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In-air and underwater sounds of hooded seals during the breeding season in the Gulf of St. Lawrence

Héloïse C. Frouin-Mouy[1,a)] and Mike O. Hammill[2]
[1]JASCO Applied Sciences, 2305-4464 Markham Street, Victoria, British Columbia V8Z 7X8, Canada
[2]Maurice Lamontagne Institute, Fisheries and Oceans Canada, 850 Route de la Mer, Mont-Joli, Québec G5H 3Z4, Canada

ABSTRACT:
The hooded seal is a migratory species inhabiting the North Atlantic. Passive acoustic monitoring (PAM) conducted over spatial scales consistent with their known and potential habitat could provide insight into seasonal and spatial occurrence patterns of this species. Hooded seal airborne and underwater acoustic signals were recorded during the breeding season on the pack ice in the Gulf of St. Lawrence in March 2018 to better characterize their acoustic repertoire (notably underwater calls). In-air and underwater signals were classified into 12 and 22 types, respectively. Signals produced by males through the inflation and deflation of the proboscis and septum were the predominant sounds heard on the ice surface. Five of the 22 underwater signals were proboscis and septum noises. The remaining underwater signals (17) were categorized as voiced calls and further analyzed using two classification methods. Agreement with the initial subjective classification of voiced calls was high (77% for classification tree analysis and 88% for random forest analysis), showing that 12–13 call types separated well. The hooded seal's underwater acoustic repertoire is larger and more diverse than has been previously described. This study provides important baseline information necessary to monitor hooded seals using PAM.
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I. INTRODUCTION

The hooded seal (*Cystophora cristata*) is an abundant, pelagic, deep-diving pinniped distributed throughout the North Atlantic and adjacent Arctic marine areas (Sergeant, 1974). Hooded seals spend most of the year dispersed and offshore, presumably foraging regularly outside the breeding and molting periods (Sergeant, 1974; Folkow and Blix, 1995; Folkow and Blix, 1999; Andersen *et al.*, 2009). They breed synchronously during mid- to late March on the pack ice around Jan Mayen, in Davis Strait, in the Gulf of St. Lawrence (the Gulf), and off the northern coast of Newfoundland (the Front) (Sergeant, 1974; Hammill, 1993; Folkow *et al.*, 1996; Bajzak *et al.*, 2009). These four breeding herds belong to two management stocks (Northwest Atlantic and Northeast Atlantic), which are not distinguished morphologically (Wiig and Lie, 1984) or genetically (Sundt *et al.*, 1994; Coltman *et al.*, 2007). Northwest Atlantic hooded seals breed in Davis Strait, the Gulf, and the Front and then migrate to southeastern Greenland by late June or early July to molt (Hammill, 1993). Hooded seals in the Northeast Atlantic population whelping near Jan Mayen disperse broadly after breeding but return to the pack ice east of Greenland in July to molt (Folkow *et al.*, 1996; Vacquie-Garcia *et al.*, 2017).

Habitats of hooded seals are difficult to survey during certain times of the year as they are inaccessible due to heavy pack ice, remoteness of those areas, and the requirement of expensive icebreaker ships and/or helicopters. Until now, information on hooded seal distributions has been provided by shore-based observations, capture of tagged individuals, vessel surveys, aerial surveys, and satellite telemetry methods (Sergeant, 1974; Hammill, 1993; Øritsland and Øien, 1995; Andersen *et al.*, 2009). Significant gaps still exist in our knowledge about this species, some of which might be addressed using long-term passive acoustic monitoring (PAM). PAM has become a common method for investigating acoustic behavior as well as for measuring temporal and spatial distributions of marine mammals over large and remote areas (e.g., Mellinger *et al.*, 2007; Van Parijs *et al.*, 2009). While acoustic monitoring is less suited than tagging studies for tracking individuals, it can sample larger fractions of populations to obtain temporal distributions of habitat use at selected locations. PAM could serve in this regard as a reliable and cost-effective method to study the year-round distribution of hooded seals.

