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THE UNIVERSITY OF ALBERTA

UNDERWATER VOCALIZATIONS OF THE BEARDED SEAL (*ERIGNATHUS BARBATUS*).

by

HOLLY JOAN CLEATOR

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

SPRING 1987

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Date 16 April /87

Abstract

The underwater vocalizations of bearded seals (*Erignathus barbatus*) were recorded between March and June in 1982 and 1983 at six sites in the Canadian Arctic. 970 vocalizations were measured for temporal and spectral structures and then classified into one of six call types. Calls were narrow in frequency bandwidth and frequency-modulated. The repertoires of vocalizing bearded seals varied amongst the six recording sites. Between-site differences in temporal and spectral features, call use, and sequential organization were measured. The results suggest that bearded seals may be relatively sedentary and that geographically different vocal repertoires may be characteristic of discrete breeding stocks. A prominent daily cycle in rate of calling during April and May was found at two sites; rate of calling was higher during the early morning hours (i.e., 0300–0400 hrs sun time) than at other times of day. No distinct temporal cycle occurred during late May and early June. Rate of calling appeared to be negatively correlated with pattern of haul-out. In paired recordings, made simultaneously using two hydrophones, a few (14 of 163) of the recorded bearded seal calls were heard up to a distance of 30 km underwater.

Vocalization surveys were conducted in Penny Strait, N.W.T. and surrounding waters in April-June 1982, April 1983, and April 1984 to study the winter and spring distribution of bearded seals. Before ice break-up, bearded seals appeared to avoid areas of stable, landfast ice or areas heavily used by walruses (*Odobenus rosmarus*); regions where the ice was less stable and where break-up occurred early were preferred. Water depth did not appear to influence distribution. Numbers of calls increased between mid-April and early June, probably because of an increase in rate of calling by individual seals. Vocalization surveys can be used to separate preferred habitats from unsuitable ones. It is not possible to determine the absolute number of bearded seals at or near a site using vocalizations, however it is possible to measure the relative abundance of seals for spatial and temporal comparisons.

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1. INTRODUCTION

Bearded seals (*Erignathus barbatus*) are northern phocids with a circumpolar distribution. Several external features make them readily distinguishable from other northern phocids. They are the largest of all arctic seals, although the head is small relative to the rest of the body. The mystacial vibrissae are conspicuously long, giving rise to the name "bearded" seal. The third digit in the foreflipper is slightly longer than the others, which gives the flipper a square shape, and accounts for the common name "square flipper" bestowed on them by Norwegian sealers. Female bearded seals have four mammary glands; other northern phocids have two.

Based on differences in external appearance and cranial measurements, bearded seals have been divided into two subspecies (Ognev 1935; Manning 1974). The distribution of the Pacific subspecies (*Erignathus barbatus nauticus* Pallas 1811) is reported to extend from the Canadian Central Arctic west to the Laptev Sea. The distribution of the Atlantic subspecies (*Erignathus barbatus barbatus* Erxleben 1777) is reported to include the eastern Canadian Arctic and North Atlantic east to the Laptev Sea (Manning 1974). The exact boundary between the two subspecies has not been clearly defined and there is disagreement in the literature on whether the differences in body size and growth rates of cranial bones between specimens taken from the two regions are sufficient to warrant the subspecies distinction (Kosygin and Potelov 1971; Manning 1974; Smith 1981).

Historically, bearded seals were of great importance to the Inuit, who have long used their meat for food, their blubber for fuel, and their skin for dog-team traces, harpoon lines, footgear, and any other use that required strength and durability. However, with increased availability of substitutes during the past 20 years, many of the traditional uses of seal by-products have stopped and the importance of this species to local economies has markedly declined. Commercial exploitation of bearded seals has been limited to small operations by Soviet, and occasionally Norwegian, sealers. Until recently, research on the biology of bearded seals has mostly focussed on what could be gained from animals killed by hunters. Very little is understood about the social behaviour of this species. For example, it is thought that bearded seals are promiscuous in their breeding habits (Stirling 1983), but no one has verified or refuted this supposition using data collected in the field. In the spring, during the breeding season, bearded seals produce a vocalization thought to be associated in some way with mating (Dubrovskii 1937; Chapskii 1938; Ray *et al.* 1969; Burns 1981; Stirling *et al.* 1983). These calls have been examined in the Bering Sea and at sites in the Canadian High Arctic (Ray *et al.* 1969; Stirling *et al.* 1983). In this study, I examined the vocalizations of bearded seals in an effort to learn more about their behaviour and ecology.

The first paper in my thesis describes and compares the structure of vocalizations and repertoire of bearded seals at one site in the Alaskan Beaufort Sea and five sites in the Canadian Arctic. Short ($\leq$ 7 day) temporal cycles in rates of calling were looked for at two of the sites, and distances over which the calls propagate in water were measured. The primary objective of the study was to learn more about bearded seal vocalizations and what they tell us about the behaviour and ecology of the species. A practical offshoot of the research was to develop quantifiable and repeatable methods of collecting data on vocalizations for future studies.

Mature males produce vocalizations during the spring to advertise their breeding condition, territoriality, or both (Ray *et al.* 1969). Males probably reach sexual maturity at 6 or 7 years of age (McLaren 1958; Tikhomirov 1966; Burns 1967; Potelov 1975; Burns and Frost 1979; Smith 1981). In arctic waters most breeding probably occurs between mid-April and late May, although males are in breeding condition from about mid-March to late June (McLaren 1958; Tikhomirov 1966; Burns 1967; Potelov 1975; Burns and Frost 1979; Burns 1981). Females may begin to ovulate at 3 or 4 years of age (Burns and Frost 1979; Burns 1981; Smith 1981), but most probably become sexually mature at 5 or 6 years of age (McLaren 1958; Tikhomirov 1966; Burns 1967; Potelov 1975; Burns and Frost 1979). Early researchers concluded that females breed every other year (Sleptsov 1943; McLaren 1958), however more recent studies have shown that most ($\geq$ approximately 82%) sexually mature females reproduce annually (Chapskii 1938; Tikhomirov 1966; Burns 1967; Fedoseev 1973; Burns and Frost 1979; Smith 1981). Females with pups ovulate and mate before their pups are fully weaned (Burns and Frost 1979). Implantation is delayed and occurs between mid-July and early August;

approximately two months after breeding (Chapskii 1938; Burns and Frost 1979). Pups are born on the ice in spring; neonates are first observed in late April and early May (Chapskii 1938; McLaren 1958; Johnson *et al.* 1966; Potelov 1975; Burns 1981). Some researchers have reported a lactation period of nearly one month (Chapskii 1938; Tikhomirov 1966), while others have reported a 12 to 18 day lactation period (Burns and Frost 1979). Pups are capable of independent feeding when they are weaned (Burns and Frost 1979).

At birth, the sex ratio is close to unity, while in older age classes females are often more numerous (Sleptsov 1943; Fedoseev 1973; Burns and Frost 1979) which suggests that mortality rates for males are higher than for females (Smith 1981). Longevity in the wild ranges between 23 and 31 years of age (Benjaminsen 1973; Burns and Frost 1979; Smith 1981). The chief predators of bearded seals are man and polar bears (Stirling and Archibald 1977; Burns 1981). Though rare, parts of young bearded seals have been found in the stomachs of walruses (Lowry and Fay 1984).

The boreoarctic distribution of bearded seals extends as far south as the Sea of Okhotsk and Tartar Strait in the North Pacific, and between northeastern Newfoundland and northern Norway in the North Atlantic (Sleptsov 1943; Ray *et al.* 1982). In many parts of their range, bearded seals appear to be relatively sedentary and move only short distances in response to local changes in ice conditions (Fedoseev 1973; Burns and Frost 1979). In a few areas, such as the Bering and Chukchi Seas, they migrate long distances each year in order to maintain contact with ice (Burns and Frost 1979). Generally, in winter and spring bearded seals seem to prefer areas of shallow water (i.e., < 100 m) where the ice is broken and openings are available for breathing and haul-out (McLaren 1962; Mansfield 1967, 1975; Burns and Frost 1979; Stirling *et al.* 1981, 1982; Kingsley *et al.* 1985), however, they are not restricted to these areas. Some animals have been seen during spring in waters more than 500 m deep (Finley and Renaud 1980); others have maintained breathing holes in fast ice far (400 km) from open water (Stirling and Smith 1977).

To date, aerial visual counts are the principal way in which information on distribution and abundance has been collected for this species. However, most aerial surveys were primarily designed to determine the distribution of ringed seals; bearded seals were counted incidentally (Stirling *et al.* 1977, 1982; Kingsley *et al.* 1985). Stirling *et al.* (1983) have suggested that vocalizations may be an alternative or a supplement to aerial surveys for studying the distribution of this species during the late winter and spring. The second paper in my thesis examines the winter distribution of bearded seals in an area of the Canadian High Arctic as determined by their vocalizations, and discusses the disadvantages of using this technique.

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2. UNDERWATER VOCALIZATIONS OF THE BEARDED SEAL: REPERTOIRE, GEOGRAPHICAL VARIATION, CYCLES IN RATES OF CALLING, AND PROPAGATION IN WATER

2.1 Introduction

Bearded seals (*Erignathus barbatus*), the largest of the northern phocids, are distributed throughout the Arctic and in the most northerly areas of the Pacific and Atlantic Oceans (Sleptsov 1943; Burns 1981; Ray *et al.* 1982). Adult animals usually weigh between 180 kg and 290 kg; females may be slightly larger than males (McLaren 1958; Johnson *et al.* 1966; Burns 1967; Benjaminsen 1973; Burns and Frost 1979; Burns 1981). They are semi-solitary in nature and patchily distributed at low densities although in areas where they are common, groups of up to 10–15 seals may haul out on the ice together from about April through June.

Although opportunistic in their feeding habits, bearded seals prefer bottom-dwelling organisms (McLaren 1962; Burns 1967; Burns and Frost 1979; Lowry *et al.* 1980; Smith 1981; Finley and Evans 1983). The highest densities of seals are found in areas of wide coastal shelves and shallow waters rich in benthic fauna. In winter, bearded seals usually inhabit shallow waters with broken shifting pack ice, but also occur in areas of thin stable landfast ice or fast ice adjacent to polynyas or leads (Mansfield 1967; Stirling and Smith 1977; Stirling *et al.* 1981; Kingsley *et al.* 1985). Little is known about their distribution in open water in summer.

Based on histological evidence, active spermatogenesis in males occurs from about mid-March to mid-June (McLaren 1958; Tikhomirov 1966; Burns 1967; Potelov 1975; Burns 1981), although mating begins sometime late in or at the end of lactation, usually in May (McLaren 1958; Tikhomirov 1966; Burns 1967; Potelov 1975; Burns and Frost 1979). The data are incomplete, but male bearded seals are thought to be promiscuous (Stirling 1983). Most females probably pup each year (Chapskii 1938; Tikhomirov 1966; Fedoseev 1973; Burns and Frost 1979; Smith 1981); pups are born on the ice in late April or early May and are weaned within 12 to 18 days (Burns and Frost 1979).

Bearded seals produce a frequency-modulated vocalization (Freuchen 1935; Dubrovskii 1937; Chapskii 1938; Poulter 1966; Ray *et al.* 1969; Burns 1981; Stirling *et al.* 1983). In the Canadian Arctic, these distinctive underwater calls are heard from late March to late June or early summer (Stirling *et al.* 1983), and are loud enough to be audible to the unaided human ear on a calm day if the seal is nearby. Ray *et al.* (1969) suggest that only mature males produce the trills and that they function to advertise breeding condition, territoriality, or both. More recently, vocalizations have been studied because of the potential they appear to have for providing more information on distribution, relative abundance, and social structure (Stirling *et al.* 1983). In this study, underwater recordings of bearded seal vocalizations were used to measure temporal and spectral characteristics of the calls, compare the repertoires recorded at six sites in the Arctic, examine daily changes in rate of vocalization, and roughly measure the distance that calls travel in water.

2.2 Materials and Methods

2.2.1 Repertoire

Vocalizations used in the repertoire analysis were recorded at the six arctic sites: five in Canada and one in the waters north of Alaska, U.S.A. (Fig. 1-1). Three km south of Ramsay Island (71°33'N, 119°08'W), in the western Arctic, bearded seal calls were recorded between 20 April and 23 May 1982, from a camp on the sea ice. On two occasions during that time, a lone bearded seal was thought to be vocalizing within about a 50 m radius of the hydrophone because the calls were of similar intensity and none overlapped. In both instances, recording was continuous until the seal stopped calling. Underwater recordings were also made 0.5 km N of Dundas Island (76°10'N, 94°53'W) between 27 May and 14 June 1982, and 8 km S of Table Island (77°05'N, 95°15'W) during April and June of 1982 and 1983. On 1 and 2 May 1979, I. Stirling recorded bearded seal vocalizations in the waters east of Hall Peninsula, S.E. Baffin Island (approx. 63°13'N, 64°38'W), in the eastern Arctic. On 12 and 17 March 1983, I. Stirling recorded along the western coast of Hudson Bay, within 20 km of Churchill, Manitoba (approx 58°51'N, 93°52'W). D. Ljungblad made two recordings on 2 and 3 May 1982 in Alaskan waters near Point Barrow (approx 71°33'N, 155° 18'W). Recordings were made opportunistically at various times of day.

Where possible, at least 100 calls were analyzed for each site to ensure a representative sample of the commoner calls for geographic comparison of repertoires. The same calls were used for examining all aspects of the repertoire, including frequency of occurrence of each call type. Clear vocalizations with little background noise were preferred. In some instances, however, it was necessary to include poorly-recorded calls in the analysis to ensure that the sample of calls chosen for a site was representative of the frequency of occurrence of all call types recorded at that site. In total, 970 trills were measured for start frequency, end frequency, duration, and change in frequency (range). At each recording site, the distributions for start frequency and end frequency (in Hz) were positively skewed. To correct the skewness, start frequency and end frequency were both expressed as octaves above 1 Hz. An octave is the difference between two frequencies expressed as logarithm to base 2, i.e. $\log_2 f_1 - \log_2 f_2$, where f_1 and f_2 are given in Hz. To calculate start and end frequencies for a call, a reference value of 1 Hz was used for f_2. For range, f_1 was start frequency (in Hz) and f_2 was end frequency (in Hz). In practice, Hz values were transformed to natural logarithms and the result was divided by ln 2 to convert to $\log_2$.

There were two benefits derived from transforming the Hz values to octaves. Firstly, the transform values gave symmetrical frequency distributions. Secondly, in humans, at least, the basilar membrane in the inner ear perceives differences in pitch in terms of octaves, not by the absolute frequencies of the sound(s) heard. Because octaves had the potential for being biologically relevant to bearded seals, as well as removing skewness in the frequency (Hz) data, all frequency values were given in octaves.

A Kay Sona-graph ® 7029A set on 13 dB high shape using a narrow-band filter (45 Hz at 80–8000 Hz setting) was used to make sound spectrograms from which measurements were taken. A Scientific-Atlanta SD345 Spectrascope III and SD348 Waterfall (25 Hz bandwidth at 0–10,000 Hz setting) were also used to measure calls.

Some trills were measured using both sets of equipment for comparison. The mean difference in values between the two sets of equipment was 7.7% (s.d.=8.4% ; N=122).

Trills were sorted into call types based on whether they ascended or descended in frequency, and had a constant or variable rate of frequency change (Fig. 1-2). The correct call type for each trill was distinguished first aurally, then confirmed visually. Trills that descended in pitch at a relatively constant rate were classified as call type T1 (Fig. 1-3a). Trills that ascended in pitch at a relatively constant rate were catalogued as call type T2 (Fig. 1-3b). Trills that descended in pitch at a variable rate were classified as call type T3 (Fig. 1-3c). The usual pattern of frequency change in T3 calls was an ever-decreasing drop in pitch as the call progressed. None of the ascending-frequency trills rose in pitch at a variable rate; however had any been recorded they would have been classified as a separate call type. The call types were subdivided into two categories: those calls given singly and those given in a sequence with one or more other trills by the same seal. For a call to be classified as part of a sequence, the connection(s) between it and one or two other calls had to be either visible on spectrographic displays or clearly audible. Solitary vocalizations were denoted with the symbol A (e.g., T1A) and those in sequence with the symbol S (e.g., T1S).

The means and standard deviations for start frequency, end frequency, duration, and range were calculated for the six call types at each of the recording sites and for all sites pooled. One-way analysis of variance (ANOVA) was used for each call type to test for differences in start frequency, end frequency, and duration between sites. Because examination of differences amongst sites might yield false results if very small sizes were used, a minimum sample of 10 calls was arbitrarily chosen for the ANOVA. Separate variance (Welch) pairwise t tests were made between all possible pairs of sites (having > 10 calls) for each call type. To adjust for the large number of tests made, Bonferroni probabilities were used for determining statistical significance. A probability value of $\leq$ 0.0167 was chosen for the level of significance in the Bonferroni tests; this value is equivalent to a $p \leq 0.05$ significance level used in most standard t tests. The ANOVA and t tests were run using Biomedical Data Processing (BMDP) statistical packages (Dixon *et al.* 1983). The frequency of occurrence of each call type in the repertoire at each site was calculated as a percentage of the total number of vocalizations recorded there. Comparison of the frequency of occurrence of each call type between sites was done by means of a Chi-square test. The total number of solitary calls (i.e., T1A+T2A+T3A) and sequences were compared amongst the six sites.

At the Ramsay Island site where recording conditions were clearest, 1692 calls were classified according to call type. Eighty-six calls (5.1%) did not fit into any of the established call types because they were atypical in one or more structural characteristics. Although more difficult to quantify because of generally greater background noise, the frequency of occurrence of unusual calls was similar at the other recording sites. For example, Figure 1-4h contains a trill recorded at the Baffin Island site which descends in frequency, yet in such an unusual way that it cannot be classified as either a T1 or T3 call. Atypical trills, such as the one shown, were excluded from the repertoire analysis.

In addition to trills, at the Ramsay Island site, some low-pitched vocalizations were recorded. Mean and standard deviation values were calculated for several features of the calls: start frequency, end frequency, call duration, and time interval between calls.

2.2.2 Daily cycles in rates of calling

To determine whether bearded seal trills show a daily cycle in calling rate, 10- or 20-min. recordings were made every 2 hrs at the Ramsay Island and Dundas Island sites. Before about mid-April, calling rates were too low to be measured in 10 minutes, so 20-min. recordings were made at the Dundas Island site in April. Recordings began there at 1600 hrs on 7 April 1982 and ended at 1200 hrs on 21 April 1982. No recordings were missed. Another set of recordings at Dundas Island began at 1400 hrs on 27 May 1982 and ended at 0400 hrs on 7 June 1982; of the 128 scheduled recordings, 8 (6.3%) were missed. At Ramsay Island, recording began at 1800 hrs on 20 April 1982 and ended at 2000 hrs on 23 May 1982. Of 398 scheduled recordings, 33 (8.3%) were missed. Most of the missed recordings were lost as a result of equipment malfunctions.

The calls heard in each recording were counted in the laboratory. Vocalizations varied greatly in volume, presumably because calling seals were located at different distances away from the hydrophone, so that a decision on whether some faint noises were parts of the same call, or even calls at all, had to be made subjectively. Background noise during a recording also made it difficult for the listener to hear clearly and to tally the calls. In poorer-quality recordings, there was as much as a 10% difference in the number of calls counted on the same recording in two different listening sessions. For that reason, each recording was played three times and the mean number of calls heard during the three listening bouts was used in analyses.

Stirling *et al.*(1983) have reported that background noise resulting from ice and water movement and surface winds, and type of equipment can degrade the quality of underwater recordings. Equipment malfunctions and environmental conditions were potential sources of concern in the Ramsay Island and Dundas Island recordings. At the Ramsay Island site, for example, another make of hydrophone was used during the last ten days of recording because the first hydrophone malfunctioned and an identical replacement was not available. At the same site, the batteries in the pre-amplifier power supply discharged to below-satisfactory levels during 15 (3.8%) of the recording sessions. Overall, bearded seal calls recorded near Ramsay Island were clearer than the calls recorded near Dundas Island; consequently the former were used to test the importance of type and condition of equipment and level of background noise in explaining variation in calling rates over time. Background noise level was subjectively quantified for each recording on a scale of 1 to 5. Rates of vocalization were then regressed against time of day, Julian day, background noise level, make of hydrophone, and condition of pre-amp power supply (satisfactory vs fading) using a step-wise multiple regression. The differences in calling rate between low to moderate background noise levels (ranks 1-3) and high background noise levels (ranks 4 and 5), between the two makes of hydrophone (ITC 6050C and LC-50), and between fully charged and partially or fully discharged batteries in the pre-amp power unit were tested using Student's t test.

Daily patterns in rate of calling were investigated by means of time-series analysis. Vocalization rates were plotted against time to test for temporal trends or patterns. Missing data were replaced with values calculated by interpolation. The data set was then smoothed using a moving average that included the value of interest plus one value taken immediately preceeding and following it in time. Spectral analysis was performed on the smoothed data (frequency bandwidth = 0.07). All statistical analyses were run using BMDP packages except where otherwise noted.

2.2.3 Propagation of calls

In order to determine how far from the source bearded seal vocalizations can be heard underwater, simultaneous recordings were made on two sets of recording equipment. One set of recordings was made from the ice camp near Ramsay Island; a concurrent series of 15 recordings was made at distances 5 km to 30 km away. The mobile recording unit was transported in a Bell 206B helicopter to sites at 5 km intervals along linear transects radiating out from camp (Fig. 1-5). Six recordings were made to the east of camp (5–30 km), three to the south (15, 25, and 30 km), one to the southwest (15 km), two to the west (5 and 10 km), and three to the north (5, 10, and 15 km).

For the first eight recordings (5–30 km E, 25 and 30 km S), 6050C hydrophones equipped with pre-amplifiers were used at both the camp and remote sites. The hydrophone at Ramsay camp then malfunctioned and the remaining seven recordings at camp were made using an LC-50 hydrophone with an LG-1324 pre-amplifier. Single-side-band HF radios provided communication between the two recording teams. Recordings were started simultaneously. Underwater vocalizations at each site were recorded on one of the two channels of both recorders. Distinct calls heard at Ramsay camp were described by the camp observer via radio to the helicopter team; the description was recorded on the second channel of both tape recorders. Transects were terminated when identifiable calls could no longer be heard at both recording sites.

