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Variation of Weddell seal (*Leptonychotes weddellii*) underwater vocalizations over mesogeographic ranges

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Abstract

The goal of this study was to determine if Weddell seal (*Leptonychotes weddellii*) underwater vocalizations exhibit regional differences over mesogeographic ranges (600–2000 km). Recordings were made along the Eastern Antarctic coastline at Mawson, Davis and Casey research stations. Differences in vocalizations were examined on three levels: (1) presence of unique call types/categories. (2) rate of occurrence of call types/categories, and (3) call features (number of call elements, start frequency, frequency shift, and duration). A total of 33 different call types within 13 categories were identified. Two call types were unique to Davis and one to each of Mawson and Casey. One category was unique to Davis. Significant differences in the proportion of call usage among the three stations were found for 23 of the 26 shared call types and all 11 of the shared call categories. All call features varied among stations when compared simultaneously or individually. While differences in vocalizations were observed over the mesogeographic range, some temporal variations also were observed at two of the levels; call usage and call features. Weddell seal groups separated by >600 km exhibited different vocal patterns.

Key words: Weddell seals, *Leptonychotes weddellii*, underwater vocalizations, geographic variations, temporal variations, mesogeographic ranges.

Introduction

Weddell seals (*Leptonychotes weddellii*) have a circumpolar coastal distribution around Antarctica and adjacent islands (Bertram, 1940). They are not a migratory species and the main factor controlling their seasonal distribution is the stability of the land-fast ice (Kooyman, 1981*a*). Weddell seals are polygamous with one male mating up to ten females (Kooyman, 1981*b*). Females exhibit site fidelity at McMurdo Sound with little noticeable exchange between both sides of the Sound (90 km) (Stirling, 1974). Females also have been observed to return yearly to the same area to give birth (Stirling, 1969*a*). Stirling (1971) suggested the limiting factor for the number of pups in a colony is related to the number of suitable cracks in the sea ice. When emigration occurs in Weddell seals, it tends to be to the closest colony to their birth site. They are able to show enough behavioural plasticity to adapt and be accepted by this neighbouring colony (Stirling, 1969*b*; 1974).

Weddell seals are very vocal and possess a large and varied underwater vocal repertoire with call frequencies ranging from <0.1 kHz to >20 kHz and durations ranging from 10–20 ms for clicks to over a minute for trills (Thomas & Kuechle, 1982; Thomas & Stirling, 1983; Thomas *et al.*, 1988; Pahl *et al.*, 1997). Weddell seals are most vocal during the breeding season beginning in September with a gradual increase in the number of calls to a maximum in November (Thomas *et al.*, 1987; Green & Burton, 1988).

The first documentation of macrogeographic (transcontinental) variations in Weddell seal underwater vocalizations compared recordings taken from the Palmer Peninsula and McMurdo Sound which are approximately 5000 km apart (Thomas & Stirling, 1983). A further study comparing underwater vocalizations from Palmer Peninsula, McMurdo Sound and Davis Station in East Prydz Bay (which lies on the opposite side of Antarctica from Palmer Peninsula and McMurdo Sound) also found variations in Weddell seal underwater vocalizations around the Antarctic continent (Thomas *et al.*, 1988). McMurdo sound is approximately 3000 km along the coast from Casey.

A study by Pahl *et al.* (1997) found no evidence of microgeographic variation over a range of 150 km in the Vestfold Hills (Davis, Australian

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Antarctic Territory). Vocal patterns varied slightly between breeding groups, but no discernable consistent patterns were noted. In addition, Pahl *et al.* (1997) found that most seals that were tagged were not present in the Vestfold Hills two years in a row. Therefore, different individuals were likely acoustically active at a same site over different years.

Four other pinniped species have been shown to possess geographical variations in vocalizations. These are the Northern elephant seal (*Mirounga angustirostris*) (LeBoeuf & Peterson, 1969), bearded seal (*Erignathus barbatus*) (Cleator *et al.*, 1989), harp seal (*Pagophilus groenlandicus*) (Perry & Terhune, 1999) and leopard seal (*Hydrurga leptonyx*) (Thomas & Golladay, 1995). Similarly, variations in cetacean vocalizations of blue whales (*Balaenoptera musculus*) (Stafford *et al.*, 2001), humpback whales (*Megaptera novaeangliae*) (Cerchio *et al.*, 2001; McSweeney *et al.*, 1989), killer whales (*Orcinus orca*) (Ford, 1991), and sperm whales (*Physeter macrocephalus*) (Weilgart & Whitehead, 1997) also have been reported. In many cases, the differences in vocalizations within species have been attributed to reproductive isolation.