There are few data on hooded seal underwater calls because of the limited access by researchers to the constantly changing pack-ice habitat and difficulty with accessing the species during the mating period. To date, only two scientific papers describe the acoustic repertoire of this species, with a special emphasis on the airborne acoustic repertoire. Terhune and Ronald (1973) describe few airborne and

[a)]Also at: Department of Biology, University of Victoria, 3800 Finnerty Road, Victoria, British Columbia V8P 5C2, Canada. Electronic mail: heloise.frouin@gmail.com, ORCID: 0000-0003-2693-1105.

underwater sounds recorded in the Magdalen Islands, Québec, Canada. Their analysis is based on acoustic data recorded in March of 1968 and 1971 with a total recording duration of 2 h. Their recordings included three underwater short calls ("grung," "snort," and "buzz") produced by adult males. The grung had highest intensity in the 0.2–0.4 kHz range. The snort was a broadband call containing energy from 0.1 to 1 kHz and occasionally harmonics up to 3 kHz. The buzz had most of its energy at 1.2 kHz with side bands and harmonics reaching 6 kHz. The male adult sounds in air were produced by the filling and deflating of the proboscis. Terhune and Ronald (1973) also recorded a call produced in air by a female while in a "defensive" posture and a call produced by a pup. Ballard and Kovacs (1995) describe the in-air and underwater acoustic repertoire of hooded seals in the Gulf of St. Lawrence, Canada. Data were recorded from 18 to 21 March 1988 and from 15 to 21 March 1989, with a total recording duration of 36 h in air and 9 h underwater. The acoustic repertoire was composed of three major classes of sounds. The class A calls contained in-air and underwater short-duration voiced calls with a continuous repetition rate. Call type A1 included two categories of signals, A1i ("airy exhalation") and A1ii. The A1ii category was subdivided into two subcategories, A1iia ("brief guttural growl") and A1iib ("moaning growl"). Call type A2 included two categories of signals, A2i ("long-duration growl") and A2ii ("roars"). Class B calls contained in-air voiced signals and included two categories of signals, B1 ("frequency-modulated growls") and B2 ("alternating moaning and growling vocalizations"). Class C sounds contained in-air and underwater signals created through the use of the hood (proboscis) and septum as well as several other voiced sounds recorded underwater. The acoustic repertoire described in Ballard and Kovacs (1995) included five call types, seven categories, and eight subcategories (for a total of 20 signals described in the paper).

In the present study, we used passive acoustics to record and describe the hooded seal acoustic repertoire in the Gulf of St. Lawrence during the breeding season, with a special focus on underwater sounds. Our detailed description of underwater acoustic repertoire provides an essential step toward using PAM for monitoring hooded seals in the Northwest Atlantic.

II. METHODS

A. Data collection

The southern Gulf of St. Lawrence was chosen as the study site because of relative ease of access (it requires a helicopter, but the hooded seal herds are rarely more than 60–70 km from land). In this area, the hooded seals normally select the drifting pack ice with larger pans, roughly 100 m across and approximately 50 cm thick. However, with the movement of the ice, pans will break, and with ridging, the pans may be over a meter in thickness (Hammill *et al.*, 1992; M.O.H., personal observation). Females with pups are on average 50 m apart, but the distances can vary from approximately 10 m to as much as 100 m or more between them, depending on whether the ice is smooth or ridged (Kovacs, 1990). Lactation lasts for 4 days, during which the pups double in size (Kovacs and Lavigne, 1992).

The trios (or "triads") composed of an adult hooded seal female, her pup, and an attending male make up the social structure of the hooded seal herd during the breeding season. Male hooded seals do not attend a female with a newborn; they only show up at the end of the second day, i.e., about a day before weaning (M.O.H., personal observation). Male hooded seals are polygynous to some degree during the breeding season, in the form of serial monogamy (Kovacs, 1990). A male may defend access to the female while she is nursing, and then at weaning, the male follows the female to the water for mating and then returns to the ice to defend access to a different female during the short lactation period (McRae and Kovacs, 1994; Kovacs *et al.*, 1996). Hooded seals are large (adults 200–400 kg; Kovacs and Lavigne, 1992; Kovacs *et al.*, 1996) and can be aggressive. Animals normally do not flee and therefore must be approached with caution.

