Variation of harp seal (*Pagophilus groenlandicus*) underwater vocalizations among three breeding locations

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Abstract

We compared the underwater vocalizations of harp seals *Pagophilus groenlandicus* Erxleben, 1777 recorded during the breeding season at three locations: Jan Mayen Island (north of Iceland); Gulf of St Lawrence; and the 'Front' ice east of Labrador. The three herds shared 17 call types. The Jan Mayen herd had one call type not found in the Gulf or Front. One of the Gulf and Front call types was not found at Jan Mayen. Based on ANOVA *post hoc* pairwise comparisons between locations, the three herds exhibited a similar number of within-call type differences in duration, number of elements, start pitch and end pitch. There were no differences in proportional usage of call types between the Gulf and Front herds but both differed in a similar manner from those of the Jan Mayen herd. These findings support tagging studies that indicate that the Gulf and Front herds may be interbreeding and both are reproductively isolated from the Jan Mayen herd. We found no evidence of acoustic adaptation to the site-specific ice and environmental conditions associated with the three study locations.

Key words: harp seal, *Pagophilus groenlandicus*, underwater vocalizations, variation, call type, interbreeding

INTRODUCTION

Harp seals *Pagophilus groenlandicus* Erxleben, 1777 (Perry *et al.*, 1995) are the most abundant pinniped species in the North Atlantic and are noted for their long annual migrations (Sergeant, 1991). They have been divided into three separate populations on the basis of their breeding sites in: (1) the White Sea; (2) the Greenland Sea near Jan Mayen Island; (3) the North-west Atlantic (Fig. 1). The Northwest Atlantic population has been further subdivided into a Gulf of St Lawrence (Gulf) population and a population north of Newfoundland and east of Labrador (Front; see Fig. 1). Although harp seal populations have been described by the location of discrete breeding congregations, there is evidence of some mixing between populations on summer feeding grounds (Øien & Øritsland, 1991; Sergeant, 1991).

Morphological and genetic data suggest that there is a clear division between east and west Atlantic populations but some degree of mixing between the Gulf and Front subpopulations within the Northwest Atlantic (Sergeant, 1991). Further, extensive tagging programmes within the Gulf and Front breeding herds have demonstrated that immature animals move between herds but mixing decreases as animals mature. Only a single adult female tagged in the Gulf has been found at the Front while no Front animals, tagged as adults, have been recovered in the Gulf (Sergeant, 1991). Because harp seals from both breeding locations are known to mix on summer feeding grounds, between the Canadian Arctic and south-east Greenland (Sergeant, 1991), and probably migrate along similar routes at least as far south as the Front, it is possible that Gulf animals move between breeding sites while Front animals may be philopatric.

Polar, ice-breeding phocids such as Weddell *Leptonychotes weddellii*, bearded *Erignathus barbatus*, leopard *Hydrurga leptonyx* and harp seals are well-known for their varied and complex underwater vocalizations (Møhl *et al.*, 1975; Thomas & Kuechle, 1982; Cleator *et al.*, 1989; Terhune, 1994; Thomas & Golladay 1995). Geographic variation in vocalizations has been demonstrated in bearded, leopard and Weddell seals (Thomas & Stirling, 1983; Thomas *et al.*, 1988; Cleator *et al.*, 1989; Thomas & Golladay, 1995) and attributed to reproductive isolation of breeding populations within species. Geographic variation of underwater calls has also been found between harp seals breeding in the Gulf and those at Jan Mayen (Terhune, 1994). The purpose