Preliminary analyses of narrow bandwidth calls collected at Australian research stations Casey and Davis have showed differences in many call features between both populations (Terhune *et al.*, 2001). The present study collected recordings at three Australian bases separated by 600–2000 km to determine if variations in underwater vocalizations of Weddell seals can be detected over mesogeographic ranges. If variations over these distances cannot be identified, there is little hope that underwater vocalizations can be a useful tool to identify discreet breeding populations of Weddell seals around Antarctica. A secondary objective was to determine if temporal variations can be observed in underwater vocalizations of Weddell seals within a short timeframe. This will help determine if reliable geographic variation comparisons can be made using datasets collected in different years.

Materials and Methods

Recording equipment

Recordings were made off the Eastern Antarctic coastline near three Australian Antarctic stations: Casey (66°17′S, 110°32′E) in 1997, Davis (68°35′S, 77°58′E) in 1992, and 1997 and Mawson (67°36′S, 62°52′E) in 2000 (Fig. 1). Mawson lies approximately 600 km west of Davis along the Antarctic coastline. Davis lies approximately 1400 km west of Casey along the coastline. Recordings were taken from breeding colonies (Abgrall, 2002) accessible through sea-ice travel from the stations. The recordings from breeding colonies around a station were pooled to form the data set for each station. Eight to ten recordings were taken opportunistically between 21 October and 1 December at each station.

At each recording site, a hole was drilled through the sea-ice. The hydrophone was lowered into the water approximately 2 m below the sea-ice. At all stations, different units of Sony digital audio tape (DAT) recorders (model TCD-D3) were used (frequency response: 0.02–20 kHz ± 1 dB). At Mawson, a SeaSystem (frequency response unknown) or a Vemco (frequency response: 0.03–20 kHz ± 2 dB) hydrophone was connected to a Sony DAT recorder. At Davis, a Bruel and Kjaer 8100 hydrophone equipped with a Bruel and Kjaer 2635 charge preamplifier (frequency response: 0.002–30 kHz ± 1 dB) was connected to the Sony DAT recorder. At Casey, an ITC 6050C hydrophone (frequency response: 0.03–75 kHz ± 1 dB) with built-in preamplifier was used. The recorded calls were analysed using Spectrogram version 5.1.6 (copyright 1994–1999 by R. S. Horne). Monaural sampling at a rate of 44 kHz with 16-bit resolution was used.

Data analysis

Mesogeographic (Mawson, 2000; Davis, 1997; Casey, 1997) and temporal (Davis, 1997; Davis, 1992) vocal variations were assessed using three methods: (a) differences in vocal repertoire (presence of unique call types or call categories), (b) differences in call usage (the proportional usage of call types or call categories), and (c) differences in easily measurable call features. Calls were classified into 13 broad categories described by Thomas & Kuechle (1982) and Pahl *et al.* (1997). Calls exhibiting different patterns within a category were further classified into types (Abgrall, 2002). Forty-one call types were identified and numbered starting at 301 to 341 to avoid any confusion with previous classifications existing in the literature. The call category indicator letter follows each call type number. Examples of the call types are available as .wav files and spectrograms via the Metadata Division of the Australian Antarctic Division. Only call types and categories whose absence at a base was statistically significant (Z-score) and not due to low sample sizes were used in the following analyses. Thirty-three of the forty-one call types and all thirteen call categories were used. Four standard, easily measurable call features were used in the analyses (number of elements, start frequency, frequency shift, and duration or duration of the first element in the case of multiple element calls). Only the first 100 calls of each recording site per day were used in the analyses (Perry & Terhune, 1999). If less than 100 calls were present, all the calls were analysed. Limiting the number of calls per