Vocalizations heard at both the camp and helicopter sites were later matched by alternately listening to short segments of concurrent recordings. Start and end frequencies, pattern of frequency modulation, and duration were used to identify a call on both tapes. Comments recorded over the radio aided in lining up the two tapes accurately. As radio signals from camp were received virtually instaneously at the helicopter, it was possible to use a voice signal as a constant point. By using the difference in travel time between the voice signals over the radio and trills travelling through water, and knowing the speed of sound in arctic waters and the straight-line distance between recording units, it was possible to estimate the minimum distance from a calling seal to both recording sites (Fig. 1-16). The following equation was used to calculate minimum distances.

$$X = [D - L] \div 2 \qquad \text{where:} \quad L = T\,V$$

X = distance from seal to closer hydrophone

D = distance between camp and helicopter

L = difference between distances from the calling seal to the two recording sites

T = difference in time between the arrival of a call at one recording site and its arrival at the other site

V = speed of sound in water (1.438 km/s) measured in Baffin Bay in April (Ødegaard and Danneskiold-Samsøe 1982).

2.2.4 Recording

Most underwater recordings were made using a Uher 4200 stereo recorder (frequency response 0.02 to 25.00 kHz ± 4.5 dB at 19 cm/s) and an International Transducer Corporation 6050C hydrophone (frequency response 0.03 to 75.00 kHz ± 1.0 dB). A Nagra SN recorder (frequency response 0.06 to 15.00 kHz ± 2.0 dB) was used from a helicopter during the Ramsay Island distance trials. An Atlantic Research Corporation LC-50 hydrophone (frequency response 0.10 to 10.00 kHz ± 3.0 dB) with an LG-1324 pre-amp were used at the Ramsay Island site for 10 days, after the ITC 6050C hydrophone malfunctioned. Recordings were 10 or 20 min. in duration. Tape speed was set at 9.5 cm/s or 19 cm/s when recording trills for repertoire analysis or the distance trials. Recordings made for investigating daily or seasonal trends in rates of calling were often recorded at 4.7 cm/s because the fidelity achieved from faster recording speeds was not needed and the slower speed resulted in fewer tapes being used and less time spent changing them on the recorder. Increased levels of background noise, resulting from ice or water movement and surface winds, are known to reduce the quality of recordings (Stirling *et al.* 1983). For that reason, few recordings were made when winds exceeded 15 knots, except those made to study temporal patterns in rate of calling. Active ice and water movement were also avoided when possible.

The Alaskan, Hudson Bay, Baffin Island, and Table Island sites were visited only one or a few times. Travel to and from the sites was made in a Bell 206B helicopter. The helicopter idled for 2 or 3 min after landing to cool the engine before shutting down. Using a hand auger, a 10 cm (diameter) hole was drilled through the sea ice and the hydrophone was suspended 3-5 m below the underside of the ice. Seal breathing holes and natural openings in the ice were used when available.

At the Ramsay Island and Dundas Island sites, recordings were made over periods of several weeks. The tape recorder, which was housed inside a heated Parcoll tent or wooden hut, was connected to the hydrophone by 100-300 m of cable. A 12 V lead-acid battery powered the system and an interval timer automatically turned the recorder on and off. Opportunistic recordings were made when recording conditions were good, or when unusual circumstances occurred.

2.3 Results

2.3.1 Repertoire

2.3.1.1 Geographic variation in within-call structures

Bearded seal calls are narrow-band frequency-modulated whistles which sound like warbling sirens. Of the 970 trills analyzed from all recording sites, 66.8% belonged to call type T1 (Figs. 1-4a and 1-4b). T1 calls started as high as 10,500 Hz and ended as low as 130 Hz. Call duration ranged from 0.2 s to 176 s. For most T1 trills, the rate of descent in frequency was relatively constant throughout the call. However, at some recording locations as many as one-third of the T1 trills began with a sharp-drop in frequency similar to the 'descending shoulder' of Weddell seal trills (Thomas and Kuechle 1982) (Fig. 1-4b). Most (84.3%) T1 calls occurred alone. T1A calls were typically lower in start and end frequencies and longer in duration than T1S calls (Table 1-1).

Duration of T1A calls varied considerably both within and between sites. Overall, start frequency showed a positive relationship with duration. A few solitary T1 trills were relatively short in duration (approx $\leq$ 8 s) and had a start frequency of approximately $\leq$ 800 Hz. These calls were often unmodulated and were referred to as moans (Ray *et al.* 1969) (Fig. 1-4e). Most of the T1A trills were longer in duration and some of these showed a distinct pattern of frequency modulation superimposed over the small frequency oscillations present in all trills. As these calls descended in frequency, oscillations in pitch appeared intermittently. The interval between oscillations increased as the call progressed. Examples of this pattern are shown in Figs. 1-3, 1-6f, 1-7, 1-8. At some sites, extra frequency oscillations appeared between the dominant oscillations. Calls that had major and minor frequency oscillations were called two-peak trills; those that had three or more minor frequency oscillations between the major frequency oscillations were called multi-peak trills (see Fig. 1-3). The time intervals between the major frequency oscillations were measured for 87 trills. The sequence of time intervals within each call was found to fit a logarithmic curve quite well, though not perfectly. At the Hudson Bay and Table Island sites, some T1S calls were also multi-peaked.

As many as 20% of all descending-frequency trills at some recording sites belonged to call type T3 (Fig. 1-4d); they made up 14.7% of the total number of the 970 analyzed trills. Most (66.8% of 970) T3 calls were heard in sequences. T3A calls usually began lower in pitch than T3S calls. Mean end frequency and mean duration were similar. In general, T1 and T3 calls were comparable in start frequency and end frequency, but T1 calls were usually longer in duration than T3 calls. Although most descending-frequency trills were readily distinguished by ear as belonging to either call type T1 or T3, some lay on the continuum between the two call types.

In some parts of the Canadian Arctic and Alaskan waters, ascending trills (call type T2) were heard, though less frequently than those that descended in pitch.

T2 trills made up 18.5% of the calls that were analyzed and 75% of those calls were heard in sequence. On average, T2A calls started and ended lower in frequency, and were shorter in duration than T2S calls. Typically, T2 calls rose in pitch at a relatively constant rate, beginning as low as 120 Hz and ending as high as 7250 Hz (Fig. 1-4c). Call duration varied between 0.2 s and 42 s. A small percentage (i.e., < 5%) of the calls recorded by T.G. Smith in the waters south and west of Banks I. in the Western Arctic were ascending-frequency trills that had a variable rate of frequency change (call type T4).

One-way ANOVA showed that there were statistically significant differences in start frequency and end frequency amongst the recording sites for all call types but T2A (Table 1-2). A between-site comparison was not possible for T2A calls because only one site (Ramsay Island) had ≥ 10 calls. Statistically significant differences in call duration between sites were found in call types T1A, T1S, and T2S; in contrast, there were no significant differences between sites for call types T3A and T3S. Pairwise comparisons between sites for call types T1A, T1S, and T2S showed that the differences between sites revealed by ANOVA were the result of more than just one significant pair (Table 1-3). More often, three or more pairwise comparisons were statistically significant for each call type.

Frequency bandwidth varied between calls (Fig. 1-4g), however virtually all were within the range of 50 to 300 Hz. A frequency bandwidth of 1147 Hz was measured in one trill. Typically, the higher the start frequency of a call, the wider its bandwidth. Large within-call changes in bandwidth were infrequent.

Harmonics regularly appeared on both sonagrams and waterfall displays and seemed to be associated with loud calls. Many of the lone seal vocalizations recorded at Ramsay Island, for example, had one or two harmonics visible above the fundamental. T3S calls, in particular, often had three or more harmonics, even though the T1S and T2S calls that preceeded them in sequences had only one or no harmonics (Fig. 1-6b).

2.3.1.2 Geographic variation in between-call structures

Two-thirds of all recorded bearded seal trills (637 of 970) were heard alone, the remainder occurred in sequences. Geographic differences between the number of calls heard alone versus in sequence were detected. In the western Arctic, 46.3% (31 of 67) and 43.6% (180 of 413) of recorded trills occurred in sequences (Alaska and Ramsay Island sites respectively), while in western Hudson Bay, 57.8% (89 of 154) of the recorded trills were heard in sequences. Near Table Island, trills contained in sequences made up 29.1% (30 of 103) of all recorded calls. At the Baffin Island and Dundas Island sites virtually all trills occurred alone.

Two- and three-trill sequences were most common at all sites (Fig. 1-6) (52 and 68 of 125 sequences respectively) although one sequence recorded at the Hudson Bay site contained seven trills. The most common pattern of trills in sequences (47.2% of 125) was a T1 call followed by a T2 call followed by a T3 call. Occasionally, the third call in a sequence was a T1. In two-trill sequences, one of the descending-frequency trills (T1 or T3) was absent.

Geographic differences in frequency of occurrence of call types and in the number of solitary calls versus the number of sequences were detected. Frequency of occurrence of call types was similar amongst the Alaskan, Ramsay Island, Hudson Bay, and Table Island sites, and they were different from the Baffin Island and Dundas Island sites (Fig. 1-9). Inter-site comparison of the number of solitary calls and the number of sequences yielded a Chi-square value significant at the 0.005 level ($x^2=69.2$; df=5). Contrasting Baffin Island and Dundas Island sites (together), with the other four sites gave a Chi-square value significant at the 0.005 level ($x^2=58.8$; df=1). The 1 df tested accounted for approximately 85% of the total Chi-square value. Although the degrees of freedom in a Chi-square are not additive, this one contrast is obviously the most important of all possible contrasts. At the four similar sites (Alaska, Ramsay Island, Hudson Bay, and Table Island) T1 calls made up about 58% (425 of 737) of the repertoire; T2 and T3 calls made up the remaining 42%. Approximately 25% of T1 calls occurred in sequences at the four sites. T2 and T3 calls occurred in sequences more often than alone, with the exception of the T3 calls recorded near Table Island which were mostly (approx 71% of 103) solitary. In contrast, at the Baffin Island and Dundas Island sites, T1 calls made up about 95% of the repertoire. Of 107 trills recorded at the Baffin Island site, only 2 were in sequences. No T3 calls were recorded at the site. No T1S calls or T2 calls were recorded at the Dundas Island site although I. Stirling (pers. comm.) reports having heard a very occasional T2 call during six years of recording there and at other sites nearby.

2.3.1.3 Alaska repertoire

At the Alaskan site, all call types were recorded except T3A calls. T1, T2, and T3 calls comprised 56.7%, 35.8%, and 7.5% of the repertoire, respectively. Moans and T1A trills with single-peak frequency oscillations were recorded (Fig. 1-7a). The most commonly repeated sequence (11 of 16) consisted of a T1S call followed by a T2S call.

2.3.1.4 Ramsay Island repertoire

All call types were recorded at the Ramsay Island site. The repertoire consisted of 56.7% T1 calls, 25.7% T2 calls, and 17.6% T3 calls (N=413). Moans, and T1A trills with single-peak frequency oscillations were recorded regularly (Fig. 1-7b). On average, T1A calls were shorter in duration, and T1S, T2S, and T3A calls started and ended higher in frequency at the Ramsay Island site than at the other sites. Overall there was a slight trend toward higher start and end frequencies at the Ramsay Island site when compared with the other three southern sites (i.e., Alaska, Hudson Bay, and Baffin Island). Near Ramsay Island, 20% of the (67) sequences were the two-trill sequence T1S-T2S (Fig. 1-6a) and 60% were the three-trill sequence T1S-T2S-T3S (Fig. 1-6b). The remaining 20% began with a T2S call followed by a T3S call, then another T2S call (Fig. 1-6c). Most of these sequences consisted of only three trills, however one sequence contained six trills (T2S-T3S-T2S-T3S-T2S-T3S).

2.3.1.5 Hudson Bay repertoire

At the Hudson Bay site, all call types but T2A and T3A calls were recorded. In a sample of 154 calls, 57.2% were classified as call type T1, 21.4% as call type T2, and 21.4% as call type T3. Moans and T1A calls with frequency oscillations were heard. Two-peak (Fig. 1-7c) and multi-peak trills were recorded as well as single-peak trills. Spectral and temporal structure were comparable between the Hudson Bay calls and calls recorded elsewhere, although generally start and end frequencies at the Hudson Bay site were on the low side of the range. Twenty-three (82.1%) of the 28 sequences examined were composed of three or more trills showing the T1S-T2S-T3S pattern (Fig. 1-6d). The five remaining sequences each contained two trills: T2S-T3S. No T1S-T2S sequences were recorded.

2.3.1.6 Baffin Island repertoire

Off S.E. Baffin Island, one T1S, three T2 calls, and no T3 calls were recorded. T1 calls made up 97.3% of the repertoire and T2 calls made up the remaining 2.7% (N=111). Moans were recorded. Approximately 80% of the T1A trills with frequency oscillations were single-peaked (Fig. 1-7d); the rest showed the two-peak pattern. T1 calls recorded at the Baffin Island site were comparable with T1 calls recorded at the other sites. The one T2A and two T2S calls, however, had unusually low start frequencies when compared with T2 calls recorded elsewhere. Only two sequences were heard in the Baffin Island recordings. Both sequences contained two trills: a T2S call was followed by a short (1-2 s) T1S call.

2.3.1.7 Dundas Island repertoire

In the waters near Dundas Island, only T1A and T3A calls were recorded. Most (94.3%) were classified as T1A calls; of those 6.0% were moans. Many T1A calls showed a repeating pattern of frequency oscillations, with one major and several (3-6) minor oscillations per cycle (Fig. 1-8a). The time interval between major oscillations increased to about 1 s in 75% of the "peaked" T1A trills. In the remaining 18 (of 122) trills, the length of time between major frequency oscillations increased to a maximum of 14.4 s ($\bar{x}$=9.4 s ; s.d.=2.5 s). Mean start frequency and duration of the T1A trills were higher than the mean values calculated for the four southern sites. Start frequencies for T3A calls, however, were an average of 1.0-2.2 octaves lower than at other sites where the calls were recorded. No sequences were heard (Table 1-1).

2.3.1.8 Table Island repertoire

All call types were recorded near Table Island. Over half (63.1%) of the 103 recorded calls were classified as type T1 calls. T2 and T3 calls accounted for the remaining 12.6% and 24.3% of the repertoire, respectively. Moans and T1A calls with frequency oscillations were recorded. Two-peak T1A trills were common. T1S trills had a complex pattern of frequency oscillation, with as many as seven or more frequency oscillations accompanying the dominant oscillation per cycle (Fig. 1-8b). The time interval between major frequency oscillations in multi-peak trills usually reached a maximum of 19–20 s by the end of the call. Call types T1 and T2 were typically 10-16 s longer in duration near Table Island than the T1 and T2 calls recorded at the other sites, with the exception of the equally-long T1A calls recorded near Dundas Island. The Table Island and Dundas Island T1A calls were also similar in start frequency; on average they were 0.5 to 1.0 octave higher than at the other sites. Half of the trill sequences (6 of 12) recorded at the Table Island site contained two trills: a T2S call followed by a T1S call. The other six recorded sequences each contained three trills. The call pattern in five of these sequences was T1S-T2S-T1S (Fig. 1-6f). In the sixth sequence, a T3S call was followed by a T2S call and then a T1S call. In four of the six three-trill sequences, the T1S that ended the sequences had frequency oscillations.

2.3.1.9 Comparison between "lone-seal" and "multiple-seal" recordings

Vocalizations were recorded from a lone seal on two occasions at Ramsay Island. The first recording session lasted for 72 min. and 244 trills were recorded; the second session lasted for 29 min. and 78 trills were recorded. It was not known whether it was the same seal calling both times, however the close similarity in start frequency and end frequency between the two recordings (Table 1-4) suggests that both calling bouts could have been recorded from the same seal. The lone seal(s) produced an assortment of calls typical of other calls recorded in the area. Comparison of start frequency, end frequency, and duration between the trills recorded from the lone seal(s) and 91 calls taken from other recordings made at the site, showed statistically significant differences between the 'lone seal' recordings and the 'general' recordings for start frequency, end frequency, and duration in T2 calls and start frequency and duration in T3 calls (Table 1-3). ANOVA and pairwise t tests did not reveal any significant differences between the two 'lone seal' recordings. The vocalizations of the lone seal(s) were slightly higher in frequency and the two recordings contained more call sequences (44.3% of 247 calls and 66.7% of 78 calls) than was found in the 'general' recordings (20.9% of 91 calls). Use of call types was comparable (Fig. 1-10).

2.3.1.10 Groans

A number of recordings made at the Ramsay Island site contained vocalizations I have called groans (Fig. 1-4f). Circumstantial evidence suggests the sounds were made by bearded seals, because they occurred in association with other bearded seal vocalizations, but not with ringed seal calls. Aside from those two species of pinnipeds, no other marine mammals are known to occur near the Ramsay Island site in April. Groans usually occurred in series although occasionally a solitary call was heard. Seventeen groan series were analyzed. As many as 12 groans were counted in one series, however 3 to 6 was more typical. The repetition rate was generally even with an interval of about 1–1.5 s ($\bar{x}$=1.2 s ; s.d.=0.3 s ; N=64) between calls. Each groan ranged from 0.2 s to 1.7 s in duration, with a mean duration of 0.6 s (s.d.=0.3 s ; N=80). Groans were low in pitch (approx. 80–340 Hz): on average they started at 177 Hz (s.d.=39 Hz ; N=80) and ended at 113 Hz (s.d.=27 Hz ; N=80). Ninety percent of the groans dropped in pitch, from the start to the end of the call, by 20 Hz to 150 Hz; one by as much as 205 Hz. In the two 'lone seal' recordings, groans constituted roughly 3% (10 of 332) of the total number of calls heard. They seemed to appear at the end of T1S-T2S-T3S trill sequences, sometimes after a moan that followed the T3S call. Groans were not recorded at the other sites and possibly they don't occur there. More likely, these calls do not propagate well and as seals at the other sites tended to be farther away from the hydrophone, groans may not have been detected.

2.3.2 Daily cycles in rates of calling

The number of calls recorded was significantly greater when the background noise level was low to moderate in volume, than when it was high ($t=5.25$; $df=323$; $p<0.001$). On average, more calls were recorded when the ITC 6050C hydrophone rather than the LC-50 hydrophone was used ($t=3.53$; $df=323$; $p<0.001$), and when the batteries in the pre-amp power supply were fully charged than when they were partially or fully discharged ($t=2.32$; $df=323$; $p<0.05$). Step-wise multiple regression revealed that time of day was the most important variable in explaining variation in calling rates, and date of recording was second. Ambient noise level was third in order of importance and make of hydrophone was fourth. Condition of the pre-amp power supply batteries had an F value of less than the pre-assigned value in the statistical computer package used, so it was not entered into the regression equation.

Spectral analysis of the Ramsay Island data revealed a prominent 24.2 hr cycle in rate of calling (Fig. 1-11a). A secondary 12.1 hr cycle also appeared on the periodogram. The daily peak in rate of calling ($\bar{x}=7.5$ calls/min ; s.d.$=1.4$) occurred at 0306 hrs (sun time) (Fig. 1-12a, d); the lowest mean daily vocalization rate ($\bar{x}=4.0$ calls/min ; s.d.$=1.5$) was recorded at 1506 hrs.

A 24.0 hr cycle and a 12.0 hr cycle in calling rate was found in the recordings collected at the Dundas Island site in April (Fig. 1-11b). In addition to the two prominent cycles, small harmonic peaks were also visible on the periodogram. Rate of calling peaked twice each day: the larger peak ($\bar{x}=3.5$ calls/min ; s.d.$=1.4$) occurred at 0342 hrs and the smaller peak ($\bar{x}=2.6$ calls/min ; s.d.$=1.3$) occurred at 1742 hrs (Fig. 1-12b, d).

Spectral analysis of the data collected at the Dundas Island site in late May and early June revealed several minor cycles, two of which roughly matched the harmonic cycles seen in the Ramsay Island and April Dundas Island periodograms (i.e., at 12 hrs and 6 hrs) (Fig. 1-11c). No 24-hr cycle was evident in the late spring recordings at Dundas Island. Higher rates of calling occurred in the early morning with a slight peak at 0242 hrs ($\bar{x}$=4.6 calls/min ; s.d.=1.5), and in the early evening with a slight peak at 1842 hrs ($\bar{x}$=4.4 calls/min ; s.d.=0.9) (Fig. 1-12c, d).

2.3.3 Propagation of calls

During 263 minutes of recordings made simultaneously at Ramsay Island site and 15 locations within a 30 km radius of the site, 2482 vocalizations were heard. Of these, 496 calls were heard at both sets of recording sites. It was possible to apply time-lag analysis to 160 of those calls in order to estimate the distance between a vocalizing seal and the two recording sites. For four calls, the time lag between detection of a vocalization at one site and detection at the other exceeded the absolute time lag between the two sites based on straight-line measurement.

Sixty-three percent of the vocalizations were estimated to originate within a 5 km radius of Ramsay camp. The remainder were scattered along the helicopter transects at distances up to 20 km from camp and almost 30 km from the helicopter (Fig. 1-13). These data suggest that bearded seal calls can be heard underwater for a minimum of 25 km under similar weather, ice, and topographical conditions.

There were, however, several factors which might have caused small errors in the call location estimates. The speed at which the tape recorders played varied slightly between sites and recorders. At most, this may account for a 0.2 km difference from the calculated values. Small errors may also have been made in the actual timing of the lag measurements. Eighty-three percent of the location estimates were calculated using the call description given from Ramsay camp. In the remainder, the voice marker was not recorded by the hydrophone at the helicopter. The response of the helicopter observer to the description was used as the point from which the time lag was measured in those cases. It is possible that as much as two or three seconds may have elapsed between the time at which a call description was first heard, and a verbal response was given by the helicopter team. This may have resulted in the location estimates being as much as 3–4 km off the true value in such cases.

Approximately 32% of the calls heard at concurrently-recorded sites occurred in association with one or two other calls. It was possible to apply time-lag analysis to each call contained within 17 vocalization sequences in order to determine the degree of precision in the location estimates. The mean maximum difference in location estimates within those trill sequences was 0.3 km (s.d.=0.3). In two of the sequences, the location estimates calculated for two or three calls were as much as 1.0 km apart.