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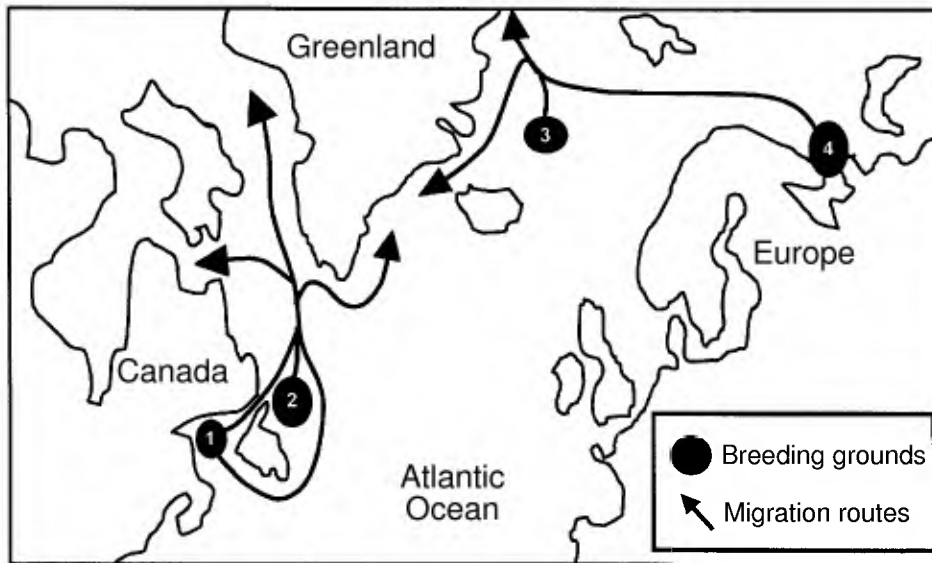
Fig. 1. Map of North Atlantic with relative locations of the four harp seal *Pagophilus groenlandicus* breeding grounds: (1) Gulf; (2) Front; (3) Jan Mayen; (4) White Sea.

of our study is to characterize underwater vocalizations of harp seals breeding at the Front, and to compare these to previous recordings from the Gulf and Jan Mayen breeding sites.

METHODS

Recordings for this study were obtained during the pupping season in the Gulf of St Lawrence in 1983, north of Jan Mayen Island in 1990 and at the Front in 1994. All recordings were obtained using a Bruel and Kjaer 8100 hydrophone and a Bruel and Kjaer 2635 charge preamplifier. In addition, in 1983 and 1990, a Bruel and Kjaer 2203 sound level meter was used to further amplify the signals. During these 2 years a Uher 4200 tape recorder operated at 19 cm/s was used to record the calls. The frequency response of this system was flat within ±1 dB between 0.02 and 15 kHz. In the 1994 recordings, a Sony digital audio tape recorder (model TCD D3) recorded the signals directly from the 2635 preamplifier. The frequency response of this system was flat within ±1 dB between 0.02 and 22 kHz.

For all recordings, the hydrophone was placed between 1 and 4 m below the under-surface of the ice. Recordings were made during daylight hours from a number of sites within each herd. The recording procedures were similar to those reported by Møhl *et al.*, (1975) and Terhune & Ronald (1986). The Jan Mayen recording sites were a minimum of 5 km from the stationary research ship and those at the Front were a minimum of 20 km from the ship to avoid interference from engine noises.

The underwater sounds were examined by listening to playbacks and simultaneously viewing the real time spectral analysis (sonagram) provided by a Uniscan II spectrum analyser (Multigon Industries model 4600). A

Gould 1425 storage oscilloscope monitored the signal waveform.

A total of 1000 calls, consisting of the first 100–200 consecutive calls per recording, from each of the 3 herds were analysed. Any calls, within these sets of consecutive calls, that were masked by other noises or too faint to allow for repeated measures were excluded from the analyses. The following features were noted for each call:

(1) duration of the first element (ms; an element is a single sound);

(2) inter-element duration (ms; within multiple element calls only);

(3) number of elements;

(4) start (or maximum for a vertical pattern) frequency (Hz);

(5) end (or minimum for a vertical pattern) frequency (Hz);

(6) waveform (coded along a continuum where 9 = frequency modulation; 7 = sinusoidal; 5 = complex; 3 = burst pulse; 1 = click);

(7) call shape (coded such that 9 = regularly rising pitch; 7–8 = constant frequency and rising pitches; 6 = pitch increase and decrease; 5 = constant pitch; 4 = pitch decrease and increase; 2–3 = constant frequency and falling pitches; 1 = regularly falling pitch and 0 = a 'click' – a vertical pattern on the sound spectrogram);

(8) call type based on the nature of the sound and the spectrograph pattern; each call type was assigned to 1 of the arbitrary 19 call types described by Møhl *et al.*, (1975) and Terhune (1994).

