

Stability of the underwater vocal repertoire of harp seals (*Pagophilus groenlandicus*)

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Abstract

Underwater vocalizations of harp seals (*Pagophilus groenlandicus*) were recorded in the Gulf of St. Lawrence, Canada, in late February and March over seven years between 1968 and 1999. Harp seals produced seventeen call types. No new call types or major changes in the repertoire were observed over three decades. Call type proportional usage varied significantly among years. Only call type 13 showed significant differences in the number of elements per call per year. Call type 14 was the only call type that showed a significant difference for element duration. The proportional usage of call types varied significantly between early and late in the breeding season in four of the seven years. No call types showed a significant difference in the number of elements per call between early and late in the breeding season. The stable nature of the vocal behaviour of harp seals may enhance recognition of the various call types and thus serve to enhance conspecific communication.

Key words: harp seals, *Pagophilus groenlandicus*, vocal repertoire stability, seals, underwater vocalizations.

Introduction

Most species of marine mammals use underwater vocalizations as their primary means of communication (Thomson & Richardson, 1995). Harp seals (*Pagophilus groenlandicus*) have a diverse underwater vocal repertoire during the breeding season, but the behavioural significance of adult harp seal vocalizations is essentially unknown (Møhl *et al.*, 1975; Watkins & Schevill, 1979; Terhune, 1994; Serrano, 2001a). Harp seals in the Gulf of St. Lawrence produce at least 18 or more call types (Møhl *et al.*, 1975; Terhune 1994; Serrano 2001a).

Møhl *et al.* (1975) organized the classification along a continuum from constant frequency pure tones (type 1; horizontal patterns on sound spectrograms) to varying frequency broadband calls (types 14–18; vertical patterns on sound spectrograms). Many of the calls regularly repeated elements and may possess features that will help them stand-out against background noise. Vocalizations occur at other times of the year (Serrano & Miller, 2000), but their structural variety, incidence, and social significance are just becoming known (Serrano & Miller, 2000; Serrano, 2001b).

Few studies have examined changes in the vocal repertoire of mammals over time, and particularly of marine mammals. Terrestrial mammals generally do not modify their vocal repertoires over time (Janik & Slater, 1997; Seyfarth & Cheney, 1997). On the other hand, some marine mammals modify their vocalizations presumably through learning (Ralls *et al.*, 1985; Janik & Slater, 1997; Tyack & Sayigh, 1997). Repertoire changes over time are found in a variety of species, such as humpback whale breeding songs (*Megaptera novaeangliae*; Guinee *et al.*, 1983; Payne *et al.*, 1983; Payne & Payne, 1985; Noad *et al.*, 2000), killer whale signature calls (*Orcinus orca*; Ford, 1991), and bottlenose dolphin whistles (*Tursiops truncatus*; Tyack & Sayigh, 1997). Harp seals (Perry & Terhune, 1999), bearded seals (*Erignathus barbatus*; Cleator *et al.*, 1989), and Weddell seals (*Leptonychotes weddellii*; Thomas *et al.*, 1988) exhibit regional differences in their calls. Regional differences can occur through reproductive or geographic isolation.

Repertoires are not always successfully transmitted through social learning; by chance some calls might be lost, particularly in small populations (Ford, 1991; Lynch, 1996; Snowdon *et al.*, 1997). Changes in call structure are usually subtle, and new calls may arise as variations of existing calls (Payne & Payne, 1985; Ford, 1991; Lynch, 1996; Snowdon *et al.*, 1997). Even though vocal repertoires may change over time, the extent of these changes is constrained by social, environmental, and genetic factors. Social factors constrain

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changes because changes have to be made throughout the population to prevail. The environment will constrain vocal structure changes to favour enhanced transmission (Payne & Payne, 1985; Ford, 1991; Lynch, 1996; Snowdon *et al.*, 1997). Few studies have examined changes in the vocal repertoires of mammals, particularly in marine mammals (Janik & Slater, 1997).

Terhune (1994) reported that there were no differences in harp seal call types and numbers of call elements over a 19-year period, but changes within call structure were not analyzed.

