Aquatic Mammals 2003, **29.2,** 261–267

Can the sex of a Weddell seal (*Leptonychotes weddellii*) be identified by its surface call?

Melanie L. Oetelaar[1], John M. Terhune[1] and Harry R. Burton[2]

[1]*Department of Biology, University of New Brunswick, P.O. Box 5050, Saint John, New Brunswick, Canada E2L 4L5*
[2]*Australian Antarctic Division, Channel Highway, Kingston, Tasmania, Australia 7050*

Abstract

Pinnipeds predominately use underwater vocalizations for social interactions during the breeding season. Knowing the sex of the vocalizing individual can be of significant value for interpreting aquatic behaviour. However, it is usually difficult to identify the sex of the caller because the individual cannot be seen underwater. Weddell seals (*Leptonychotes weddellii*) produce a wide variety of underwater vocalizations, as well as a number of closed-mouth call types in air, which sound very similar to the underwater versions. This study used surface calls to determine whether Weddell seals produce sex-specific calls or whether there are differences in the attributes of calls made by both sexes. In-air recordings were made of adult male and female Weddell seals in breeding colonies near Davis Station, Antarctica. Trill call types were produced only by males in air, presumably underwater these are used for the purpose of territorial defence, advertisement, dominance and/or warning calls. Assuming males and females are equally likely to use the trill call type, the probability of a trill being part of the female repertoire, but not being recorded because of sample size problems, was less than 0.0001. The DL234 (roar) and DM (mew) call types also appeared to be male-specific calls, while, DWA242 (a whistle that increases in frequency in discrete steps) is a female-specific call. The DWAG call type (alternating ascending whistles and grunts) was used by both males and females; however, there were differences between the sexes in the start and end frequency measures. Assuming that what is heard in air is reflective of underwater calling, specific underwater call types could identify the sex of the caller in Weddell seals.

Key words: Weddell seal, *Leptonychotes weddellii*, vocalization, sex-specific, trill, call identification.

Introduction

The vocal repertoires of pinnipeds range from a single call type reported for crabeater seals (*Lobodon carcinophagus*; Stirling & Siniff, 1979) to the complex vocalization cycles of walruses (*Odobenus rosmarus*; Stirling *et al*., 1987). Although the specific functions of most pinniped sounds are unknown, their occurrence during the breeding season suggests that many are associated with aquatic mating (Thompson & Richardson, 1995). The reproductive strategies of nearly half of the pinniped species are unknown (Van Parijs *et al*., 2000). It is usually not possible to directly observe aquatic behaviour, particularly for those species which breed under sea ice. Monitoring vocalizations made by pinnipeds can be useful in determining their presence or behaviour where the sea ice precludes direct observation (Stirling *et al*., 1983). If underwater vocal behaviour monitoring is to be useful in elucidating pinniped reproductive behaviours, it will be important to know the sex of the caller. At least two phocid species produce calls both in air and under water: the Ross seal (*Ommatophoca rossi*; Watkins & Ray, 1985) and the Weddell seal (*Leptonychotes weddellii*; Thomas & Kuechle, 1982). In this study, we use the Weddell seal to examine whether in-air calls from known sex individuals can serve as an indicator for sex determination of underwater calls.

Weddell seals produce a wide variety of underwater vocalizations (Thomas & Kuechle, 1982; Thomas & Stirling, 1983; Thomas *et al*., 1988*a*; Pahl *et al*., 1997; Abgrall *et al*., 2003). Underwater vocalizations can be heard in-air through land-fast ice more than 4 m thick (Thomas & Kuechle, 1982). High source levels of some Weddell seal calls indicate the potential for long distance communication underwater (Thomas & Kuechle, 1982). Underwater, females generally are less vocal than males (Thomas & Kuechle, 1982). Weddell seals exhibit geographic variation in their vocal repertoire between widely separated areas (Thomas & Stirling, 1983; Thomas *et al*., 1988a; Abgrall *et al*., 2003). The vocalizations of Weddell seals seem to be associated with breeding and social interactions (Thomas & Kuechle, 1982; Thomas *et al*., 1987; Green & Burton, 1988). Thomas and Kuechle

(1982) suggested that at McMurdo Sound some call types may be used exclusively by males.