The data were compared between breeding locations to identify: call types specific to breeding sites (Z scores); call element repetition differences among sites (paired t-tests and χ^2); variation in relative frequency of occurrence of call types between sites (Pearson Product Moment Correlation); and within-call,
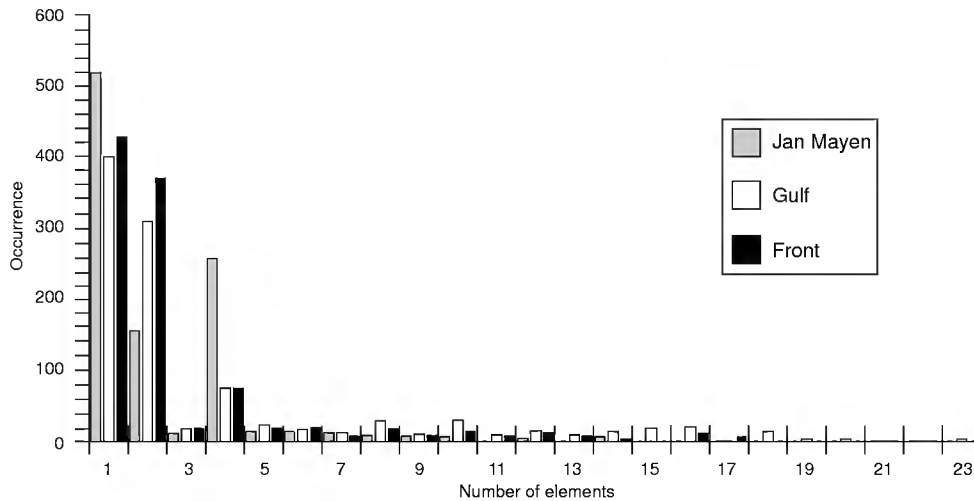
Fig. 2. Number of call elements per 1000 harp seal *Pagophilus groenlandicus* underwater vocalizations recorded at three breeding sites.
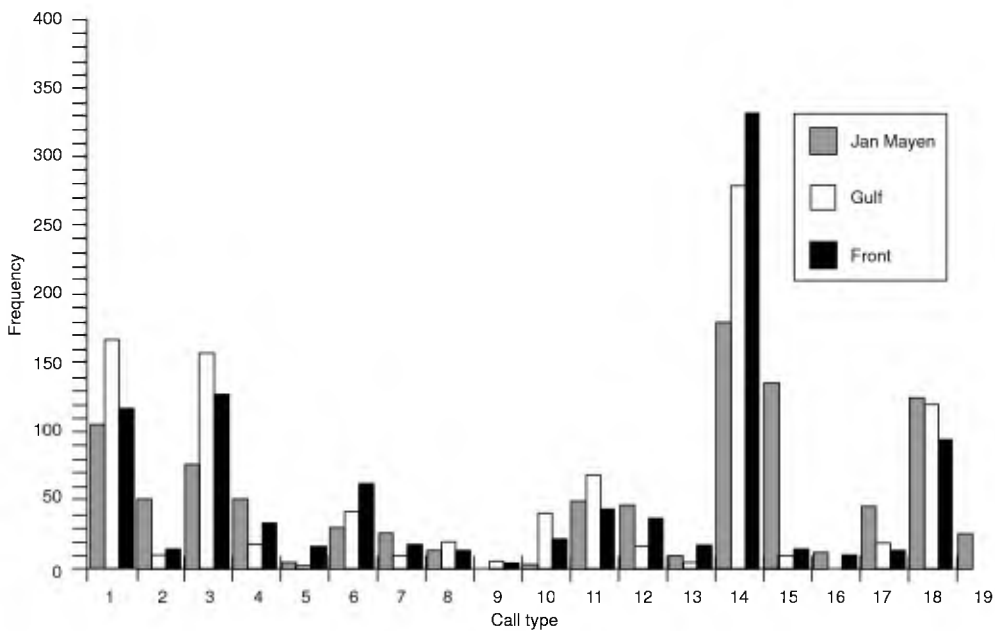
Fig. 3. Frequency of occurrence of harp seal *Pagophilus groenlandicus* underwater vocalization types (Møhl *et al.*, 1975; Terhune, 1994) per 1000 calls recorded at three breeding sites.