The purpose of the study was to determine if the underwater vocal repertoire of harp seals was stable with respect to the occurrence and structure of the different call types over time. This study extends Terhune's (1994) study and looks in more detail at possible changes over time in different call characteristics, such as duration, frequency, and proportional usage of the call types. For these purposes, we analyzed three decades (1968 to 1999) of recordings of harp seal vocalizations from the Gulf of St. Lawrence.

The functional significance of individual harp seal call types are unknown, although many are associated with the breeding season (Möhl *et al.*, 1975; Serrano & Miller, 2000). The highly synchronous harp seal breeding season means that most of the females are nursing pups during the first half of the breeding season and mating behaviours occur during the second half, after most of the pups are weaned (Sergeant, 1991). We compared the stability of call usage early and late in the breeding season to identify calls that might serve exclusively for reproductive purposes.

Materials and Methods

Recording equipment

Recordings of harp seal underwater vocalizations were made in the Gulf of St. Lawrence, near the Magdalen Islands, during the breeding season (February–March; Sergeant, 1991). Recording sessions were made on an opportunistic basis. The underwater recording gear consisted of Uher 4000 and 4400 reel-to-reel recorders and Sea Horse hydrophones with built-in preamplifiers, Atlantic Research LC32 hydrophones with Grass P15 preamplifiers, a Bruel and Kjaer 8100 hydrophone with a Bruel and Kjaer 2635 charge preamplifier, and a Sony WM-D3 tape recorder, a Benthos AQ-4 hydrophone and a Sony TCD-D8 digital audiotape (DAT), Sony TCD-D3 DAT or Sony TCD-D100 DAT. More information on recording procedures and equipment response is described in Möhl *et al.* (1975) and Terhune (1994). To decrease the likelihood of analysing the calls of the same few seals over and over again, approximately 100 consecutive

Table 1. Number of recording sites and total number of harp seal underwater calls analyzed per year.

Year	Number of Recording Sites	Total Number of Calls Analyzed
1968	4	388
1969	4	367
1970	6	520
1971	14	1131
1993	5	422
1997	2	197
1999	8	733
Total	43	3758

calls per haul-out site per year were examined (Table 1).

Data analysis

Calls were digitised with a 10-bit A/D converter at a sampling rate of 44 kHz. Underwater sounds were analysed using Multi-Speech version 2.2 (Kay Elemetrics Co., Pine Brook, New Jersey, USA 07058). Measurements were made using an analysing-filter bandwidth of 46 Hz, giving measurements accurate to ± 23 Hz and ± 2.2 ms.

We familiarized ourselves with the harp seal vocal structures by listening repeatedly to calls while watching the real-time spectrogram. We classified the calls to match the call types proposed by Möhl *et al.* (1975) and Terhune (1994). Analyzing the first 100 calls at each recording site allowed the proportional usage to be determined for each call type, independent of the total number of calls recorded.

The variables measured were: call type proportional usage, number of elements per call, element duration, and highest dominant frequency (kHz) of the call. Call type proportional usage is the number of calls of each type in a recording site divided by the total number of calls counted in that recording session. Call element was defined as a discrete sound having a clearly distinguishable start and end. The highest dominant frequency was measured for all calls. A contingency table was used to test the null hypothesis that proportional usages have not changed over three decades. A linear regression was used to test the null hypotheses that elements per call, duration, and highest dominant frequency of the call have not changed over the three decades (Sokal & Rohlf 1995). Tests were performed using Sigma Stat Version 2.02. An alpha level of 0.05 was used.