In October and November, Weddell seal males establish underwater territories along tidal cracks (Bartsch *et al*., 1992; Harcourt *et al*., 2000). They use vocalizations, especially trills (long duration, sinusoidal or frequency-modulated descending frequency sweeps) to defend their territories (Thomas & Kuechle, 1982). The defending males lie on the ice near a breathing hole or patrol in the water, make territorial calls and prepare for confrontations (Thomas & Kuechle, 1982; Harcourt *et al*., 2000). Vocal activity decreases after the mating season (Green & Burton, 1988; Thomas *et al*., 1988*b*.). Other social behaviour in Weddell seals appears to occur underwater so vocalizations would seem to be important for communication between seals (Thomas *et al*., 1988*b*).

When recording underwater vocalizations it is difficult to identify the sex of the caller because in most instances the caller cannot be observed (but see Thomas & Kuechle, 1982). Calls produced on the ice are similar to those produced underwater (Thomas & Kuechle, 1982; Terhune *et al*., 1993). By monitoring sex-specific surface calls, the sex of seals that are underwater could be identified by their calls. This information is crucial when interpreting underwater behaviours of Weddell seals.

For this study, only in-air closed-mouth (with closed nostrils) calls were considered (i.e., not open-mouthed calls used by mothers and pups). The objectives were to: (1) determine if surface call types are specific to males or females in Eastern Antarctica and (2) identify differences in the attributes of call types made by males and females.

Materials and Methods

The recordings for this study were made in 1990 and 1997. The 1990 recordings were made at a single site near Davis, Antarctica (68°31.9′S, 78°11.5′E). On 10 November 1990 there were 34 mother–pup pairs and four adult males; however, the composition changed slightly as males and females left and entered the breeding area over the next 3 weeks. Pups ranged from a few days old, where the umbilical cord was present, to those that were beginning to moult (about 4 weeks of age; Stirling, 1971; Terhune *et al*., 1993). A Radio Shack 33-2050 sound level meter (C-weighting) was used as a microphone and preamplifier. This was connected to a Sony WD-D6C cassette recorder. The cassettes were Sony UX100 and TDK SA 90 type II. The frequency response for this recording gear was 0.06–10 kHz ± 3 dB. The 1997 recordings were made at four different breeding groups (composed of 13 to 32 mother–pup pairs, plus at least one male at each site) near Davis Station, Antarctica. The recording gear was a Sennheiser ME66 microphone fitted with an MZW 20 windscreen (frequency response 0.05–20 kHz ± 2.5 dB). The tape recorder was a Sony DAT TCD-D7 (frequency response 0.02–22 kHz ± 1.0 dB). The cassettes were Sony DT-120. All recordings were made in periods of low wind and no precipitation (Terhune *et al*., 1993).

During recordings, the sound level meter, or microphone was held close to the researcher's body to reduce wind sounds and was brought within 0.3–3.0 m from the seal's throat or mouth. The seals were approached from the front while they were laying on the ice or swimming in a melt pool (Terhune *et al*., 1993). The recordings were made in an opportunistic manner in that calling seals were recorded longer (up to 39 min per day) than silent seals (as short as 29 s). The seal tag number and sex was recorded for each individual. The sex of each seal was determined by visual examination when the tapes were recorded. The location of any untagged seals was noted and they were recorded only once.

For the analysis, the recordings were simultaneously listened to and viewed using the spectrogram program GRAM (version 6.0.9; analysing bandwidths were 43, 22, 11 or 5 Hz when frequency ranges 0–22, 0–11, 0–5.5 or 0–2.7 kHz were used). The calls were then assigned to categories based on the classification systems developed by Thomas & Kuechle, (1982), Terhune *et al*. (1994) and Pahl *et al*. (1997). For each call type, the first letter (D) denotes the call was recorded near Davis, the subsequent letters indicate broad call categories and, where distinguishable, the numbers indicate specific call types within the broader categories (see Pahl *et al*., 1997 for descriptions and examples of spectral patterns of most call categories). The common names assigned to the calls are in English phonetics.