The effect of submarine topography on the obstruction of sound was examined by recording at a site about 100 m off the eastern shore of Ramsay Island, about 5 km north of camp. No vocalizations were heard at the site during five minutes of listening. Hydrographic information for the area indicated very shallow waters (<5 m) immediately around the island with steep slopes dropping off to 30 m.

The simultaneous pairs of recordings made while the helicopter was stationed 5 km, 10 km, and 15 km east of camp were so clear that it was possible to trace all calls heard at the stationary and mobile sites to determine whether each call was heard at both sites. These data were examined to figure out whether some call types travelled farther than others. The percentage of calls heard at both pairs of sites of all those heard at either site was similar for the three sets of recordings: 43.6% (5 km E), 40.7% (10 km E), 47.7% (15 km E). Frequency of occurrence of each call type was also comparable at the camp and helicopter sites for the three pairs of recordings. T1 calls made up 52.0%–59.2% of the calls recorded, T2 calls made up 12.1%–22.1%, T3 calls made up 14.8%–28.0%, and miscellaneous calls made up 3.6%–11.3%. As the three pairs of recordings were comparable the data were pooled.

The number of calls heard at both the camp and helicopter in each pair of recordings of the total number of calls heard at each was calculated as a percentage for each call type. Of 144 T1 calls and 42 T2 calls, 43.8% (63) and 41.5% (17) were heard at both sites (Fig. 1-14). About one-half (51.8% of 54) of the T3 calls and one-third (31.3% of 16) of the miscellaneous calls were heard at both locations in the three pairs of recordings. Of all the calls heard at both sites in the simultaneous pairs of recordings, 58.5% were T1 calls, 16.3% were T2 calls, and 25.2% were T3 calls. Figure

1-15 provides a comparison between those results and the frequency of occurrence of call types in the two 'lone seal' recordings. The percentage of T1 calls was similar between the two sets of data (58.5% vs 56.8%). In the 'call propagation' recordings, however, T2 calls were less frequent (16.3% vs 25.8%) and T3 calls more frequent (25.2% vs 17.4%). These differences were statistically significant ($\chi^2=13.8$; df=5 ; $p<0.025$).

2.4 Discussion

2.4.1 Repertoire

The bearded seal trills recorded in this study were narrow in bandwidth and usually frequency modulated, and most often descended in frequency. Six basic call types were identified. Temporal and spectral measurements covered a range of values as did other features of the calls (e.g., number of frequency oscillations per cycle in "peaked" T1 calls). However, some values occurred more frequently than others and an experienced listener was often able to differentiate between similar values or patterns. For example, the difference between an average of 3–6 frequency oscillations per cycle at the Dundas Island site and 7+ frequency oscillations at the Table Island site (Fig. 1-8b) was easily recognizable to an experienced ear.

In this study, few data were collected on between-seal variation in repertoire. At present, it is difficult to identify individual calling seals during late winter and spring because they are hidden from view under the ice. Nonetheless, on two occasions a lone seal was recorded calling close to the hydrophone at the Ramsay I. site. Data obtained from those recordings provide preliminary information on between-seal variation in vocalization structure and use. The similarity in the frequency of occurrence of call types between the repertoire of the lone seal and the repertoire of all seals near Ramsay Island suggests that individual seals can produce all of the call repertoire in their area. Unfortunately, it was not known whether the two sets of 'lone seal' vocalizations were from one individual or two. If male bearded seals are territorial during the breeding season, which they probably are, it is likely that the same individual was recorded on both occasions. Additional evidence of this is the similarity in start frequency, end frequency, and duration of T2 and T3 calls between the two 'lone seal' recordings, and their dissimilarity with the 'general' Ramsay Island recordings.

The vocalizations of bearded seals recorded at six arctic locations were compared to determine whether or not these seals show geographical variation in the structure and use of their repertoire. Within-call structures (i.e., start frequency, end frequency, duration, range within a call, and pattern and complexity of frequency modulation) differed noticeably between areas. Small sample sizes for most call types at most sites limited the number of statistical comparisons between sites, but with the exception of duration for T3A and T3S calls, all between-site tests for start and end frequency and duration yielded statistically significant differences. There were also clear differences in between-call features amongst the six sites. Frequency of occurrence of each call type, percentage of calls heard alone versus in sequences for each call type, and sequential organization of call types within sequences differed geographically. Unfortunately, the values calculated for the Alaskan, Hudson Bay, and Baffin Island sites were each based on only a few (2–4) short recordings. It was not known how many seals were vocalizing during each recording session. However, comparison of call use between the 'lone seal' recordings and 'general' site recordings made near Ramsay Island showed that lone seal(s) produced each call type with the same frequency of occurrence as other seals recorded at the site. As for within-call structures, even for sites at which calls were taken from recordings made over a period of two weeks or more, statistically significant between-site differences were measured. These data suggest that it is valid to make preliminary geographical comparisons of call structure and use based on a limited number of recordings from different areas. The results obtained in this study likely reflect true differences in within- and between-call features between areas, rather than results of inadequate sampling.

Bearded seal calls have been described by others (Freuchen 1935; Dubrovskii 1937; Chapskii 1938; Poulter 1966; Ray *et al.* 1969; Stirling *et al.* 1983). Freuchen described them as being "siren-like", while Dubrovskii likened them to the whistle of a locomotive. Ray *et al.* provided the most detailed account of bearded seal trills and characterized them as a "long siren-like oscillating warble". Although most descriptions in the literature are brief and onomatapoetic, rudimentary comparisons can be made between them and calls recorded in this study.

Dubrovskii (1937) and Chapskii (1938) described calls heard in the waters along the eastern coast of Novaya Zemlya, in the western Soviet Arctic. Dubrovskii reported call durations of 20–30 s and sequences in which ascending-frequency calls were followed by descending-frequency calls. The durations are comparable with those of the high arctic trills. The call sequences seem similar to those recorded in Hudson Bay and the western Arctic. Chapskii described a bearded seal call as a "descending chromatic scale which greatly resembled the sound of a siren dying away". His description matches the T1A call type.

Freuchen's (1935) description of bearded seal trills he heard in Hudson Bay and Foxe Basin matches T1A calls. He also mentioned a "strange, dull, deep-toned sound or very deep whistle", sometimes heard at the end of descending-frequency calls, which he called a "sigh". It seems likely that Freuchen's description refers to calls which have been designated in this study as moans.

Poulter (1966) also described the trills of bearded seals. He reported typical start frequencies of a "few" thousand hertz and call durations that occasionally exceeded one minute. The trill he presents in a sound spectrogram is a solitary descending-frequency call with frequency oscillations. It is similar in appearance to the T1A calls recorded at the Dundas Island and Table Island sites. Unfortunately, Poulter did not mention where the trills were recorded, although it was most likely in Alaskan waters.

The calls of bearded seals in the Bering Sea, as described by Ray *et al.* (1969) have some features in common with the calls recorded at some sites in this study. Start and end frequencies are comparable. Rate, magnitude, and pattern of frequency modulation are also generally similar. Some temporal differences, however, are evident. Time intervals between frequency oscillations were 9–20 s for some of the trills recorded at the Dundas and Table Island sites, while Ray *et al.* reported time intervals of 5–10 s in the Bering Sea trills. On average, call durations given by Ray *et al.* were longer for T1S calls and shorter for T2S calls than those recorded in this study. In the Bering Sea, T1S calls lasted for about 20–40 s and T2S calls lasted for about 3.5 s. In the waters of the Canadian Arctic and northern Alaska, T1S and T2S calls averaged approximately 9 s in duration.

Ray *et al.* (1969) described a 'four-phrase pattern' for the sequences in the Bering Sea in which the order of calls was similar to, but not identical with, some of the sequences recorded at a few sites in this study. In the Bering Sea sequences a rising introductory trill (phrase 1) was followed by a long descending trill with frequency oscillations (phrase 2). Another short ascending trill (phrase 3) was then followed by a repetition of the descending trill (phrase 2a), to complete the trill sequence pattern. This four-phrase pattern in its entirety was not recorded at any site visited during this study, although portions of it were. Ascending calls followed by descending calls with frequency oscillations were recorded at the Alaskan and Table Island sites (Fig. 1-6a). Descending oscillating-frequency calls followed by ascending calls formed part of the three-call sequences recorded at the Hudson Bay site (Fig. 1-6f).

Ray *et al.* (1969) reported that moans followed many of the Bering Sea sequences by intervals of up to 30 s. In this study, not as many moans were recorded as trills or sequences. However, occasionally a moan was associated with a trill or trill sequence. The number of overlapping calls usually made it impossible to determine what moans and trills might have been associated.

Stirling *et al.* (1983) provided a brief description of the calls recorded in the waters of Penny Strait and around Dundas and Table Islands. The calls they examined were similar in structure to the trills recorded in the same area during this study. Stirling also recorded bearded seal calls in 1972–75 in the western Arctic near Ramsay Island (unpubl. data). Of the 914 trills he recorded, 65.2% were T1 calls, 12.0% were T2 calls, and 22.8% were T3 calls. Of the 413 trills recorded near Ramsay Island in 1982, 56.5% were T1 calls, 25.7% were T2 calls, and 17.7% were T3 calls, a difference that is statistically significant ($\chi^2=39.9$; $df=2$; $p < .005$). Loss or addition of new vocalizations was not found between the two sets of recordings. No temporal or spectral measurements were made on the trills recorded during 1972–75, so comparison with the trills recorded in 1982 was not possible.

Male bearded seals attain sexual maturity at 5 or 7 yrs of age (McLaren 1958; Burns 1967; Burns and Frost 1979; Smith 1981) and can reach 23 yrs of age (Smith 1981). Age of reproductive senescence, if it occurs, is not known. If males show fidelity to particular breeding sites it is possible that some of the same seals were recorded during the 1970's and 1982. Data are sparse for marine mammals, however adult northern elephant seal bulls are reported to give consistent individual vocal patterns over periods of up to 14 months (Shipley *et al.* 1986). Comparison between site-specific bearded seal repertoires recorded in 1972-75 and 1982 show that the rate at which bearded seals give each call type can change within a period of 7-10 years. Dropping or adding new call types may occur over longer periods of time.

Comparison of the calls recorded in this study with descriptions of calls reported for other regions of the Arctic confirms that bearded seals produce descending frequency-modulated trills throughout the Arctic. However, there are site-specific differences in repertoire between areas, as shown by the differences between the six sites and between those calls and trills recorded in other regions of the Arctic. Seals inhabiting bodies of water separated by permanent barriers (e.g., land) or long distances (e.g., >1000 km) probably do not come into contact even during the open-water season, so geographical differences in repertoire between such groups are understandable simply as a result of geographic isolation over time. In some regions of the Arctic, large areas of multi-year ice remain year-round and probably also act to restrict movements of seals.

In addition to macrogeographical variation in repertoire, local variations or microgeographical variations were also found. The recording sites near Dundas Island and Table Island are separated by a body of water, Penny Strait, approximately 150 km in length. Polynyas regularly occurred in Penny Strait and around Dundas Island during the late winter and spring (Smith and Rigby 1981). Recordings were made at 4 sites in Penny Strait and around Dundas Island for several years. Frequency of occurrence of call types was consistent throughout the Dundas Island-Penny Strait area during that time. There were clear differences in repertoire, however, between northern Penny Strait and the Table Island area. Trill sequences and T1 trills with 7+ frequency oscillations per cycle were recorded near Table Island; no sequences and T1 trills with 3-6 frequency oscillations per cycle were recorded in the waters of Penny Strait and around Dundas Island. During the winter and spring, the northern end of Penny Strait was separated from the Table Island area by relatively stable ice that usually persisted until June. Although the stable ice may have restricted the movement of seals between the two areas for part of the year, during the open-water season they were free to move to new locations for overwintering in the following year. Yet consistent year-to-year differences in repertoire were evident between the Table Island and Dundas Island-Penny Strait areas. These data suggest that bearded seals may be relatively sedentary, particularly in areas where ice patterns restrict movement for part of the year.

The sharp contrast between the Table Island repertoire and the Dundas Island-Penny Strait repertoire shows that disjunct variations in repertoire can occur, even over relatively small distances. The subtle and gross differences that exist between these two neighbouring sites are typical of the kind and degree of differences found between any of the six sites despite the 800+ km distances that separate the rest of them. The Alaskan and Baffin Island sites, for example, are approximately 3500 km apart yet the degree of difference in repertoire between those sites was comparable to that found between the Table Island and Dundas Island-Penny Strait sites. More sampling is needed to determine whether clinal or disjunct variations in repertoire are more usual.

Ray *et al.* (1969) referred to the underwater vocalizations of bearded seals as songs. In birds, songs are produced chiefly by males during the breeding season, and consist of one or more sounds consistently repeated in a specific pattern (Pettingill 1970). Available data show that bearded seal calls are produced only during the breeding season and suggest that only males produce them. Notwithstanding geographical variations, bearded seal trill sequences consist of sounds that are often repeated in specific patterns and may be analogous to bird songs. Nevertheless it seems prudent to avoid using the word "song" when referring to calls or call sequences until it is clear their use fits the established definition.

The distinctiveness, repetitive nature, and long transmission distances of bearded seal calls strongly suggest that the trills are used for communication. For a number of mammalian species, vocalizations composed of pure tones with harmonious quality are associated with courtship and mating (Hawkins and Myrberg 1983). Weddell seals (*Leptonychotes weddelli*) in the Antarctic produce frequency-modulated trills that sound very similar to bearded seal trills (Thomas and Kuechle 1982). Only male Weddell seals are known to produce trills, which are heard only during the breeding season, and are thought to be used for proclamation of breeding territory. Ray *et al.* (1969) suggest that male bearded seals may produce trills for the same reason. Burns (1981) suggests that female bearded seals also produce trills. He bases this assertion on the large number of calls he has heard simultaneously in some areas relative to the number of males observed in the vinicity. However, given the long distances the calls travel in water, their relatively long durations (mean duration for all call types was 12.2 s, N=970) and hence frequent overlapping, and difficulty of counting numbers of individual calls when more than about six overlap at one time, it seems likely that only male bearded seals produce the trills.

Like bearded seals, Weddell seals also show geographic variation in their trill repertoire (Thomas and Stirling 1983). Interestingly, in one region of the Antarctic, Weddell seals produce ascending trills as well as descending trills. The ascending-frequency calls are the mirror-image of the descending-frequency calls, and follow them in sequence. This pattern is identical to some bearded seal sequences recorded in the western Arctic, Hudson Bay, and near Table Island in the High Arctic. Distinct geographic differences in call use and sequential organization occur in both species; but while the spectral and temporal features of Weddell seal calls differ only subtly between areas, those of bearded seal calls appear to be more geographically distinct.

Weddell seals exhibit a strong degree of fidelity to specific breeding areas, which is thought to account for their geographic variation in repertoire. It is possible that strong fidelity to breeding sites or areas may also be responsible for the geographical differences found in the repertoire of bearded seals. Unfortunately not enough is known about the behaviour of this species to allow us to determine whether adult male bearded seals are sedentary and remain in productive areas year-round, or whether they move around during the year but return to specific breeding areas each spring.

Bearded seals are not known to produce vocalizations other than trills and groans. In contrast, Weddell seals produce a variety of calls in addition to trills (Thomas and Keuchle 1982; Thomas and Stirling 1983). Gregarious polygynous pinnipeds typically have a more developed repertoire than species that are solitary and exhibit a monogamous approach to breeding. The social and polyngyous Weddell seal and harp seal (*Phoca groenlandica*) produce 55 and 16 different calls respectively (Møhl *et al*, 1975; Thomas and Stirling 1983). Solitary species, which are thought or known to be serially monogamous breeders, produce only a few different calls. Three underwater vocalizations have been identified from the hooded seal (*Cystophora cristata*) (Terhune and Ronald 1973), two from the Ross seal (*Ommatophoca rossi*) (Watkins and Ray 1985), and one from the crabeater seal (*Lobodon carcinophagus*) (Stirling and Siniff 1979). The solitary but likely polygamous ribbon seal (*Phoca fasciata*) produces two underwater vocalizations (Watkins and Ray 1977). Walruses (*Odobenus rosmarus*) produce only five different calls (Stirling *et al.* 1983) yet these animals are polygynous. Male walruses may compensate for their limited array of call types by producing high-intensity calls almost continuously during the breeding season (I. Stirling, pers. comm.). The repertoire of bearded seals consists of trills and I have identified six call types. The calls produced by breeding males are loud and, although the length of individual calling bouts and the time intervals between them are not yet known, individual males seem to call much of the time. This pattern is similar to that of the polygynous walrus, although bearded seals are usually semi-solitary and suspected of being promiscuous (Stirling 1983). Parturient females do not appear to aggregate in breeding colonies; consequently, males likely have only limited control over the reproductive success of neighbouring males. In summary, bearded seals do not have a well-developed repertoire, however the loudness of their calls and frequent rate of calling suggest a promiscuous or possibly polygynous mating system rather than a monogamous one.

2.4.2 Daily cycles in rates of calling

Time of day was found to be the most important factor in explaining the changes in rate of calling in the Ramsay Island data. Prominent daily cycles were evident in both the Ramsay Island and Dundas Island recordings. The spectral pattern in the Ramsay Island periodogram indicated the presence of a strong fundamental cycle at 24.2 hrs with a weak first harmonic cycle at 12.2 hrs. The 24-hr cycle did not fit a sine curve. The spectral pattern in the early spring Dundas periodogram showed the presence of both a 24.0 hr cycle and a 12.0 hr cycle. The 12-hr cycle was strongest and that indicated that there were two peaks per day; because the two peaks were not quite equal in strength, a 24-hr component appeared. The late spring Dundas periodogram did not show any distinct cycles although a slight rise in calling rate occurred early in the morning, as it did in the April and early May recordings at both sites.

Biological events with a daily period length are well known in many organisms (Halberg 1959; Aschoff 1960; Bruce 1960; Bunning 1967). With the present knowledge of bearded seal physiology and behaviour it is not yet possible to identify the endogenous or exogenous factors that influence their calling rates. However, in harp seals, crabeater seals, and leopard seals, rate of calling is negatively correlated with the number of seals hauled out on the ice (Terhune and Ronald 1976; Thomas and DeMaster 1982). During the spring, bearded seals haul out during the day. Casual observations at the Ramsay Island site revealed that in late April bearded seals typically hauled out in the late morning or afternoon and returned to the water in early evening. By late May, seals were hauling out earlier in the morning and staying up on the ice until later in the evening. Ringed seals have a similar haul-out pattern. As spring progresses, ringed seals haul out earlier in the morning and remain on the ice until later in the evening (Smith and Hammill 1981; M. Kingsley, unpubl. data). By mid-June in the High Arctic, individual ringed seals may remain hauled out for 24+ hours. The daily periodicity in haul out becomes much less pronounced than it was earlier in the year. Data on the haul-out behaviour of bearded seals were not collected during the late spring Dundas Island recordings, but it seems likely that at that time of year bearded seals, like ringed seals, show less daily rhythmicity in the time of day at which they are hauled out. If so, this may explain the daily peak in rate of calling during early morning in the early spring, and the absence of a daily cycle during the late spring. The effect of seasonal factors (e.g., daylength, temperature) and weather (e.g., day-to-day unpredictability in temperature and wind) on haul-out in bearded seals has not yet been investigated. A quantitative study of the pattern of bearded seal haul-out is needed to test the hypothesis that rate of calling is negatively correlated with the number of seals hauled out on the ice.

2.4.3 Propagation in water

The results from my study confirm that bearded seal calls can be heard for up to 30 km. Although the intensity of the calls was not measured at source, a little over one-half were subjectively evaluated as either moderate or loud in intensity at both concurrently-recorded sites. I did not record at distances greater than 30 km; consequently, I was not able to determine whether bearded seal calls travel farther ~~than~~ that distance in water. Stirling *et al.* (1983) suggest that under ideal conditions, some bearded seal vocalizations may travel as far as 45 km in water.

Several factors contribute to the attenuation of sound in arctic marine waters: cylindrical spreading in and absorption by sea-water, and absorption by and reflection from the bottom and undersurface of the ice (see review by Mansfield 1983). Water depth and roughness of ice cover influence sound propagation in water even further, especially at higher frequencies (Verrall 1981). The Ramsay Island 'call propagation' trials were conducted in shallow water (<100 m) with a relatively smooth cover (approx 1.5 m thick) of annual shore-fast ice. Although the attenuation of sound under smooth ice should be less rapid than under a surface ~~roughened~~ by rafting and ridging, scattering losses due to reflection from the ice surface ~~and absorption~~ by and reflection from the shallow bottom were higher than would have occurred in deeper water (>150 m) (Verrall 1981). In spite of the shallow waters, 8.6% (14 of 163) of the recorded calls were heard up to a distance of 30 km. However in the nearshore waters (< 5 m deep) around the perimeter of Ramsay Island, bearded seal calls originating from deeper waters were apparently absorbed or deflected by the steep submarine banks around the island.

Ice, which may have extended to the bottom in places, may have also blocked the transmission of calls.

Preliminary data suggest that some bearded seal call types may travel farther in water than others. The first piece of evidence for this is the difference in percent occurrence of calls heard (simultaneously) at both the camp and helicopter sites between the three call types. The percentage of T3 calls heard simultaneously at each pair (camp/helicopter) of sites, of the total number of T3 calls recorded at either site, was higher than was the case for call types T1 and T2. The percentage of T1 calls was slightly greater than the percentage of T2 calls. The second piece of evidence was found in a comparison of the frequency of occurrence of each call type between the calls heard at both sites in the 'call propagation' recordings and the calls heard in the two 'lone seal' recordings. T1 calls were produced at the same frequency of occurrence in both sets of recordings. T2 calls were heard more often in the 'lone seal' recordings than in the 'call propagation' recordings, and T3 calls were heard less often. These data suggest that, of the three call types, T2 calls are the poorest and T3 calls are the best at propagating through water. Although the 'lone seal' recordings were made when a seal was calling within about 50 m of the hydrophone so it was possible to classify all calls made by the seal, the frequency of occurrence of each call type may vary between individuals. Consequently, it may be inappropriate to ascribe the differences in the percent occurrence of each call type between the 'call propagation' recordings and 'lone seal' recordings to differences in the transmission properties of each call type. Nonetheless, during many hours of listening to bearded seal calls I noticed that often in sequences such as T1-T2-T3, the T2 call was faint and difficult to hear while the T3 call was loud and clear. The sharply descending start of T3 calls appears to contain a lot of energy which may account for the harmonics typically associated with those calls and their greater propagation. It has been suggested that in some bird species, individuals may be capable of assessing their distances from one another by assessing the degradation of calls caused by distance and environmental acoustics (Morton 1982). It is possible that bearded seals may also be able to roughly determine how far away a caller is by assessing how well the T3 call can be heard relative to the T2 call.