between-site differences in features (1), (3), (4) and (5) (as above; ANOVA *post hoc* comparisons using Tukey honest significant difference tests for unequal sample sizes – low sample sizes of some call types precluded some pairwise comparisons).

RESULTS

The Front and Jan Mayen recordings were characterized by high levels of ambient noise resulting from grinding and moving ice floes and a low incidence of seal calls. In contrast, the Gulf recordings were characterized by lower ambient noise levels and, within the herd, higher numbers of harp seal vocalizations. Comparisons of ambient noise levels among the breeding

sites were beyond the scope of this study and, therefore, were not analysed statistically.

No new call types were detected from the Front herd and, therefore, all calls could be assigned to the 19 patterns previously described for harp seals (Møhl *et al.*, 1975; Terhune, 1994). There was complete overlap in the call types detected at the Front with those recorded at the Gulf except that call type 16 was not detected in the Gulf sample of 1983. A clerical error was found in the 1983 Gulf recordings data set such that the previously reported absence of call type 5 (Terhune, 1994) was an error. Call type 9 (frequency shift keying) recorded at both the Front and Gulf was not detected in the Jan Mayen herd. Call type 19 (tink) recorded at Jan Mayen was not detected in the Front or Gulf herds. The frequency shifting within each element of call type 9 and

Table 1. Numbers of harp seal *Pagophilus groenlandicus* underwater call types exhibiting inter-herd differences between four call features (1 = element duration; 3 = number of elements; 4 = start pitch; 5 = end pitch). Significant differences ($P < 0.05$) were determined by ANOVA *post hoc* comparisons of means using Tukey honest significant difference tests for unequal sample sizes. The maximum number of differences for each call feature is equal to the number of call types compared for that pair of sites

| | Call feature | | | | No. of call |
Locations	1	3	4	5	types compared
Gulf–Front	6	7	5	6	15
Gulf–Jan Mayen	4	4	6	7	13
Front–Jan Mayen	8	4	6	8	14
Totals	18	15	17	21	42

the high pitch of call type 19 were distinct and clearly different from the other call types. Assuming the null hypothesis that both call types had an equal probability of occurrence in all herds, the probability of not detecting call type 19 in the Front and Gulf herds was $P < 0.00003$ ($Z = -7.95$). Similarly, the probability of not detecting call type 9 in the Jan Mayen herd was $P < 0.0001$ ($Z = -3.69$).

The most common numbers of elements per call (in descending order) were 1, 2 and 4 for the Front and Gulf herds and 1, 4 and 2 for the Jan Mayen herd (Fig. 2). The mean numbers of call elements were 2.5 (SD = 2.6) for the Front, 3.4 (SD = 3.9) for the Gulf and 2.3 (SD = 1.9) for the Jan Mayen herds. There was no significant difference in the numbers of elements per 1000 calls per herd between the Jan Mayen and Front herds ($t = -1.32$, $P = 0.187$) but there were differences between the other two pairs of herds (Gulf–Jan Mayen, $t = -7.69$, $P < 0.001$; Gulf–Front, $t = 6.21$, $P < 0.001$).