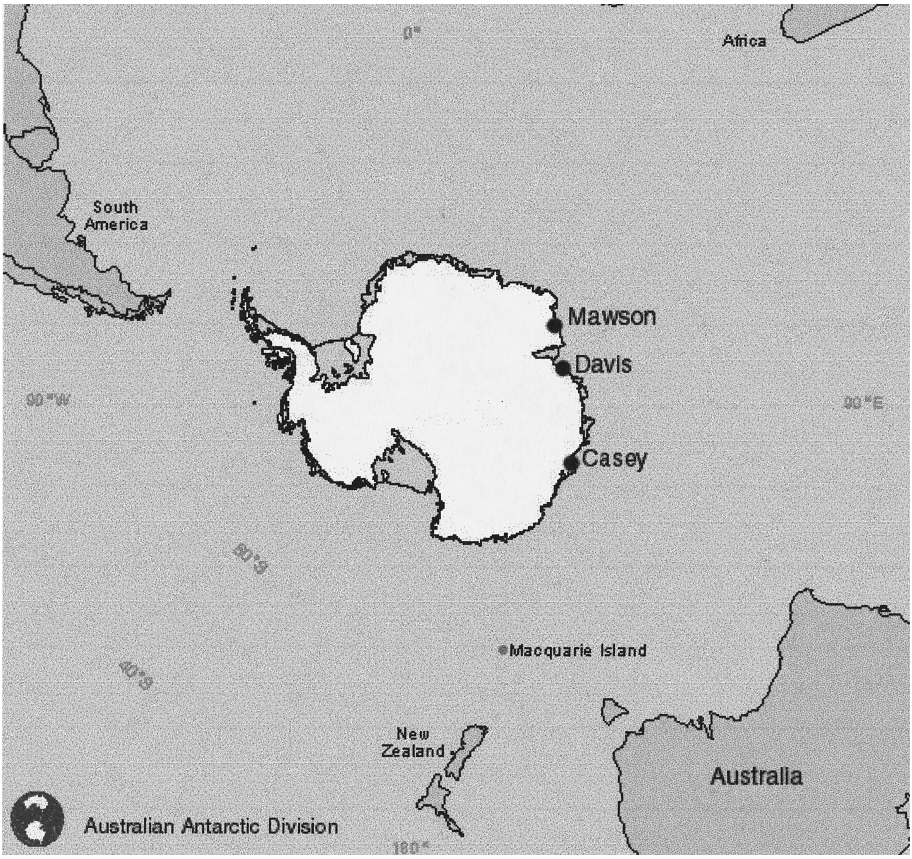

Figure 1. Map of Antarctica showing Casey, Davis, and Mawson stations on the Eastern Antarctic coastline.

recording allowed approximately equal sample sizes for each station. It also limited the potential impact of a few very vocal seals that could be present at certain breeding colonies. Classifying consecutive call types enabled determining the proportional usage of each type. Significance was assessed at an α-level of 0.05 for all statistical analyses.

Vocal repertoires
Both narrow (call types) and broad (call categories) classifications were used to insure that the conclusions reached would be based on geographic variations and not call classification. Differences in vocal repertoires were considered to be present if one or many call types or call categories were found at one station while being absent from the other two.

Temporal differences in vocal repertoires were assessed through the presence of unique calls between Davis 1997 and Davis 1992. Again, both a narrow and a broad classification were used. The presence of temporal differences in vocal repertoires was concluded if one or many call types or call categories were found at one station while being absent from the other one. Strictly, the geographic difference in vocal repertoires was also assessed by looking for unique call types or call categories between Davis 1997 and Casey 1997.

Call usage
Mesogeographic comparisons of call usage were first done with all three stations together and then by examining each set of stations two-by-two. The analysis then compared the rate of occurrence of all call types or call categories found among the stations, first simultaneously and then, individually.

Temporal differences in call usage were examined by comparing the rate of occurrence of the different call types or call categories between Davis 1992 and Davis 1997. Again, differences in call usage were examined by looking at both overall differences in call type and call category, and differences in individual call type and call category usage.

Chi-square analyses were used to test for statistical differences in rate of call usage.

Call features

Mesogeographic variations in the above-mentioned call features were tested for both call categories and call types. Because of the rare occurrence of certain calls at some stations, only the most common call categories and call types were used. Seven call categories were tested: O (tone), L (growl), T (trill), WD (whistle descending), M (mew), C (chug), and G (grunt). Ten call types were tested: 302-0, 303-L, 313-T, 318-WD, 321-WD, 322-WD, 325-M, 326-C, 328-C, and 329-G.

Variations in call features also were tested for all calls combined. This was done because of problems that exist in call classification. By not classifying the calls and comparing all the call features per station at once, it provided a comparison test that did not include an observer-created classification. Standard transformations were applied to the frequency ($\log_2$) and duration ($\log_{10}$) values for analysis purposes.