Bearded seal trills seem well designed for easy detection and recognition in spite of degradation from environmental acoustics and the passage through water. Male Weddell seals also produce trills very similar to those of bearded seals. Weddell seal trills are thought to travel long distances in water which enables the caller to communicate with seals far away and with those hauled out on nearby ice. Sound pressure levels ranging from 148 to 193 dB *re* 1μPa at 1 m have been measured for Weddell seals, however no field tests to measure actual transmission distances have been reported (Thomas and Kuechle 1982).

2.4.4 Technical considerations for future data collection

The results from this and other studies suggest that environmental factors and recording equipment should be taken into account when trying to compare the relative abundance of bearded seals between areas using data from single recordings. Recording while surface winds are $\geq$ 22 km/hr, or when ice or water is moving near the hydrophone should be avoided. Time of day for recording should also be considered. Although recording during the early morning (i.e., 0200–0600 hrs) may be preferable for maximizing the numbers of calls recorded, it may be difficult to record at that time of day if the sites have to be reached by aircraft. The number of bearded seal calls recorded per unit time also increases as spring progresses so that it becomes progressively more difficult to count the number of calls or to select calls for spectral analysis because so many overlap. For that reason, in late spring it may be preferrable to record during mid-day when calling rates are low. Bearded seal calls are loud, so calling individuals can be detected over long (up to 30 km) distances. These results are important to keep in mind when designing a vocalization survey intended to compare the relative abundance of bearded seals between areas. The recording locations should be a minimum of 50 km apart to ensure that none of the same animals are recorded at two or more locations. In areas where submarine obstacles are present, recording locations may be closer together.

Many questions regarding bearded seal vocalizations are unanswered and will remain so without the aid of more advanced technology. Hydrophone arrays look promising as a means for providing relatively accurate measurements of distances between calling seals and the distances over which calls can still be heard. They may also help provide information on individual calling rates and the time interval between calling bouts, as well as the differences in vocal repertoire between individuals.

TABLE 1-1. Mean values for start frequency, end frequency, duration, and change in frequency (range) for each call type recorded at the six sites. Start frequency and end frequency are given in number of octaves above 1 Hz. Duration is given in number of seconds and range in number of octaves. Hertz values for mean start and end frequencies are shown in brackets.

Call type	Feature	ALASKA $\bar{x}$	ALASKA s.d.	ALASKA N	RAMSAY I. $\bar{x}$	RAMSAY I. s.d.	RAMSAY I. N	HUDSON BAY $\bar{x}$	HUDSON BAY s.d.	HUDSON BAY N
T1A	Start freq	10.2	1.0	28	10.4	1.4	181	10.3	1.2	65
		(1176 Hz)			(1351 Hz)			(1261 Hz)		
	End freq	8.9	0.6		9.3	1.1		9.3	1.0	
		(478 Hz)			(630 Hz)			(630 Hz)		
	Duration	14.1	19.7		8.3	9.2		14.3	18.8	
	Range	1.3	1.0		1.1	0.9		1.0	0.9	
T1S	Start freq	10.7	0.6	10	11.8	1.1	53	9.3	0.6	23
		(1663 Hz)			(3566 Hz)			(630 Hz)		
	End freq	9.2	0.6		10.8	1.1		8.1	0.6	
		(588 Hz)			(1783 Hz)			(274 Hz)		
	Duration	2.4	0.7		4.0	4.6		11.1	2.8	
	Range	1.5	1.1		1.0	0.7		1.2	0.3	
T2A	Start freq	7.9	0.1	8	8.3	0.7	34			
		(239 Hz)			(315 Hz)					
	End freq	9.0	0.4		9.1	0.7				
		(512 Hz)			(549 Hz)					
	Duration	2.8	1.9		3.8	6.0				
	Range	1.1	0.4		0.8	0.5				
T2S	Start freq	9.6	0.8	16	10.3	1.4	72	8.3	0.7	33
		(776 Hz)			(1261 Hz)			(315 Hz)		
	End freq	10.3	0.6		11.8	1.2		9.4	0.6	
		(1261 Hz)			(3566 Hz)			(676 Hz)		
	Duration	2.1	0.9		9.4	8.8		8.8	3.2	
	Range	0.7	0.4		1.5	0.9		1.1	0.4	
T3A	Start freq			--	11.1	0.6	18			
					(2195 Hz)					
	End freq				9.3	0.7				
					(630 Hz)					
	Duration				3.1	1.5				
	Range				1.8	1.0				
T3S	Start freq	11.1	0.2	5	12.1	0.9	55	9.4	0.6	33
		(2195 Hz)			(4390 Hz)			(676 Hz)		
	End freq	8.8	0.6		9.2	0.6		8.3	0.6	
		(446 Hz)			(588 Hz)			(315 Hz)		
	Duration	13.1	11.9		3.8	2.5		3.6	2.3	
	Range	2.3	0.8		2.9	0.8		1.1	0.3	
Total number of calls				67			413			154

TABLE 1 (continued)

Call type	BAFFIN I. x̄	s.d.	N	DUNDAS I. x̄	s.d.	N	TABLE I. x̄	s.d.	N	ALL SITES x̄	s.d.	N
T1A	10.3	1.3	107	10.9	1.3	115	11.2	1.1	50	10.6	1.3	546
	(1261 Hz)			(1911 Hz)			(2352 Hz)			(1552 Hz)		
	9.0	0.8		8.5	0.9		8.8	1.0		9.0	1.0	
	(512 Hz)			(362 Hz)			(446 Hz)			(512 Hz)		
	12.9	17.8		31.5	29.4		24.4	24.5		16.3	21.4	
	1.3	1.2		2.4	1.0		2.4	1.3				
T1S	9.3	-	1			--	10.5	1.3	15	10.9	1.4	102
	(630 Hz)						(1448 Hz)			(1911 Hz)		
	9.0	-					8.8	1.0		9.7	1.5	
	(512 Hz)						(446 Hz)			(814 Hz)		
	1.2	-					33.2	43.8		9.3	18.5	
	0.3	-					1.7	1.3				
T2A	7.6	-	1			--	8.5	-	1	8.2	0.6	44
	(194 Hz)						(362 Hz)			(294 Hz)		
	9.1	-					9.4	-		9.1	0.7	
	(549 Hz)						(676 Hz)			(549 Hz)		
	5.4	-					21.3	-		4.1	5.9	
	1.5	-					0.9	-				
T2S	7.6	0.3	2			--	9.5	1.8	12	9.6	1.5	135
	(194 Hz)						(724 Hz)			(776 Hz)		
	9.3	0.8					10.5	1.3		10.9	1.4	
	(630 Hz)						(1448 Hz)			(1911 Hz)		
	5.1	0.8					16.7	11.4		9.0	8.1	
	1.7	0.3					1.0	0.7				
T3A			--	8.9	0.2	7	9.9	0.7	22	10.2	1.0	47
				(478 Hz)			(955 Hz)			(1176 Hz)		
				7.8	0.3		7.9	0.7		8.4	1.0	
				(223 Hz)			(239 Hz)			(338 Hz)		
				3.2	1.5		3.3	2.1		3.2	1.8	
				1.1	0.2		2.0	0.7				
T3S			--			--	12.1	1.6	3	11.1	1.5	96
							(4390 Hz)			(2195 Hz)		
							10.2	2.9		8.9	0.9	
							(1176 Hz)			(478 Hz)		
							8.5	0.6		4.3	4.0	
							1.9	1.5				
Total no. of calls			111			122			103			970

TABLE 1-2. Inter-site comparison of mean start frequency, mean end frequency, and mean duration for all call types. To be included in the ANOVA, a site had to have 10 or more calls of that type.

Call type	Sites compared*	Start frequency	End frequency	Duration
T1A	A,R,H,B,D,T	$F = 6.31$ $p < 0.001$	$F = 10.98$ $p < 0.001$	$F = 22.04$ $p < 0.001$
T1S	A,R,H,T	$F = 32.5$ $p < 0.001$	$F = 48.92$ $p < 0.001$	$F = 12.37$ $p < 0.001$
T2A	(R)			
T2S	A,R,H,T	$F = 19.82$ $p < 0.001$	$F = 38.73$ $p < 0.001$	$F = 8.39$ $p < 0.001$
T3A	R,T	$F = 35.19$ $p < 0.001$	$F = 46.42$ $p < 0.001$	$F = 0.06$ $p > 0.05$
T3S	R,T	$F = 210.33$ $p < 0.001$	$F = 38.20$ $p < 0.001$	$F = 0.10$ $p > 0.05$

* A=Alaska R=Ramsay Island H=Hudson Bay B=Baffin Island D=Dundas Island T=Table Island

TABLE 1-3. Pairwise comparisons of mean start frequency, mean end frequency, and mean duration between all sites for T1A, T1S, and T2S calls. Only those comparisons with a significance level of p 0.05 (Bonferroni probability of 0.0167) are given.

Call type	Feature	Alaska	Ramsay I.	Hudson Bay	Baffin I.	Dundas I.	Table I.
T1A	Start freq	D,T	D,T	D,T	D,T	A,R,H,B	A,R,H,B
	End freq	R,	A, H,B,D,T	R, D	R, D	R,H,B	R
	Duration	D	D,T	D,T	D,T	A,R,H,B	R,H,B
T1S	Start freq	R,H	A, H, T	A,R T	---	---	R,H
	End freq	R,H	A, H, T	A,R			R
	Duration	H	H	A,R			
T2S	Start freq	H	H	A,R	---	---	
	End freq	R,H	A, H, T	A,R			R
	Duration	R,H	A	A			A

A=Alaska. R=Ramsay Island H=Hudson Bay B=Baffin Island D=Dundas Island T=Table Island

TABLE 1-4. Mean values for start frequency, end frequency, duration, and change in frequency (range) for each call type in the two 'lone seal' recordings and 'general' recordings from Ramsay Island site. Start frequency and end frequency are given in number of octaves above 1 Hz. Duration is given in number of seconds and range in number of octaves. Hertz values for mean start and end frequencies are shown in brackets.

Call type	Feature	Lone seal (72 min.) $\bar{x}$	s.d.	N	Lone seal (29 min.) $\bar{x}$	s.d.	N	General $\bar{x}$	s.d.	N
T1	Start freq	10.7 (1667 Hz)	1.6	147	11.0 (2048 Hz)	1.6	36	10.4 (1351 Hz)	1.0	51
	End freq	9.7 (832 Hz)	1.3		9.6 (776 Hz)	1.3		9.5 (724 Hz)	0.8	
	Duration	6.9	7.8		9.6	11.6		7.1	8.0	
	Range	1.0	0.9		1.4	1.0		0.9	0.7	
T2	Start freq	9.7 (832 Hz)	1.5	59	10.1 (1098 Hz)	1.4	24	8.9 (478 Hz)	1.3	23
	End freq	10.9 (1911 Hz)	1.6		11.7 (3327 Hz)	1.3		9.9 (955 Hz)	1.5	
	Duration	6.8	5.5		11.7	10.9		6.4	11.1	
	Range	1.2	0.7		1.6	1.1		1.0	0.7	
T3	Start freq	12.1 (4390 Hz)	0.8	38	12.0 (4096 Hz)	1.0	18	10.9 (1911 Hz)	0.9	17
	End freq	9.3 (630 Hz)	0.7		9.0 (512 Hz)	0.6		9.2 (588 Hz)	0.5	
	Duration	3.7	2.2		4.3	2.8		2.5	1.2	
	Range	2.8	0.8		3.0	0.9		1.7	1.1	
Total number of calls				244			78			91

TABLE 1-5. Comparison of mean start frequency, mean end frequency, and duration for T1, T2, and T3 calls amongst three sets of vocalizations recorded at the Ramsay Island site: vocalizations recorded from a lone seal on two occasions and vocalizations chosen from the general Ramsay Island recordings. All pair-wise t tests with a significance level of $p \leq 0.05$ (Bonferroni probability of ≤ 0.0167) are given.

Call type	Start frequency	End frequency	Duration
T1	$F = 1.37$	$F = 0.38$	$F = 1.47$
	$p > 0.05$	$p > 0.05$	$p > 0.05$
Significant t tests	--	--	--
T2	$F = 3.79$	$F = 8.18$	$F = 3.24$
	$p < 0.05$	$p < 0.001$	$p < 0.05$
Significant t tests	l.s.^{1} + general	l.s.^{1} + general l.s.^{2} + general	--
T3	$F = 11.14$	$F = 0.84$	$F = 3.45$
	$p < 0.001$	$p > 0.05$	$p < 0.05$
Significant t tests	l.s.^{1} + general l.s.^{2} + general	--	l.s.^{1} + general l.s.^{2} + general

l.s.^{1} = 1st 'lone seal' recording (N=244)

l.s.^{2} = 2nd 'lone seal' recording (N=78)

general = 'general' recordings (N=91)

FIGURE 1-1. Locations of the six sites at which underwater recordings of bearded calls were made.

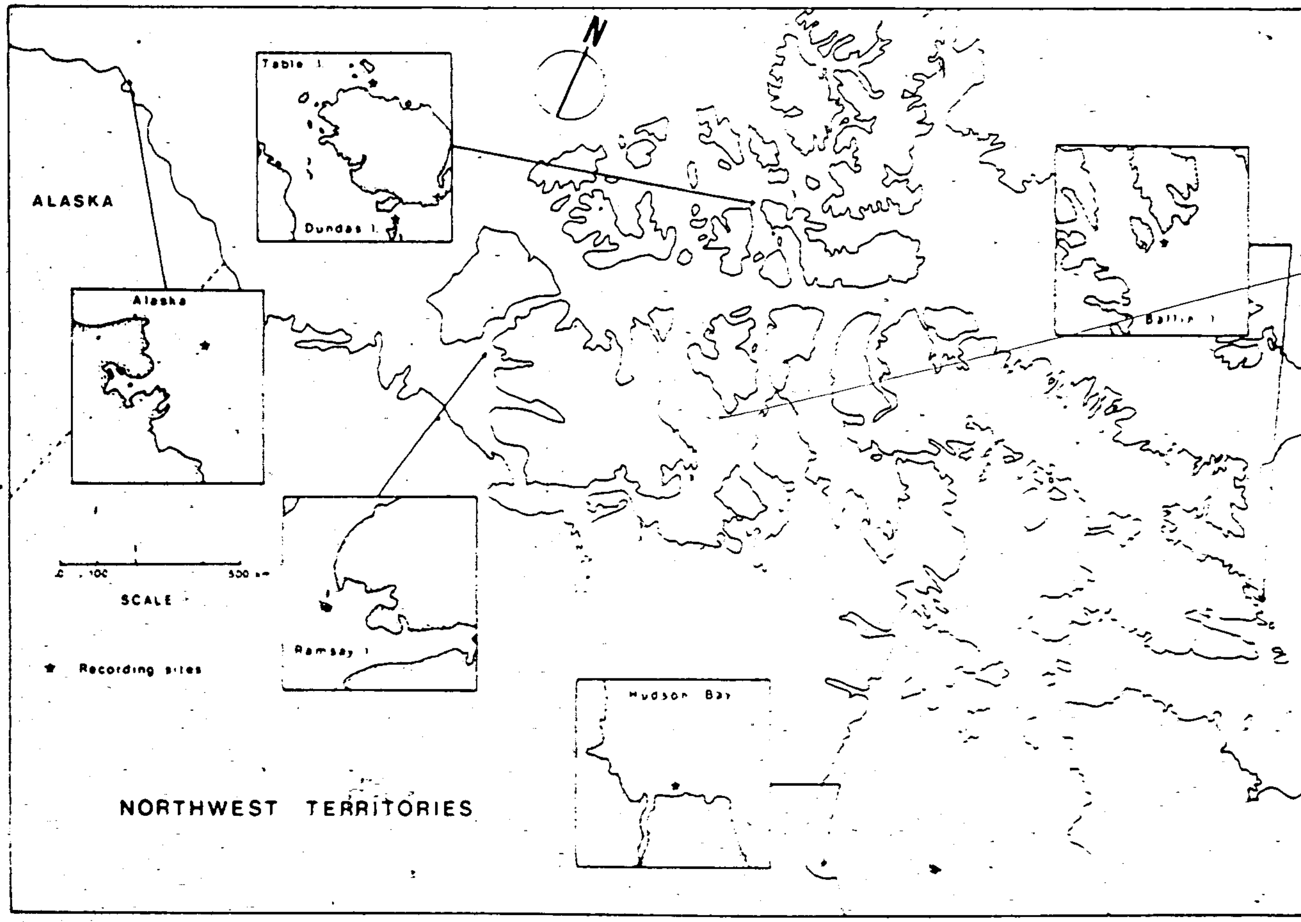


FIGURE 1-2. Classification scheme for bearded seal vocalizations.

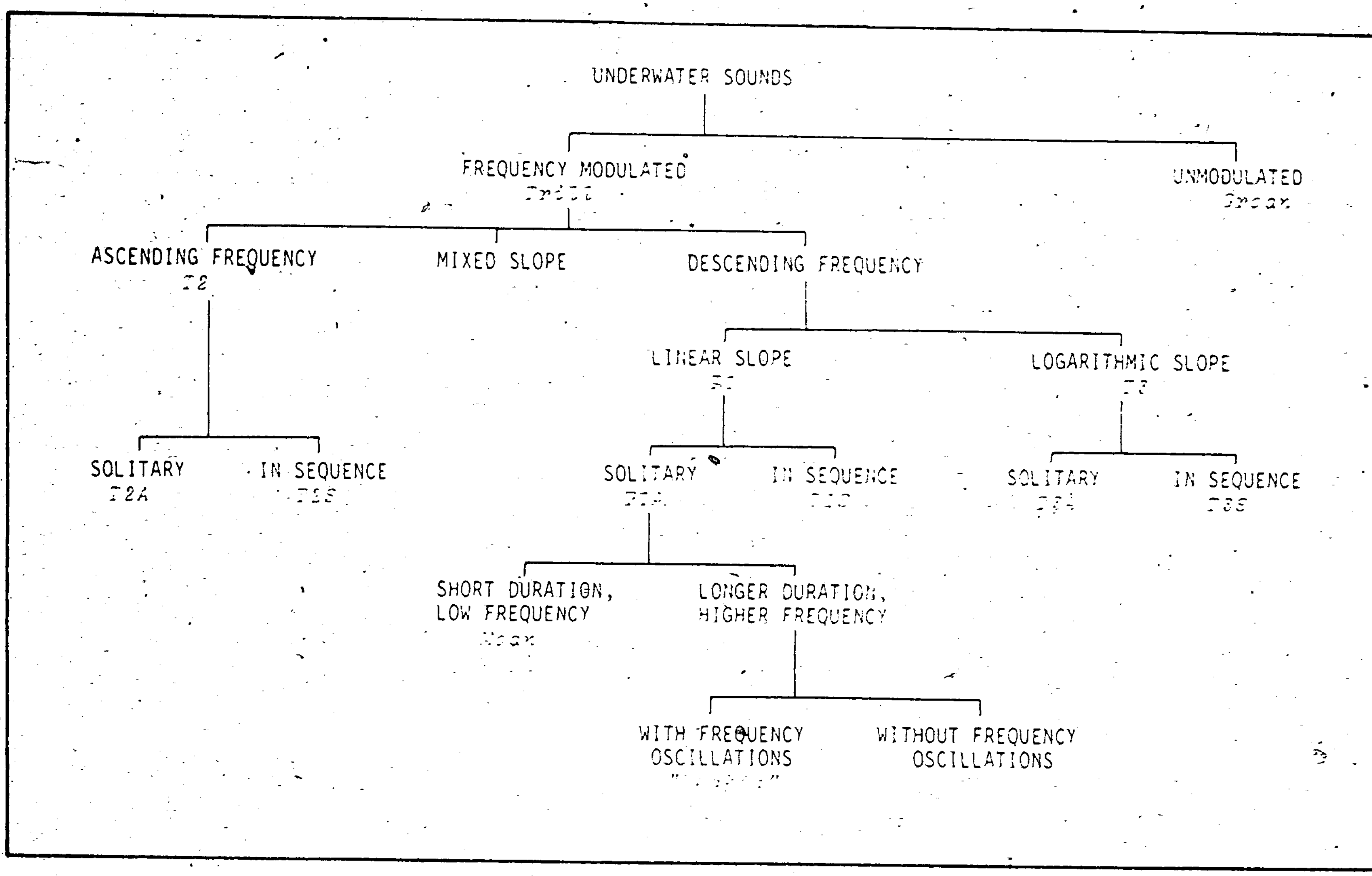


FIGURE 1-3. Line drawings showing the basic shapes of the three call types (T1, T2, and T3). The drawings to the right show the basic shapes of the T1 calls with frequency oscillations.