The numbers of calls with one to eight elements inclusive did not differ significantly between the Front and Gulf herds ($\chi^2 = 10.70$, d.f. = 7, $P = 0.15$) but there were significant differences between both the Front and Jan Mayen ($\chi^2 = 208.33$, d.f. = 7, $P < 0.000001$) and the Gulf and Jan Mayen ($\chi^2 = 184.63$, d.f. = 7, $P < 0.000001$) herds.

The Front and Gulf herds exhibited similar call type usage ($r = 0.95$, $n = 19$, $P < 0.0001$). The correlations of call type usage between the Front and Gulf herds and the Jan Mayen herd were lower ($r = 0.76$, $n = 19$, $P < 0.0002$ for each). The Front and Gulf herds had a greater incidence of type 14 (grunt pairs) and type 3 (morse) calls than the Jan Mayen herd (Fig. 3). The Jan Mayen herd had a greater incidence of type 15 (knocks) calls than the other two herds.

Within each call type, a number of differences in the four call features existed between herds, although there was no clear pattern in the inter-herd differences (Table 1). Of 168 ANOVA *post hoc* pairwise comparisons between sites, 71 exhibited significant differences; 8.4 would be expected due to chance alone. There were only 11 instances in which all four features of a

call type exhibited no differences between a pair of herds.

DISCUSSION

Comparisons of harp seal underwater vocalizations between breeding locations (Front, Gulf and Jan Mayen) provide evidence of geographic isolation between the Jan Mayen herd and the other two populations. The similarity of calls between the Gulf and Front herds suggests mixing between these breeding sites.

The harp seal repertoires of the Front and Gulf of St Lawrence do not include call type 19. The absence of type 16 calls from the Gulf recordings in 1983 is probably due to sampling problems as this type has been present in earlier and later recordings (Møhl et al., 1975; Terhune, 1994). The Jan Mayen repertoire does not include the type 9 call. Call types 9 and 19 both contain repeated elements and have distinctive pitch patterns. It is unlikely that these would have been misclassified as other call types or not detected because of masking by ambient noises or other harp seal calls.

The 19 call type categories are relatively broad and include sets of calls along a continuum. They were initially classified subjectively (Møhl et al., 1975; Terhune, 1994). The effect of conservatively decreasing the repertoire to 19 call types is that potentially different call types may have been amalgamated (Møhl et al., 1975; Terhune, 1994). By reducing the number of call type categories, there is less possibility of identifying a variation of a major call type as being a unique type found in only one of the herds. The fact that 71 of 168 pairwise comparisons of four call features, per pairs of herds, exhibited statistically significant differences suggests that the repertoires between the three herds may be more different than is indicated by the presence of only two unique call types. The number of differences found was similar for the four call features and the three between-herd pairwise comparisons. This uniformity suggests that the within-herd variability for the various call types is not greatly different from the between-herd variability. To some extent, the data presented in Table 1 reflect the 'noise level' of the classification system. The absence of trends between the call features used or the pairs of herds examined, suggests that it is unlikely that more than the two previously described clearly distinctive call types were present or absent from each breeding location. Some less distinctive within-type call differences, however, may have been present.

The Front and Gulf herds have similar patterns in the mean number of elements per call, especially for one to eight elements with two element calls being more common than four element calls. The element repetitions of two common call types (grunt pairs at the Gulf and Front, and quadruplicate knocks at Jan Mayen) clearly influence the overall element repetitions per herd. The maximum number of elements per call in the Front and Gulf herds is also higher (17 and 23, respectively) than has been found for the Jan Mayen herd (14;

Fig. 2). Our results, however, indicate that the numbers of elements per call are similar in the Jan Mayen and Front herds.