Call types were summarized by sex to see how many seals made each call type. A *t*-test was performed on the sampling duration data to determine if there was a difference in the sampling times of males and females. We used a Fisher Exact Probability Test to determine if the potential sex-specific calls were made equally by both males and females. Next, we performed a Z-score test to determine the probability of the potential sex-specific call types being part of the female or the male repertoire, assuming each call type was used at the same rate for both genders, and was not recorded because of a small sample size. Lastly, gender-related differences in call attributes (start frequency, end frequency, and duration of the first element; Fig. 1) for three related call types, DWA207 (points 'a' and 'b' in Fig. 1), DG230 (points 'c' and 'd' in Fig. 1) and DWAG (both pairs of points in Fig. 1) were analysed using Discriminant Function Analysis. Because of the similarity of

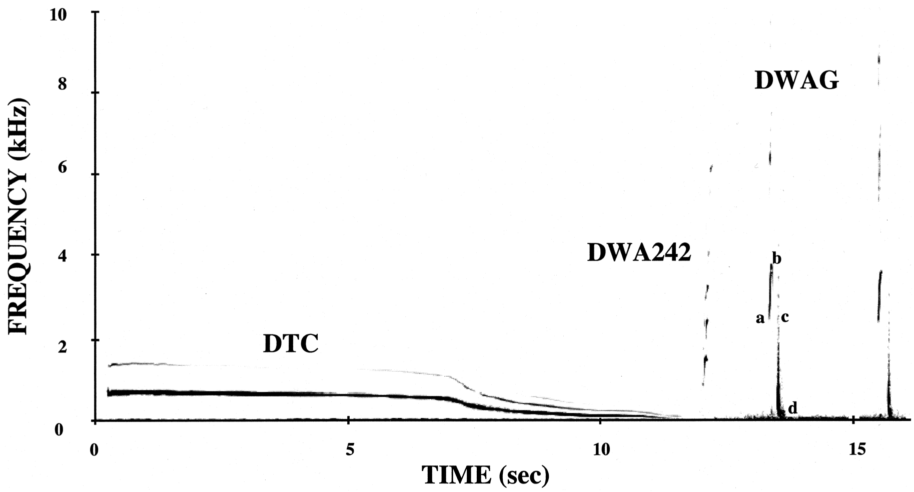

Figure 1. Sound spectrogram of a typical adult Weddell seal trill (DTC), a stepped ascending whistle showing the discrete frequency increments (DWA242) and two repetitions of alternating ascending whistle–grunt pairs (DWAG) recorded in-air near Davis, Antarctica. Labels 'a' and 'b' indicate the start and end frequency measurement points respectively of the ascending whistle component with the element duration being the time between them and 'c' and 'd' indicate the start and end frequency measurement points respectively of the grunt component with the element duration being the time between them. Analyzing bandwidth = 21.5 Hz.

most elements within multiple element calls, only the attributes of the first element of one randomly selected call per seal were measured.

Results

All closed-mouth (with closed nostrils) calls were matched to previously described underwater patterns (Pahl *et al.*, 1997). A total of 15 different closed-mouth call types were used in air by Weddell seals:

(1) DT: narrow to broad bandwidth trill, beginning with a pronounced frequency downsweep. By definition, the call has to be longer than 2 s (to distinguish it from a descending whistle).
(2) DTC: a narrow bandwidth trill with a constant frequency beginning, sinusoidal or frequency-modulated waveform ending with a pronounced descending frequency sweep. By definition, the call has to be longer than 2 s (Fig. 1).
(3) DL234: a constant frequency roar; a broadband call with predominant sound energy above 300 Hz.
(4) DM: a mew beginning with an abruptly descending frequency that is followed by a long constant frequency.
(5) DWA242: an ascending frequency whistle that increases in frequency in discrete steps (Fig. 1).
(6) DWA207: a constantly ascending frequency whistle, narrow bandwidth call, less than 2 s.
(7) DWAG: a brief ascending whistle followed by a grunt (or guttural glug), alternating in a regular pattern and typically contains multiple elements (repetitions) (Fig. 1).
(8) DWD: a descending frequency, narrow bandwidth whistle that can be repeated and can be followed by a constant frequency ending; by definition the total duration is less than 2 s.
(9) DG230: low descending frequency grunt, narrow bandwidth, short call.
(10) DG244: a low constant frequency grunt, broad bandwidth, short call.
(11) DC: an abruptly descending frequency chug, narrow to medium bandwidth, low frequency and often followed by a brief constant frequency ending.
(12) DO: a constant frequency tone, predominantly sinusoidal call.
(13) DQ: a whoop; a constant frequency, narrow bandwidth call with a brief terminal upsweep.
(14) DS: A short, narrowband squeak with constant or rising frequency and an irregular waveform.
(15) DL218: a constant frequency growl with predominant sound energy below 300 Hz, broadband, pulsed, long call, can have a slight increase in frequency at the end.