A contingency table was used to test the null hypothesis that proportional usage or the number of elements per call did not change between early in

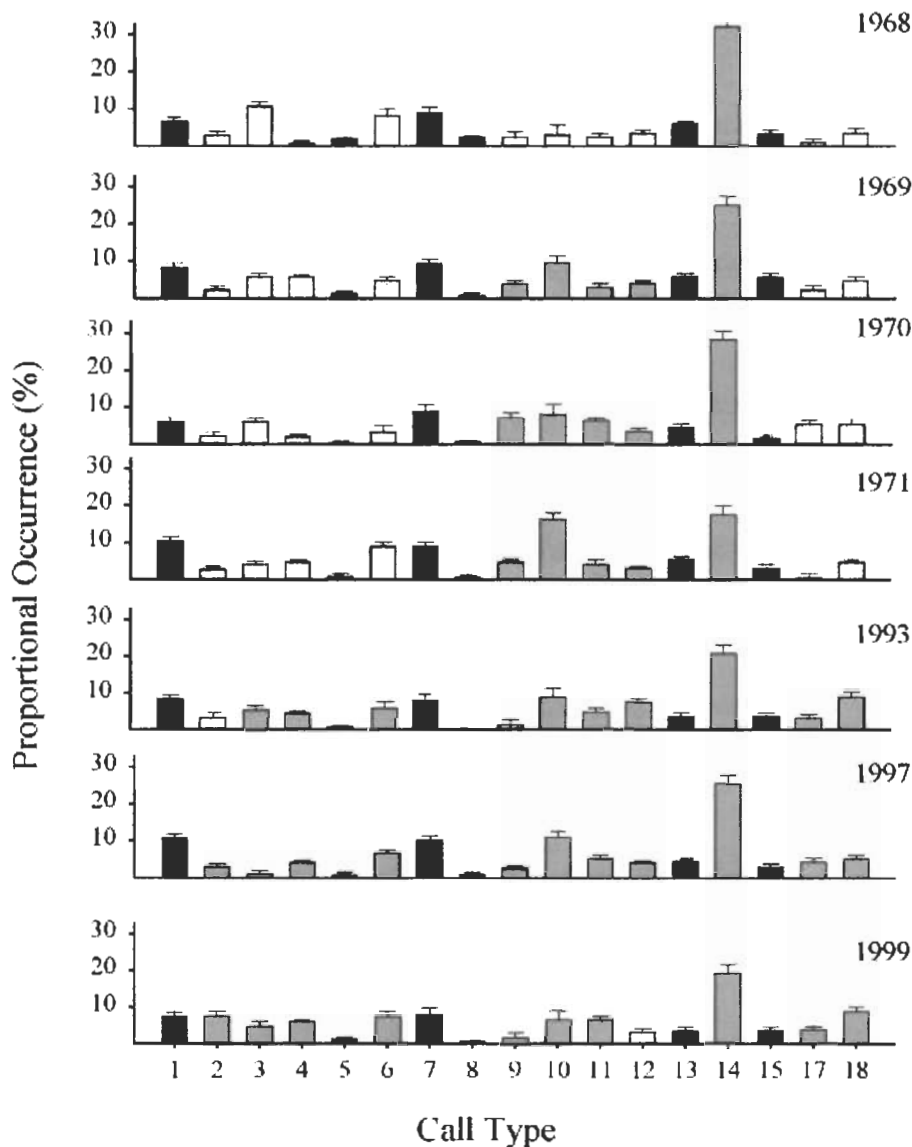


Figure 1. Mean per cent occurrence (\pm s.e.) of underwater call types by year from the Gulf of St. Lawrence harp seal herd. A contingency table analysis found differences between years. Grey bars indicate significant differences.

the breeding season (28 February to 14 March) and late in the breeding season (15 March or later). Data from all years were combined for this analysis.

Results

The same 17 call types were observed in the years surveyed. Call type 16, a single click, was not detected in sufficient numbers to permit detailed analyses. Overall, the call type proportional usage

showed similar patterns over the years (Fig. 1). Call type proportional usage varied significantly among years ($X^2=439.56$, $df=96$, $P=0.001$). Eleven calls showed a significant difference among years (Fig. 1). In all the years, call type 14 (double grunts) was the most frequently used (Fig. 1). The least used call type varied from year to year.

Only call type 13 ($r=0.85$, $df=1$, $F=4.00$, $P=0.015$; Fig. 2) showed significant differences in the number of elements per call per year.