Mesogeographic differences in call features among the stations were tested using a multivariate analysis of variance (MANOVA). This allowed comparing the overall variation in all four call features among the three stations when all calls were combined, for each call category, and for each call type. Each call feature also was examined individually among the three stations using a one-way analysis of variance (ANOVA) test. A discriminant function analysis (DFA) also was performed using all calls from each station to test whether call features could be used as a reliable indicator of group identity. DFA also were performed for each individual call category and call type.

Temporal variations in features of all calls combined, call categories, and call types were tested between Davis 1992 and 1997. Davis 1997 and Casey 1997 stations were used to test strictly geographic variations. The same statistical tests as for mesogeographic variations in call features were used (MANOVA, ANOVA, and DFA). All statistical analyses in this section were done using SPSS 10.1.4 for Windows (© SPSS Inc., 1989–2000). Additional statistical tests and results are included in Abgrall (2002).

Results

Call repertoire

Unique call types were found at all three locations (Table 1). These call types combined represent 205 out of a total of 2439 calls sampled from the three locations. Only one unique call category was found (category WAG) at Davis. Other noticeable absences include the lack of WA calls at Casey and the lack of K calls at Davis.

Temporally, only one unique call type was found between Davis 1997 and Davis 1992, and represented 12 out of 1693 calls sampled at Davis 1997 and Davis 1992 (Table 1). No unique call categories were found. Strictly geographically, Davis 1997 and Casey 1997 had a total of nine call types unique to one or the other station and combined for a total of 231 out of the 1514 calls sampled (Table 1). Three unique call categories were found (categories WA and WAG at Davis 1997 and K at Casey 1997). Davis 1997 and Davis 1992 shared 29 out of 30 call types. Davis 1997 and Casey 1997 shared 23 out of 32 call types.

Call usage

The rate of occurrence of calls among Mawson 2000, Davis 1997, and Casey 1997 were significantly different when all calls types and call categories were compared simultaneously (d.f.=64, χ^2= 1586.50, P<0.001; and d.f.=24, χ^2=711.01, P<0.001, respectively). When each call type and call category was compared individually, 23 of the 26 call types and all 11 call categories that were numerous enough to be analysed had a significant difference in rate of occurrence (d.f.=2, χ^2>5.991, P<0.05 for all significant individual call types and call categories; Table 2). When looked at by pair of stations, all three pairs had significant variations in the frequency of occurrence when all call types or call categories were compared simultaneously and all pairs had similar proportions of significant individual call types and call categories (Table 2).

Temporal differences in rate of occurrence between Davis 1997 and Davis 1992 were significant when all call types and categories were compared simultaneously (d.f.=29, χ^2=355.72, P<0.001 and d.f.=11, χ^2=161.54, P<0.001, respectively). When each call type and call category was compared individually, 19 of the 27 call types and 7 of the 11 call categories that were numerous enough to be analysed had significant differences in rate of occurrence (d.f.=1, χ^2>3.841 for all significant individual call types and call categories; Table 2).

Call features

A mesogeographic multivariate analysis of variance among Mawson 2000, Davis 1997, and Casey 1997 found a significant difference in call features when all calls were combined (P<0.001; Fig. 2). When the analysis looked at each call feature, the ANOVAs for each call feature were significantly different among the three stations (all P<0.001; Fig. 2). Mesogeographic MANOVAs also found significant differences in call features for each call category and for each call type (P<0.001 for all call categories and call types; Table 3). Table 3 also shows the

Table 1. Rate of occurrence of the 33 Weddell seal underwater call types at all four stations.

Call type	Mawson 2000	Casey 1997	Davis 1997	Davis 1992
301-O	0	1	62	23
302-O	61	69	57	165
303-L	45	58	10	47
304-L	2	1	42	24
305-Q	12	3	2	3
306-S	81	8	47	4
307-S	2	0	12	0
308-WA	23	0	57	41
309-WA	**104**	**0**	**0**	**0**
310-TC	0	19	34	15
311-TC	5	2	4	7
312-TC	2	10	7	44
313-T	14	51	19	23
314-T	0	6	19	30
315-T	1	0	18	61
316-WD	2	37	22	55
317-WD	3	28	2	38
318-WD	36	155	40	42
319-WD	**0**	**5**	**0**	**0**
320-WD	0	43	8	4
321-WD	47	51	21	12
322-WD	77	34	20	4
323-WD	7	0	7	7
324-WD	83	0	21	45
325-M	63	36	87	110
326-C	14	17	22	9
327-C	11	15	2	10
328-C	208	20	50	28
329-G	15	19	17	15
330-G	6	2	4	1
331-G	**0**	**0**	**25**	**4**
332-WAG	**0**	**0**	**71**	**13**
333-K	1	15	0	0
Total	925	705	809	884