Clear differences exist in the occurrence of call types 14, 15, and 3 between the Jan Mayen and two West Atlantic herds (Fig. 3). Call usage of the Front and Gulf herds has a higher correlation than between either of these and the Jan Mayen herd. This supports the previous measures, which suggest that the harp seal underwater vocalizations from the Gulf and Front herds are similar and both differ in the same way from the calls of the Jan Mayen herd.

Seal tagging studies have been conducted on the harp seal breeding herds in the Gulf of St Lawrence, Front and the Jan Mayen areas (Sergeant, 1991). There have been no recaptures of the Western Atlantic tagged seals in the Jan Mayen herd, nor have animals tagged in the Jan Mayen herd been recaptured in the Front, Gulf, or White Sea breeding herds (Øien & Øritsland, 1991, 1992). It appears that seals from the Jan Mayen and Western Atlantic (Front and Gulf) herds may overlap outside of the breeding season, during their summer foraging but are reproductively isolated (Øien & Øritsland, 1991; Sergeant, 1991).

The discreteness of the Jan Mayen breeding stocks presents a mechanism that would permit vocalization differences to develop and be maintained by this group, particularly if harp seal vocalizations are predominately associated with courtship and mating (Møhl et al., 1975; Terhune & Ronald, 1976). If like Weddell seals (Thomas et al., 1987), harp seals do not vocalize extensively outside of their breeding season, then animals mixing on summer feeding grounds would not be exposed to the full repertoire of each other's calls and thus would not be likely to learn those call types.

Sergeant (1991) reviewed a number of lines of evidence concerning the mixing of the Gulf and Front herds. A female that was tagged as an adult in the Gulf was recovered on the Front ice (Sergeant, 1991). An unknown proportion of both immature and mature harp seals moves between the two Western Atlantic herds. Sergeant, (1991, p. 56) concludes that 'the Gulf and Front substocks mix sufficiently that they can be treated as a common stock for the purpose of management'.

The absence of differences between vocalizations of the Gulf and Front herds also implies that the seals of these two herds are interbreeding, as suggested by Sergeant (1991). It is not possible to determine the extent of mixing between the two herds from the vocalization data, but if mixing between the Front and Gulf herds is common, then new call types could be maintained in both herds.

Geographic variations in vocalizations are thought to result from acoustic adaptations to site-specific environmental conditions (Date & Lemon, 1993) or to reflect functionless cultural or genetic divergence caused by isolation (Ford, 1991). The nature and types of background noise at the Jan Mayen and Front breeding locations are similar and both are different from that of the Gulf. Generally, background noises at the Gulf location are predominately associated with calls of other harp seals (Terhune & Ronald, 1986). In periods of low wind, the ambient non-biological noise levels are below those of a zero sea state (Payne, 1964). The thicker ice normally found at the Front and Jan Mayen breeding locations causes the predominate background noise to be associated with wind and ice movements. These two different patterns of ambient noise do not appear to markedly influence the structures or usage of vocalizations, otherwise we would expect the Jan Mayen and Front call patterns to be more similar to each other. The proportion of within-call differences for this pair (26 of 56 possible differences) is higher than for the other two pairwise herd comparisons (24 of 60 and 21 of 52 possible differences). Therefore, there is no evidence of acoustic adaptations to site-specific environmental conditions in the harp seal vocalizations that we recorded.

Our results suggest that there are geographical variations in the underwater vocalizations of harp seals across the Atlantic. In the Gulf and Jan Mayen herds, these differences appear to be stable over time periods of at least two decades (Terhune, 1994). As with the Weddell (Thomas & Stirling, 1983; Thomas et al., 1988), leopard (Thomas & Golladay, 1995) and bearded (Cleator et al., 1989) seals, vocalization variations are attributed to reproductive isolation. The differing types of ice and conspecific noises between the Gulf and Front or Jan Mayen herds do not appear to be influencing vocalizations. The absence of significant vocalization differences between the Gulf and Front herds, which are known from tag returns to mix at least to a small degree (Sergeant, 1991), supports reproductive isolation as the mechanism allowing for the establishment and maintenance of call differences between the east and west Atlantic breeding herds.