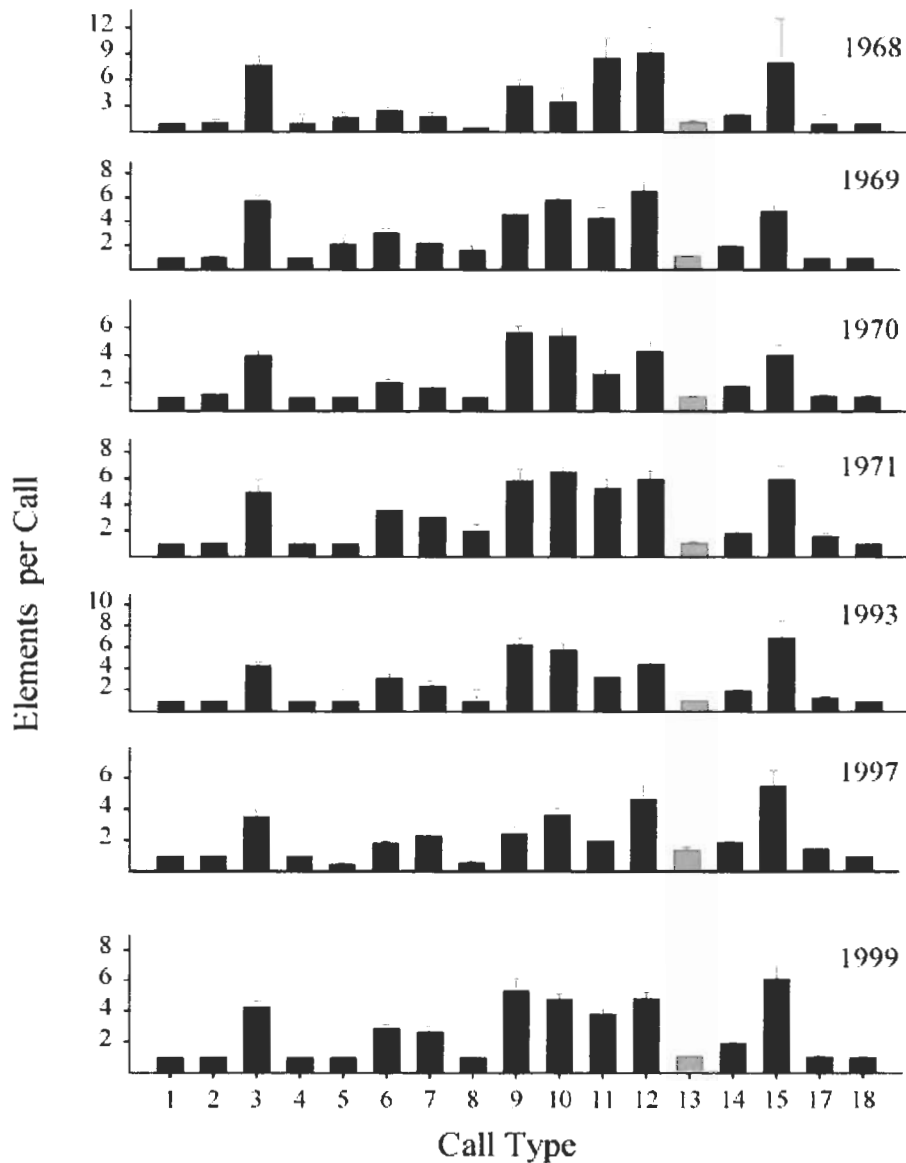


Figure 2. Number of elements (mean \pm s.e.) per call type by year from the Gulf of St. Lawrence harp seal herd. Grey bars indicate significant differences.

Call type 14 was the only call type that showed a significant difference ($r=0.87$, $df=1$, $F=16.36$, $P=0.010$) for element duration (Fig. 3).