Bolded call types indicate call types unique to a station.

proportions of individual call types and categories that had significant differences for each individual call feature from ANOVAs.

Multivariate analyses of variance between Davis 1992 and Davis 1997 (temporal variation), and between Davis 1997 and Casey 1997 (strictly geographic variation) found a significant difference in call features when all calls were combined (P<0.001; Fig. 3). When the analysis looked at each call feature, the ANOVAs for two of the four call features (number of elements and start frequency) were significantly different between Davis 1992 and Davis 1997 (both P<0.01; Fig. 3a), and for all four call features between Davis 1997 and Casey 1997 (all P<0.001; Fig. 3b). Temporal and strictly geographic MANOVAs also found significant differences in call features for six of seven and all seven call categories, respectively and for six of nine and seven of nine call types, respectively (Table 3).

The DFA found that call features could be used as statistically significant indicators of station origin among Mawson 2000, Davis 1997, and Casey 1997 (P<0.001). However, the overall classification success of a call was 58.3%, with a high of 71.2% for Mawson 2000 calls and a low of 44.6% for Davis 1997 calls. When calls were divided into categories or types, call features were a significant indicator of station origin for all of the call categories and call types (P<0.001).

The DFA found that call features could be used as statistically significant indicators of station origin between Davis 1992 and Davis 1997, and between Davis 1997 and Casey 1997 when all calls were combined, for all call categories, and for six of nine and eight of nine call types, respectively (P<0.05 for

Table 2. Results of the chi-square analyses performed on the frequency of occurrence of Weddell seal underwater call types and call categories at three stations simultaneously or between each set of two stations (the Davis 1997–Davis 1992 pair refers to the temporal variations) when all call types or call categories were compared simultaneously (Observed χ^2) or individually (Significant Call Types).

Stations Compared	d.f.	Critical χ^2 at $\alpha=0.05$	Observed χ^2	Significant Call types
Call Types				
Mawson 2000–Davis 1997–Casey 1997	64	83.675	1586.5	23/26
Mawson 2000–Davis 1997	31	44.985	641.1	20/26
Davis 1997–Casey 1997	31	44.985	594.2	22/27
Mawson 2000–Casey 1997	30	43.773	692.9	15/21
Davis 1997–Davis 1992	29	42.557	355.7	19/27

Stations Compared	d.f.	Critical χ^2 at $\alpha=0.05$	Observed χ^2	Significant Call Categories
Call categories				
Mawson 2000–Davis 1997–Casey 1997	24	36.415	711.0	11/11
Mawson 2000–Davis 1997	12	21.026	302.14	10/12
Davis 1997–Casey 1997	12	21.026	346.1	10/12
Mawson 2000–Casey 1997	11	19.675	363.13	9/12
Davis 1997–Davis 1992	11	19.675	161.54	8/11

all significant measures). The overall classification success of a call temporally and strictly geographically was 54.2% and 69.6% when all calls were combined.

Discussion

The main objective of this study was to determine whether Weddell seal call variations could determine if sub-populations were present over mesogeographic ranges. Vocal variations were observed using three techniques: call repertoire (presence of unique call types or categories; Table 1), call usage (rate of occurrence of call types or categories; Table 2), and call features (variations in four call features when all calls were combined, by call category, or by call type; Table 3). Unique call types can be used to identify specific Weddell seal sub-populations.

The presence of the WAG calls at Davis only while both WA and G elements were found individually at Mawson suggests that cultural learning, and not strictly genetic factors, plays an important role in Weddell seal vocal patterns. The WAG call was a fairly important constituent of the Davis 1997 vocal repertoire, representing 8.8% of the calls analysed (Table 1). This percentage was on the rise from 1.5% of the total calls at Davis in 1992 (Table 1). It is possible that the combination of the WA and G calls at Davis is a fairly new event explained by its increase in usage through the years, although only two years are available to be compared in this case. The absence of the WAG at Mawson and Casey could be explained by the lack of exchange in individuals between Davis and Mawson or Casey during this timeframe.