REFERENCES

Cleator, H. J., Stirling, I. & Smith, T. G. (1989). Underwater vocalizations of the bearded seal (*Erignathus barbatus*). *Can. J. Zool.* **67**: 1900–1910.

Date, E. M. & Lemon, R. E. (1993). Sound transmission: a basis for dialects in birdsong? *Behaviour* **124**: 291–312.

Ford, J. K. B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. *Can. J. Zool.* **69**: 1454–1483.

Møhl, B., Terhune, J. M. & Ronald, K. (1975). Underwater calls of the harp seal, *Pagophilus groenlandicus*. In *Biology of the seal*. Ronald, K. & Mansfield, A. W. (Eds). *Rapp. P.-v. Réun. Cons. Int. Explor. Mer* **169**: 533–543.

Øien, N. & Øritsland, T. (1991). Recaptures of harp seals (*Phoca groenlandica*) tagged as pups in the Greenland Sea; pup production and dispersion patterns. Joint ICES/NAFO Working Group on Harp and Hooded Seals, WP SEA-33, Copenhagen 14–18 October 1991: 1–21.

Øien, N. & Øritsland, T. (1992). Using mark-recapture methods to estimate pup production of harp seals (*Phoca groenlandica*) in the Greenland Sea. *Int. Counc. Explor. Mer, Mar. Mamm. Comm., C.M.* 1992/No. 10 - Ref. D.: 1–10.

Payne, F. A. (1964). Effect of ice cover on shallow-water ambient sea noise. *J. Acoust. Soc. Am.* **36**: 1943–1947.

Perry, E. A., Carr, S. M., Bartlett, S. E. & Davidson, W. S. (1995). A phylogenetic perspective on the evolution of reproductive behavior in pagophilic deals of the Northwest Atlantic as indicated by mitochondrial DNA sequences. *J. Mammal.* **76**: 22–31.

Sergeant, D. E. (1991). Harp seals, man and ice. *Can. Spec. Publ. Fish. Aquat. Sci.* No. 114: 1–153.

Terhune, J. M. (1994). Geographical variation of harp seal underwater vocalizations. *Can J. Zool.* **72**: 892–897.

Terhune, J. M. & Ronald, K. (1976). Examining harp seal behavioural patterns via their underwater vocalizations. *Appl. Anim. Ethol.* **2**: 261–264.

Terhune, J. M. & Ronald, K. (1986). Distant and near-range functions of harp seal underwater calls. *Can. J. Zool.* **64**: 1065–1070.

Thomas, J. A. & Golladay, C. L. (1995). Geographic variation in leopard seal (*Hydrurga leptonyx*) underwater vocalizations. In *Sensory Systems of Aquatic Mammals*: 201–221. Kastelein, R. A., Thomas, J. A. & Nachtigall, P. E. (Eds). Woerden: De Spil Publishers.

Thomas, J. A. & Kuechle, V. B. (1982). Quantitative analysis of Weddell seal (*Leptonychotes weddelli*) underwater vocalizations at McMurdo Sound, Antarctica. *J. Acoust. Soc. Am.* **72**: 1730–1738.

Thomas, J. A. & Stirling, I. (1983). Geographic variation in the underwater vocalizations of Weddell seals (*Leptonychotes weddelli*) from Palmer Peninsula and McMurdo Sound, Antarctica. *Can. J. Zool.* **61**: 2203–2212.

Thomas, J. A., Ferm, L. M. & Kuechle, V. B. (1987). Silence as an anti-predator strategy by Weddell seals. *Ant. J.* **22**: 232–234.

Thomas, J. A., Puddicombe, R. A., George, M. & Lewis, D. (1988). Variations in underwater vocalizations of Weddell seals (*Leptonychotes weddelli*) at the Vestfold Hills as a measure of breeding population discreteness. *Hydrobiologia* **165**: 279–284.