Highest dominant frequencies showed significant differences across years for four call types. The call types that showed a significant difference were: 2 ($r=0.80$, $df=1$, $F=8.98$, $P=0.030$), 7 ($r=0.76$, $df=1$, $F=7.05$, $P=0.045$), 17 ($r=0.84$, $df=1$, $F=12.72$, $P=0.016$), and 18 ($r=0.77$, $df=1$, $F=16.36$, $P=0.040$; Fig. 4).

The proportional usage of the call types between early and late in the breeding season varied significantly in 4 years (1968 $X^2=31.93$, $df=16$, $P=0.011$; 1969 $X^2=34.68$, $df=16$, $P=0.011$; 1970 $X^2=32.03$, $df=16$, $P=0.011$; 1999 $X^2=42.52$, $df=16$, $P=0.001$). As with the proportional usage of the call types, the number of elements per call did not vary much between early and late in the season (Fig. 5). Only call type 14 showed a significant difference ($X^2=31.93$, $df=1$, $P=0.011$).

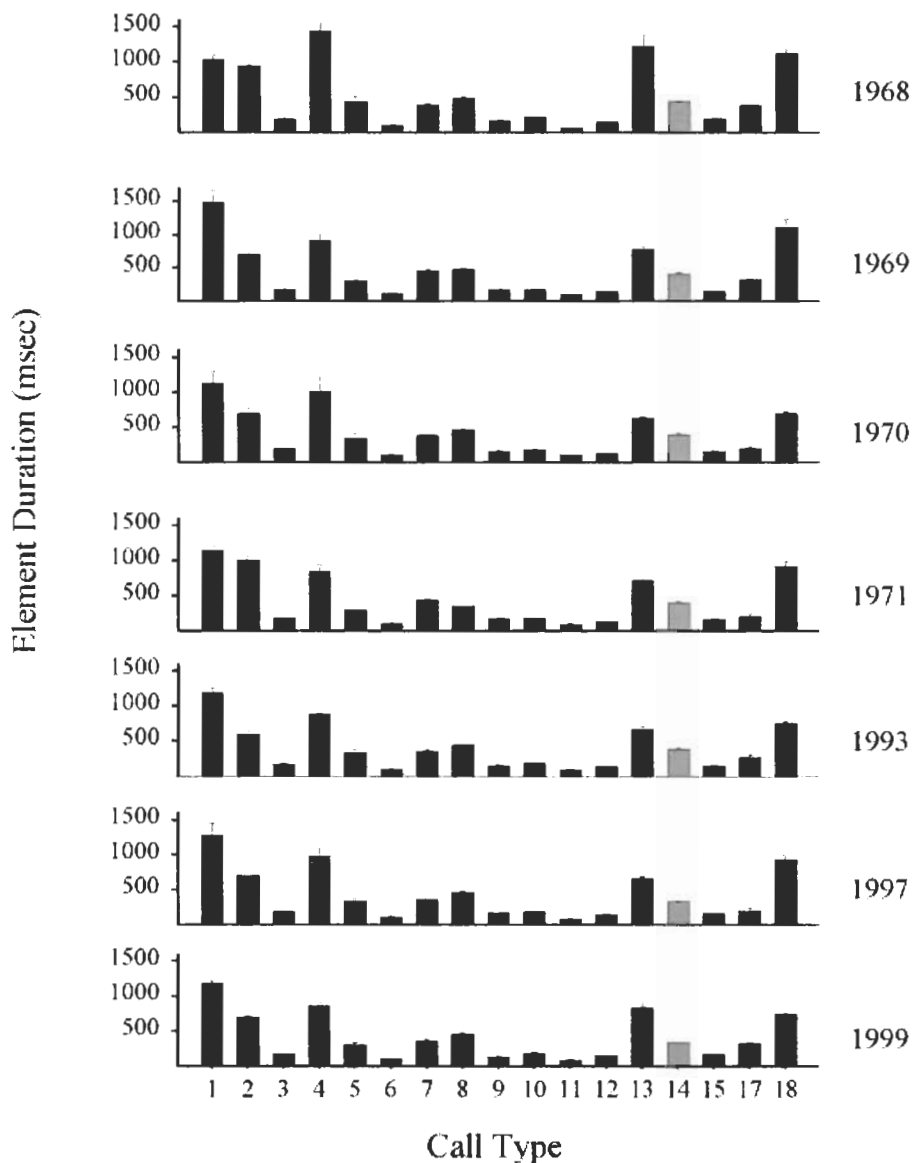


Figure 3. Element duration (mean \pm s.e.) per call type by year from the Gulf of St. Lawrence harp seal herd. Grey bars indicate significant differences.