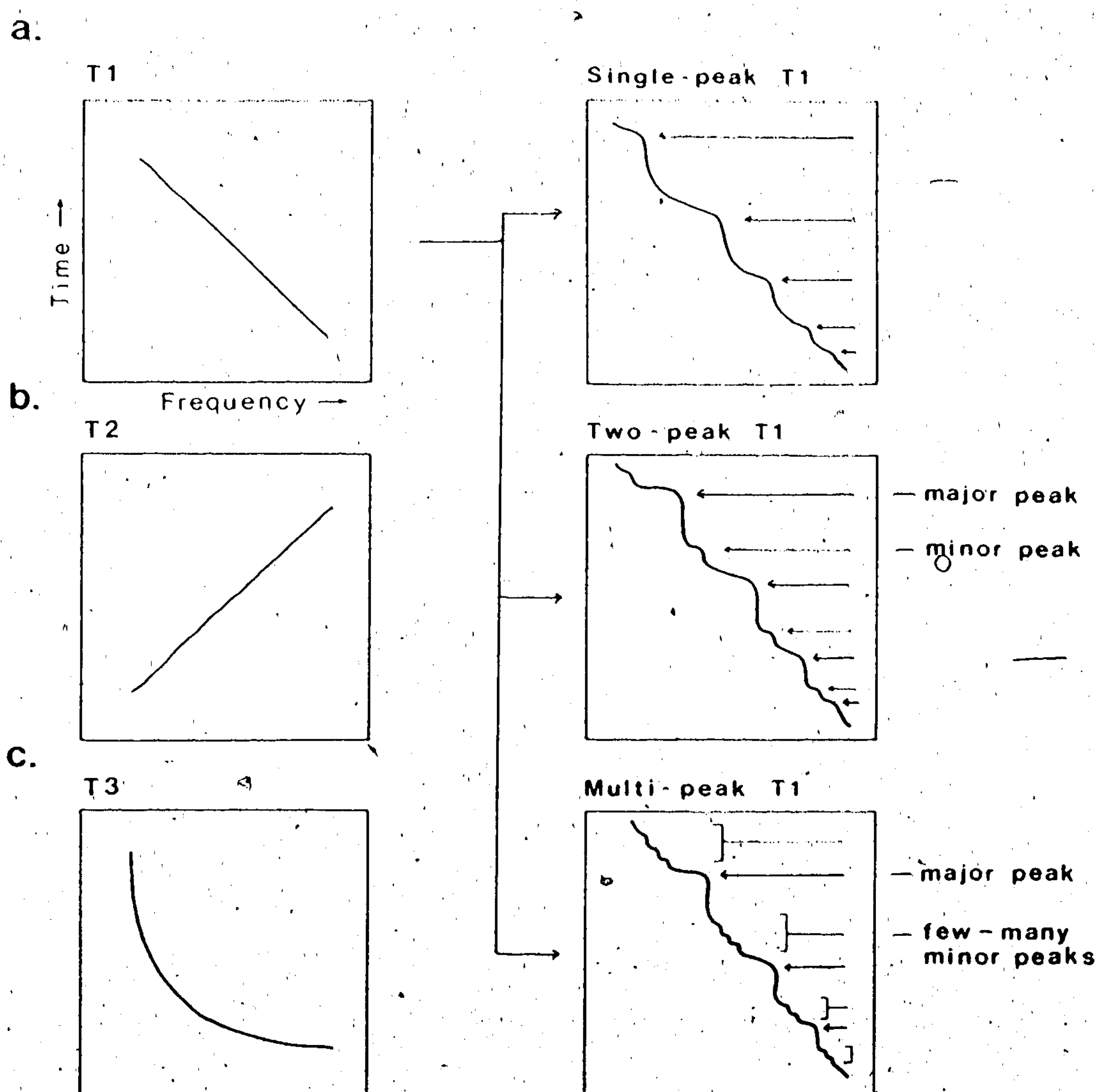


FIGURE 1-4 Waterfall displays showing examples of solitary bearded seal calls.

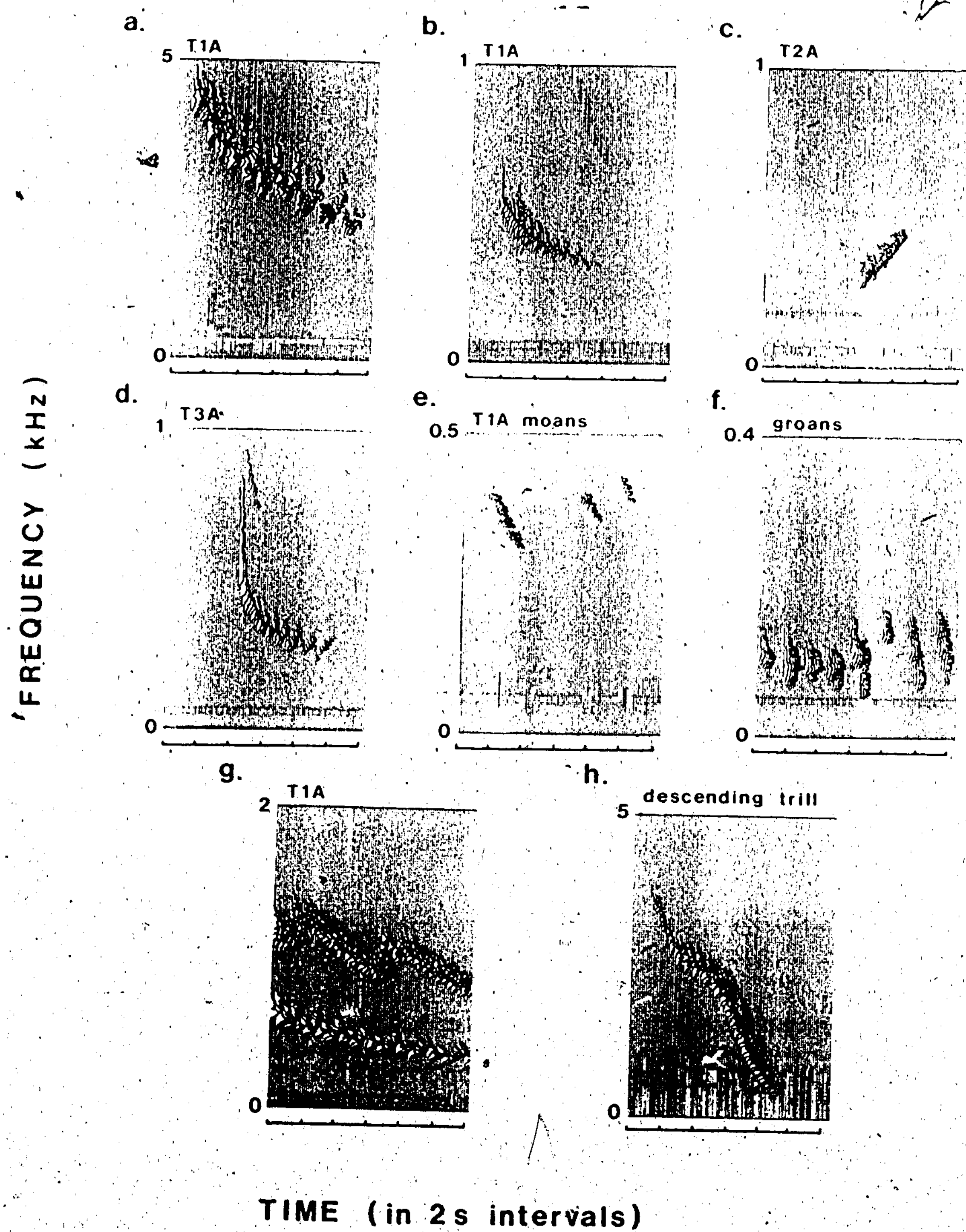


FIGURE 1-5. Locations of the ice camp and the helicopter recording sites near Ramsay Island. Each helicopter site is labelled with the direction and distance (in km) it was from Ramsay camp.

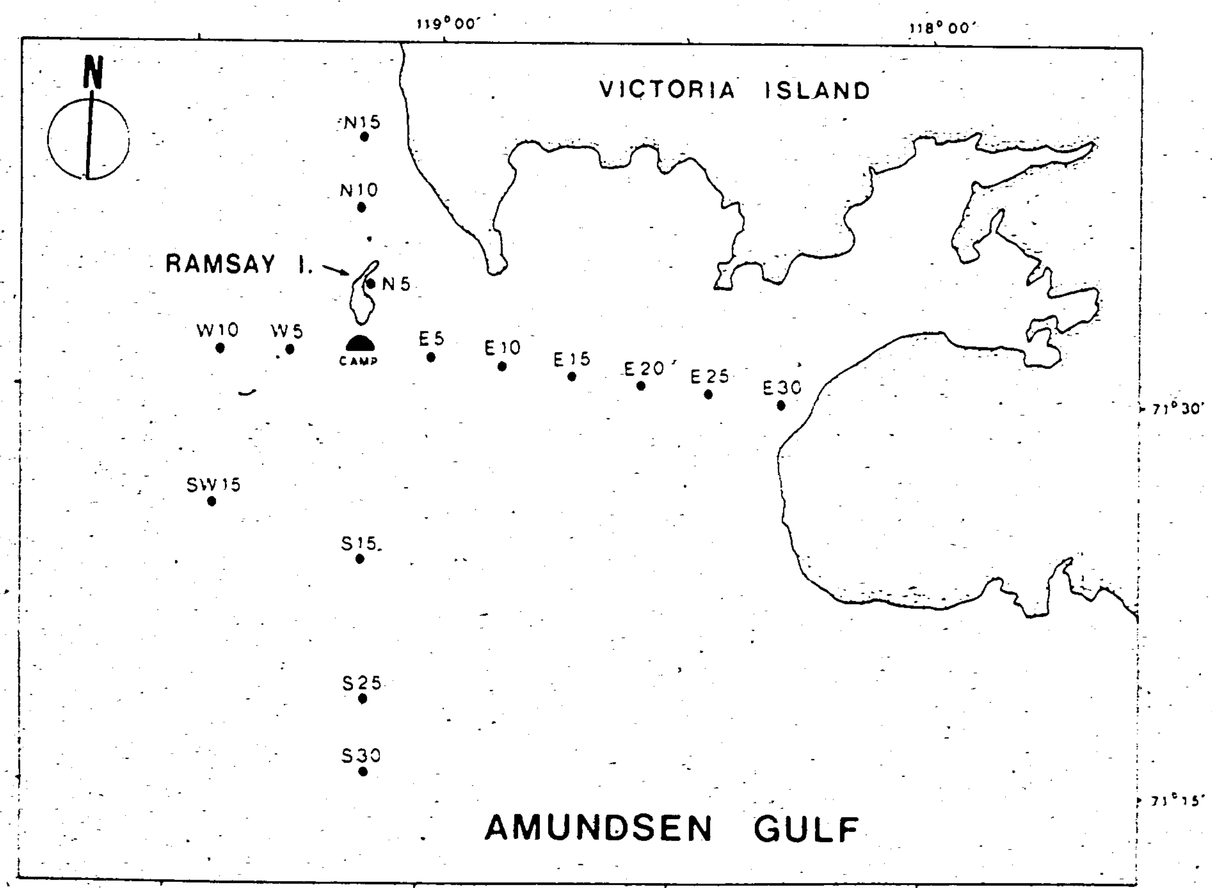


FIGURE 1-6 Waterfall displays showing examples of bearded seal trill sequences.

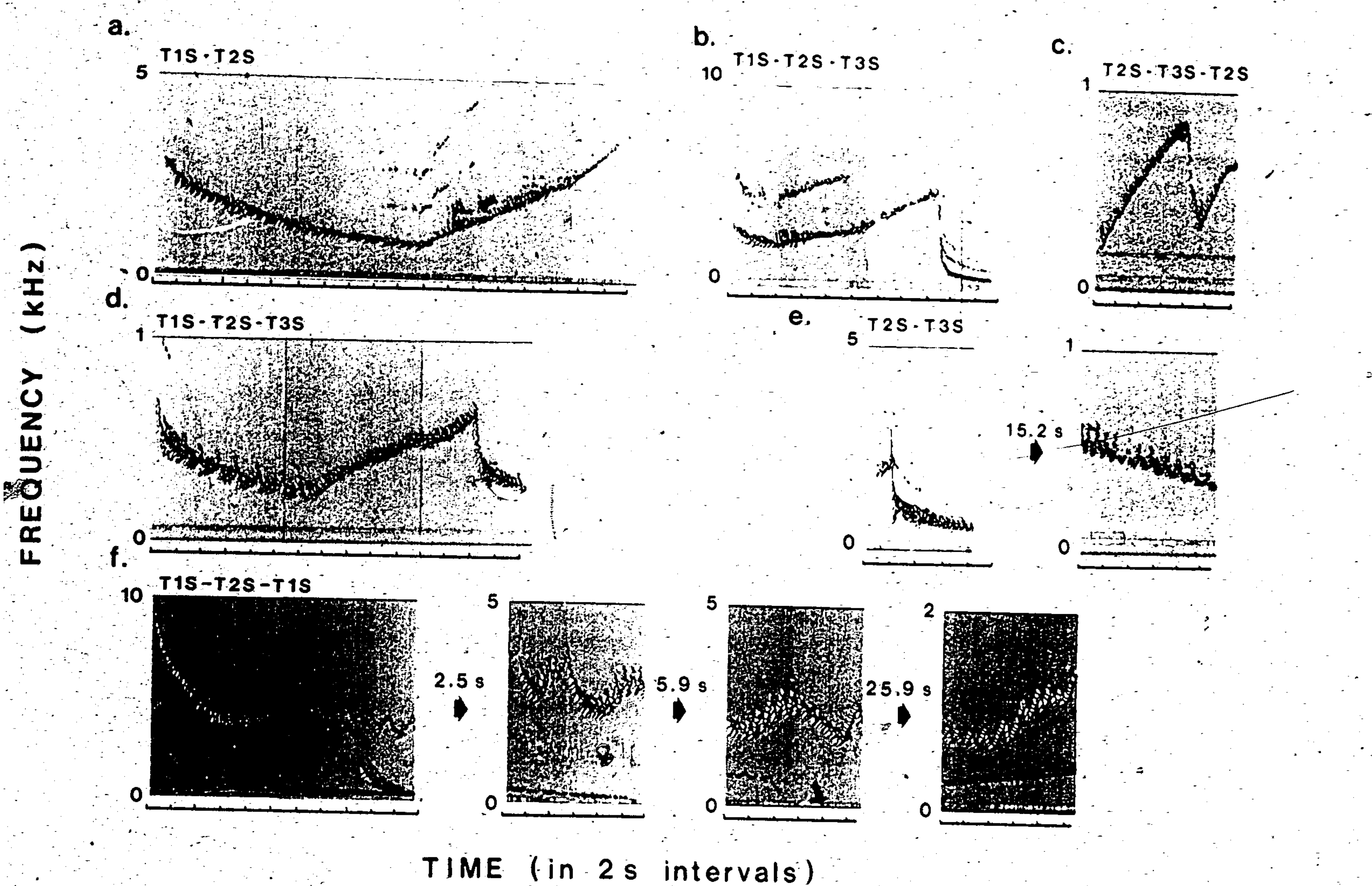


FIGURE 1-7 Waterfall displays showing examples of bearded seal T1A trills recorded at the Alaska, Ramsay Island, Hudson Bay, and Baffin Island sites.

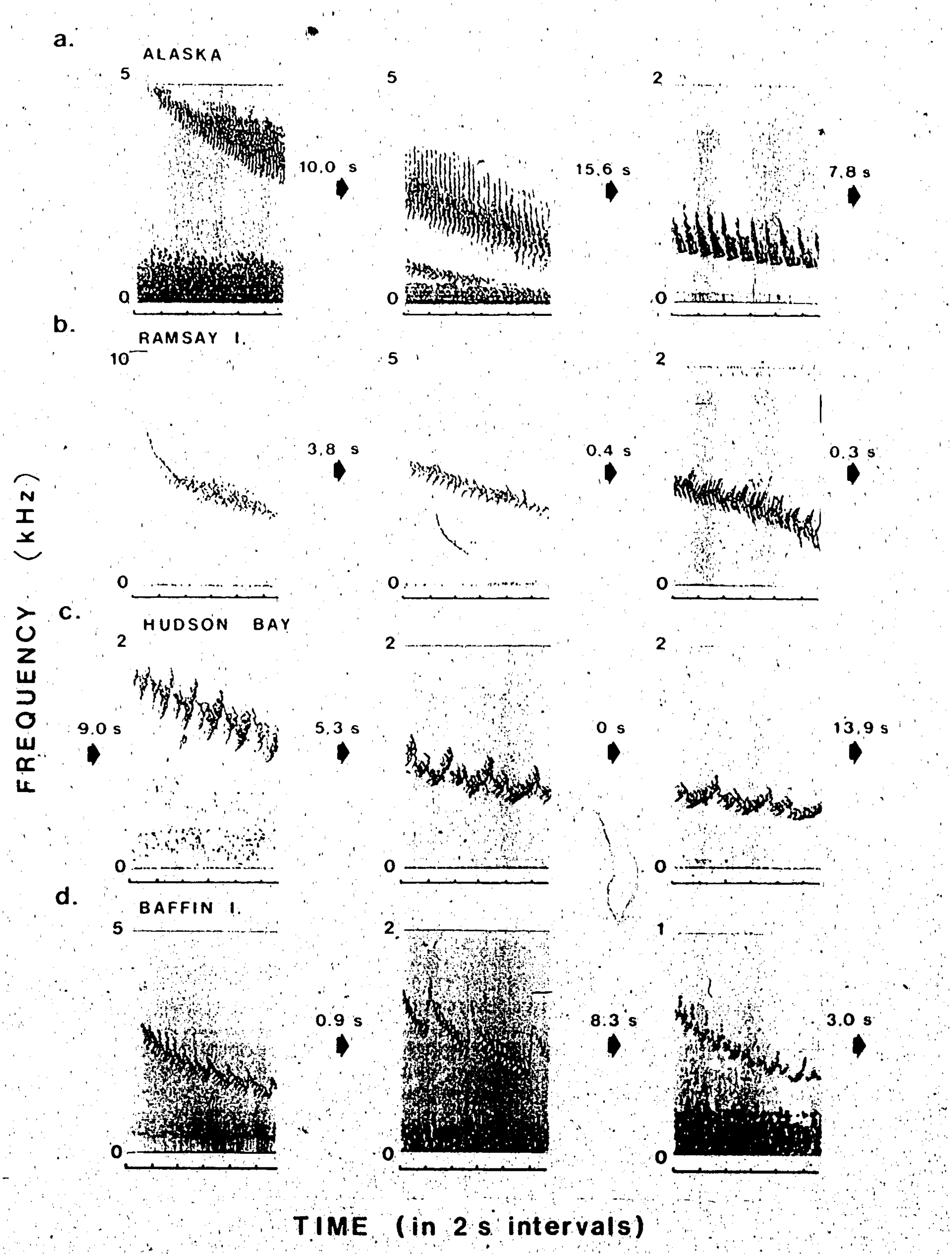


FIGURE 1-8 Line drawings and waterfall displays showing the complex cycles of frequency oscillations that occur in the T1A trills at the Dundas Island site and in the T1S trills at the Table Island site.

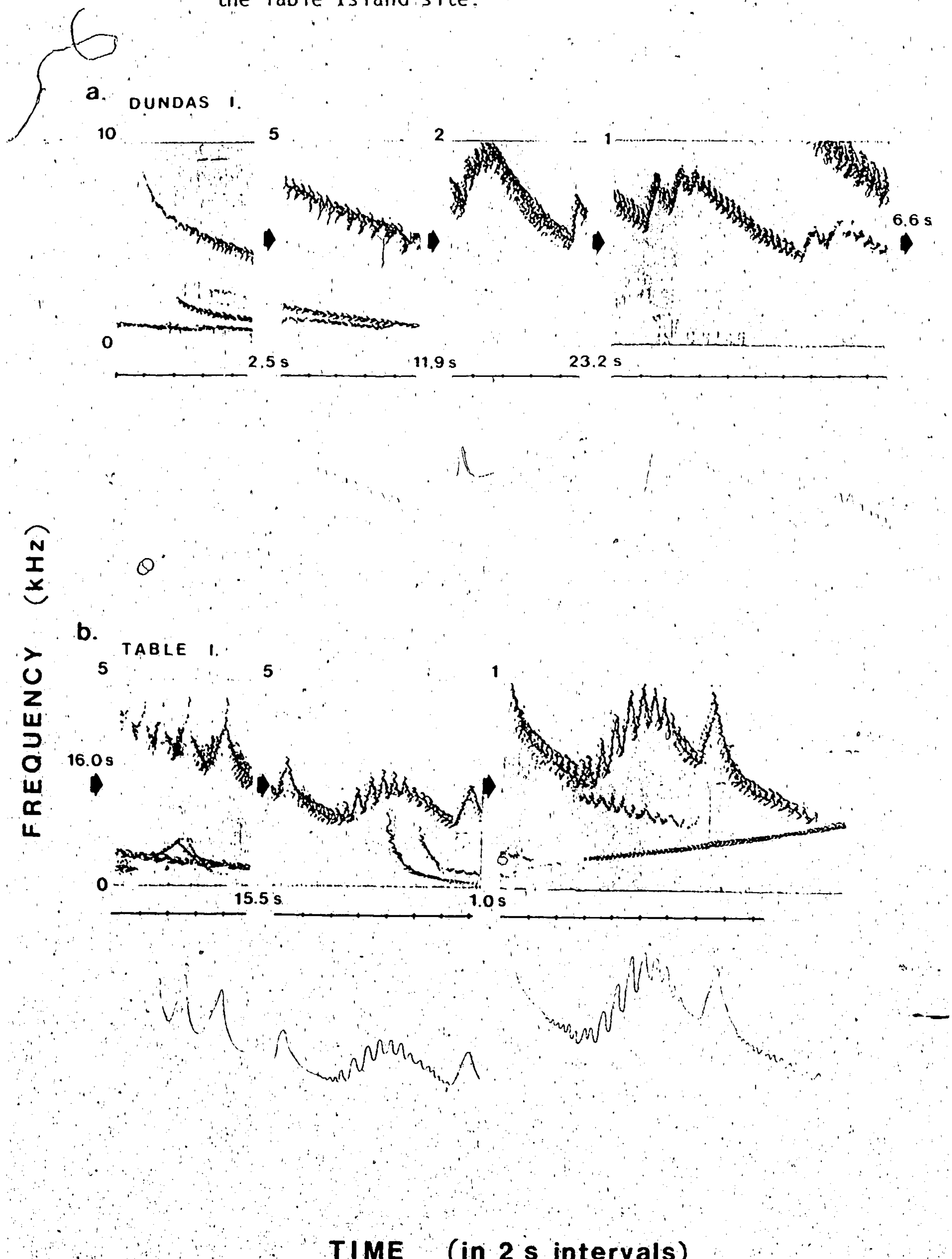


FIGURE 1-9. Frequency of occurrence of each call type at all recording sites.

