

Quantitative classification of harbor seal breeding calls in Georgia Strait, Canada

Katrina Nikolich^{a)}

Department of Biology, Western Washington University, 516 High Street, Bellingham, Washington 98225, USA

Héloïse Frouin-Mouy

JASCO Applied Sciences Canada Ltd., 2305-4464 Markham Street, Victoria, British Columbia V8Z 7X8, Canada

Alejandro Acevedo-Gutiérrez

Department of Biology, Western Washington University, 516 High Street, Bellingham, Washington 98225, USA

(Received 12 February 2016; revised 21 June 2016; accepted 29 July 2016; published online 24 August 2016)

During breeding season, male harbor seals (*Phoca vitulina*) produce underwater calls used in sexual competition and advertisement. Call characteristics vary among populations, and within-population differences are thought to represent individual variation. However, vocalizations have not been described for several populations of this widely-distributed and genetically diverse species. This study describes the vocal repertoire of harbor seals from British Columbia, Canada. Underwater recordings were made near Hornby Island during the summer of 2014 using a single hydrophone. A wide variability was detected in breeding vocalizations within this single breeding site. Four candidate call types were identified, containing six subtypes. Linear discriminant analysis showed 88% agreement with subjective classification of call types, and 74% agreement for call subtypes. Classification tree analysis gave a 92% agreement with candidate call types, with all splits made on the basis of call duration. Differences in duration may have reflected individual differences among seals. This study suggests that the vocal repertoire of harbor seals in this area comprises a vocal continuum rather than discrete call types. Further work with the ability to localize calls may help to determine whether this complexity represents variability due to propagation conditions, animal orientation, or differences among individual seals. © 2016 Acoustical Society of America.

[<http://dx.doi.org/10.1121/1.4961008>]

[WWA]

Pages: 1300–1308

I. INTRODUCTION

While all pinnipeds give birth on land, almost half of the extant pinniped species mate aquatically (Van Parijs, 2003). All pinniped species that mate underwater, the majority of which are phocids or “earless seals,” produce underwater vocalizations during the breeding season (Van Parijs *et al.*, 2003). The cryptic nature of underwater mating presents challenges to the study of breeding behavior in these species; consequently, much of the early study of breeding systems in pinnipeds focused on terrestrially-mating species (e.g., Le Boeuf, 1974; Anderson and Fedak, 1985; Boness, 1991; Cassini, 1999). With the development of remote sensing technology, biologists have gained the ability to learn more about the mating systems and strategies of aquatically-mating pinnipeds. One such emerging method is the use of passive acoustics to describe breeding vocalizations. Cataloguing the breeding vocal repertoire of aquatically-mating species enables us to define the temporal and spatial patterns of breeding activity, giving insight into mating systems and strategies (Van Parijs, 2003; Van Opzeeland *et al.*, 2008).

In phocid seals, vocal repertoire varies at both the species and population levels (Rogers, 2003; Van Opzeeland *et al.*, 2008, 2010). Phocid species produce anywhere from 1 to 34 call types, often differing between populations in species that show geographic isolation (see reviews in Stirling and Thomas, 2003; Rogers, 2003; Van Opzeeland *et al.*, 2008). Differences in repertoire size among populations of the same species may be due to proximal environmental factors, or the development of vocal dialects as a result of geographic isolation of populations (Thomas and Stirling, 1983; Thomas and Golladay, 1995). Further, some pinniped species exhibit vocal learning, resulting in the divergence of vocal characteristics between populations (Janik and Slater, 1997; Abgrall *et al.*, 2003; Van Parijs *et al.*, 2003; Reichmuth and Casey, 2014). To better enable comparisons of calls among populations, acoustic datasets should encompass the species’ global geographic range. For species that are widely distributed with limited individual ranges, there may exist a number of breeding stocks in a relatively small geographical area. It is then important to sample among these stocks extensively to achieve a representative sample.

Harbor seals are phocids that occupy coastal ranges throughout the northern hemisphere (Stanley *et al.*, 1996) and are composed of several subspecies (Stanley *et al.*,

^{a)}Electronic mail: katrinan@uvic.ca

1996; Burg *et al.*, 1999). Individuals tend to be philopatric (Härkönen and Harding, 2001), resulting in genetic isolation between parapatric populations over relatively short distances (Stanley *et al.*, 1996; Burg *et al.*, 1999; Huber *et al.*, 2012). Harbor seals engage in lekking, a polygynous mating system wherein males aggregate in an area frequented by females and perform visual and/or vocal displays which advertise sexual fitness (Hanggi and Schusterman, 1994; Hayes *et al.*, 2004a; Boness *et al.*, 2006). The traits upon which females base their choices are still unclear in harbor seals, and are thought to be a combination of surface-active displays and underwater vocalizations (Sullivan, 1981; Hanggi and Schusterman, 1994; Nicholson, 2000).

Hanggi and Schusterman (1994) first described underwater vocalizations for adult harbor seals *in situ* in Moss Cove, central California, and hypothesized that these calls were related to breeding activity. One vocalization type, the “roar,” shows a significant variation between individuals, but little intra-individual variation (Hanggi and Schusterman, 1994; Van Parijs *et al.*, 2000a; Hayes *et al.*, 2004b). The roars of different individuals can vary in both duration and frequency parameters (Hanggi and Schusterman, 1994; Van Parijs *et al.*, 2000a; Hayes *et al.*, 2004b) and are hypothesized to serve as a reliable indicator of body size and condition (Nicholson, 2000; Hayes *et al.*, 2004b). Male harbor seal underwater vocalizations have been described for populations in Norway and Sweden (Björgesæter *et al.*, 2004), Scotland (Van Parijs *et al.*, 1997, 1999, 2000a, 2000b; Björgesæter *et al.*, 2004), the west coast of the United States (Nicholson, 2000; Hayes *et al.*, 2004b), and eastern Canada (Coltman *et al.*, 1997; Van Parijs and Kovacs, 2002; Boness *et al.*, 2006). In each of these populations, the roar call has been associated with male breeding behavior, and is often heard during short dives between bouts of surface active behavior (Coltman *et al.*, 1997; Van Parijs *et al.*, 1997).

As is seen in other widely-distributed pinniped species, harbor seal roars exhibit geographic variability in vocal characteristics. For instance, males in Orkney and Moray Firth, Scotland, display more vocal variation between sites than between individuals within a site (Van Parijs *et al.*, 2000a). Harbor seals from six locations in the North Sea also vary in the frequency contours of their roars (Björgesæter *et al.*, 2004). Harbor seal roars from ten locations throughout their global range were compared and found to be ~90% distinguishable among populations (Van Parijs *et al.*, 2003). These clear differences among populations suggest the development of site-specific dialects on a small spatial scale, perhaps facilitated by a combination of genetic distance, vocal learning, and site-specific environmental conditions (Van Parijs *et al.*, 2003).

