.42 (19)

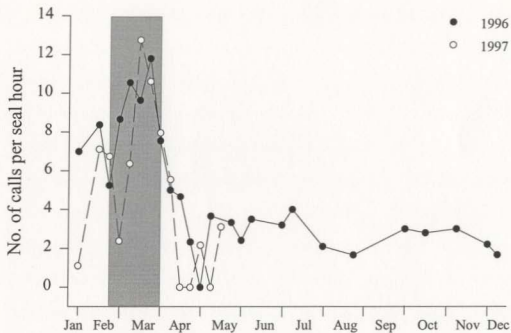


Figure 4.1. Seasonal variation in rate of vocalizations, based on weekly means. Shaded area indicates breeding season.

the non-breeding season the maximal weekly mean rate of vocalization was 6.7 calls/hour and the minimum was 0 calls/hour (Fig. 4.1). As in 1996, in 1997 there was a significant difference between seasons.

The rate of vocalization did not differ significantly between the breeding or non-breeding seasons of 1996 and 1997. However, the breeding season of 1996 differed significantly from the non-breeding season of 1997, and the breeding season of 1997 was significantly different from the non-breeding season of 1996. The calling rate was significantly higher in the breeding than in the non-breeding season for both years.

Rate of calling did not differ significantly between morning and evening in 1996 or between morning and evening in 1997 (Fig. 4.2). In 1996, the highest rate of morning calling was 11.7 calls/hour during the breeding season and the lowest was 1.5 calls/hour during the non-breeding season. The highest rate of evening calling was 21.7 calls/hour during the breeding season and the lowest was 0 calls/hour during the non-breeding season (Fig. 4.2).

In 1997 the highest rate of morning calling was 15.7 calls/hour emitted during the breeding season and the lowest rate was 0 calls/hour the non-breeding season. The highest rate of evening calling was 19.6 calls/hour presented during the breeding season and the lowest was 0 calls/hour during the non-breeding season (Fig. 4.2).

The levels of vocal activity during non-breeding and breeding seasons peaked at different times of the day in 1996 and 1997. Comparisons of calling rates in NV, LV and

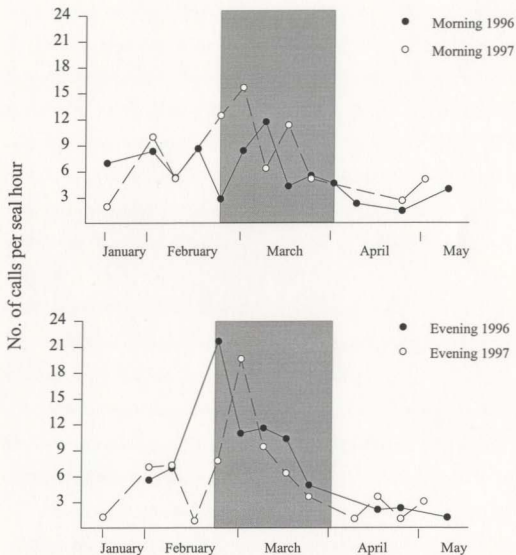


Figure 4.2. Seasonal variation in rate of vocalizations, based on weekly means. Shaded area indicates breeding season.

HV during non-breeding and breeding seasons in 1996 and 1997 are shown in Table 4.4. NV differed significantly between years in both seasons. Mean time of day for NV during the non-breeding season of 1996 was 1100 h, and in 1997 was 0700 h. Mean time of day for NV for the breeding season of 1996 was 2300 h and in 1997 was 1800 h. Mean time of day of LV was significantly different between years. LV occurred around 1100 h during the non-breeding season of 1996 and at 0700 h during the non-breeding season of 1997. Mean time of day for LV was 0200 h during the breeding season of 1996 and at 2100 h breeding season of 1997. Mean time of day of HV did not differ significantly during the non-breeding seasons of 1996 and 1997. However, mean time of day of HV was significantly different during the breeding seasons of 1996 and 1997.