Temporal variations over five years also were observed. These were found to be negligible for the call repertoire analysis (one unique call type representing 0.7% of the total calls sampled and no unique call categories; Table 1), but not for the call usage and call features analyses. Call repertoires (unique call types and categories) are thus practical vocal indicators of sub-populations, while call usage and within-call differences are not as effective due to the temporal variation observed in the chi-square (Table 2), MANOVA (Table 3) and DFA tests. These temporal variations; however, are less than the geographic variations observed (Tables 2 and 3) and discussed above.

Some Weddell seal females do not breed every year (Stirling, 1974). Pahl *et al.* (1997) observed that over two consecutive years, only five out of 55 tagged Weddell seals were re-sighted at the Vestfold Hills. Thus, the same seals were not necessarily recorded at Davis in different years. The sampling of different individuals at a single station over a

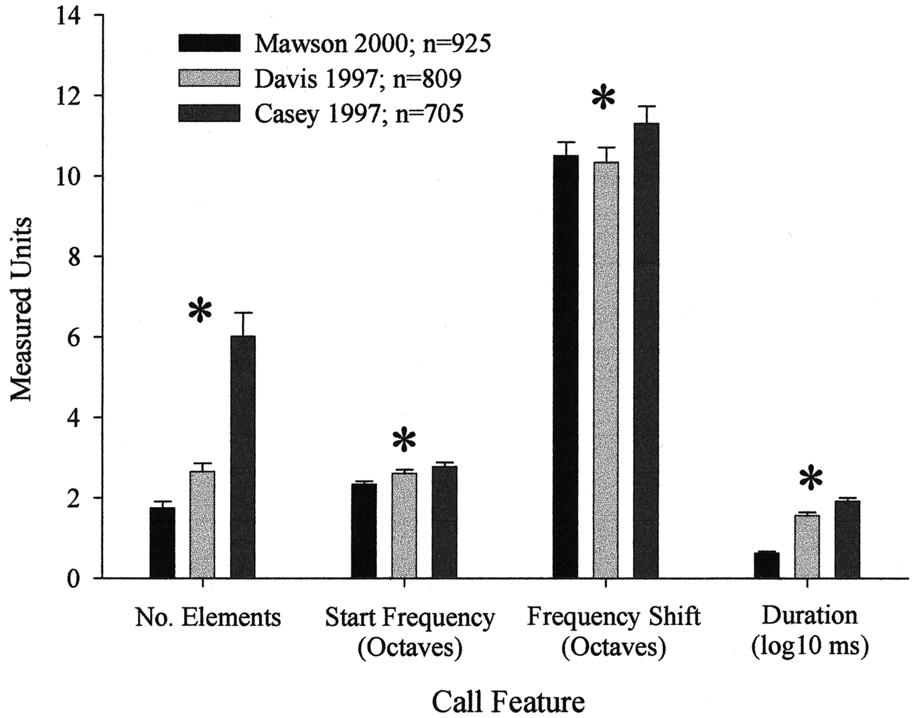

Figure 2. Multivariate analysis results of mesogeographic variation of Weddell seal underwater calls at Mawson 2000, Davis 1997, and Casey 1997 for all calls combined ($P<0.001$) (*refers to call features that showed individual significant variation among Mawson 2000, Davis 1997, and Casey 1997).

Table 3. Proportion of call categories and call types of Weddell seal underwater vocalizations that had significant (at $\alpha=0.05$) variations in call features (MANOVAs when all features combined and ANOVAs for each individual call feature) among Mawson 2000, Davis 1997, and Casey 1997 (Mesogeographic), between Davis 1997 and Davis 1992 (Temporal), and between Davis 1997 and Casey 1997 (Strictly Geographic).