The size of the harbor seal’s vocal repertoire also varies by population. Hanggi and Schusterman (1994) identified and described five unique call types in Monterey Bay, California, that were used to varying degrees by each individual male. Nicholson (2000) described three related call types: the preroar, step, and roar, all of which are interchangeable parts of a typical roar. Van Parijs *et al.* (2000a) described two roar types at a single study site in Orkney,

Scotland. At this site, however, individual harbor seals have highly stereotyped vocalizations. This lack of intra-individual variation suggests that each individual harbor seal uses only one roar type. Similarly, Björgesæter *et al.* (2004) found two distinct call types within two sites in Norway, but could not confirm whether this finding reflected differences within or among individuals at each site. Vocal plasticity within individuals (i.e., the use of more than one distinct call type per individual) has not been explicitly described for any population of harbor seals other than in Moss Cove, CA (Hanggi and Schusterman, 1994). This is also the only population for which calls have been formally described that are not roars.

The Pacific harbor seal subspecies *P. v. richardii* ranges from California to Alaska, including the coasts of Oregon and Washington, and British Columbia, Canada (Stanley *et al.*, 1996). The work by Hanggi and Schusterman (1994) suggests the potential for vocal variation within this subspecies; however, harbor seal vocal breeding behavior has not been formally described for any populations north of California (Hanggi and Schusterman, 1994; Nicholson, 2000; Hayes *et al.*, 2004b). To obtain a more representative dataset from this subspecies, the vocalizations of other populations in its range should be described. The inland waters of Washington State and southern British Columbia, collectively called the Salish Sea, support a high density of harbor seals (Olesiuk, 2010). This sea is therefore an advantageous location to begin characterizing the roars of the Pacific Northwest populations of harbor seals.

Vocalizations of harbor seals were recorded at a haul-out site in the northernmost waterway of the Salish Sea: Georgia Strait, British Columbia. From this single haul-out, a wide variability was detected in the acoustic parameters of roars, as well as three distinctive calls which do not fit the typical definition of a roar. This study describes the within-site vocal variability exhibited in this population of harbor seals, and we propose that this population exhibits a wide vocal range including a repertoire of four call types.

II. METHODS

A. Data collection

Acoustic observations were conducted during the summer of 2014 at a haul-out site on Heron Rocks, which is located near the southwestern tip of Hornby Island, BC. Hornby Island lies about 10 km off the east coast of Vancouver Island, near the northern end of Georgia Strait. An Autonomous Multichannel Acoustic Recorder (AMAR; JASCO Applied Sciences, JASCO Applied Sciences, Halifax, NS, Canada) system, fitted with a single omnidirectional hydrophone (M8E from GeoSpectrum Technologies Inc.; nominal sensitivity -165 dB re: 1 V/ μ Pa; flat frequency response ± 0.3 dB from 10 to 24 000 Hz), was deployed on a weighted mooring at approximately 6.4 m depth (low tide) in a location central to the haul out ($49^{\circ}29.307'N$, $124^{\circ}39.313'W$; Fig. 1). The AMAR was deployed on June 15th and recorded continuously in the bandwidth of 10 Hz to 24 kHz (24-bit sampling resolution; 48 000 Hz sampling frequency) until it was retrieved by a diver on September 10th.

B. Data processing and analysis

Twenty days were randomly selected from the breeding season for analysis, and only files containing seal calls were examined for call variability. Acoustic recordings were viewed spectrographically and calls were annotated using the MATLAB-based program Osprey (Mellinger, 1994) with a 2048 point fast Fourier transform (FFT), Hann window, and 50% overlap. Each call was measured using the Noise Resistant Feature Set (NRFS) in Osprey (Mellinger and Bradbury, 2007), which includes parameters that produce the same results in varying levels of ambient noise. This feature set was designed for calls such as seal roars, which tend to fade at high frequencies and overlap with natural background noise, making it difficult to use traditional spectrographic measurements to define them (Mellinger and Bradbury, 2007). The NRFS reduces a manual annotation box into a “feature box.” The feature box is defined as the frequency and time vectors within the annotation box where 90% of the energy in the annotation box is located, thus defining the call relative to ambient noise. Measurements are then taken from this feature box, making them robust to varying noise levels (Mellinger and Bradbury, 2007). The NRFS took a total of 27 measurements for each call, including the mean signal-to-noise ratio (MSNR). For analysis, only seal roars that had a definitive start and end time, judged visually and audibly in Osprey, were measured. All roars with null values for any of the 27 NRFS measurements were excluded, and only roars with a MSNR >30 dB were used for analysis. A threshold of 30 dB was judged visually and audibly to be that at which all calls were clearly defined and that all measurements would therefore be most accurate, regardless of noise level.

Of the calls that had all measurements and an acceptable MSNR, a subset of 500 was randomly selected. Because the

recordings had no directionality, calls could not be localized or attributed to an individual seal. We attempted to avoid individual bias by verifying that this sample contained a representative numbers of calls from each day of the breeding season, as well as a representative distribution of call durations and bandwidths. This subset of calls was analyzed both aurally and visually and placed into subjective classes. Roars were considered to be any call over 5 s in duration that had a low-frequency component and a broadband “pulse” component, as defined by Van Parijs *et al.* (2000a). Calls that were <5 s or did not contain both low-frequency and broadband components were considered non-roar call types, and were subjectively placed into hierarchical call type groups.

Quantitative classification was conducted using linear discriminant analysis (LDA; Klecka, 1980) and classification tree (recursive partitioning) analysis (Breiman *et al.*, 1984). Because our data contained a large number of measurements, we wished to use a multivariate technique that would prioritize the most important variables for grouping samples, without losing any information by grouping the variables into single components, as in principal components analysis (Dunlop *et al.*, 2007). Discriminant function analyses such as LDA have been used to successfully classify harbor seal vocalizations (Van Parijs *et al.*, 2000a; Van Parijs *et al.*, 2003), and are useful for determining whether groups can be reliably separated. To determine the ways in which the groups separated, and which variables were most important in determining each call type, we used classification tree (recursive partitioning) analysis. Classification tree analysis has been suggested as a superior method for classifying marine mammal calls from a single recorder because it does not require the data to conform to parametric assumptions: namely, homoscedasticity of groups, normality of data, and independence of samples, the latter of which is important in