The total number of females recorded was 133 (91 were previously tagged) over 16 days for a

Table 1. Total number of in-air closed-mouth call types/number of Weddell seals making that call type. Thirty-eight female and 12 male adult seals made at least one closed mouth call. Call types were matched to the underwater call types as classified by Pahl *et al.* (1997). Calls identified by an asterisk were only detected from that sex in one year.

Call type	Females	Males
DT	0/0	37/6
DTC	0/0	12/5
DL234	0/0	24/4
DM	0/0	16/4
DWA242	94/22	0/0
DWA207	119/29	20/5
DG244	94/22	13/3
DG230	43/17	7/2
DWD	89/13	23/5
DWAG	31/10	27/4
DC	53/10	13/4
DO	3/2*	13/3
DQ	30/3	4/1*
DS	3/3	2/1*
DL218	2/1*	1/1*

duration of 996 min (n=561 calls; Table 1). The total number of males recorded was 22 (13 were previously tagged) over 15 days for a duration of 268 min (n=212 calls; Table 1). Some individuals produced only open-mouth calls and some made no sounds at all. Due to the opportunistic nature of the sampling protocol some seals were recorded longer than others, which may bias the results. A Pearson Product-Moment Correlation was performed to determine if there was a relationship between sampling duration and the probability of a seal calling. There was a significant relationship between increasing recording duration and the chance of a seal producing most call types (Pearson's correlation=0.821, R^2=0.673, $P<0.0001$, n=155). Only seals sampled for more than 500 s were included in further statistical analyses of the sex-specific call types.

Thirty-eight females and 12 males made closed-mouth calls (Table 1) and 13 females and 11 males were recorded for 500 s or longer. Five call types were identified as potential sex-specific calls (Table 1). No female made a DT, DTC, DL234, or DM call type and no males made the DWA242 call type. For seals recorded for 500 s or longer, only males produced the call types DT, DTC, DL234, and DM and only females produced the call type DWA242 (Table 2). All other types were made by both sexes. One female seal was heard making a DO that lasted for more than 2 s, which was followed by a pause and a DWD. Without the pause between the two calls, it would be similar to a DTC. A few seals made closed-mouth calls while they appeared to be sleeping. With the exception of one male that made a trill, we did not hear seals using closed-mouth calls when an observer was not close to a seal. Some of the seals reacted to the presence of the observer by lunging forward with their head while snapping their jaws open and shut.

The t-test s showed no significant differences in individual sampling durations between males and females when analysing the whole sample ($t = -1.642$, df=153, P=0.1027) or when analysing the seals sampled for a minimum of 500 s ($t = -0.303$, df=40, P=0.7636).

A Z-score test was performed to determine the probability of sex specific calls being part of the female (for the two types of trills, DL234 and DM) or the male (for DWA242) repertoire, assuming that each call type was used at the same proportion for both genders. The expected value for the two types of trills, DL234 and DM, was the proportion of calls made by males in air (i.e., the females were assumed to make DT, DTC, DL234 and DM, in the same proportion as the males). The expected value for the DWA242 was the proportion of calls made by females in air (i.e., the males were assumed to make the DWA242 in the same proportion as the females). For DT, DTC, DL234 and DM, the Z-scores were 10.89, 5.80, 8.46 and 6.77, respectively, which corresponded to $P<0.000001$. For the DWA242, the Z-score was 6.53 which corresponds to $P<0.000001$.

Table 2. Numbers of call types from 13 female and 11 male Weddell seals sampled in air for over 500 s that made possible sex-specific call types.