Calls Compared	All Features	Number of Elements	Start Frequency	Frequency Shift	Duration
Categories					
Mesogeographic	7/7	2/5	4/7	5/7	5/7
Temporal	6/7	2/3	3/7	4/7	6/7
Strictly Geographic	7/7	2/3	3/7	4/7	5/7
Types					
Mesogeographic	10/10	3/6	8/10	7/10	7/10
Temporal	6/9	1/4	4/9	2/9	5/9
Strictly Geographic	7/9	3/4	5/9	4/9	3/9

5-year period also could be responsible for the temporal variations observed. The term 'temporal' was used for this within-station variation analysis because it was the only controlled factor that changed. Variations in vocalizations observed are not necessarily a direct result of variations over time for the same individuals and the 'temporal' study does not solely control for temporal variation. A longer timeframe is needed to assess vocal pattern stability (see Serrano & Terhune, 2002).

Thomas *et al.* (1988) observed macrogeographic variations (transcontinental) in Weddell seal underwater vocalizations. As in this study, the presence of unique call types was found to be a good

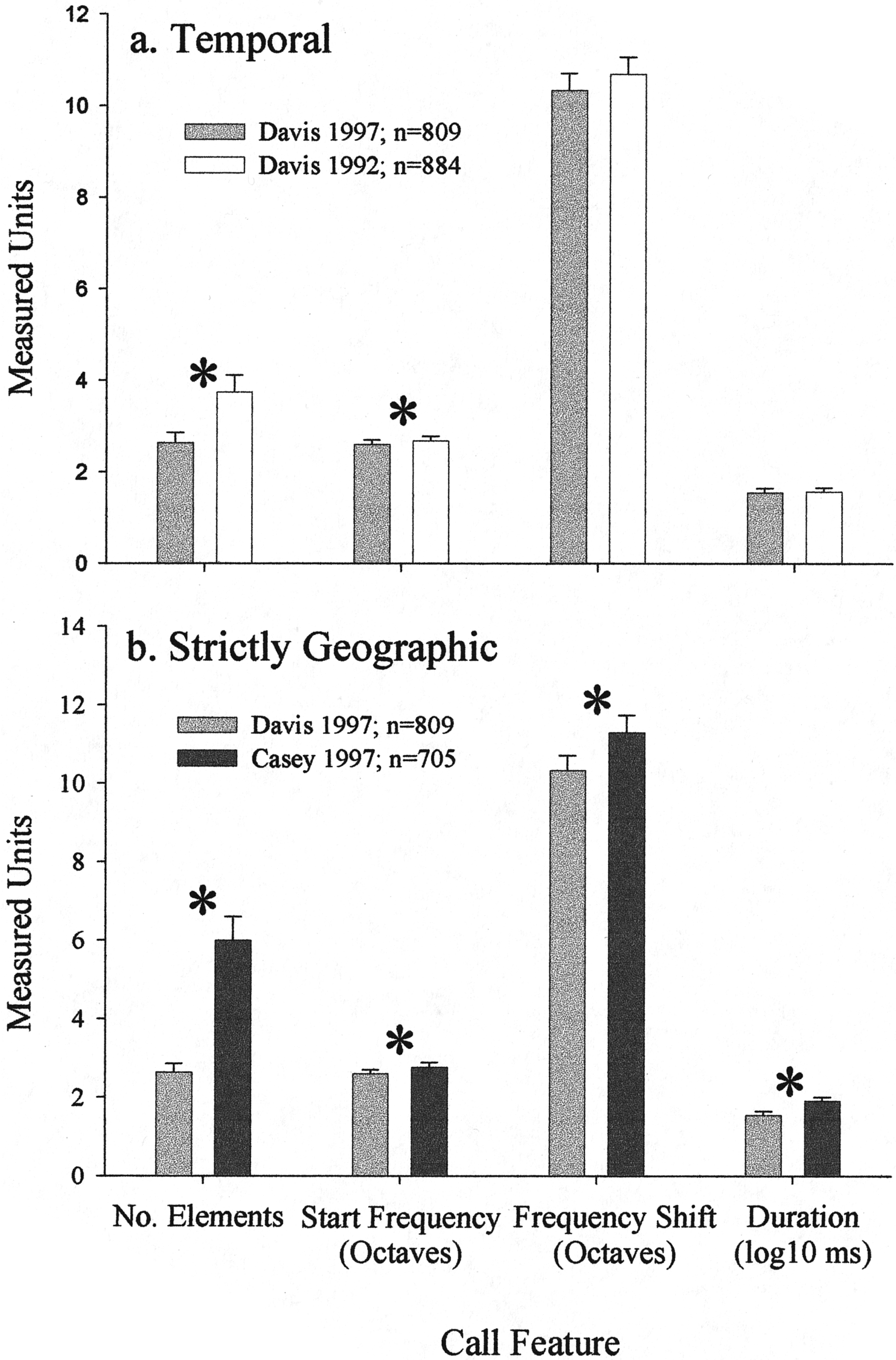

Figure 3. Multivariate analysis results of mesogeographic variation of Weddell seal underwater calls between Davis 1997 and Davis 1992 (a. Temporal), and between Davis 1997 and Casey 1997 (b. Strictly Geographic) for all calls combined ($P << 0.001$) (*refers to call features that showed significant individual variation).