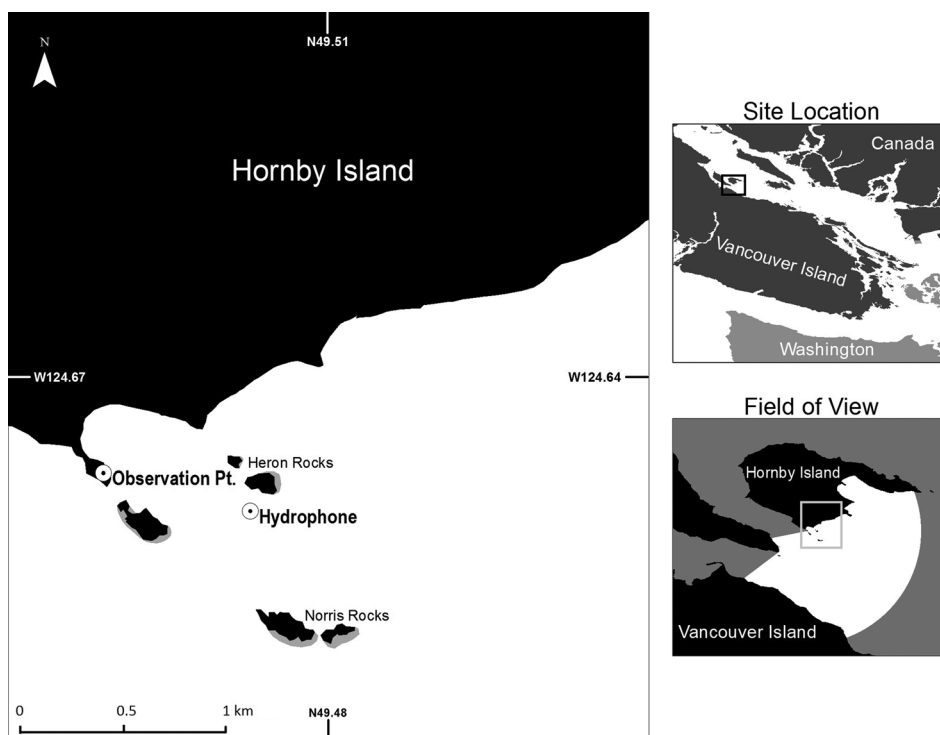


FIG. 1. Map showing the Salish Sea and indicating the region of study (top right), the field of view visible from the observation site (bottom right), and a close-up view of the study site at Heron Rocks (left), including the location of the hydrophone, observation point, and haul-out area. Created in ArcGIS using the North American 1983 datum and GCS NA1983 coordinate system. Units are in decimal degrees. Map created by Erin Harker (Western Washington University); used with permission.

TABLE I. Descriptions and shorthand codes of key features from the NRFS in Osprey used in linear discriminants analysis to classify harbor seal mating calls at Hornby Island, Canada.

Measurement	Notation	Description
Duration (s)	Duration	The length of the feature box
Temporal interquartile range (s)	Time quartile	The amount of time where a cumulative 25%–75% of the energy in the call is represented
Temporal concentration	Time concent.	The number of time blocks (21.3 ms each) that contain a cumulative 50% of the energy in the call
Amplitude modulation rate	AM rate	The dominant rate of amplitude modulation in the call
Overall entropy	Entropy	Average measure of how evenly the energy is spread among frequency blocks in every time block
Upsweep mean (Hz)	Upsweep	Average change in median frequency between successive time blocks in the trimmed spectrogram

situations where pseudo-replication is a possibility due to the inability to localize calls to an individual (Breiman *et al.*, 1984; Rekdahl *et al.*, 2013; Garland *et al.*, 2015). The LDA was run using the MASS library in R, and the classification tree analysis was run using the Rpart library in R (version 3.1.3; R Foundation for Statistical Computing, 2012).

For LDA, redundant variables (defined as having a correlation value greater than $|0.85|$ using a Spearman’s correlation matrix) were identified and excluded from further analysis. Graphical analysis was used to determine whether each of the remaining variables contributed to separation of the candidate call types. Those variables that showed differences among call types were considered “key variables” (Table I), and were used in the LDA. Five of the six key variables were log-transformed to better conform to the assumptions of the model. Because some upsweep mean values were less than zero, these data were log transformed by their absolute value (Table I). To avoid overfitting, we trained the LDA model with a subset of the data, then used the resulting model to predict classifications of the remaining dataset. First, LDA was used to classify call types by randomly selecting 100 calls to build the model, then predicting classifications for the remaining 400 calls based on this model. Roars were then excluded from the dataset and a subset of 50 of the remaining calls was used to train a model classifying non-roar call subtypes. The agreement between aural-visual and LDA classification systems was then tested using chi-squared association analysis and by comparing error rates. The LDA models were each trained ten times with different random samples of calls; if the results were consistent across models, we interpreted this as an indication that the classification was non-random.

For the classification tree analysis, all of the NRFS variables were used. Because this method is robust to departures from parametric assumptions, none of the variables were transformed. Trees were split into nodes using the Gini index as the measure of impurity or “goodness of split” (Breiman *et al.*, 1984). Trees were overgrown and V-fold cross-validation was performed by dividing the data into ten subsets; the trees were then pruned using the 1 SE rule (i.e., the best tree is the simplest one within 1 standard error of the smallest cross-validated error; Breiman *et al.*, 1984; Van Parijs *et al.*, 2003). As with LDA analysis, a classification tree was produced using all 500 calls and separating by call type, then roars were excluded and another tree was produced classifying the remaining calls to subtype. Misclassification rates were examined to determine agreement with qualitative classification.

III. RESULTS

A. Qualitative classification

A total of 1764 seal calls were determined to be of sufficient quality for classification. Of these calls, 500 were randomly selected for analysis. Roars formed the majority of the calls analyzed (383/500 calls). There was a large amount of variability in temporal components of roars, but less variation in the frequency components (see Fig. 2 and Table II for examples). However, there was no evidence that roars could be subdivided into types. Rather, roar characteristics fell along a broad continuum with notable variation in total call duration, temporal interquartile range, and maximum frequency. A typical roar is shown in Fig. 3(a).

Three non-roar call types were distinguishable both visually and audibly from the roar. We have termed these non-roar call types the growl, the short call, and the sweep (Fig. 3). A growl was characterized as any call that lacks a component >1000 Hz, and comprised only 27 of the 500 calls analyzed (Table II). Growls were characterized by their narrow bandwidth and low frequency, but were variable in duration, with the median duration around 7 s. Growls were further subdivided: growls ≤ 7 s in duration were classified as short growls [Fig. 3(b)], and growls >7 s were termed long growls. The short call was defined as a call with a duration <5 s and an upper frequency >1000 Hz. This call type

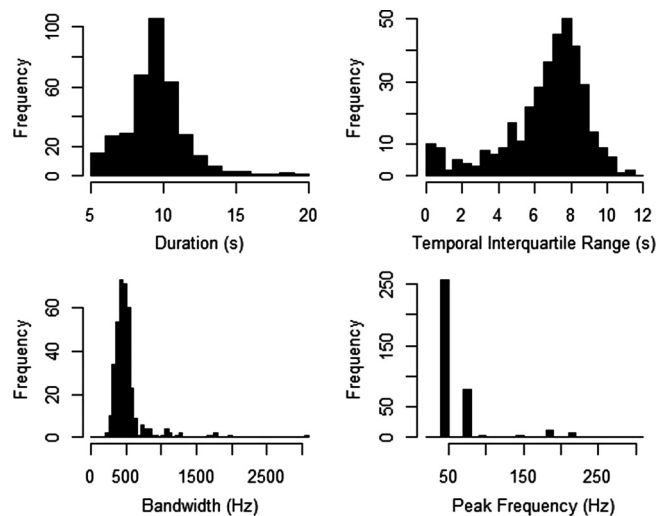


FIG. 2. Histograms of four acoustic variables for calls that were designated roars by qualitative analysis. $N = 383$ calls. There was a large amount of variability in duration and temporal interquartile range, and less variability in peak frequency and bandwidth.