Hooded seal signals included in this study were recorded during their breeding season on the pack ice in the Gulf of St. Lawrence from 12 to 17 March 2018. Four different recording locations were used, each on a different day. Data collection was carried out in conjunction with hooded seal monitoring conducted by the Department of Fisheries and Oceans Canada. A helicopter was used for transport to the ice. The actual site was selected if at least two triads were within 50 m of each other and another 2–4 triads were within 200 m. Where these conditions were observed, the helicopter landed, and a hole was drilled to ensure a minimum ice thickness of 50 cm for observer safety. Harp seals (*Pagophilus groenlandicus*) also breed in the Gulf during early March but have finished pupping activities by 12 March and in 2018 were located near the Magdalen Islands, more than 80 km away.

The breeding aggregations were situated off the coast of Prince Edward Island starting at 47°01′ N, 63°45′ W and finishing at 46°59′ N, 63°23′ W after 5 days. See SuppPub1.pdf for a map illustrating the four recording locations used in this study (Fig. S1).[1]

Eighteen hours of recordings were made, including 7 h of sampling in air and 11 h of sampling underwater (see SuppPub1.pdf for a photograph of the in-air and underwater recording setup; Fig. S2).[1] During recording in air, the distance from the microphone to the vocalizing animal was approximately 5–10 m. Sounds were recorded continuously with a sampling rate of 96 kHz to produce an acoustic bandwidth of 10 Hz to 48 kHz by using a Dayton Audio EMM-6 microphone (Dayton Audio, Springboro, OH) connected to a Sound Devices 722 digital recorder (Sound Devices LCC, Reedsburg, WI). One group of seals at each of the four recording locations was visited for in-air recordings. Groups of seals contained from two to eight individuals each. The age, sex, and behavior of the animal emitting the signal were noted. No other marine mammal species was observed during recordings.

Underwater sounds were sampled with an ocean sound meter (JASCO Applied Sciences, Dartmouth, NS, Canada). The ocean sound meter recorded continuously and used a sampling rate of 32 kHz to produce an acoustic bandwidth of 10 Hz to 16 kHz, and a GeoSpectrum M36 hydrophone [with sensitivity of −165 dB V/μPa and a frequency response which is flat (within 1 dB) from 10 Hz to 10 kHz] (Geospectrum Technologies Inc., Dartmouth, NS, Canada) was lowered 10 m into the water (approximately 5 m below the underside of the ice). A GoPro camera (Hero 5) captured in-air videos of surrounding areas on the ice (not underwater). With the aim of distinguishing sounds produced underwater and sounds produced at the water surface (when animals were in the water) that might be recorded on the hydrophone, animal behavior recorded by the videos (GoPro) at the ice edge near to the hydrophone was analyzed in combination with the underwater and in-air recordings.

B. Data analysis

1. Subjective classification

Acoustic analyses were completed by an experienced acoustician (HFM). Acoustic signals were defined by visual inspection of the sound spectrogram as continuous units of sound separated by silent periods. Based on consistent differences in time and frequency features, signals were divided into types. Signals were initially classified subjectively through aural and visual matching of signals to signal types following the classification scheme of Ballard and Kovacs (1995). For new signal types, naming was based primarily on the signal category (e.g., moan) or acoustic similarity to familiar sounds (e.g., howl). Additional subdivision of categories was also undertaken where a variation of a signal category was consistent (e.g., Moan1 and Moan2). Overall, as in other classification systems for marine mammal signals (e.g., Risch *et al.*, 2007; Garland *et al.*, 2015), the frequency range and modulation of a signal as well as its duration were most important for its initial categorization. Intra-observer variability as experience (and signal type classification) increased over time could influence results. To ensure consistent analysis, all data were re-inspected by the same acoustician after the first round of manual annotations.