indicator of geographic variations. Thomas *et al.* (1988) indicated that more research needed to be done to detect the minimal range over with these geographic variations can be detected. Pahl *et al.* (1997) found no microgeographic variations over a range of 150 km, but did note variability between nearby breeding groups and among years. The mesogeographic range (600 km) used in this study is likely close to the minimal distance over which geographic variations can be detected through underwater vocalizations.

Perry & Terhune (1999) used the same three analysis techniques as in the present study to compared underwater vocalizations of harp seals between three populations (Jan Mayen Island, Gulf of St. Lawrence, and the 'Front' ice east of Labrador). Perry & Terhune (1999) found that the Gulf and 'Front' herds are likely interbreeding while being reproductively isolated from the Jan Mayen herd. This was consistent with results obtained from tagging studies (Sergeant, 1991). The differences in harp seal underwater vocalizations can be further attributed to geographic variations in light of recent evidence, suggesting that harp seal vocal repertoires have changed little over the past three decades (Serrano & Terhune, 2002). In light of the observed underwater vocalization variations among all three stations, it would seem that the Weddell seal populations at Mawson, Davis, and Casey stations would all be reproductively isolated from one another.

The results are also consistent with those obtained using similar techniques on other marine mammals species. Differences in call repertoire and call features (duration, start frequency, and end frequency) also were used to identify geographic variations in bearded and leopard seals (Cleator *et al.*, 1989; Thomas & Galloday, 1995). Cleator *et al.* (1989) also observed geographic variations in call usage for bearded seals. Unique call types were used to differentiate between two blue whale populations in the North Pacific (Stafford *et al.*, 2001). Hawaiian and Mexican humpback whales population were found to differ acoustically according to 44 variables (Cerchio *et al.*, 2001).

In the case of regional dialects, Ford (1991) found that within 16 pods of killer whales off the coast of British Columbia, four distinct acoustic clans could be identified from the presence of unique call types in each clan. Ford (1991) noted that the formation of a new pod within a clan also was accompanied with a divergence in call repertoire (call innovation and call extinction). Ford (1991) hypothesized that these divergences resulted from errors in learning across generations. Since it is likely that Weddell seals at Mawson, Davis, and Casey stations do not mix they do not have the potential to interbreed (from Davis-based tagging studies, no Davis-tagged seals travelled to Mawson or Casey), as the killer whale clans off the coast of British Columbia, Weddell seal vocal repertoire variations cannot be interpreted as regional dialects.

Weilgart & Whitehead (1997) identified regional dialects in sperm whale repertoires in the South Pacific. Weilgart & Whitehead (1997) found strong group-specific dialects that seemed to persist over years. The lack of DNA differences among the groups studied in this region supported the claim that the geographic variations were indeed regional dialects. If future DNA analyses of the three Weddell seal populations examined in this study fail to differentiate among the populations, and contradict the observed results from tagging studies at Davis, then the mesogeographic variations discussed in the present study could be interpreted as regional dialects.

Unique call types (such as call type 332-WAG, which is unique to Davis) can be used to identify Weddell seal reproductive groups in the absence of known physical barriers separating the populations. This, however, cannot be done using only measures of vocal attributes. The DFA percentages of correct allocation are too low (58.3% overall among the three stations) to be useful indicators of reproductive groups.

What we need to better understand at this point is the biological significance of the geographic variations of underwater vocalizations of Weddell seals observed in this study and its use as an accurate natural tag of distinct breeding populations. This will be partly addressed once the genetic variation between the populations is assessed and available for comparison with the underwater vocalizations variations observed in this study. Longer-term monitoring of certain rare calls such as call type 307-S that was absent at Davis 1992, but was present twelve times in the Davis 1997 sample (Table 1) would also be useful. It would be interesting to see if this, or other infrequent call types, increase in occurrence over the next generations.

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