TABLE II. Counts and summary statistics for the four call types characterized for harbor seals at Hornby Island, Canada. $N=500$ calls. For measurements taken using the NRFS in Osprey, means are presented with standard deviation in parentheses. Key features are denoted with an asterisk (*). See Table I for full names of measurements and descriptions.

Call Type	Roar	Growl	Short call	Sweep
# Sampled	383	27	78	12
% of N	76.6	14.5	12.0	10.3
Duration (s)*	9.3 (2.3)	8.2 (3.2)	3.3 (0.9)	2.5 (0.2)
Low freq. (Hz)	41.4 (13.8)	41.2 (10.5)	38.2 (9.3)	43.0 (15.3)
Bandwidth (Hz)	510 (255)	398 (164)	420 (102)	279 (87)
Time quartile (s)*	6.4 (2.5)	4.5 (2.9)	1.3 (1.0)	0.4 (0.2)
Time concent.*	6.9 (3.4)	3.7 (4.0)	1.0 (1.3)	0.2 (0.3)
AM rate*	0.2 (0.3)	0.3 (0.5)	0.9 (0.6)	2.4 (1.6)
Entropy*	68.3 (15.8)	56.0 (10.7)	57.5 (12.5)	38.8 (5.9)
Upsweep (Hz)*	-4.7 (28.4)	-5.5 (11.8)	-14.1 (16.4)	-18.8 (9.3)

was more common than the growl, with 78 examples in 500 calls (Table II). Short calls were subdivided into two subtypes: the step and the abrupt call. Steps were calls that contained a low-frequency component as well as a pulse over 1000 Hz; much like a roar but with a duration <5 s. Abrupt calls were >1000 Hz, contained no low-frequency component, and appeared to be the pulse section of a normal roar with the low-frequency component absent [Fig. 3(c)]. The

sweep call type was characterized as a call lasting 2–3 s and consisting of a broadband knock followed by a noisy upsweep with an upper frequency that extends up to 6 kHz [Fig. 3(d)]. Sweep calls were the rarest call type, comprising only 12 of the 500 calls classified (Table II).

B. Linear discriminants analysis classification

To verify call type classification (roar, growl, short call, or sweep) quantitatively, all calls that were classified using aural-visual analysis were assessed using LDA. After 10 independent trials using different training sets, LDA classification agreed with aural-visual classification for 83%–90% of calls [mean \pm standard deviation (SD) = $87.9 \pm 2.0\%$]. The percentage of variation explained in the first linear discriminant was $91.8 \pm 3.4\%$, indicating that the model was trained sufficiently to interpret the untrained data. The majority of roars were classified correctly; however, some were often misclassified as short calls or growls. Growls were often misclassified as roars or short calls, and short calls were often classified correctly, although some were often misclassified as other call types. Sweeps were the most unique call type, and as a result were rarely misclassified; when they were misclassified, they were grouped as short calls (Table III). High weightings were given to amplitude modulation rate, duration, and temporal interquartile range in the first two linear discriminants. These

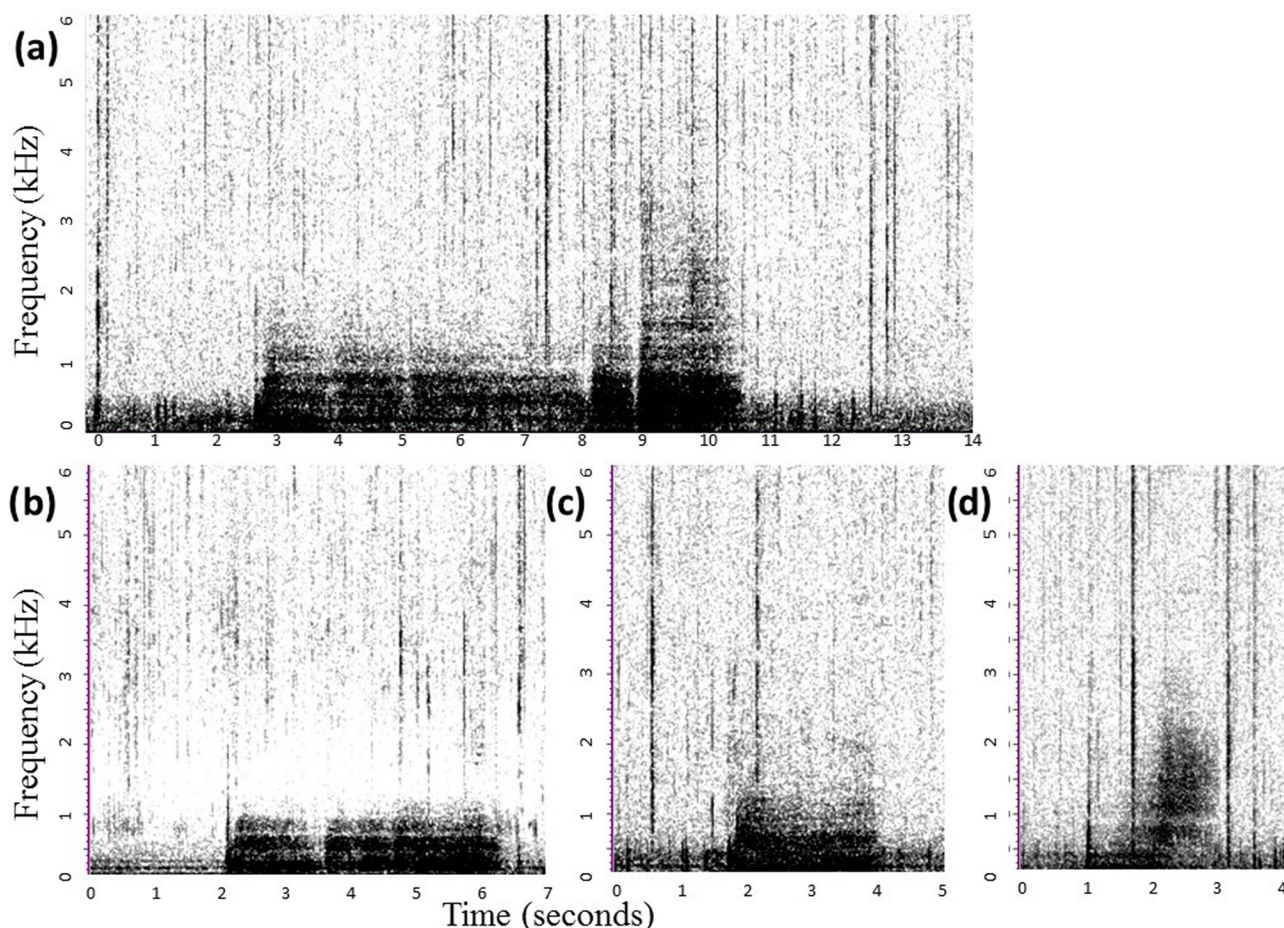


FIG. 3. (Color online) Spectrograms of the three non-roar call types (containing five subtypes) of harbor seal breeding call characterized at Hornby Island, Canada. Spectrograms generated by Raven Pro 1.5 (Cornell Lab of Ornithology) with smoothed 2456 point FFT, Hann window, and 50% overlap: (a) Roar; (b) Growl (Short); (c) Short Call (Abrupt subtype); (d) Sweep. Axes are scaled the same in each spectrogram.