Call type	Female	Male	Phi^2	Fisher Exact Probability
DT	0	6	0.1912	0.0208
DTC	0	5	0.1693	0.0368
DL234	0	4	0.1444	0.0667
DM	0	4	0.1444	0.0667
DWA242	12	0	0.2200	0.0059

Table 3. Discriminant Function Analysis results of Weddell seal in-air, closed-mouth call types made by both sexes. The females (F) and males (M) were compared to determine any differences in the call attributes of start and end frequency and duration of the first element.

Call type	Sex	% Correctly identified	Female	Male	Wilks' λ	*P*
DWAG	F	100	10	0	0.0076	0.0013
	M	100	0	4		
DWA207	F	97	28	1	0.713	0.0188
	M	25	3	1		
DG230	F	88	7	1	0.764	0.378
	M	71	2	5		

Three common call types with overlapping call characteristics (DWAG, DWA207 and DG230) and having a sample size of four or more seals of both sexes making the call were analysed for gender-related differences in call attributes. Discriminant Function Analysis correctly identified all of the male and female DWAG calls (Table 3). There were sex-related differences (Wilks' $\lambda=0.076$, $F_{6,7}=14.172$, $P=0.0013$) attributable to the start frequency of the ascending whistle component (Wilks' $\lambda=0.156$, $P=0.030$) and the start (Wilks' $\lambda=0.480$, $P=0.0005$) and end (Wilks' $\lambda=0.276$, $P=0.003$) frequencies of the grunts. There were no significant sex-related differences between the other call parameters. The sex of the male DWA207 calls could not be reliably determined (Table 3) even though the differences were statistically significant (Wilks' $\lambda=0.713$, $F_{3,29}=3.891$, $P=0.018$). The significant difference was present in the start frequency (Wilks' $\lambda=0.826$, $P=0.040$), but not the other two call attributes. The sex associated with call type DG230 could not be determined by call attributes (Wilks' $\lambda=0.764$, $F_{3,11}=1.135$, $P=0.378$; Table 3).

Discussion

Thomas & Kuechle (1982) suggested that five Weddell seal call types appear to be used exclusively by males at McMurdo Sound, Antarctica. Our findings provide quantitative evidence that some Weddell seal call types in Eastern Antarctica are sex-specific. Trills produced by Weddell seals at Davis were only made by males. Females have the ability to make calls that are similar to DTC calls (i.e., a constant frequency tone >2 s followed by a descending whistle that drops in frequency), but probably do not produce trills because of behavioural factors. Trills are likely used under water by males for territorial defence, advertisement, dominance and/or warning calls (Thomas & Kuechle, 1982; Thomas & Stirling, 1983; Thomas *et al.*, 1983).

The small sample sizes make it difficult to determine if DL234 or DM are also made only by males. The statistical test using the number of calls per sex was significant, but the test employing the number of seals calling was not significant. Further sampling will be required to determine if these are male-only calls.

The stepped ascending whistle (DWA242) is likely a female identification call. None of the 12 males recorded made this call and it was produced by 22 of the 38 females that made closed-mouth calls. The Z-score test indicated that the absence of the DWA242 in our male recordings is not likely attributable to the sample size. This vocalization would enable a male to identify a female seal that is in his territory so that he does not attack a potential mate. High frequency tone-like sounds often are submissive call types in mammals (Morton, 1977; Thomas *et al.*, 1988*b*).

Although sample sizes were low, the Discriminant Function Analysis correctly identified the sex of all DWAG calls from males and females. When call types that were similar to the two components of the DWAG call were examined, the sexes could not be correctly identified. This suggests that there could be some shared calls between males and females that convey sex identification. Again, because of the small sample sizes, further sampling is warranted.

Despite the wide variety of underwater calls exhibited by Weddell seals, some call types may not have been displayed in air due to the method in which the recordings were collected. For example, seals could be less likely to display submissive calls when closely approached by a human observer. The functional significance of the different underwater call types produced in air may also not be the same because of the manner in which the vocalizations were recorded. The recording situation was clearly confrontational because the observer was so close to the seal. The seals did not produce closed-mouth vocalizations, except while apparently sleeping. In this situation, it was not possible to link specific call types to natural behavioural acts. Future monitoring of seal calls in undisturbed conditions could allow for a greater variety of sex-specific call types to be identified.