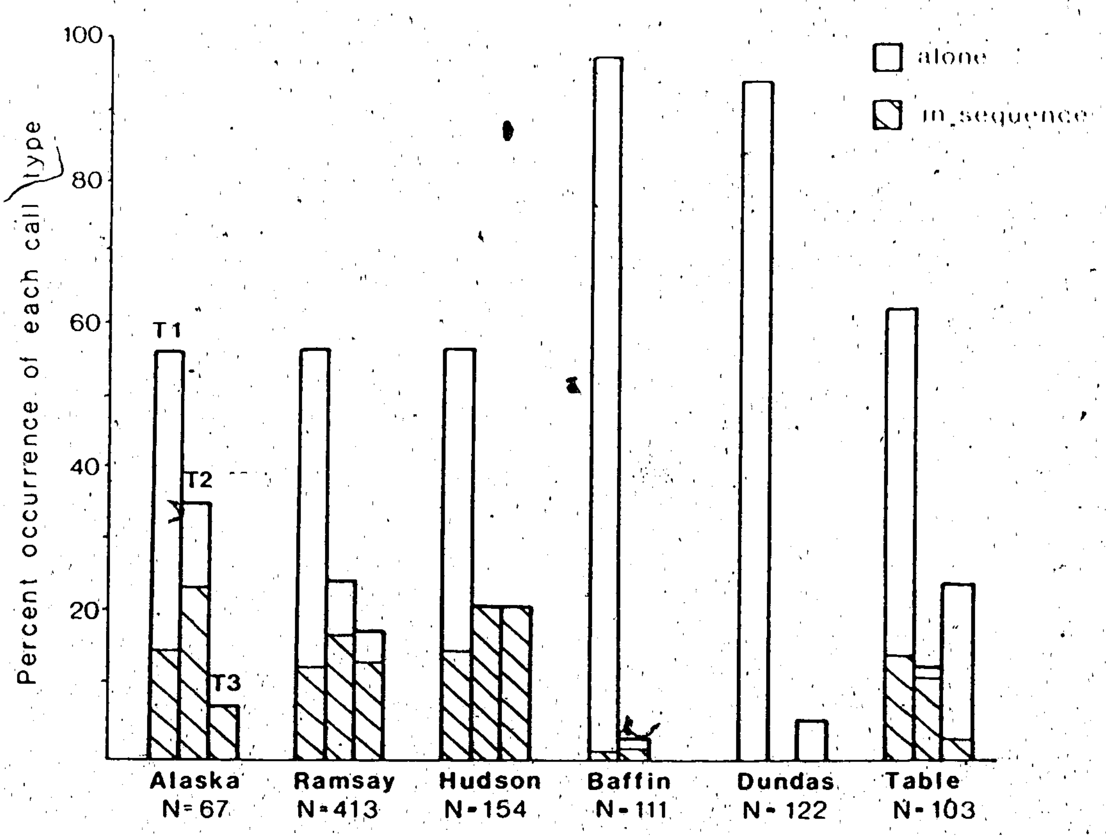


FIGURE 1-10. Frequency of occurrence of each call type in both 'lone seal' recordings and the 'general' recordings made at the Ramsay Island site.

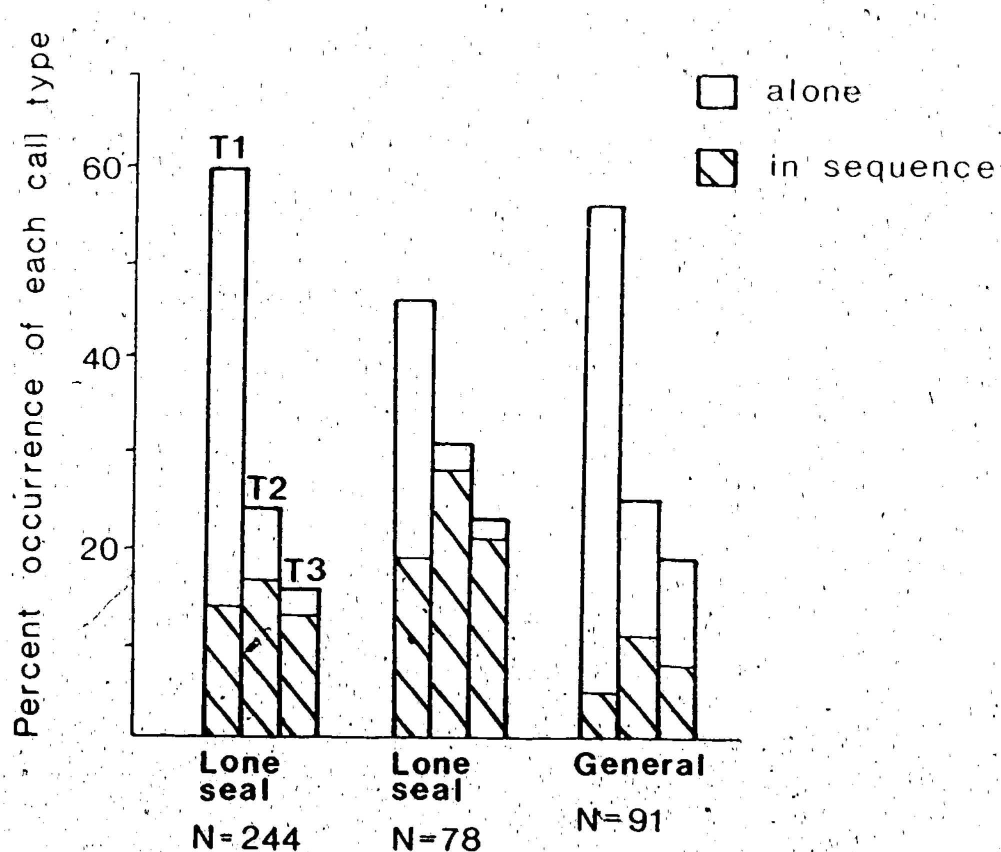


FIGURE 1-11. Power spectra showing the relative abundance of all possible temporal cycles in the vocalization rate data collected at Ramsay Island and Dundas Island sites in early and late spring.

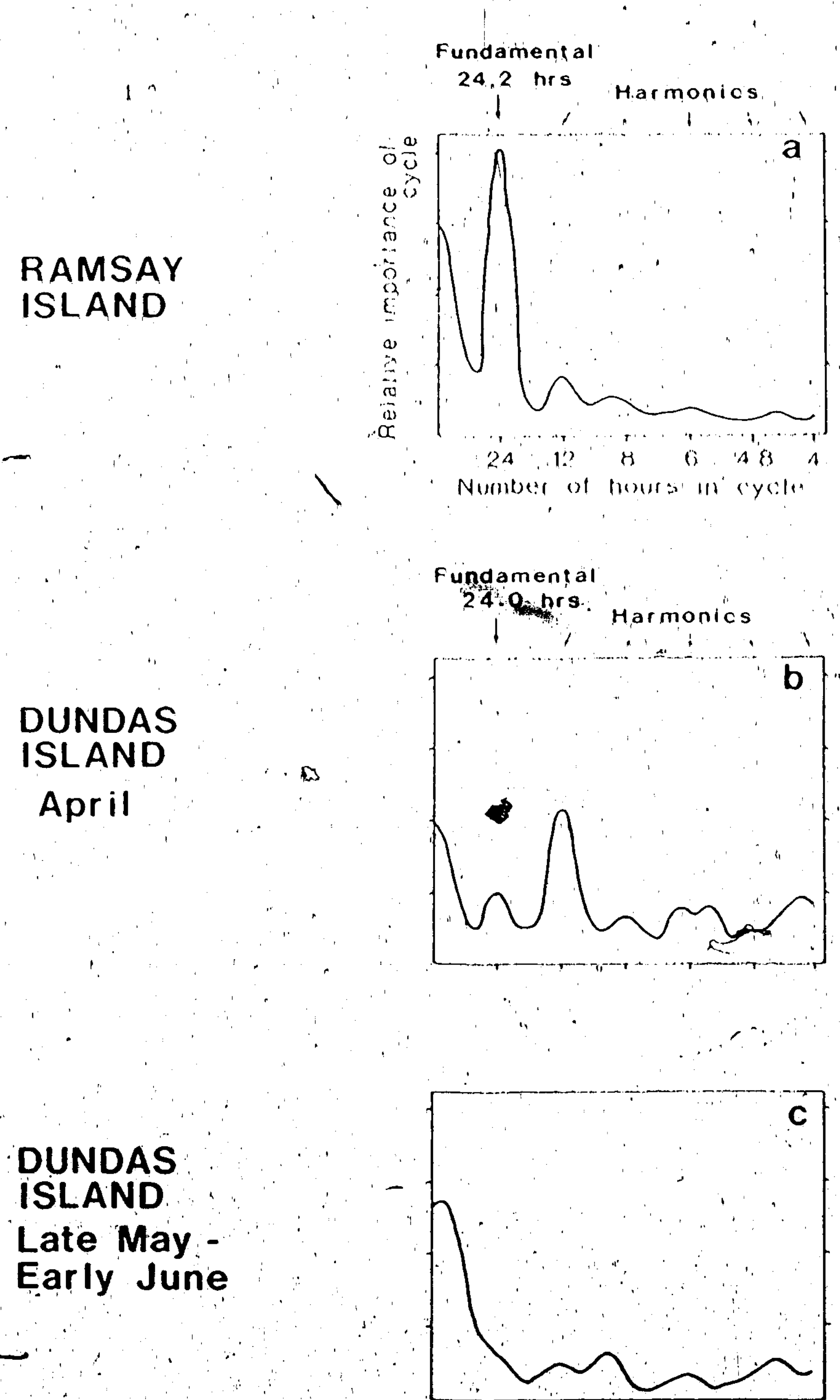


FIGURE 1-12. Daily cycles in mean rates of calling at the Ramsay Island and Dundas Island sites. The error bars in the upper three graphs show plus and minus one sample standard deviation of the data about the mean. The bottom graph provides a comparison of the patterns in rate of calling for the three data sets.

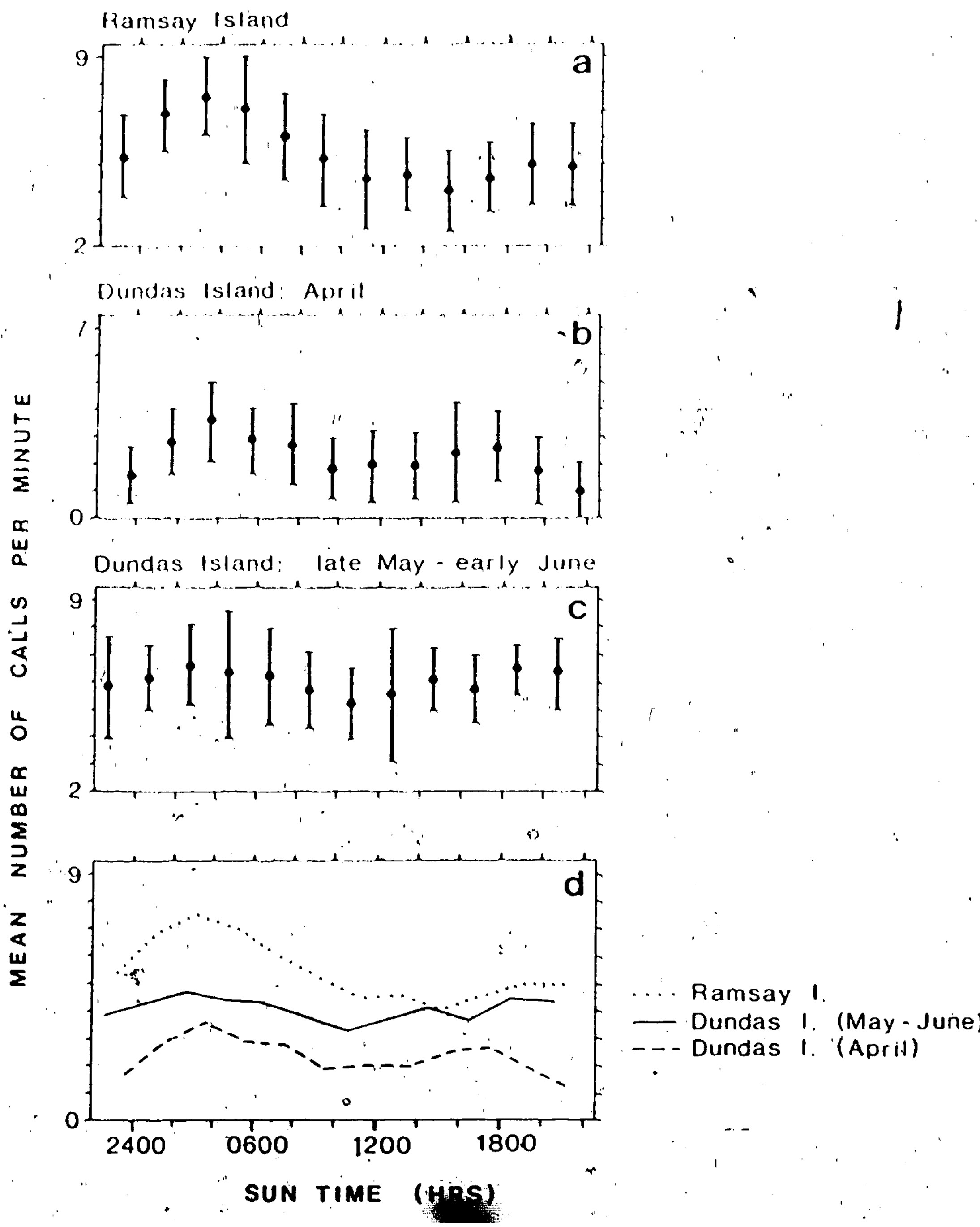


FIGURE 1-13. Distances that 156 bearded seal vocalizations were estimated to have travelled in water based on straight-line measurements between two hydrophones (see text for method). The vocalizations are grouped by call type. Only one distance value is shown for each call: the distance between the calling seal and the hydrophone farther from it.

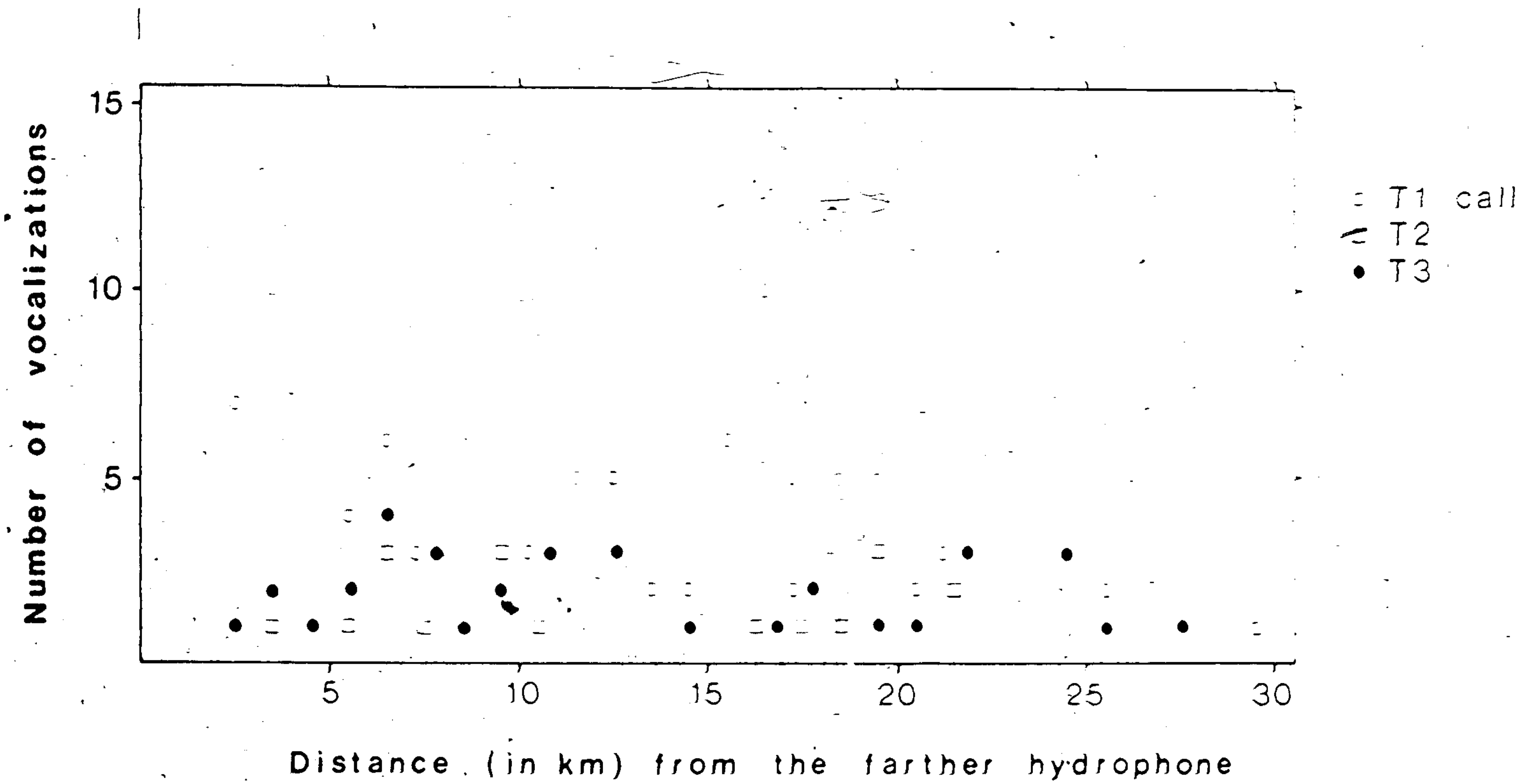


FIGURE 1-14. Frequency of occurrence, by call type, of calls heard at both the camp and helicopter recording sites near Ramsay Island. The graphed data are the pooled results taken from simultaneous camp-helicopter recordings made while the helicopter was 5 km, 10 km, and 15 km east of the camp. Of 239 individual calls recorded at either the camp or helicopter sites, 108 (45.2%) were recorded at both locations.

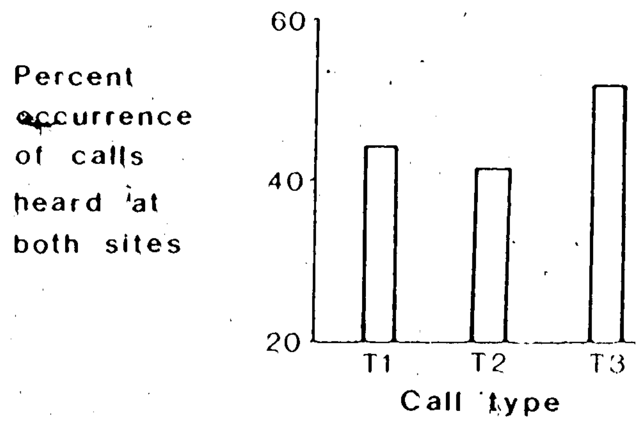


FIGURE 1-15. Comparison of the frequency of occurrence of each call type between the 'call propagation' and 'lone seal' recordings. Only those calls heard at both the camp and helicopter sites were used in the 'call propagation' recordings (N=473). The two 'lone seal' recordings were pooled together (N=322).

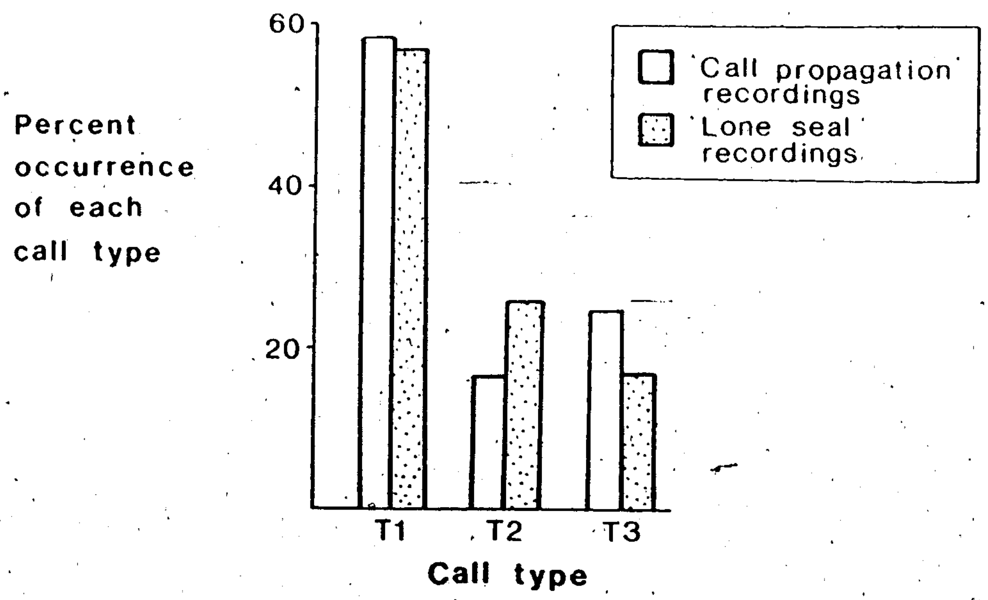
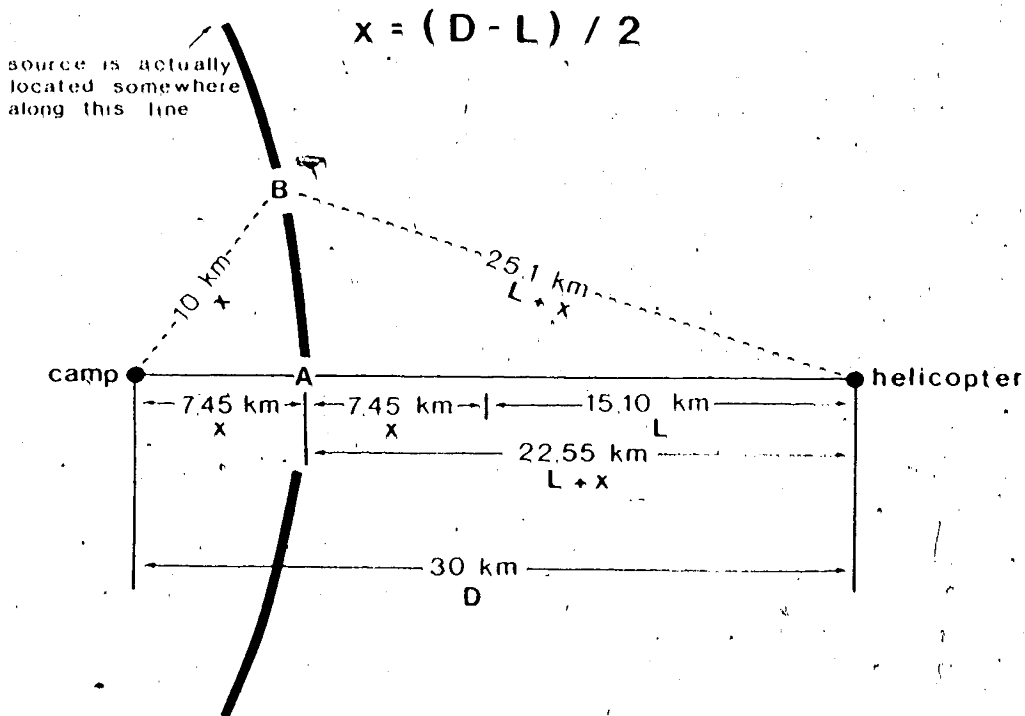


FIGURE 1-16. Calculations used to determine the minimum transmission distance between a vocalizing seal and the two recording sites.