In the non-breeding season of 1996, the most commonly used calls were of low frequency (≤ 3 kHz) and had few harmonics (≤ 3) (call types 13, 1, 7, 2, 3 and 22; 56 % of the calls). In the breeding season of the same year this pattern changed, and calls of high frequency with many harmonics became more common (call types 22, 26, 27, 21 18 and 23; 67 % of the calls).

The non-breeding and breeding seasons of 1997 had a similar pattern. In the non-breeding season the most commonly used calls were of low frequency (≤ 3 kHz) and had few (≤ 3) harmonics (call types 13, 1, 7, 2, 3 and 22; 57 % of the calls). In the breeding season calls of high frequency with many harmonics were more common (call types 22, 27, 26, 21 18, and 23; 63 % of the calls). Call type 13 was the most frequently used in

Table 4.4. Summary of data on calling rates in 1996 and 1997. Mean \pm sd (n) are shown.

	1996	1997
Non-breeding		
NV*	11 \pm 0.9	7 \pm 0.3
LV*	11 \pm 0.1	8 \pm 0.1
HV	8 \pm 0.8	8 \pm 0.6
Breeding		
NV*	23 \pm 0.3	18 \pm 0.4
LV*	2 \pm 0.4	21 \pm 0.2
HV*	22 \pm 0.9	10 \pm 0.4

Note: * $p < 0.05$
based on Watson's *F*-test comparing years.

1996 and the second most used in 1997, call types 26, 27 and 3 were recorded only during 1996 and call type 15 was only recorded during 1997. Overall there was no significant correlation between the relative frequency of use of call types between years ($p < 0.05$; Kendall's rank-correlation coefficient = -0.133).

4.4 Discussion

The tendency for call rates to increase in February and to peak in March was consistent with the observed timing of males congregating close to females, the peak of courtship behaviour, and the presumed period of copulations (Terhune and Ronald, 1976; Lavigne and Kovacs, 1988; Sergeant, 1991). This pattern of vocal activity during the breeding season is also consistent with the pattern exhibit by harp seals in the Gulf of Lawrence their call rate peaked by mid March (Terhune and Ronald, 1976).

The function of repetitive calling in the breeding season is to distinguish the signaler from the random background noise, due to its regularity (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 about the actor is reduced (Krebs and Davies, 1993). Calls produced at high rates function better for long-range

communication, signaling an individual's location; other processes of communication function better over short distances, signaling gender, individual identity, hierarchical status, or signaler intentions (Watkins and Schevill, 1979; Terhune and Ronald, 1986). The low rates of calling when males and females were segregated could indicate that calls are mainly used in male-female interactions or might function in mate choice. Similar behaviour has been observed in harbor seals (*Phoca vitulina*; Riedman, 1990).

A decline in the rate of vocalization in late March and early April was similar in 1996 and 1997. The moulting period begins in April in harp seals in the northwestern Atlantic (Sergeant, 1991). Møhl et al. (1975) found no sounds attributable to harp seals during recordings near moulting herds in the wild. My recordings support this suggestion. The silence of the seals at this time might simply reflect the few social interactions at this time and the small percentage of time spent by seals in the water (Møhl et al. 1975; Moulton, 1997).

Contrary to the results reported by Terhune and Ronald (1976), calling rates of captive seals at day or night did not differ significantly. During the breeding season of 1996 the mean time of HV was concentrated in the nighttime (2200 h), however, in 1997 HV was concentrated in the daytime (1000 h). The same happened with the mean time of LV. Only the mean time of NV was consistently at night in both years. The differences between the results reported by Terhune and Ronald (1976) and my study could be due to: population differences, sampling and analysis methods, or captivity.

Gene flow among the three populations is low (Lavigne and Kovacs, 1988; Sergeant, 1991). Terhune (1994) reported geographical differences in call repertoire between the populations of the Gulf of St. Lawrence and the Jan Mayen Sea. Repertoire differences were also found between those populations and captive seals in this study (discussed on Chapter 3).