Discussion

The same call types were recorded in all the years of the study. There were no new distinctive underwater harp seal call types in the Gulf of St. Lawrence between 1968 and 1999. This repertoire stability differs from that of other marine mammals, such as killer whales (Ford, 1991), bottlenose dolphins (Tyack & Sayigh, 1997), possibly bearded

seals (Cleator *et al.*, 1989), and other mammals such as primates (Snowdon *et al.*, 1997). The classification of the harp seal repertoire is difficult because many calls lie along a continuum and it is possible to subdivide putative call types into more categories (Möhl *et al.*, 1975; Terhune, 1994; Serrano, 2001a). However, distinctly different call types, such as one present in the Jan Mayen Island harp seal herd, but not in the Gulf of St. Lawrence herd (Terhune,

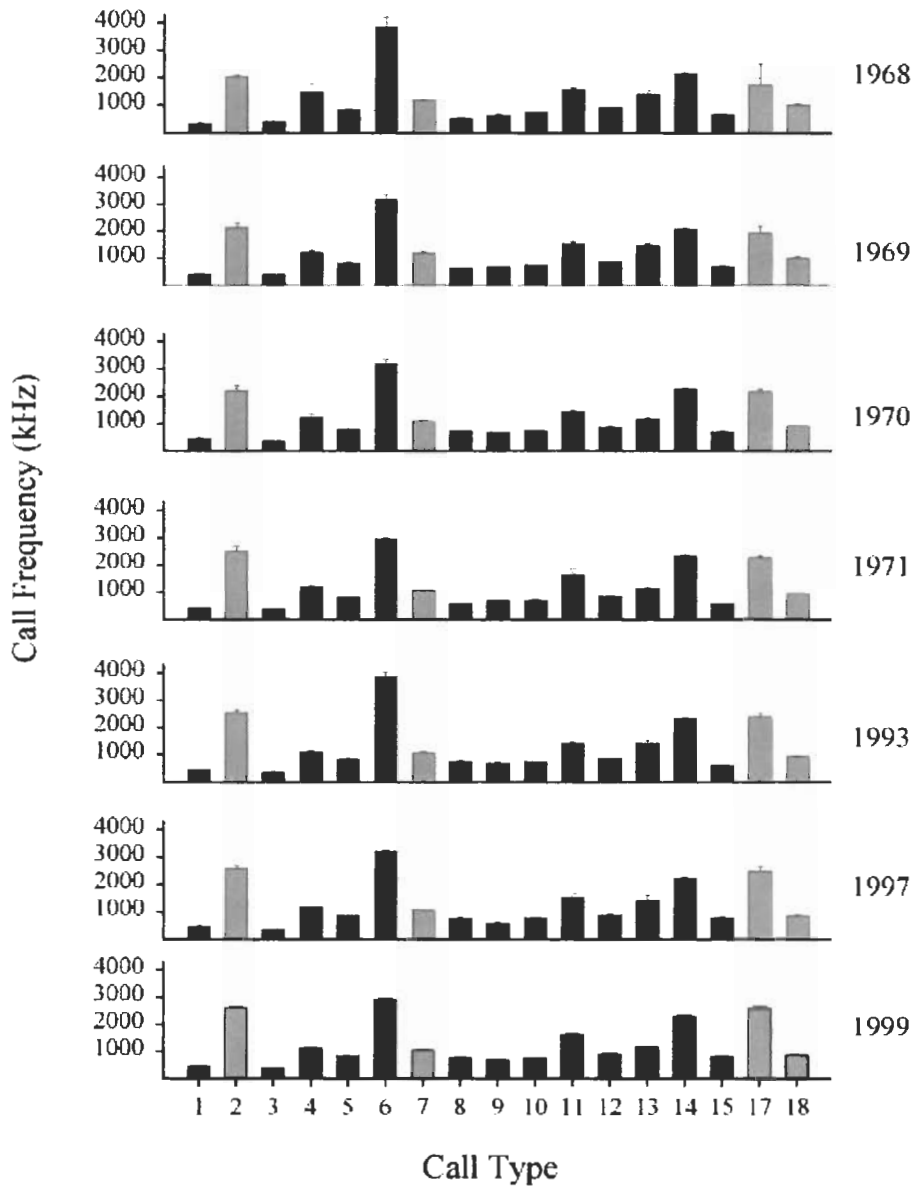


Figure 4. Highest dominant frequency (mean \pm s.e.) of underwater call types by year from the Gulf of St. Lawrence harp seal herd. Grey bars indicate significant differences.

1994), would have been readily discernible. Some of the variables associated with different call types were statistically different between some years, but no new call types were developed.

The average number of elements per call (this measure included all call types and incorporated the frequency of occurrence of each call type) differed between the Gulf of St. Lawrence and the Jan Mayen Island harp seal herds (Terhune, 1994). In

decreasing order of occurrence, the Gulf of St. Lawrence herd underwater calls most commonly contained 1, 2 or 4 elements, while those from the Jan Mayen Island herd were usually made up of 1, 4 or 2 elements per call. These differences were stable over a 20- and 19-year period, respectively (Terhune, 1994).

The frequency of occurrence of the call types and the number of elements per call early in the