CASE A
Minimum-distance location of source

D = 30 km
V = 1.438 km/s
L = T V
= 10.5 s x 1.438/km s
= 15.10 km
X = (D-L) ÷ 2
= (30 - 15.1) ÷ 2
= 7.45 km

CASE B
Source is not on line joining camp and helicopter

suppose that source is 10 km from camp, then:

D = 30
L = T V
= 10.5 s x 1.438 km/s
= 15.10 km
L + X = 25.10 km

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3. WINTER DISTRIBUTION OF BEARDED SEALS IN THE PENNY STRAIT AREA, NORTHWEST TERRITORIES, AS DETERMINED BY UNDERWATER VOCALIZATIONS

3.1 Introduction

Arctic pinnipeds are often difficult to census. Being aquatic, they spend most of their time in water where they are hard to see, and frequently are far enough from land to preclude land-based surveys. In most of the Canadian Arctic the open-water season lasts from July to September. During the remainder of the year, the waters are usually ice-covered except for a few relatively small recurring openings (i.e., polynyas or leads). Consequently, efforts to study the distribution and abundance of arctic seals are limited to times when they haul out on ice for purposes such as pupping or moulting. Inclement weather and darkness during the winter further limit the periods during which surveys may be done and increase the difficulties and danger, particularly with aerial surveys.

Techniques of population estimation usually require either the capture of some individuals in a population, such as in mark-recapture or catch per unit effort studies, or visual counting of animals. Indirect counts of such signs of abundance as tracks, nests, or vocalizations make up a third category. Singing or calling surveys have been used to study the density and distribution of birds (McClure 1939; Kimball 1949; Petraborg *et al.* 1953; Kozicky *et al.* 1954; Gates and Smith 1972). The possibility of using underwater vocalizations to census pinnipeds, or at least estimate their relative abundance, has been noted (Ray 1970; Thomas and DeMaster 1982). More recently, Stirling *et al.* (1983) reported using the underwater calls of ringed seals (*Phoca hispida*), bearded seals (*Erignathus barbatus*), and Atlantic walruses (*Odobenus rosmarus rosmarus*) to determine their relative abundance at sites in the Canadian High Arctic in late winter and spring. Prior to that, visual aerial survey was the only census technique successfully used on bearded seals. However, most of the aerial surveys reported in the literature were specifically designed for ringed seals, and simply included sightings of bearded seals made during survey flights. Designing a reliable and accurate aerial survey for bearded seals is difficult because, in addition to the problems already outlined, they tend to occur at lower densities than ringed seals, their distribution is more clumped, and the details of their haul-out are not as well-known as they are for ringed seals (Smith 1981).

Bearded seals are circumpolar and boreoarctic in distribution. Results from aerial surveys and other studies show that during the late winter (March-April) and spring (May-June) bearded seals prefer areas of moving ice and open waters in shallow-bottomed areas, and avoid areas of thick shorefast ice (McLaren 1962; Mansfield 1967; Burns 1970; Davis *et al.* 1975; Burns and Frost 1979; Stirling *et al.* 1982; Kingsley *et al* 1985). There are a few areas where bearded seals maintain breathing holes in landfast ice throughout the winter (Mansfield 1967; Stirling and Smith 1977; Smith 1981), however this situation likely occurs only in waters that freeze-up late and open early (Stirling *et al.* 1983). Bearded seals have been observed in waters over 500 m deep during March and April (Finley and Renaud 1980).

During the breeding season, sometime between late winter and early summer, bearded seals produce trill-like vocalizations (Dubrovskii 1937; Chapskii 1938; Ray *et al.* 1969; Burns 1981; Stirling *et al.* 1983). Males are thought to produce most, if not all, trill vocalizations for the purpose of advertising breeding condition, or ownership of territory, or both (Ray *et al.* 1969). The primary objective of this study was to examine the winter distribution of bearded seals in Penny Strait and surrounding waters by listening for their underwater calls in April. A secondary objective was to document their distribution by means of vocalization surveys during the period between late winter and break-up (in late June).

3.2 Materials and Methods

Sub-ice recordings were made at seven locations during April-June 1982, and at six of the locations in April 1983 and April 1984 (Fig. 2-1). The recording sites varied with respect to several features: water depth; snow thickness; thickness, stability, age (annual vs multi-year) and type (landfast vs pack) of ice cover (Table 2-1).

Most recording stations were located in northern Queens Channel (76°11'N, 96°00'W) and Penny Strait (76°30'N, 97°00'W). Site 4 was located in southern Belcher Channel (77°15'N, 95°00'W). In shallow waters (<100 m), under a relatively smooth cover of landfast ice, bearded seal trills can be heard up to 30 km from the vocalizing animal, although only a small percentage (≤ 15%) can be heard for distances greater than 20 km (this study, Chapter 2). To reduce the likelihood of recording the same seal at two or more sites, the recording stations were located at least 20 km apart. Where possible, land masses (usually islands) were used as submarine barriers between sites to dampen or block the transmission of calls from one recording station to another (Fig. 2-1).

In 1982, sites 1 and 2 were visited on 18 April, 29 April, 4 June, 14 June, and 29 June. The remaining five sites were visited on either three or four of those dates. Some recordings were lost because poor weather precluded reaching the site or because of equipment malfunction. Since few or no vocalizations were heard at site 3 in spring 1982, it was excluded from subsequent surveys. In 1983 and 1984, underwater recordings were made on 17 and 26 April and 12 and 25 April respectively. In the Canadian High Arctic, ice conditions remain relatively stable through the winter until late April or early May. Therefore the distribution of bearded seals at that time of year should reflect their winter (December-March) distribution.

Recordings were made using Uher 4200 Report Monitor tape recorders with either Ampex or BASF tapes and an ITC (International Transducer Corporation) 6050C hydrophone. Travel to and from recording sites was made in a Bell 206B helicopter. After landing on the sea ice, the helicopter had to idle for 2–3 min to cool the engine before it was turned off. A 10 cm (diameter) hole was drilled through the ice using a hand auger. Thickness of ice was recorded and the hydrophone was suspended 3–5 m below the underside of the ice. When available, seal breathing holes or cracks in the ice were used for installing the hydrophone. Recordings were usually made between 0900 hrs and 1800 hrs CST and most were 20 min in duration.

In the laboratory, each recording was listened to three times and the number of vocalizations heard was tallied. Presumably because calling seals were located at different distances away from the hydrophone, vocalizations varied greatly in volume and the decision on whether or not to include a very faint call was necessarily subjective. Recordings in which high background noise levels predominated were more prone to variable results than those with low background noise. Because there could be as much as a 10% difference in the number of calls counted between listening sessions on the same recording, the mean of three counts for each recording was used.

The mean number of vocalizations per minute per 10^4 hectares was calculated for each site. The area measurements were taken from 1:250,000 topographic maps using an HP9864A digitizer, HP 9866A printer, and HP 9830A keyboard. A circle was drawn on the map around each recording site then traced using the digitizing wand. A circle with a radius of 20 km was used and, to be conservative, it was assumed that the transmission of calls occurred only in straight lines. All bodies of water whose 'sound path' to the recording sites were blocked by land were eliminated from the calculation.

Three comparions were made by means of a Kruskal-Wallace test: among sites in April-June 1982, among sites in April 1982-84, and among years (April 1982-84). Calling rates recorded in April 1982-84 at sites 1 and 2 were then compared with the values obtained at sites 4-7 by means of Scheffe's S test on the ranked values. Because of the limited number of replications and extent of missing data a critical level of 0.05 was chosen for all tests.

3.3 Results

Statistically significant differences in calling rates were found amongst the seven sites visited in spring 1982 ($H=20.0$; $df=6$; $p<.005$). Overall, sites 1-3 ~~had lower~~ rates of vocalization than sites 4-7 (Table 2-2). To determine whether the vocalization rates were simply a reflection of the amount of area actually surveyed at each site rather than an indicator of real differences in the density of vocalizing seals at or near sites, the mean rate of calling at each recording station was divided by the area sampled there, Normalizing vocalization rate values for area at each site did produce a few changes in the ranking order amongst the sites. Nonetheless, significant differences between sites remained ($H=12.2$; $df=6$; $p < 0.05$): generally fewer vocalizations were recorded at sites 1–3, than at sites 4–7.

Site 7 had the highest mean vocalization rate in April-June 1982 and April 1982–84 and the largest sampling area (113,760 hectares). Dividing the rate of calling at site 7 by an estimate of the area sampled dropped the site in rank from the highest mean calling rate in the April-June 1982 surveys to second highest below site 4 (Table 2-2), and from the highest mean calling rate in April 1982–84 to fourth highest, below sites 4, 5, and 6 (Table 2-3).

Site 3 consistently had the lowest vocalization rates during the 1982 surveys and the smallest sampling area (8,292 hectares). When ranked against the other sites, site 3 maintained the lowest mean rate of vocalization during the 1982 surveys (Table 2-2). The lowest rate of calling was recorded there in all surveys except one. On 14 June, five faint calls (60.3 calls/min./ha x 10^6) were recorded at site 3; they probably originated from near the mouth of Barrow Harbour. The waters depths around the site were shallow (approx 30 m) and stable landfast ice persisted there throughout the study period.

When the rates of vocalization at all sites were normalized for area, site 2 rose in rank from sixth highest to third highest in 1982 (Table 2-2). However, during the April 1982–84 recordings, site 2 remained second lowest in rank (i.e., 5th of 6) (Table 2-3). During April-June 1982, the rate of vocalization varied considerably between surveys at site 2 (Fig. 2-2). From 18 April to 29 April the vocalization rate increased by 52 times. Between the three June surveys the rate of calling decreased by a factor of 11 and then increased by a factor of 14. Changes of that magnitude were not recorded at any other site.

In absolute terms, the number of vocalizations per minute at all sites increased between April and early June 1982, although with the exception of site 2 the rates of calling remained relatively stable amongst the sites during that period (Fig. 2-2). Calling rates of ≥ 100 calls/min./ha x 10^6 were recorded at four of the seven sites on 4 June.

Some vocalization rates are missing for sites 5, 6, and 7 during the mid- and late June surveys, nevertheless the rates of vocalization decreased at those sites during the latter half of the month. In contrast, rates of calling continued to increase at sites 1-3 in June.

Comparison of calling rates (normalized for area) between the sites visited in April 1982–84 revealed statistically significant differences ($H=19.7$; $df=5$; $p<0.005$). Overall, lower rates of vocalization were recorded at sites 1 and 2 than at sites 4–7 (Scheffe's S statistic=8.5 ; $df=5,30$; $p<0.001$) (Fig. 2-3). The mean numbers of calls recorded per minute in April 1982–84 at sites 1 and 2 were 12.0 calls/min./ha x 10^6 and 9.1 calls/min./ha x 10^6 respectively. Although three times as many calls were heard at site 2, the calls recorded at site 1 were moderate to loud in intensity, while those at site 2 were weaker. Most calls recorded at site 1 likely originated closer to the hydrophone whereas calls recorded at site 2 likely originated farther offshore in Penny Strait and northern Queens Channel. Sites 4, 5, 6, and 7 had comparable rates of calling in April 1982–84 ($\bar{x}_4=85.5$ calls/min./ha x 10^6; $\bar{x}_5=81.5$ calls/min./ha x 10^6; $\bar{x}_6=85.4$ calls/min./ha x 10^6; $\bar{x}_7=78.2$ calls/min./ha x 10^6). In spite of the similarity in mean values amongst the four sites, vocalization rates varied considerably between sites and dates: from a low of 42.7 calls/min./ha x 10^6 to a high of 121.8 calls/min./ha x 10^6. None of the four sites was consistently higher or lower than the rest over the three-year period.

Comparison among years of the rates of vocalization in April at the six recording sites showed that between-year differences were not statistically significant ($H=3.6$; $df=2$; $p>0.05$). The highest mean calling rate was recorded in 1984 ($\bar{x}=70.0$ calls/min./ha x 10^6 ; s.d.=36.4). In 1982 and 1983, the mean rates of calling for the six sites were 61.4 calls/min./ha x 10^6 (s.d.=36.6) and 57.1 calls/min./ha x 10^6 (s.d.=36.7) respectively.

3.4 Discussion

Calling rates were used to determine the relative abundance of bearded seals at seven sites in Penny Strait and environs, and to determine whether these values varied greatly between years. With a few exceptions, sites 1–3 had lower rates of calling than sites 4–7 in all surveys conducted during 1982–84. Although time of day may have influenced the number of vocalizations recorded (this study, Chapter 2), there were no obvious indications in the survey data that differences in calling rates amongst the sites were the result of time of day at which the recordings were made. Examination of habitat information at each site revealed some similarities between vocalization rate values and environmental features.

Sites 2 and 3 were located in relatively shallow waters covered by thick (i.e., ≥150 cm), stable landfast ice. Very low rates of calling were recorded at site 3 during all surveys in 1982 but one (14 June), and most calls recorded at site 2 were weak in volume. These data suggest that during the winter and early spring, bearded seals avoid areas such as the inner reaches of inlets, bays, and harbours because of the stable ice conditions that occur there. Previous studies on the habitat preferences of bearded seals gave similar results (McLaren 1962; Mansfield 1967; Burns and Frost 1979; Stirling *et al.* 1982, 1983; Kingsley *et al.* 1985).

In determining the area of water actually surveyed at each site, the assumption was made that bearded seal calls travelled only in straight lines. This is an oversimplification of what likely occurs. Some field experiences suggest that bearded seal calls can bend around points of land in some situations, but attenuate noticeably as a result of doing so. On 14 June 1982, five faint calls were recorded at site 3. It is possible some or all of the calls originated within the 8,292 ha of water surrounding the site, but the weak volume of the calls suggests they originated from near the mouth of Barrow Harbour and travelled along a curved path to reach the head of the harbour. It seems likely that the relatively high rate of calling (60.3 calls/min./ha x 10^{6}) for that date resulted from dividing the five calls by an unrealistically small survey area calculated using straight line borders. The geography of the other six sites poses less concern with respect to the 'straight-line' assumption because the ratios of water to land were considerably greater than at site 3.

Bearded seals are reported to overwinter most frequently in areas of broken, moving ice over shallow water ($\geq$100 m) (Mansfield 1967; Burns 1970; Davis *et al.* 1975; Burns and Frost 1979; Stirling *et al.* 1982; Kingsley *et al.* 1985). Areas where the ice contains openings such polynyas and leads are preferred (Burns and Frost 1979; Smith *et al.* 1979; Stirling *et al.* 1981). Stirling *et al.* (1981) stated "the winter distribution of bearded seals in the Canadian Arctic could for the most part be superimposed over the polynya areas". Site 1 (Dundas polynya) is a relatively ice-free area which persists throughout the winter months at the north-eastern edge of Queens Channel. Strong currents and predominantly shallow water are the likely causes of this recurring feature; it usually reaches its maximum size in late April or early May (Smith and Rigby 1981), before break-up in the rest of the study area. Based on the number of calls recorded in April 1982–84 it appears site 1 receives little use by bearded seals at that time of year. Two factors relating to walruses may help to account for the relative absence of bearded seals.

Atlantic walruses overwinter in the vicinity of Dundas polynya because of the shallow water it provides for benthic feeding, and openings in the ice available for breathing and haul-out (Stirling *et al.* 1983). Bivalve molluscs are the predominant food of walruses although secondarily they eat other types of benthic invertebrates (Vibe 1950; Mansfield 1958; Loughrey 1959; Krylov 1971; Lowry *et al.* 1980; Fay 1982). Bearded seals are also primarily benthic or epibenthic feeders. However, in contrast to walruses, bearded seals will use a wide variety of food items including pelagic fishes such as arctic cod (*Boreogadus saida*) (Chapskii 1938; Vibe 1950; McLaren 1962; Burns 1967; Kosygin 1971; Burns and Frost 1979; Lowry *et al.* 1980; Smith 1981; Finley and Evans 1983). The specific diet of an individual seal appears to vary with age, location, and time of year (Burns and Frost 1979; Finley and Evans 1983). Bearded seals are able to switch prey if the availability of certain food items becomes reduced (Lowry *et al.* 1980), nonetheless Dundas polynya would likely provide few pelagic species for alternate foods. As a result of inter-specific competition with walruses for benthic prey, most bearded seals in the region may be forced to move into the deeper waters of Penny Strait and

Queens Channel in order to find adequate quantities of food.

Another possible explanation for the low calling rates recorded at site 1 may relate to the fact that walruses sometimes prey on seals (Gray 1927; Freuchen 1935; Chapskii 1936; Vibe 1950; Fay 1982; Krylov 1971). Recent data from the Bering and Chukchi seas have shown that walruses may prey upon several species of seals, including bearded seals (Lowry and Fay 1984). Since only young seals were taken, only females with pups and unaccompanied pups or juveniles may be directly affected by the presence of walruses. Indirectly, however, the distribution of adult male bearded seals may be influenced because breeding occurs soon after a female weans her pup (Kumlien 1879; Chapskii 1938; McLaren 1958; Burns 1981). In some cases, females will breed while still lactating (Burns 1981). A breeding male is unlikely to establish a territory and vocalize in an area distant from where females give birth and wean their pups. Consequently, the distribution of adult males may ultimately be affected by the distribution and movements of walruses. Adult bearded seals may also avoid walruses because of the predator avoidance behaviour learned as a pup or juvenile. A similar predator-prey relationship in the Antarctic exists: leopard seals (*Hydrurga leptonyx*) prey on pup and subadult crabeater seals (*Lobodon carcinophagus*). Adult crabeater seals, although not as vulnerable, still avoid leopard seals perhaps because of avoidance behaviour learned early in life (I. Stirling, pers. comm.).

Similar rates of calling were recorded at sites 4, 5, 6, and 7 during the 1982–84 surveys. The presence of both first-year and multi-year ice, and the thickness of ice and snow cover were similar between years at sites 4, 5, and 7. One striking difference, however, was the range of water depths: 60 m–325 m. Site 6 was different from the other three sites. The three islands surrounding site 6 were only 5 km apart; prevailing winds and currents were channelled through the inter-island waters. Consequently, the annual ice at site 6 was usually thinner ($\bar{x}$=71 cm s.d.=37 cm) than at sites 4, 5, and 7 ($\bar{x}$=116 cm s.d.=31 cm) and the ice cover there may have tended to break-up earlier that at the other three sites. Despite differences in water depth, snow thickness, and age, type, and thickness of ice cover between sites 4–7, differences in rates of calling were not statistically significant amongst the four sites.

In summary, the results of the 1982–84 vocalization surveys show that during late winter and early spring, bearded seals in Penny Strait and northern Queens Channel avoid waters covered by thick, stable landfast ice which tends to break up late (i.e., like sites 2 and 3). With the possible exception of areas heavily used by walruses, they seem to prefer areas of thinner and less stable ice where break-up occurs early (i.e., like sites 4–7). These results concur with data collected from most other areas examined to date, although in a few reported cases bearded seals have been reported overwintering in stable annual ice, far from open water (Mansfield 1967; Stirling and Smith 1977). They can maintain breathing holes like the ringed seal, however it seems that they usually do so only in waters where break-up occurs early and freeze-up occurs late (Stirling *et al.* 1983). The distribution of bearded seals was once thought to be limited to relatively shallow waters where benthic prey is available (Vibe 1950; Burns 1967; Mansfield 1967; Davis *et al.* 1975; Burns and Frost 1979; Stirling *et al.* 1982; Kingsley *et al.* 1985). Recent field studies in other areas have shown that bearded seals also overwinter in deeper waters (Mansfield *et al.* 1975; Finley and Renaud 1980). All of the 37 bearded seals sighted during aerial surveys conducted in the North Water of Baffin Bay in March 1979 were in areas where the average water depth was greater than 200 m and at least 21 (60%) occurred in areas where the water depth exceeded 500 m (Finley and Renaud 1980). In Penny Strait and northern Queens Channel, water depths generally ranged between 75 and 300 m except over shoals near islands. The results from this study indicate that bearded seals occurred throughout much of the study area, over a range of water depths.

In 1982, a general rise in vocalization rate occurred between mid-April and early June at most sites. Stirling *et al.* (1983) also reported a general increase from late winter to early summer at the sites they examined. There are two possible explanations: an increase in calling rates of individual seals or an increase in the number of seals within range of the hydrophone. Bearded seals are thought to produce trill vocalizations for the purpose of proclaiming breeding condition, or ownership of territory, or both (Ray *et al.* 1969). The limited data available indicate that only males produce trills. Male Weddell seals (*Leptonychotes weddelli*) produce a similar trill during the breeding season for advertisement of location (Thomas and Kuechle 1982). Males of that species are polygynous and breed in fast-ice habitat where they defend three-dimensional territories under the ice (Ray 1967; Stirling 1969; Siniff *et al.* 1974). The mating system of the bearded seal is unknown, although promiscuity is suspected, and most breeding is thought to occur in the pack ice zone where space may be less limited than in fast ice areas (Stirling 1983). Whether or not bearded seals defend territories, as do Weddell seals, is not known but seems probable. Based on histological evidence, the breeding season for males is reported to extend from late winter or early spring until early or mid-June (McLaren 1958a; Tikhomirov 1966; Burns 1981). In eastern Canadian arctic waters, between northern Hudson Bay and northern Baffin Island, the peak breeding period occurs in mid-May (McLaren 1958a). It does not seem unreasonable that males may call more during the peak of breeding activity than earlier in the breeding season. Penny Strait and Queens Channel are surrounded by waters covered with ice types mostly unfavourable for bearded seals so that extensive underwater movements of bearded seals into Penny Strait and Queens Channel from adjacent areas prior to break-up seem unlikely. Thus, the most likely explanation for an increase in calling rates between mid-April and early June is an increase in the rate of calling by individual seals.