TABLE III. Example association analysis table from the ten LDA models used to classify harbor seal call types at Hornby Island, Canada. High agreement between subjective and LDA classification is indicated in bold. Models were trained with a random subset of 100 calls, which was then used to predict classification of the remaining 400 calls. Classifications for call types are: Growl = G, Roar = R, Sweep = S, and Short call = SC.

Subjective	LDA classification			
	G	R	S	SC
G	4	13	0	6
R	8	283	0	12
S	0	0	10	0
SC	0	5	3	56

$X^2 = 579.7, p < 0.0001$
 Agreement between AV and LDA: 88.3%
 Variance explained by first LD: 94.3%

variables most often showed good separation of means among different call types; however, growls had a similar duration and amplitude modulation rate to roars.

Before a trained LDA model was used to classify non-roar calls into subtypes, four of the six key variables (namely, Duration, Time Quart, Time Concent, and AM Rate) were log-transformed to meet the assumptions of the model. Average agreement with aural-visual classification after 10 independent trials was lower than for call types ($73.6 \pm 4.5\%$), and much more variable. The percentage of variation explained by the first linear discriminant was $90.3 \pm 3.5\%$. Long growl, sweep, and step subtypes were most often classified correctly. When steps were misclassified, they were most often misclassified as abrupt calls, and vice versa. Short growls were also often misclassified as steps. Thus, many of the subtypes shared a similarity in some features, but were variable in others, suggesting that these call subtypes formed a continuum, rather than discrete groups.

C. Classification tree analysis

The classification tree for call type, originally grown with seven nodes, was pruned using the 1 SE rule to three

nodes (two splits) by examining cross-validation results. The main factor determining splits was duration. The misclassification rate for this tree was 39/500 or 7.8%. Sweeps and short calls were classified correctly; however, just as with the LDA, growls and roars were unable to be separated and constituted one group, likely due to overlap in duration between these two call types (Fig. 4). Overall, the separation of call type groups was moderately successful. When used to classify subtypes, the original 5-node classification tree was once again pruned to three nodes, with all splits based on duration. Sweeps and long growls showed good separation, due to their distinctly short and long duration, respectively. Steps, abrupt calls, and short growls were all placed together (Fig. 4). The misclassification rate was 24/117, or 20.8%. As with the LDA, call subtypes did not all separate well, suggesting that they lie along a continuum.

IV. DISCUSSION

The goal of this study was to describe the breeding vocalizations of harbor seals in British Columbia, in order to compare their call characteristics and repertoire size with those of other populations of this species. We propose that the repertoire of this population is larger than many previously-studied sites: through spectrographic analysis, four candidate call types were suggested which were distinguished primarily by duration and maximum frequency. Quantitative classification showed that three call types (the roar, sweep, and short call) separated moderately well, while the fourth (growl) was not distinguishable from a roar. The main feature separating the proposed call types was call duration; thus, growls and roars were likely classified quantitatively as the same group because these proposed call types were similar in duration. Similarly, call subtypes did not separate well unless they were markedly different in duration from other subtypes. While measures of duration were variable within and across call types, many other measurements showed poor separation among call types. Therefore, we posit that the call types we identified represent variations on

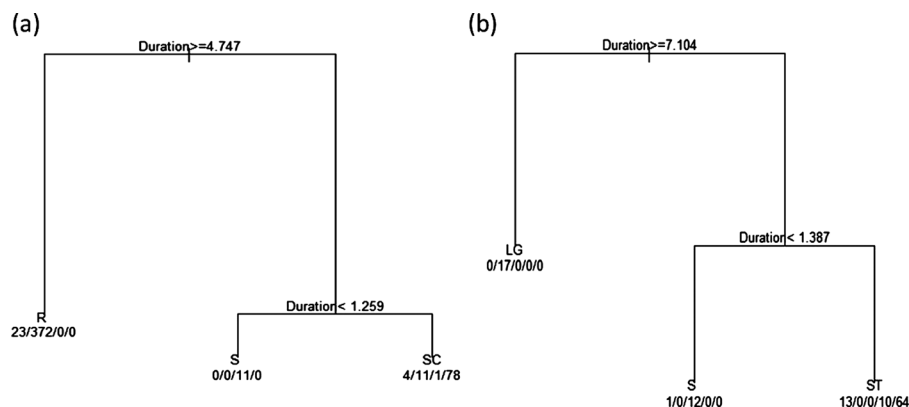


FIG. 4. Classification trees of harbor seal (a) call types and (b) call subtypes at Hornby Island, Canada. Variables consisted of 27 acoustic measurements taken by the NRSF in Osprey (Mellinger and Bradbury, 2007). Nodes were split using the Gini index, and cross-validation was performed with ten subsets. No minimum bin size was specified. Trees were pruned according to the 1 SE Rule, as determined by cross-validated error values. The variable used at each split is given, as well as splitting criteria (numeric values). Earlier splits explain more variability in the data than do later splits (toward the bottom). The vertical depth of each split (relative to those on the same tree) is proportional to the amount of variability explained by that split. Call types are labeled as in Table III, and subtypes are assigned as follows: A = Abrupt call, ST = Step, LG = Long Growl, SG = Short Growl, and S = Sweep. The number of calls assigned to each node is given as (a) G/R/S/SC and (b) A/LG/S/SG/ST.

the roar—produced by animals of different size/age classes—forming a vocal continuum in this breeding haul-out.

The roar has been associated with breeding harbor seals throughout their global range (Van Parijs *et al.*, 2003). Because this call is stereotyped within an individual and varies between individuals, it is considered to be the primary means by which males display dominance to other males and likely to females (Van Parijs *et al.*, 1997, 2000a; Nicholson, 2000; Hayes *et al.*, 2004a, 2004b). Seals at Hornby Island showed a high degree of variation in time parameters of calls, including total duration and temporal interquartile range, but did not differ widely in frequency components such as bandwidth, minimum frequency, and peak frequency. The duration of the broadband section of the roar differs among individuals (Van Parijs *et al.*, 2000a): it is longer in more dominant individuals, as reflected by body size and behavior (Nicholson, 2000; Hayes *et al.*, 2004b). Nicholson (2000) found that the roars of dominant males have a lower minimum frequency, and this was confirmed with playback experiments (Hayes *et al.*, 2004b). However, all call types at Hornby Island had comparatively similar frequency measurements; our results are more similar to those found in Moray Firth, Scotland, where individual seals have significantly different roar durations, but do not differ significantly in frequency measurements (Van Parijs *et al.*, 2000a). Calls that differ in certain variables but that have overlap in others are said to make up a vocal continuum, or a series of graded calls, as is proposed for harp seal (*Pagophilus groenlandicus*; Serrano and Terhune, 2002) and beluga (*Delphinapterus leucas*; Garland *et al.*, 2015) calls.