Second, Terhune and Ronald (1976) recorded seal calls every three hours during seven days, recording for three minutes every hour. I did daily continuous recordings for up to 6 hours over one-and-a-half months. For their analyses Terhune and Ronald (1976) just considered high-frequency calls, and obtained a relative index of occurrence throughout their study period. For my analyses, I considered all types of call, and used F-statistics to analyze it.

Third, captive animals behave differently from wild animals (Martin and Bateson, 1994), so vocal activity of the seals studied might be affected by captivity.

During the breeding seasons of 1996 and 1997, high-frequency calls with many harmonics were used more commonly than low-frequency calls with few harmonics. During the non-breeding seasons of both years this pattern was reversed. Signals described as being easily distinguished at close range during the noisy environment of the breeding season (Møhl et al. 1975; Watkins and Schevill 1977; Terhune and Ronald 1986) were most similar to my recordings from the breeding season. These structurally complex call types probably are used not only to contrast with ambient noise, as proposed by Watkins and Schevill (1977), but also to convey information about the signaler.

Similar findings in Steller sea lions (*Eumetopias jubatus*) showed that these animals might identify individuals by the call-frequency characteristics of the signaler (Lisitsyna, 1979). Møhl et al. (1975) suggested that high-frequency calls with many harmonics could be used at close range in courtship and mating, so they likely provide more information than just signaler location.

Chapter 5: Plasma testosterone concentration in captive male harp seals

5.1 Introduction

Pinnipeds have diverse social and reproductive behaviour, which includes extreme aggression among males and high levels of polygyny (Bartholomew, 1970; Le Boeuf, 1991). This diversity has led to numerous studies on the social behaviour of pinnipeds, but surprisingly few investigations on the physiological basis of male behaviour. For example, endocrinology has been investigated in only five species (Boyd, 1991). Harbor seal (*Phoca vitulina*) testosterone levels were studied for 8 months in a captive seal, which exhibited seasonal changes (Kirby, 1990). Testosterone concentration changes in two hooded seals (*Cystophora cristata*) were monitored by Noonan et al. (1991), who suggested that the breeding season extends over several months. Hawaiian monk seals (*Monachus schauinslandi*) testosterone levels were investigated by Atkinson & Gilmartin (1992), who found a long period of activity. Territorial behaviour and breeding frequency of Weddell seals (*Leptonychotes weddellii*) were studied in relation to testosterone and cortisol concentrations, age and size, by Bartsh et al. (1992). They proposed that territorial Weddell seal males have the highest testosterone concentrations and are the biggest males. The sub-Antarctic fur seal (*Arctocephalus tropicalis*) presents two peaks in plasma testosterone concentration and mean testicular weight during the summer (Bester, 1990). Bester (1990) showed that the first peak occurs during the breeding season and the second occurs during moult. These few studies suggest that testosterone levels influence

male reproductive behaviour of seasonal breeders.

Some aspects of harp seal biology, such as migration patterns, feeding habits, and reproductive physiology, have been studied due to the importance of this species to commercial fisheries. However, no studies on male reproductive hormones and their influences on mating behaviour have been carried out. Harp seals are interesting because they are seasonal breeders with precisely timed reproduction each year with births occurring only over about three weeks (Lavigne and Kovacs, 1988; Sergeant, 1991). Harp seals share these reproductive characteristics with other seals, so they could be a good model to describe seasonal behavioural patterns in other seal species. Furthermore, they are economically important in Newfoundland, and if a rational exploitation of this species is intended, it can only be made with a thorough knowledge of its biology.

5.2 Methods

Blood samples from four captive adult harp seal males were collected from January 1996 to April 1997. Male 1 was captured as an adult in 1991, males 2 and 4 were captured as adults in 1995, and male 3 was 1 week old when captured with his mother in 1990. Body mass of the four males from March 1996 to March 1997 are summarised in Table 5.1.