Acoustic recordings were viewed spectrographically using the custom software program, PAMlab (JASCO), allowing all hooded seal signals to be selected manually from the spectrograms (3.91 Hz frequency resolution, 0.05 ms frame length, 0.01 ms time step, Hamming window). The minimum frequency, maximum frequency, duration, and frequency bandwidth were logged for each signal. All 5-min (underwater) and 30-min (in air) audio files containing signals were used in the subjective analysis to allow signal classification.

Underwater signals that were clearly distinguishable with a good signal-to-noise ratio (SNR) measuring more than 6 dB above background noise levels, measured within a time duration equivalent to the signal immediately preceding and following the signal, were included for further analysis. To reduce the contribution of other hooded seal sounds to the SNR, the time windows were automatically selected to lie between the annotated hooded seal signals.

2. Quantitative classification and statistical analysis of underwater signals

Data (from PAMlab) containing underwater signals (voiced calls and proboscis/septum sounds) with a SNR > 6 dB were imported into R. Data were analyzed using the *warbleR* package in R (version 1.1.23; Araya-Salas and Smith-Vidaurre, 2017) using the following spectrogram parameters: fast Fourier transform (FFT) window size 512 points (pts), overlap 95%, and Hanning window (frequency resolution = 62.5 Hz). Of each signal, 29 parameters (Table I) were measured from the time envelope and the frequency spectrum (e.g., Fig. 1). The determination of these parameters is based primarily on the Acoustat approach of Fristrup and Watkins (1992). Acoustic parameters that were automatically generated by *warbleR* and measured on all signals included duration; mean frequency, median frequency; first quartile frequency; third quartile frequency, interquartile frequency range; median time, first quartile time, third quartile time, interquartile time range; skewness; kurtosis; spectral entropy, time entropy, spectrographic entropy; spectral flatness; average, minimum, and maximum of fundamental frequency measured across the acoustic signal; average, minimum, and maximum of dominant frequency measured across the acoustic signal; range of dominant frequency measured across the acoustic signal; modulation index; dominant frequency measurement at the start and at the end of the signal; slope of the change in dominant frequency through time; peak frequency and mean peak frequency. All signals were analyzed, but only voiced calls were included in further analyses.

As we had no concurrent underwater visual data to estimate the number of individuals within range of the recorder, multiple calls from an individual animal are likely included in the analysis. Due to the potential for pseudo-replication of calls per individual, a non-parametric classification tree analysis with cross-validation was undertaken on the measured variables using the *rpart* package in R (version 4.1–15; Therneau *et al.*, 2019) following the method of Risch *et al.* (2007) and Garland *et al.* (2015). Classification and regression tree analyses (CART) have become popular in marine mammal acoustic literature (Risch *et al.*, 2007; Rekdahl *et al.*, 2013; Garland *et al.*, 2015) due to their robustness to outliers, data with non-normal distributions, and non-independent (correlated) data (Breiman *et al.*, 1984). Thus, they are preferable to discriminant function analyses (DFA) and principal component analysis (PCA), which require independence of samples, normal distributions of discriminating variables, homogeneity of variances, linearity, and uncorrelated discriminating variables. All variables in CART are considered in each splitting decision in the classification tree, and the analysis is strengthened by correlated or co-linear variables (Breiman *et al.*, 1984). Trees are grown by separating the original multivariate data into increasingly homogeneous groups to obtain groups that

TABLE I. Description of 29 signal parameters measured for all signals, with those used in the quantitative classification of hooded seal underwater voiced call types noted in bold.