Weddell seal underwater vocal repertoires exhibit geographical variation (Thomas & Stirling, 1983; Thomas *et al*., 1988*a*; Abgrall *et al*., 2003). While trills have been detected at all recording locations to date, this is not the case for many of the other call types (Thomas & Stirling, 1983; Thomas *et al*., 1988*a*; Abgrall *et al*., 2003). The call type DWA242 was not reported at McMurdo Sound (Thomas & Kuechle, 1982) nor at Casey Station (1400 km east of Davis; Abgrall *et al*., 2003) and the call type DWAG was not reported at McMurdo Sound (Thomas & Kuechle, 1982), Casey, or Mawson Station (1400 km west of Davis; Abgrall *et al*., 2003). Thus, for two call types identified in this study as potentially conveying sex-specific information at Davis, neither one would be useful at other locations. This suggests that although some call types can convey sex-specific information, except for trills, their usefulness may be limited to restricted geographic regions.

Thomas and Kuechle's (1982) and our data suggest that Weddell seal repertoires include some call types that indicate the sex of the caller. Underwater, where long-range visibility is not possible, sex-specific calls would enhance communication, especially with respect to male attraction vocalizations. While male trills seem to be ubiquitous, other sex-specific call types may only be used in particular geographic locations. Further investigation will be required to determine the functional significance of the different call types underwater and in air and if the seals are using closed-mouth calls in air for inter-animal communication. Identifying sex-specific calls will enable researchers to determine the presence of Weddell seals of either sex in underwater recording situations where visual identification of the calling seal is not possible. This would enhance the information on the distribution, behaviour, and possibly abundance of Weddell seals that could be obtained via remote monitoring of underwater vocalizations (Stirling *et al*., 1983).

Many vertebrates and some invertebrates exhibit sex-specific sound patterns (Bradbury & Vehrencamp, 1998). Among marine mammals, walrus, harbour seal (*Phoca vitulina*) and fin whale (*Balaenoptera physalus*) males produce underwater sex-specific calls (Schevill *et al*., 1966; Van Parijs *et al*., 2000; Croll *et al*., 2002). Serrano (2001) identified one in-air (closed mouth, but with nostrils open) and four underwater call types made only by male captive harp seals (*Pagophilus groenlandicus*) throughout the year. Eleven other underwater call types were made by both males and females (Serrano, 2001). During the breeding season both male and female captive leopard seals (*Hydrurga leptonyx*) produce underwater long range broadcast calls that could serve a solicitation function (Rogers *et al*., 1996). This infers that both male and female leopard seals will call to attract a mate while in Weddell seals, only the males make long range attraction calls. Vocalization monitoring can be used to help elucidate reproductive strategies of pinnipeds. Such studies will be enhanced by using direct observation (Thomas & Kuechle, 1982), monitoring captive individuals (Rogers *et al*., 1996; Serrano, 2001) and, where applicable, using in-air recordings to link the sex of the caller to specific underwater call types.

Acknowledgments

We thank T. Cheesman, R. McFarlane, and A. Flaherty for making the majority of the recordings. The Davis expeditioners of 1990 and 1997 provided logistical support. The Australian Antarctic Division and the Natural Sciences and Engineering Research Council of Canada provided logistical support and funding. R. Rochette and K. Frego assisted with the statistical analyses and manuscript preparation. R. S. Horne is the author of GRAM. J. Thomas, S. Van Parijs and an anonymous reviewer are thanked for providing valuable comments on earlier drafts of this manuscript.

Literature Cited

Abgrall, P., Terhune, J. M. & Burton, H. R. (2003) Variation of Weddell seal (*Leptonychotes weddellii*) underwater vocalizations over mesogeographic ranges. *Aquatic Mammals* **29,** 268–277.

Bartsh, S. S., Johnston, S. D. & Siniff, D. B. (1992) Territorial behavior and breeding frequency of male Weddell seals (*Leptonychotes weddelli*) in relation to age, size, and concentrations of serum testosterone and cortisol. *Canadian Journal of Zoology* **70,** 680–692.

Bradbury, J. W. & Vehrencamp, S. L. (1998) *Principles of Animal Communication*. Sinauer Associates, Inc. Sunderland, MS, U.S.A.

Croll, D. A., Clark, C. W., Acevedo, A., Tershy, B., Florees, S., Gedamke, J. & Urban, J. (2002) Only male fin whales sing loud songs. *Nature* **417,** 809.