The variation in call duration but not frequency suggests that observed differences in call duration at Hornby Island were due to individual differences in roar production reflecting the age and size of the individual, rather than the existence of discrete call types. Captive juvenile males in New England were recorded producing vocalizations much like our abrupt calls and short growls (Ralls *et al.*, 1985). Harbor seals mimic other animals, giving evidence of vocal learning (Ralls *et al.*, 1985; Janik and Slater, 1997). Perhaps the shorter calls we detected were the calls of juvenile males mimicking adults. Therefore, short calls and roars may only be differentiated by the age and size of the caller. Of the four call types proposed in this study, the sweep was the most distinct with regard to quantitative analysis, and the most unlike any call that has been previously described for harbor seals. Further study at this site and nearby populations with the ability to localize calls will allow us to learn more about the context of these shortest calls in the vocal continuum.

In addition to individual differences, harbor seals display population-specific dialects in roar structure (Van Parijs *et al.*, 2000a, 2003). Therefore, it is important to compare the calls described at Hornby Island to calls heard elsewhere. For instance, roars heard at Hornby Island were on average several seconds longer than those heard in Moray Firth (average \pm SE = 4.8 ± 0.4 s), but shorter than those heard in Orkney, Scotland (14.6 ± 0.4 s; Van Parijs *et al.*, 2000a) and the southern Norwegian Sea (ranging from 8 to 12 s; Bjørgesæter *et al.*, 2004). The bandwidth of roars at Hornby Island was slightly narrower than those heard at Moray Firth (average minimum frequency 1.06 kHz lower than average

maximum frequency), Orkney (average minimum frequencies 2.38 and 1.93 kHz lower than average maximum frequencies; Van Parijs *et al.*, 2000a), and the southern Norwegian Sea (~ 1.5 kHz; Bjørgesæter *et al.*, 2004), although our average may have been biased by propagation loss at higher frequencies and was quite variable (Table II). Roars measured at two sites in Eastern Canada were similar in duration to those heard at Hornby Island (7.5 ± 3.2 s), with a slightly higher minimum frequency (average 0.4 kHz; Van Parijs and Kovacs, 2002). Roars in Moss Cove, California, were described as being much shorter than those at Hornby Island (average 4.9 s), with a higher average bandwidth (average maximum frequency 810 Hz; Hanggi and Schusterman, 1994). This description is more similar to our short call type. These comparisons suggest that harbor seals at Hornby Island produce breeding calls over a wider range of durations than observed in some other populations.

The vocal repertoire of harbor seals is difficult to define, as calls seem to lie along a continuum. While harbor seals produce a variety of calls in air (Van Parijs and Kovacs, 2002), underwater calls have almost exclusively been called roars, despite variability within this call type. Four non-roar calls were described for harbor seals at Moss Cove (Hanggi and Schusterman, 1994) which have not been formally described for harbor seals since, although Nicholson (2000) noted that these call types were heard elsewhere in Monterey Bay. In Moss Cove, individual males made use of more than one call type in different combinations during the breeding season (Hanggi and Schusterman, 1994). Different roar types within a breeding site have been noted in other populations (Van Parijs *et al.*, 2000a; Bjørgesæter *et al.*, 2004); however, these roar types are likely produced by different individuals, and not used in combination by single animals. When comparing phocid mating systems to call repertoire, Stirling and Thomas (2003) proposed that harbor seals, as promiscuous breeders, were grouped with other species producing 5–19 vocalization types. Rogers (2003) considered harbor seals to have an underwater breeding repertoire of five call types, and placed them in a vocal category with harp, ringed, and Weddell seals, all of which exhibit extensive and varied vocal repertoires and which vocalize year-round (Rogers, 2003; Van Opzeeland *et al.*, 2008). Harp seal and Weddell seal (*Leptonychotes weddellii*) calls lie along a vocal continuum, with calls varying within call types, similar to what we found with harbor seals at Hornby Island (Serrano and Terhune, 2002; Doiron *et al.*, 2012). Although these previous studies predict a large vocal repertoire for harbor seals based on ecological similarity to other species, non-roar call types in adult harbor seals have still not been described in the literature for any population since 1994. The results of our attempt to define discrete call types at Hornby Island were inconclusive, suggesting that the idea of a defined vocal repertoire in harbor seals, and perhaps other phocid species which show wide variation within call types, may be overly simplistic. Instead, we propose that harbor seal calls are graded along a vocal continuum, and that the number of call types is subjective and varies between populations.

In this study, we employed two methods to quantitatively classify harbor seal calls. Discriminant function

analyses (including LDA) and classification tree analysis are common methods to classify marine mammal vocalizations, either to call type, individual, or region. Discriminant function analyses have been used to classify calls of cetaceans (e.g., Dunlop *et al.*, 2007; Antunes *et al.*, 2011; Fournet and Szabo, 2013) and pinnipeds (e.g., Charrier *et al.*, 2010; Sauvé *et al.*, 2015), including harbor seals (Van Parijs *et al.*, 2000a, 2003; Khan *et al.*, 2006). Classification tree analysis has become popular in marine mammal acoustic literature (e.g., Breiman *et al.*, 1984; Risch *et al.*, 2007; Rekdahl *et al.*, 2013; Garland *et al.*, 2015), due to its robustness to redundant variables, lack of independence of samples, and non-parametric sample sets, all of which are common in acoustic datasets. When performing LDA, we accounted as far as possible for these issues by transforming data, excluding redundant variables, and subsampling to reduce pseudo-replication. Classification tree analysis does not require as much pre-handling of data, which makes it more appealing and often more sensitive; however, it should be noted that classification trees produced very similar results to those that we found with LDA in this study. Garland *et al.* (2015) suggest that classification trees are a superior method to classify calls that fall on a vocal continuum, and this appears to be the case for call types in the current study. While both methods produced satisfactory results in this study, we would suggest classification tree analysis as a robust and explanatory method to use rather than LDA for future studies of harbor seal calls.

We were unable to confirm the individual identity of callers at Hornby Island, as the majority of vocalizations were heard during nighttime hours, so no visual observations were available. Therefore, we could not confirm the location of males when vocalizations took place, or gauge the size or age of callers. Additionally, it was impossible to localize any vocalizations due to the use of a single omnidirectional hydrophone. Because we could not identify the range or location of the caller, we were unable to determine how much of the observed vocal variation was due to propagation loss. Sound attenuates over distance due partially to absorption by water molecules, and in shallow water, surface and bottom effects are a major contributor to propagation loss (Richardson *et al.*, 1995). Higher-frequency sounds are lost at a greater rate than low-frequency sounds, which may account for part of the difference between roars, which contain sound over 1 kHz, and growls, which are similar in duration to roars but for which no signal over 1 kHz was detectable. When the caller is close to the surface ($<1/4$ dominant wavelength), a dipole effect is created which increases propagation loss (Richardson *et al.*, 1995). Seals calling at different depths may have accounted for some of the differences in the calls that we describe, but without the ability to localize calls in three dimensions, we could not control for these effects. Finally, peak frequency and amplitude of harbor seal roars is affected by the orientation of the seal relative to the recorder (i.e., facing toward or away from the hydrophone; Nicholson, 2000), which we were also unable to control for in this study. Further investigation using a hydrophone array equipped for localization purposes may help to determine whether observed variation in call structure results from individual variation, or from differences

in propagation loss due to animals calling at different ranges from the hydrophone.