With the exceptions of sites 2 and 3, by late June in 1982 the differences in calling rates between all sites became indistinguishable. Rates of calling for sites 1 and 2 had increased from mid-April to late June, whereas the rates of calling at sites 4–6 had increased, and then decreased. Although no surveys were conducted in May, and data are missing for some sites from one or two surveys in mid- and late June, it appears that the distribution of bearded seals in late spring may be less localized than earlier in the year. After the ice begins to break up, thereby creating breathing holes in areas previously covered with unbroken ice, the seals probably start to move around to take advantage of newly-available feeding areas. Stirling *et al.* (1983) also noted the connection between ice break-up and the seals' increased freedom of movement to account for the results they obtained from vocalization surveys.

Underwater vocalizations can be used to determine the distribution and relative abundance of bearded seals. As the winter ice cover does not change appreciably until mid- to late May in the High Arctic, the results obtained from April surveys may reflect the distribution of this species throughout the winter (Stirling *et al.* 1983). No other survey technique examined thus far can provide information on bearded seals at the time of maximum ice accumulation. There are, however, several problems to resolve before the results from vocalization surveys can be interpreted further.

Unfortunately, relatively little is known about the social behaviour of this species anywhere in its range. Whether or not subadult and adult bearded seals segregate spatially during the breeding season in the Canadian Arctic, as do ringed seals (McLaren 1958; Burns 1970; Smith 1973), is not known. In some regions of the Soviet Arctic the distribution of bearded seals is reported to be differentiated by age and sex, while in other regions no prominent separation has been observed (see review by Fedoseev 1973). The age, sex, and social status of vocalizing individuals are only partially known. Available data point toward adult males but there are no data with which to reject females conclusively. Consequently, we cannot be certain whether the results of vocalization surveys provide information on all segments of a population or only particular sex and age classes. Data on the calling rates of individual seals, and how they may be affected by the calls or presence of other individuals is sparse or lacking. Until we have the answers to these questions and gain a better understanding of the general biology of the species we will not know, for example, if the absence of vocalizations at a site means, categorically, that bearded seals are not present or whether they are present but not calling. Despite the absence of hard data, it seems likely that the lack of vocalizations at a site indicates that bearded seals are not present.

Bearded seal calls can travel 20 km or more underwater (this study, Chapter 2). Under ideal conditions, trills have been recorded up to 45 km from source (Stirling *et al.* 1983). The radius of call audibility varies with type of equipment used, weather conditions, and physical environment (Stirling *et al.* 1983; this study, Chapter 2). Differences in call intensity between individuals may exist and individuals may vary the intensity of their calls over time. Because of the number of factors that affect our ability to hear bearded seal calls, it is difficult to determine the absolute abundance of seals at a location especially if the recording stations are less than about 40 km apart.

Until a relatively accurate, quick, and inexpensive technique is devised for pinpointing the locations of calling seals, vocalization counts can only be used as a general indicator of distribution and relative abundance in different habitats. In this study, for example, similar numbers of calls were recorded at sites 1 and 2. Yet a subjective evaluation of call strength at both sites suggested that while site 1 may have supported a few vocalizing seals during winter and early spring, no calling seals were in close proximity to site 2 until spring break-up began.

Calvert and Stirling (1985) found that vocalization rates of ringed seals overlapped too much amongst different habitats to permit the use of calls for determining the distribution and relative abundance of wintering and pupping areas. Dog-search techniques remain the most effective survey method for separating suitable and unsuitable ringed seal habitat. In comparison, vocalization surveys for bearded seals appear to separate preferred habitats from unsuitable ones. However, between similar habitat types there may be so much overlap in calling rates that repeated surveys are needed to reveal and verify relatively small between-site differences. Although details of habitat use may be weak or unavailable within relatively small areas (e.g., Penny Strait), surveys of underwater vocalizations seem very useful for determining wintering areas on a regional scale (e.g., as Stirling *et al.* (1983) did in the High Arctic). As yet, vocalization surveys remain the only appropriate method for investigating the winter distribution of bearded seals because environmental conditions are not conducive to collecting animals or counting them visually at that time of year. There are a number of problems that must be solved; nonetheless, the use of vocalizations for determining relative abundance and distribution contributes significantly to our efforts to understand the biology of this species.

TABLE 2-1. Habitat information for the seven recording sites. Snow and ice values represent the means calculated from measurements made in April (1982-84); standard deviations are shown in brackets.

Site Number	Lat./Long.	Hydrographic Feature	Water Depth in meters	Snow Depth in cm	Ice Depth in cm	Ice Character Age *	Ice Character Type **
1	76°10'N, 94°53'W	polynya in inter-island channel	25	variable	variable (unstable ice)	A	L + P
2	76°20'N, 95°19'W	mouth of bay	50	34 (21)	170 (37)	A	L
3	76°35'N, 95°42'W	head of harbour	30	3	200	A	L
4	77°05'N, 95°15'W	inter-island channel	60	9 (2)	104 (27)	A + M	P
5	76°32'N, 97°09'W	inter-island channel	325	9 (8)	117 (30)	A + M	P
6	76°32'N, 97°09'W	small inter-island channel	75	8 (5)	71 (37)	A	L + P
7	76°19'N, 97°02'W	inter-island channel	260	10 (9)	126 (37)	A + M	P

* A = annual ice M = multi-year ice

** L = landfast ice P = pack ice

TABLE 2-2. Effects of dividing mean rate of vocalization by area sampled at the seven sites surveyed in April - June 1982. Standard deviation values are given in brackets.

Site number	Mean number of calls per minute	Area sampled (in hectares)	Mean number of calls per minute per hectare x 10^6
1	3.4	74,893	45.4 (21.8)
2	3.0	35,845	83.7 (91.0)
3	0.2	8,292	24.1 (28.2)
4	8.0	77,158	103.7 (28.4)
5	6.4	77,310	82.8 (27.8)
6	6.5	85,451	76.1 (16.9)
7	11.5	113,760	101.1 (19.0)

TABLE 2-3. Effects of dividing mean rate of vocalization by area sampled at the six sites surveyed in April 1982-84. Standard deviation values are given in brackets.

Site number	Mean number of calls per minute	Area sampled (in hectares)	Mean number of calls per minute per hectares x 10^6
1	0.9	74,893	12.0 (16.5)
2	1.4	35,845	39.1 (25.6)
4	6.6	77,158	[illegible]5.5 (21.6)
5	6.3	77,310	81.5 (31.3)
6	7.3	85,451	85.4 (18.5)
7	8.9	113,760	78.2 (22.7)

FIGURE 2-1. Locations of the seven recording sites in Penny Strait and surrounding waters.

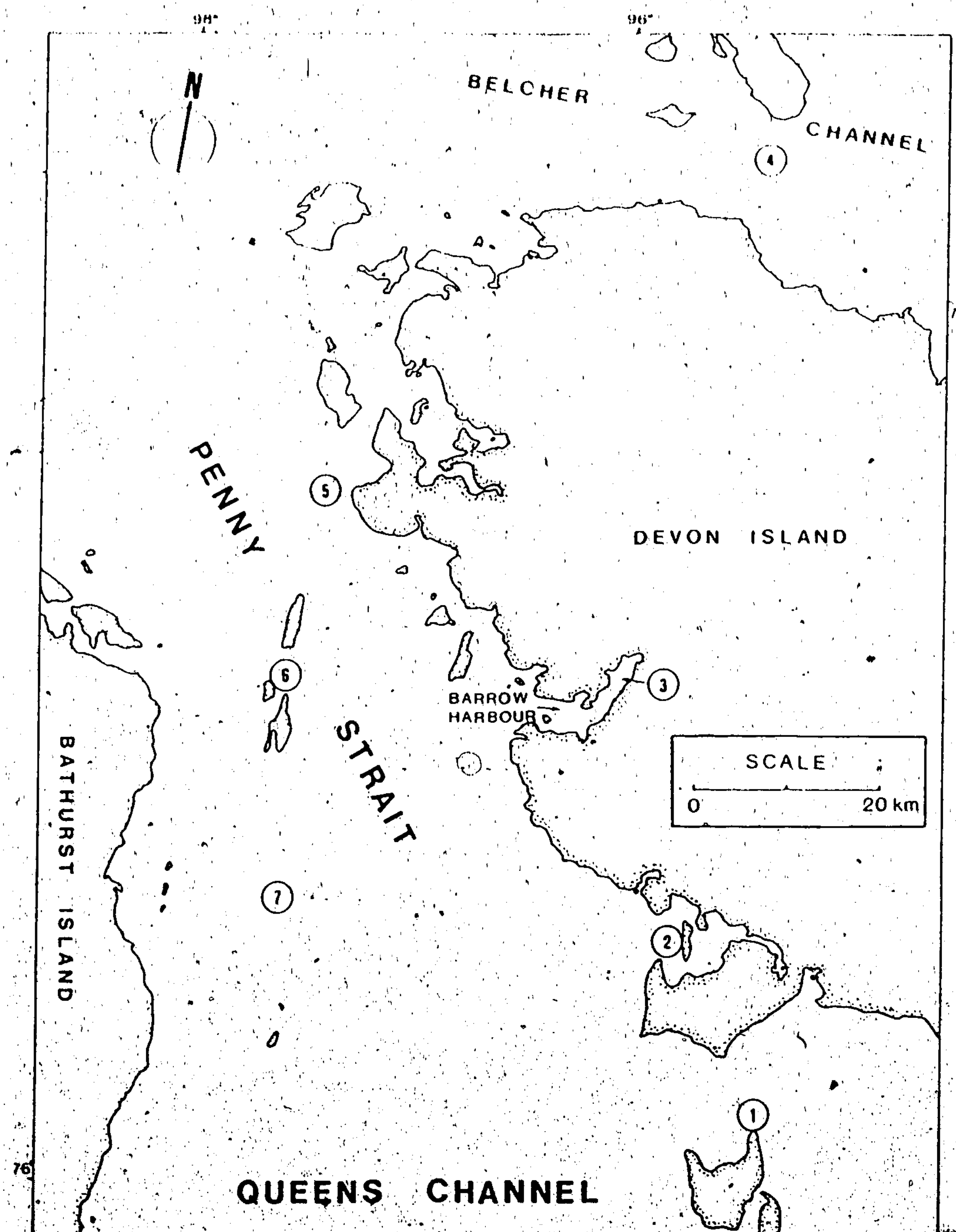


FIGURE 2-2. Mean vocalization rates recorded at each site during the April-June 1982 surveys.

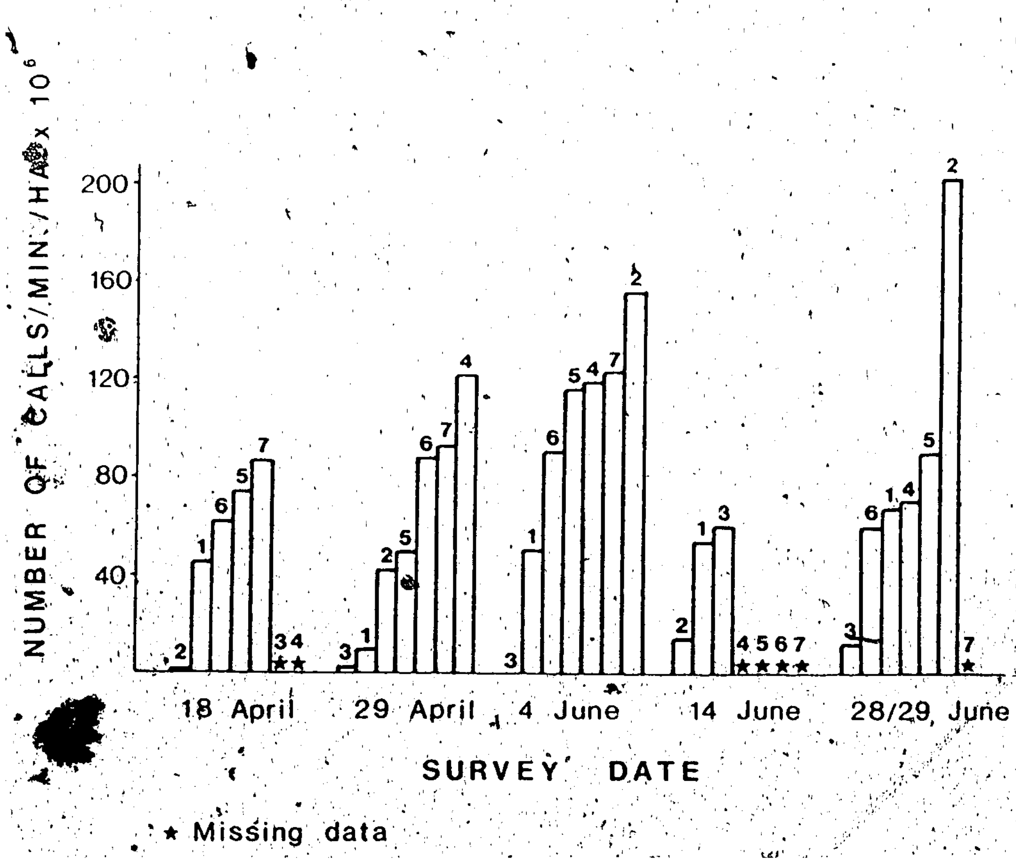
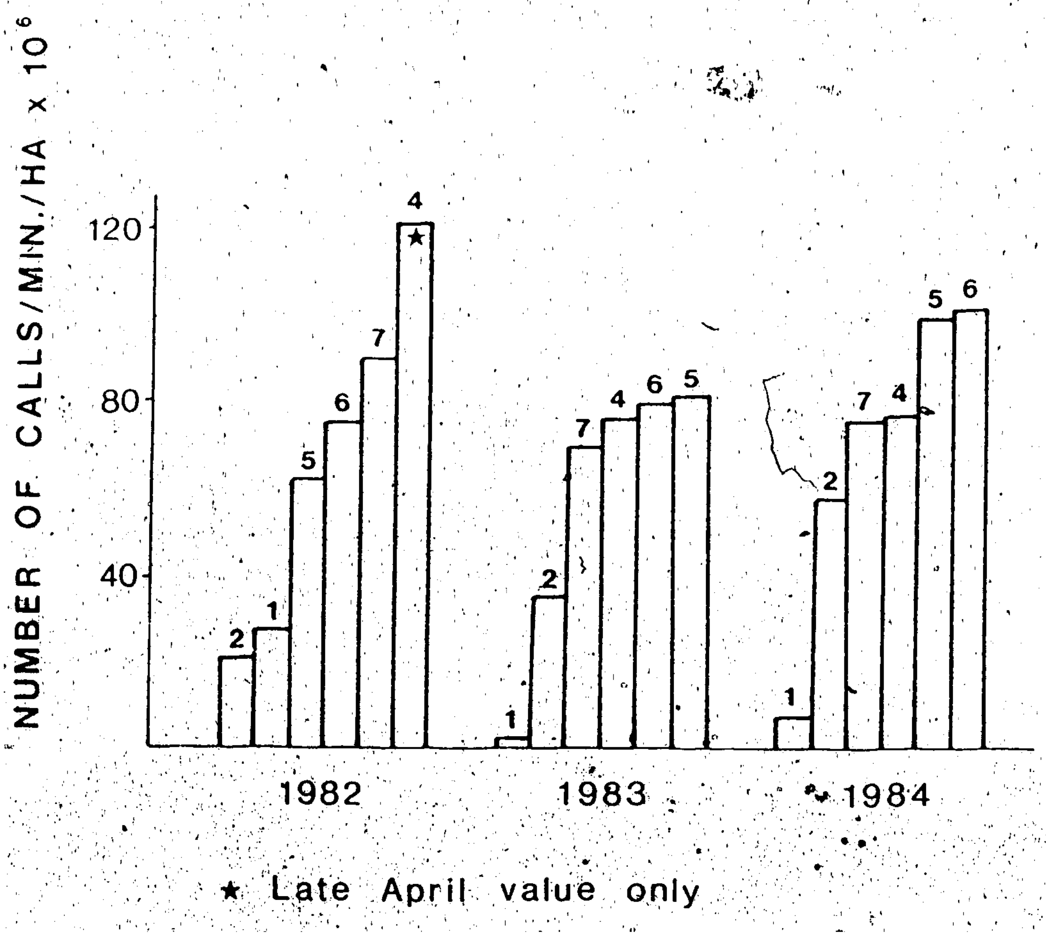


FIGURE 2-3. Mean vocalization rates recorded at each site during the April 1982-84 surveys.



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4. SUMMARY

The bearded seal is the least known of the pinnipeds in the Canadian Arctic. Because they are semi-solitary and prefer an environment of unstable ice, they are both difficult and expensive to study. Consequently, until recently, most research on bearded seals was restricted to the collection of natural history data from animals killed by Inuk hunters. In this study, I have attempted to gain a better understanding of the behaviour and general ecology of bearded seals by examining their underwater vocalizations.

Ray *et al.* (1969) and Stirling *et al.* (1983) gave brief descriptions of bearded seal vocalizations, but this study represents the most extensive investigation of the calls of this species to date. My primary objectives were to describe the vocal repertoire of bearded seals and to use their underwater vocalizations to study winter distribution. Several other questions were also addressed. Does the vocalization repertoire of bearded seals vary geographically? Does their rate of calling change on a daily or seasonal basis? How far can bearded seal trills travel in water?

Bearded seals produce calls that are narrow in frequency bandwidth and frequency-modulated. The repertoires of their underwater vocalizations vary geographically, both in structure and use. Within-call structures vary in frequency, duration, and pattern of frequency modulation. Between-call structures vary in frequency of occurrence of each call type, in the ratio of calls heard alone versus in sequence, and in the sequential organization of call types within trill sequences. These results show that clear inter-population differences in vocal repertoire exist.

Preliminary data suggested that repertoires may change over time, but not radically. Comparison of the vocalizations recorded in 1982 at the Ramsay Island site with those recorded there in 1972-75 showed that the frequency of occurrence of each call type had changed, but no calls had been added or lost. Similarly, descriptions of bearded seal trills reported by others up to 50 years ago (Freuchen 1935; Dubrovskii 1937; Chapskii 1938; Poulter 1966; Ray *et al.* 1969; Stirling *et al.* 1983) show that the calls recorded during this study are similar to those heard previously.

My study was not designed to examine individual differences in repertoire. However, the recordings from Ramsay Island allowed comparison between the repertoire of one seal and all others recorded at the site. The frequency of occurrence of each call type was similar between the two sets of recordings, although spectral and temporal values were mostly dissimilar. Sonabuoy arrays would likely permit a more controlled examination of the differences in repertoire between individual seals. With the aid of a stationary array, it should be possible to localize individual calling seals, thereby allowing comparisons of repertoire between individuals. It may also be possible to track calling seals over time to determine how extensively they move under the ice, whether they are territorial and, if so, the size of their territories. Investigating territoriality will be possible if individual seals can be identified by their vocalizations or repertoire, or if they call continuously for long periods. Another important area for future investigation is to determine the identity of vocalizing seals. Confirming the age, sex, and social status of calling individuals will assist us to understand the function of their vocalizations. Keeping animals in captivity may be the only practical way to get such detailed information.

Several factors were responsible for the variation in the number of calls recorded at a site; time of day and, to a lesser degree, date had the greatest effects. Bearded seals showed a prominent daily cycle in rate of calling during the April and early May recordings at two recording sites. Calling rates were high in the early morning (i.e., 0300–0400 hrs sun time). No distinct cycle in rate of calling occurred in the late May and early June recordings, although a slight rise occurred during the early morning. Surface wind, make and condition of recording equipment also influenced the number of calls recorded. Increased surface winds and improperly functioning equipment resulted in fewer calls than would have been recorded under ideal conditions.

Daily pattern in calling rate appears to be negatively correlated with haul-out which, in turn, is probably affected by seasonal factors (e.g., daylength, temperature) or weather (e.g., day-to-day unpredictability in temperature and wind). To determine whether rate of calling is negatively correlated with numbers of seals hauled out on the ice, a quantitative study of the temporal pattern of haul-out and the factors that may influence it is needed. No data on rate of calling or time interval between calling bouts were collected for individual seals. Hydrophone arrays may be useful for obtaining that kind of information.

Using a two-hydrophone recording system, I showed that some bearded seal calls can be heard for up to 30 km underwater when conditions are suitable. I have offered two pieces of evidence that suggest that some call types may be heard over greater distances than others. Submarine obstacles can block or severely reduce the transmission of bearded seal calls. Exactly how far each call type can be heard and the effects of submarine topography on call transmission should be quantified using a hydrophone array. Knowing individual rates of calling and frequency of calling bouts, and how far from source bearded seal calls can be heard under a variety of environmental conditions, would make it possible to estimate the density of vocalizing seals at recording sites.

Vocalization surveys conducted in the central High Arctic during April 1982-84 revealed that bearded seals appear to avoid waters covered by stable landfast ice and areas heavily used by walruses; instead they seem to prefer areas where the ice is unstable and break-up occurs early. Water depth did not appear to influence their distribution. Data from vocalization surveys conducted during April and June 1982 suggest that after the ice begins to break up, the seals begin to move around to take advantage of newly-accessible feeding areas. Numbers of recorded calls increased between mid-April and early June, probably because of an increase in the rate of calling by individual seals during that period.

More information about the winter habitat preferences of bearded seals could be obtained from the results of the vocalization surveys if more was known about social behaviour of the species and the identity (i.e., age, sex, and social status) of the calling individuals. With the aid of a hydrophone array and microprocessor to accurately pinpoint the locations of calling seals, vocalizations could be used more effectively to study distribution and abundance.

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