Blood samples were collected approximately monthly, except during February and March, when they were collected approximately weekly. Blood was taken from the hind flipper plexus and placed into heparinized tubes before seals received their daily feeding.

The sample was centrifuged at 5,000 rpm for 20 minutes, and the serum frozen at -70 °C for analysis. The University of Prince Edward Island veterinary lab analyzed the samples. Determinations of plasma testosterone concentration were done by radioimmunoassay (RIA) using the Coat-a-count procedure.

A one-way ANOVA was used to determine if there was a significant difference among seals within seasons and through the year, and to relate testosterone levels to photoperiod and behavioural activity (Chapters 3 and 4; Moulton, 1997).

5.3 Results

Testosterone concentration exhibited a clear seasonal pattern, though differences among animals were apparent. High levels of testosterone are present for only a brief period (ca. 8 days). During 1996 the baseline level of testosterone was ca. 0.01 ng/ml; this occurred from the end of April to June (the moulting season). The highest level of testosterone was 9.43 ng/ml, which was noted in male 1 in March and the beginning of April (Fig. 5.1). Male 1 was the first seal to reach his hormonal peak (27 February), followed by males 2 and 4 (both on 14 March); male 3 was last, reaching his peak on 27 March (Fig. 5.1). One week after their peaks, testosterone concentration decreased by 49% in male 1, by 53% in male 2, 74% in male 3, and 93% in male 4.

Males 3 and 4 were the first to reach baseline levels (late April), followed by male 1 on 22 May, and male 2 on 20 June (Fig. 5.1). Plasma testosterone concentration did not differ significantly across males in 1996.

Table 5.1. Summary of body mass (kg) of the four adult males for March 1996 & 1997.

Date	Male 1	Male 2	Male 3	Male 4
1996				
7 March	158.2	176.0	174.4	128.0
14 March	152.6	176.6	174.0	132.6
20 March	145.6	178.0	169.0	131.4
27 March	140.4	174.2	160.2	132.8
Mean	149.2	176.2	169.4	131.2
1997				
5 March	149.4	156.2	198.6	147.8
18 March	145.6	151.0	201.6	142.0
26 March	139.2	149.8	191.8	141.8
Mean	144.73	152.33	197.3	143.86

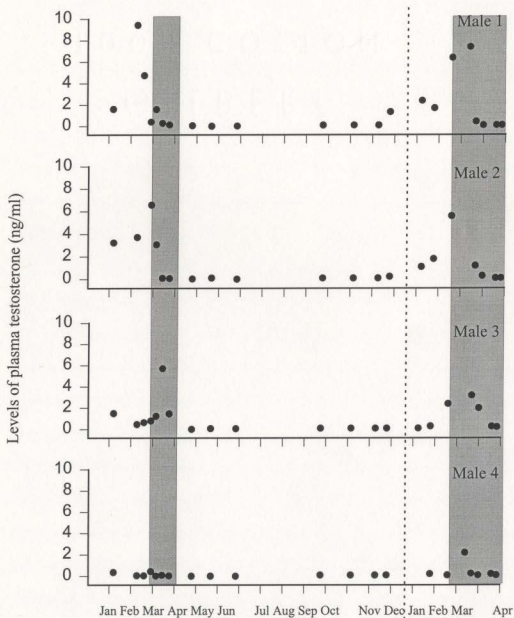


Figure 5.1. Seasonal trends in levels of plasma testosterone. Shaded area indicates breeding season (1996 and 1997).

In 1997, the lowest testosterone concentration was 0.10 ng/ml (mid April) and the highest was 7.40 ng/ml (again for male 1). Male 2 was the first to reach his hormonal peak (20 February), followed by males 1 and 4 (11 March), and lastly by male 3 (18 March; Fig. 5.1). In 1997 one week after peaking, testosterone levels decreased in male 1 by 94%, 78% in male 2, 37% in male 3 and 88% in male 4. In 1997 hormone concentrations were generally lower than in 1996, except in male 4 (Fig. 5.1). As in 1996, in 1997 there was not a significant difference within males in the breeding season or non-breeding season.