V. CONCLUSIONS

We detected a wide variability in breeding vocalizations within a single harbor seal breeding site in the Salish Sea. This variation in call length was larger than that found in many other populations. Our four proposed call types differed widely in duration but little in frequency, which suggests that the variation we observed was the result of individual differences and not intra-individual vocal plasticity. Rather than distinct call types, we propose that the breeding calls of harbor seals in this area formed a vocal continuum of variations on the roar call, in which different roars differed primarily in duration. Further investigation with the ability to localize and identify calling individuals will help to show the extent to which the observed vocal variability is the product of differences among individuals, artifacts of propagation loss, or whether individual seals modify their vocalizations.

ACKNOWLEDGMENTS

The authors would like to thank JASCO Applied Sciences in Victoria, BC for providing the hydrophone and recording equipment used in this study, and Xavier Mouy in particular, for his assistance in the field and with analysis. We would like to extend a sincere and bottomless thanks to the members of the field teams (Erin Harker, Kailey Gabrian-Voorhees, Gunnar Guddal, Amy Lepis, Kayla Litterell, Elizabeth McMurchie, Alexi Osterhaus, and Zach Pike-Urlacher), and to those who assisted with acoustic analysis in the lab (Erin Harker, Madeleine Hopkins, Allegra La Ferr, Elizabeth McMurchie, and Alexi Osterhaus). Special thanks to Erin Harker, who did double time in the field as well as with data analysis, and who contributed the map of our study site. Thanks to the Heron Rocks Camping Cooperative for providing an observation site and field accommodations, and to Hornby Island Diving for providing a boat and diver for deployment and retrieval of the acoustic equipment and other logistical support. We would also like to acknowledge the Cascades Audubon Society of Bellingham, WA for contributing funds for the field component of this study. Thanks also to Dr. Robin Matthews and Dr. Roger Anderson at Western Washington University for their helpful comments and review of the manuscript. We would like to acknowledge Western Washington University for providing funding, space, and equipment to complete this work. Final thanks go to the two anonymous reviewers for their constructive comments on this manuscript.

- Abgrall, P., Terhune, J. M., and Burton, H. R. (2003). "Variation of Weddell seal (*Leptonychotes weddellii*) underwater vocalizations over mesogeographic ranges," *Aquat. Mamm.* **29**, 268–277.
- Anderson, S. S., and Fedak, M. A. (1985). "Grey seal males: Energetic and behavioural links between size and sexual success," *Anim. Behav.* **33**, 829–838.
- Antunes, R., Schulz, T., Gero, S., Whitehead, H., Gordon, J., and Rendell, L. (2011). "Individually distinctive acoustic features in sperm whale codas," *Anim. Behav.* **81**, 723–730.
- Björge, A., Uglund, K. I., and Björge, A. (2004). "Geographical variation and acoustic structure of the underwater vocalization of harbor seal