Measurement	Abbreviation	Description
Duration (s)	Dur	Length of call
Minimum frequency (kHz)	**Min**	**Minimum frequency**
Maximum frequency (kHz)	**Max**	**Maximum frequency**
Bandwidth (kHz)	**BW**	**Maximum–minimum frequency**
Mean frequency (kHz)	MeanFreq	Mean frequency
Median frequency (kHz)	**MedFreq**	**Median frequency**
First quartile frequency (kHz)	**Freq25**	**First quartile frequency**
Third quartile frequency (kHz)	Freq75	Third quartile frequency
Interquartile frequency range (kHz)	**FreqIQR**	**Freq75–Freq25**
Median time (s)	MedTime	Median time
First quartile time (s)	Time25	First quartile time
Third quartile time (s)	Time75	Third quartile time
Interquartile time range (s)	**TimeIQR**	**Time75–Time25**
Skewness	**Skew**	**Asymmetry of the spectrum**
Kurtosis	Kurt	Peakedness of the spectrum
Spectral entropy	SpEnt	Energy distribution of the frequency spectrum
Time entropy	TiEnt	Energy distribution on the time envelope
Entropy	Ent	Spectrographic entropy
Spectral flatness	SFM	Spectral flatness
Average dominant frequency (kHz)	MeanDom	Average of dominant frequency measured across the acoustic signal
Minimum dominant frequency (kHz)	MinDom	Minimum frequency measured across the acoustic signal
Maximum dominant frequency (kHz)	MaxDom	Maximum frequency measured across the acoustic signal
Range of dominant frequency	DFrange	Range of dominant frequency measured across the acoustic signal
Modulation index	ModIn	Cumulative absolute difference between adjacent measurements of dominant frequencies divided by the dominant frequency range
Start dominant frequency (kHz)	StartDom	Dominant frequency measurement at the start of the signal
End dominant frequency (kHz)	EndDom	Dominant frequency measurement at the end of the signal
Slope of the change in dominant frequency through time (kHz/s)	DFslope	(EndDom − StartDom)/Dur
Peak Frequency (kHz)	PeakF	Frequency with the highest energy
Mean peak frequency (kHz)	MeanPeakF	Frequency with highest energy from the mean frequency spectrum

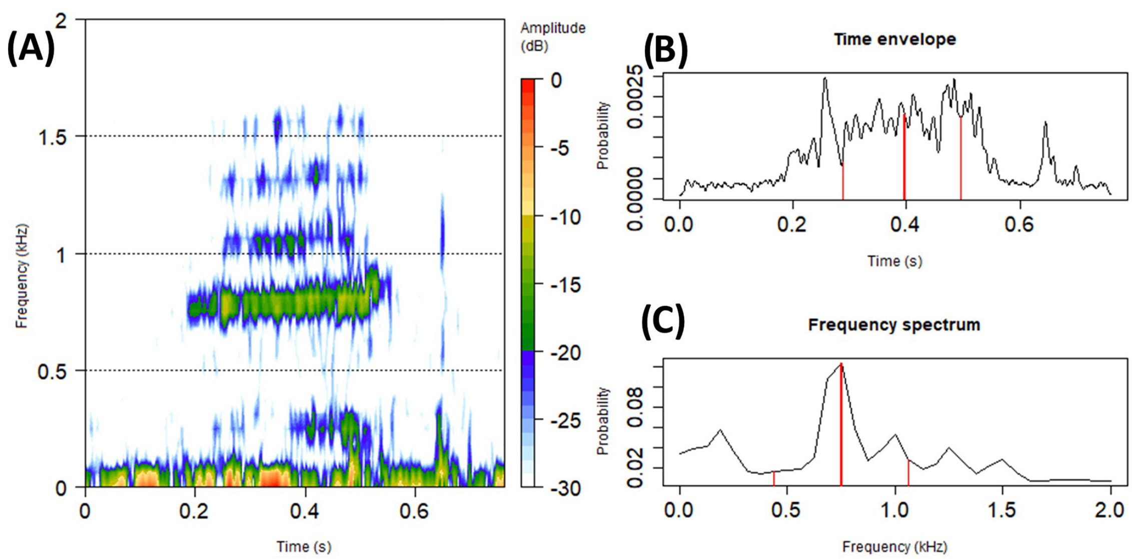

FIG. 1. (Color online) The example, here based on A1iibIII, shows the spectrogram (A) and the parametrization of the spectrogram with the time envelope (B) and the frequency spectrum (C). The median and the quartiles are indicated with vertical red segments. Spectrogram parameters: Hanning window, FFT window size: 512 pts, 95% overlap.