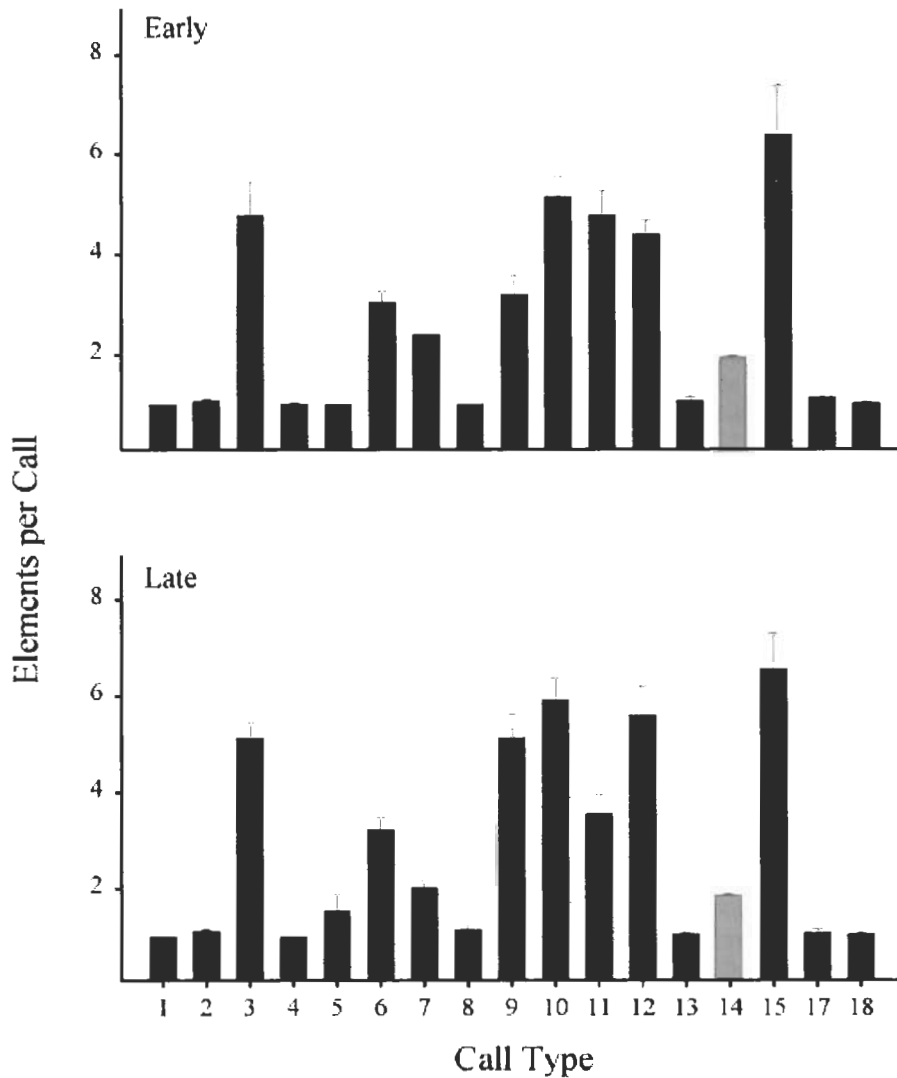


Figure 5. Comparison of the number of elements (mean \pm s.e.) between early and late in the breeding season per underwater call type by the Gulf of St. Lawrence harp seal herd. Grey bars indicate significant differences.

breeding season (when pupping occurred) differed slightly from those later in the season (when pups weaned and mating occurred; Sergeant, 1991) for some of the years studied. This is not surprising in light of the large number of different call types that have been identified for harp seals (Möhl *et al.*, 1975; Terhune, 1994; Serrano, 2001a). Call type usage in some years reflects the two different stages of reproductive behaviour. The number of elements per call did not vary much between early and late in the season. Weddell seal call type usage does not appear to reflect the two different stages of

reproductive behaviour (Pahl *et al.*, 1996). Both harp and Weddell seals have large vocal repertoires and breed on ice. The breeding season is longer in Weddell seals; however, the nursing and mating stages overlap more in Weddell than in harp seals (Pahl *et al.*, 1996).

The stability of all of the variables measured within the vocal repertoire of the harp seal could be a characteristic to reduce masking in a noisy environment for two main reasons. First, stable signals are more stereotyped, and this ensures that the signal is less likely to pass unnoticed

(Moynihan, 1970). Second, stability will ensure that any anti-masking features of the calls remain stable, and as a consequence, communication remains effective. Lynch (1996) found that sounds used by birds that do not transmit well, or are potentially confusing to conspecifics because they are new, are more likely to become extinct. He concluded that the acoustic environment would act as a selective pressure against the retention of poorly propagating new sounds. To reduce ambiguity, a signaller must increase the stereotypic nature of the signals (Krebs & Davies, 1993). If this were the case for harp seals, having a stable vocal repertoire would favour recognition of the call types.