- (*Phoca vitulina*) in Norway, Sweden and Scotland," *J. Acoust. Soc. Am.* **116**, 2459–2468.
- Boness, D. J. (1991). "Determinants of mating systems in the Otariidae (Pinnipedia)," in *The Behaviour of Pinnipeds* (Springer, Netherlands), pp. 1–44.
- Boness, D. J., Bowen, W. D., Buhleier, B. M., and Marshall, G. J. (2006). "Mating tactics and mating system of an aquatic-mating pinniped: The harbor seal, *Phoca vitulina*," *Behav. Ecol. Sociobiol.* **61**, 119–130.
- Breiman, L., Friedman, J. H., Olshen, R. A., and Stone, C. G. (1984). *Classification and Regression Trees* (Chapman and Hall, London, United Kingdom), pp. 1–359.
- Burg, T. M., Trites, A. W., and Smith, M. J. (1999). "Mitochondrial and microsatellite DNA analyses of harbour seal population structure in the northeast Pacific Ocean," *Can. J. Zool.* **77**, 930–943.
- Cassini, M. H. (1999). "The evolution of reproductive systems in pinnipeds," *Behav. Ecol.* **10**, 612–616.
- Charrier, I., Aubin, T., and Mathevon, N. (2010). "Mother–calf vocal communication in Atlantic walrus: A first field experimental study," *Anim. Cognition* **13**, 471–482.
- Coltman, D. W., Bowen, W. D., Boness, D. J., and Iverson, S. J. (1997). "Balancing foraging and reproduction in the male harbour seal, an aquatically mating pinniped," *Anim. Behav.* **54**, 663–678.
- Doiron, E. E., Rouget, P. A., and Terhune, J. M. (2012). "Proportional underwater call type usage by Weddell seals (*Leptonychotes weddellii*) in breeding and nonbreeding situations," *Can. J. Zool.* **90**, 237–247.
- Dunlop, R. A., Noad, M. J., Cato, D. H., and Stokes, D. (2007). "The social vocalization repertoire of east Australian migrating humpback whales (*Megaptera novaeangliae*)," *J. Acoust. Soc. Am.* **122**, 2893–2905.
- Fournet, M., and Szabo, A. (2013). "Vocal repertoire of Southeast Alaskan humpback whales (*Megaptera novaeangliae*)," *J. Acoust. Soc. Am.* **134**, 3988–3988.
- Garland, E. C., Castellote, M., and Berchok, C. L. (2015). "Beluga whale (*Delphinapterus leucas*) vocalizations and call classification from the eastern Beaufort Sea population," *J. Acoust. Soc. Am.* **137**, 3054–3067.
- Hanggi, E. B., and Schusterman, R. J. (1994). "Underwater acoustic displays and individual variation in male harbour seals, *Phoca vitulina*," *Anim. Behav.* **48**, 1275–1283.
- Härkönen, T., and Harding, K. C. (2001). "Spatial structure of harbour seal populations and the implications thereof," *Can. J. Zool.* **79**, 2115–2127.
- Hayes, S. A., Costa, D. P., Harvey, J. T., and Le Boeuf, B. J. (2004a). "Aquatic mating strategies of the male Pacific harbor seal (*Phoca vitulina richardii*): Are males defending the hotspot?," *Mar. Mammal Sci.* **20**, 639–656.
- Hayes, S. A., Kumar, A., Costa, D. P., Mellinger, D. K., Harvey, J. T., Southall, B. L., and Le Boeuf, B. J. (2004b). "Evaluating the function of the male harbour seal, *Phoca vitulina*, roar through playback experiments," *Anim. Behav.* **67**, 1133–1139.
- Huber, H. R., Dickerson, B. R., Jeffries, S. J., and Lambourn, D. M. (2012). "Genetic analysis of Washington State harbor seals (*Phoca vitulina richardii*) using microsatellites," *Can. J. Zool.* **90**, 1361–1369.
- Janik, V. M., and Slater, P. J. (1997). "Vocal learning in mammals," *Adv. Study Behav.* **26**, 59–100.
- Khan, C. B., Markowitz, H., and McCowan, B. (2006). "Vocal development in captive harbor seal pups, *Phoca vitulina richardii*: Age, sex, and individual differences," *J. Acoust. Soc. Am.* **120**, 1684–1694.
- Klecka, W. R. (1980). *Discriminant Analysis* (Sage, London, United Kingdom), pp. 1–71.
- Le Boeuf, B. J. (1974). "Male-male competition and reproductive success in elephant seals," *Amer. Zool.* **14**, 163–176.
- Mellinger, D. K. (1994). "Osprey 1.8 Guide," Cornell Lab of Ornithology, Ithaca, New York, pp. 1–11.
- Mellinger, D. K., and Bradbury, J. (2007). "Acoustic measurements of marine mammal sounds in noisy environments," *Second International Conference on Underwater Acoustic Measurements: Technologies and Results*, Heraklion, Greece, pp. 25–29.
- Nicholson, T. E. (2000). "Social structure and underwater behavior of harbor seals in southern Monterey Bay, California," M.Sc. thesis, San Francisco State University, pp. 64–91.
- Olesiuk, P. F. (2010). "An assessment of population trends and abundance of harbour seals (*Phoca vitulina richardii*) in British Columbia," DFO Canadian Science Advisory Secretariat Research Document 2009/105, Nanaimo, B.C., pp. 1–10.
- R Foundation for Statistical Computing. (2012). "R: A Language and Environment for Statistical Computing," R Foundation for Statistical Computing, Vienna, Austria, pp. 1–409.
- Ralls, K., Fiorelli, P., and Gish, S. (1985). "Vocalizations and vocal mimicry in captive harbor seals, *Phoca vitulina*," *Can. J. Zool.* **63**, 1050–1056.
- Reichmuth, C., and Casey, C. (2014). "Vocal learning in seals, sea lions and walruses," *Curr. Opin. Neurobiol.* **28**, 66–71.
- Rekdahl, M. L., Dunlop, R. A., Noad, M. J., and Goldizen, A. W. (2013). "Temporal stability and change in the social call repertoire of migrating humpback whales," *J. Acoust. Soc. Am.* **133**, 1785–1795.
- Richardson, W. J., Greene, C. R. J., Malme, C. I., and Thompson, D. H. (1995). *Marine Mammals and Noise* (Academic Press, New York, NY), pp. 159–204.
- Risch, D., Clark, C. W., Corkeron, P. J., Elepfandt, A., Kovacs, K. M., Lydersen, C., Stirling, I., and Van Parijs, S. M. (2007). "Vocalizations of male bearded seals, *Erignathus barbatus*: Classification and geographical variation," *Anim. Behav.* **73**, 747–762.
- Rogers, T. L. (2003). "Factors influencing the acoustic behaviour of male phocid seals," *Aquat. Mamm.* **29**, 247–260.
- Sauvé, C. C., Beauflet, G., Hammill, M. O., and Charrier, I. (2015). "Acoustic analysis of airborne, underwater, and amphibious mother attraction calls by wild harbor seal pups (*Phoca vitulina*)," *J. Mamm.* **96**, 591–602.
- Serrano, A., and Terhune, J. M. (2002). "Stability of the underwater vocal repertoire of harp seals (*Pagophilus groenlandicus*)," *Aquat. Mamm.* **28**, 93–101.
- Stanley, H. F., Casey, S., Carnahan, J. M., Goodman, S., Harwood, J., and Wayne, R. K. (1996). "Worldwide patterns of mitochondrial DNA differentiation in the harbor seal (*Phoca vitulina*)," *Molec. Biol. Evol.* **13**, 368–382.
- Stirling, I., and Thomas, J. A. (2003). "Relationships between underwater vocalizations and mating systems in phocid seals," *Aquat. Mamm.* **29**, 227–246.
- Sullivan, R. M. (1981). "Aquatic displays and interactions in harbor seals, *Phoca vitulina*, with comments on mating systems," *J. Mammal.* **62**, 825–831.
- Thomas, J. A., and Golladay, C. L. (1995). "Geographic variation in leopard seal (*Hydrurga leptonyx*) underwater vocalizations," in *Sensory Systems of Aquatic Mammals* (Woerden, De Spil), pp. 201–221.
- Thomas, J. A., and Stirling, I. (1983). "Geographic variation in the underwater vocalizations of Weddell seals (*Leptonychotes weddellii*) from Palmer Peninsula and McMurdo Sound, Antarctica," *Can. J. Zool.* **61**, 2203–2212.
- Van Opzeeland, I., Kindermann, L., Boebel, O., and Van Parijs, S. M. (2008). "Insights into the acoustic behaviour of polar pinnipeds: Current knowledge and emerging techniques of study," in *Animal Behaviour: New Research*, edited by E. A. Weber and L. H. Krause (Nova Science Publishers, Hauppauge, New York), pp. 133–161.
- Van Opzeeland, I., Van Parijs, S. M., Bornemann, H., Frickenhaus, S., Kindermann, L., Klinck, H., Plötz, J., and Boebel, O. (2010). "Acoustic ecology of Antarctic pinnipeds," *Mar. Ecol. Prog. Ser.* **414**, 267–291.
- Van Parijs, S. M. (2003). "Aquatic mating in pinnipeds: A review," *Aquat. Mamm.* **29**, 214–226.
- Van Parijs, S. M., Corkeron, P. J., Harvey, J., Hayes, S. A., Mellinger, D. K., Rouget, P. A., Thompson, P. M., Wahlberg, M., and Kovacs, K. M. (2003). "Patterns in the vocalizations of male harbor seals," *J. Acoust. Soc. Am.* **113**, 3403–3410.
- Van Parijs, S. M., Hastie, G. D., and Thompson, P. M. (1999). "Geographical variation in temporal and spatial vocalization patterns of male harbour seals in the mating season," *Anim. Behav.* **58**, 1231–1239.
- Van Parijs, S. M., Hastie, G. D., and Thompson, P. M. (2000a). "Individual and geographic variation in display behaviour of male harbour seals in Scotland," *Anim. Behav.* **59**, 559–568.
- Van Parijs, S. M., Janik, V. M., and Thompson, P. M. (2000b). "Display-area size, tenure strength, and site fidelity in the aquatically mating male harbour seal, *Phoca vitulina*," *Can. J. Zool.* **78**, 2209–2217.
- Van Parijs, S. M., and Kovacs, K. M. (2002). "In-air and underwater vocalizations of eastern Canadian harbour seals, *Phoca vitulina*," *Can. J. Zool.* **80**, 1173–1179.
- Van Parijs, S. M., Thompson, P. M., Tollit, D. J., and Mackay, A. (1997). "Distribution and activity of male harbour seals during the mating season," *Anim. Behav.* **54**, 35–43.