5.4 Discussion

The timing of peaks in plasma testosterone of the captive seals is consistent with the observed timing of births and copulations in the wild: births in this population occur around late February and the beginning of March, with copulations presumably 10-14 days later (Sergeant, 1991). Nonetheless, testosterone concentration and testicular size (Miller et al., 1998) start to decline at the time assumed to be the mating period. High levels of testosterone are present for only a brief period (ca. 8 days). This pattern is consistent with results reported for other seasonally breeding mammals (Gustafson and Shemesh, 1976; Griffiths 1984; Bubenik and Schams, 1986; Schroeder and Keller, 1989; Bartsh et al., 1992). These studies show that testosterone levels were elevated before the onset of mating season, but were declining or had already reached basal levels before the mating season was over. Three of the four seals exhibited sexual behaviour such as

chasing females, attempting copulation, and aggressive behaviour toward other males. The seal with the lowest testosterone concentration did not exhibit such behaviour. Instead, it was behaviourally subordinate to the other seals in moving away from the other animals, deferring to them at feeding time, etc. Sergeant (1991) suggested that dominance is related to size and mating experience in male harp seals. When investigating influences of testosterone levels and behaviour, Bartsh et al. (1992) grouped Weddell seal males into 3 categories: territorial, non-territorial and transitional. They found that each group had different testosterone levels, and that the levels declined at different rates in each seal. Territorial males had the highest testosterone levels and their levels declined more slowly than in non-territorial males. Bartsh et al. (1992) also suggested that territorial males had the highest body mass among the three categories studied. Our data suggest that dominance is related to testosterone levels and how rapidly it declines.

In 1996, the dominant male was male 1. This male was very aggressive towards the other males, which generally avoided him. No males displayed aggressive behaviour towards male 1. Male 1 had the highest testosterone levels, and these levels decreased more slowly than in the other males. In 1997, male 3 was the heaviest (Table 5.1), however, it never showed dominance over male 1 and 2, only over male 4. If males 1 or 2 displayed aggressively towards male 3, he usually swam away. However, his aggressive behaviour towards male 4 caused this male (male 4) to swim away. In 1997, it is likely that male 2 was dominant, because, was very aggressive towards the other males, which

generally avoided him. No males displayed aggressive behaviour towards him. Male 2 did not have the highest testosterone levels, but his testosterone levels decreased only by 78% one week after it peaked. In contrast, male 1 had the highest concentration of testosterone, but it decreased by 94% one week after it peaked. Male 3 was the heaviest, but he only showed dominance over male 4. Male 4 was subordinate to all other males in 1996 and 1997 and had the lowest concentration of testosterone and the lowest body mass in both years. This male was never observed displaying aggressive behaviour, and always swam away from the other males as soon as they were aggressive towards him. Even in the absence of the other males, male 4 never attempted copulation. These data suggest that testosterone levels, and how rapidly it declines after peaking, are the main factors underlying social dominance in harp seals. In future studies sampling from animals of known age will be important to determine how important experience is to social dominance.

In 1996, two copulations were observed (in the water): on 14 March male 3 copulated with an adult female, and on 21 March male 1 copulated with a different adult female. In 1997 no copulations were observed, however, on 5 March one of the seals gave birth to a pup.

Captive and wild Hawaiian seals showed similar plasma testosterone concentrations (Atkinson & Gilmartin, 1992). Therefore, we can expect that our results are also representative of wild harp seals. However, it is important to obtain blood samples from wild animals to corroborate these results. Coordinated field and captive

reproductive physiology studies are needed to clarify the behavioural and ecological significance of these observations.

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