Green, K. & Burton, H. R. (1988) Annual and diurnal variations in the underwater vocalizations of Weddell seals. *Polar Biology* **8,** 161–164.

Harcourt, R. G., Hindell, M. A., Bell, D. G. & Waas, J. R. (2000) Three-dimensional dive profiles of free-ranging Weddell seals. *Polar Biology* **23,** 479–487.

Morton, E. S. (1977) On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. *American Naturalist* **111,** 855–869.

Pahl, B. C., Terhune, J. M. & Burton, H. R. (1997) Repertoire and geographic variation in underwater vocalisations of Weddell seals (*Leptonychotes weddellii*, Pinnipedia: Phocidae) at the Vestfold Hills, Antarctica. *Australian Journal of Zoology* **45,** 171–187.

Rogers, T. L., Cato, D. H. & Bryden, M. M. (1996) Behavioral significance of underwater vocalizations of captive leopard seals, *Hydrurga leptonyx*. *Marine Mammal Science* **12,** 414–427.

Schevill, W. E., Watkins, W. A. & Ray. C. (1966) Analysis of underwater *Odobenus* calls with remarks on the development and function of the pharyngeal pouches. *Zoologica* **51,** 103–106.

Serrano, A. (2001) New underwater and aerial vocalizations of captive harp seals (*Pagophilus groenlandicus*). *Canadian Journal of Zoology* **79,** 75–81.

Stirling, I. (1971) *Leptonychotes weddelli*. *Mammalian Species* **6,** 1–5.

Stirling, I. & Siniff, D. B. (1979) Underwater vocalizations of leopard seals (*Hydrurga leptonyx*) and crabeater seals (*Lobodon carcinophagus*) near the South Shetland Islands, Antarctica. *Canadian Journal of Zoology* **57,** 1244–1248.

Stirling, I., Calvert, W. & Cleator, H. (1983) Underwater vocalizations as a tool for studying the distribution and relative abundance of wintering pinnipeds in the High Arctic. *Arctic* **36,** 262–274.

Stirling, I., Calvert, W. & Spencer, C. (1987) Evidence of stereotyped underwater vocalizations of male Atlantic walruses (*Obodenus rosmarus rosmarus*). *Canadian Journal of Zoology* **65,** 2311–2321.

Terhune, J. M., Burton, H. & Green, K. (1993) Classification of diverse call types using cluster analysis techniques. *Bioacoustics* **4,** 245–258.

Terhune, J. M., Burton, H. & Green, K. (1994) Weddell seal in-air call sequences made with closed mouth. *Polar Biology* **14,** 117–122.

Thomas, J. A. & Kuechle, V. B. (1982) Quantitative analysis of Weddell seal (*Leptonychotes weddelli*) underwater vocalizations at McMurdo Sound, Antarctica. *Journal of Acoustic Society of America* **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. *Canadian Journal of Zoology* **61,** 2203–2212.

Thomas, J. A., Zinnel, K. C. & Ferm, L. M. (1983) Analysis of Weddell seal (*Leptonychotes weddelli*) vocalizations using underwater playbacks. *Canadian Journal of Zoology* **61,** 1558–1456.

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

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

Thomas, J. A., Ferm, L. M. & Kuechle, V. B. (1988*b*) Patterns of underwater calls from Weddell seals (*Leptonychotes weddellii*) during the breeding season at McMurdo Sound, Antarctica. *Antarctic Journal* **23,** 146–148.

Thompson, D. H. & Richardson, W. J. (1995). Marine mammal sounds. In: W. J. Richardson, C. R. Greene, C. I. Malme & D. H. Thompson (eds.) *Marine Mammals and Noise*, pp. 159–204. Academic Press, Boston.

Van Parijs, S. M., Janik, V. M. & Thompson, P. M. (2000) Display-area size, tenure length, and site fidelity in the aquatically mating male harbour seal, *Phoca vitulina*. *Canadian Journal of Zoology* **78,** 2209–2217.

Watkins, W. A. & Ray, C. G. (1985) In-air and underwater sounds of the Ross seal, *Ommatophoca rossi*. *Journal of the Acoustical Society of America* **77,** 1598–1600.