Miller & Job (1992) proposed that the high densities of animals that characterize some breeding sites in pinnipeds may have been a major factor in promoting loud and repeated calls. The repetitive nature of many harp seal call types and the familiarity of the call types would help them stand-out from the background noise associated with conspecific calls (Watkins & Schevill, 1979; Terhune & Ronald, 1986). Thus, the stability of the underwater vocal repertoire may serve to reduce conspecific masking.

This study does not distinguish between the influences of genetics or learning on the stability of the repertoire. The life span of a harp seal is typically 20–25 years (Sergeant, 1991). If genetic factors are controlling the repertoire, the latter is unlikely to change over several years (because genetic factors themselves are unlikely to change over short periods of time). If learning is important and individuals do not change their calls during their lifetime, it could well be many decades before new sounds were incorporated into the repertoire. Harp seals in the Gulf of St. Lawrence and near the Jan Mayen Island exhibit differences in their vocal repertoires which are consistent over two decades (Terhune, 1994). This shows that this species has the potential for being able to produce different sounds and vocal patterns. Although the harp seals from different breeding groups mix during the summer (Sergeant, 1991), it is possible that they do not vocalize much at this time (Møhl *et al.*, 1975; Serrano & Miller, 2000). Thus, the seals may only hear the calls associated with breeding behaviours while they are in large breeding herds. The vocal differences between the Gulf of St. Lawrence and Jan Mayen Island herds (Terhune, 1994) could be maintained by either genetic differences and/or behavioural isolation.

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