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contain cases of predominantly one class. Each split is binary, minimizing the probability of misclassification of the response variable (i.e., call type) and thus explaining more of the original variation of the data. Splits are based on only a single explanatory variable. To decide which explanatory variable at what cutoff value is selected to perform the next split, the maximum reduction in deviation over all splits is calculated. The classification tree was split into nodes based on the Gini index to reduce the impurity of nodes or "goodness of split." The terminal nodes were set to have a minimum sample size of 10, given the sample size of most call types was larger than this. This sample size cutoff excluded five voiced calls. The tree was overgrown, and tenfold cross-validation was performed. As an alternative method, Breiman *et al.* (1984) suggested the 1 − standard error (1 − SE) rule. This is done by upward pruning of the tree until the best predictive tree with the smallest estimated classification error is obtained (estimated error rate within one SE of the minimum). The selection of the classification method used depended on the results of the initial perceptual classification. Furthermore, because of their visually distinctive features, we still included in the acoustic repertoire some sounds that did not fall out in the classification tree analysis. The classification trees were plotted using the rpart.plot package (version 3.0.9; Milborrow, 2020).

For the same dataset, we also conducted a random forest analysis (Breiman, 2001) using the RandomForest package in R (version 4.6–14; Liaw and Wiener, 2002) on the same measured variables. Random forest is a tree-based ensemble method that extends standard CART methods by creating a collection of classification trees (the forest). The classification uncertainty of each tree during construction is assessed using randomly selected cases [the out-of-bag (OOB) cases or error rate]. The importance of each predictor variable is determined by evaluating the decrease in prediction accuracy when those variables are permuted. Random forests estimate error internally so there is no need for additional cross-validation, and the splitting of nodes occurs using a specified number of predictors that are randomly selected instead of all the available variables at each split (Breiman, 2001). Based on the stability of the classification of uncertainty of each tree (lowest OOB error), the number of predictors randomly selected at a node for splitting was set to three, and 1000 trees were grown [following Rankin *et al.* (2013) and Garland *et al.* (2015)]. The error per call type and the overall OOB error rate of the forest were used to assess the overall success of classification. All variables from Table I were available for CART and random forest analyses.

III. RESULTS

A. Subjective classification

1. In-air signals

From the 1060 signals identified in the recordings, seven call types (voiced calls) and five sounds produced through the inflation and deflation of the proboscis and septum were identified subjectively (Fig. 2).

Adult females produced most A1i (airy exhalation), A1ii (brief guttural growl), A1iib (moaning growl), and A2i (long-duration growl) calls near males that were displaying with their proboscis and septum mainly in low-threat situations. However, in high-threat situations, females used B1 (frequency-modulated growl) calls in response to males (or researchers) rapidly approaching notably if the pup was nearby. Weaned pups (weaners) emitted A1iibI (wailing moan) while lying idle or moving around. Weaners also emitted B1 (frequency-modulated growl) in agonistic situations.

Most of the adult male sounds in air were produced by the inflation and deflation of the proboscis and septum in the presence of other males and near adult females. Following the inflation phase of the proboscis, the slight deflation of the proboscis produced a CI sound ("bloop sound"). Following the inflation of the septum ("septum inflation"), the male rapidly shook his head, whipping the fully inflated septum rearward, and created some (generally two) CII sounds ("whoosh sound"). Then, moving the fully inflated septum from the back to the front (and vice versa), the male produced the CIII sounds ("metallic ping sound"). Finally, the male deflated the septum, generating another sound ("septum deflation"). See SuppPub2.zip for the corresponding audio files[1] and mm.1.mp4 a video showing the sequence of sound production in air.[1]

Mm. 1. This is a file of type of type "mp4" (6886 KB).

Proboscis (CI: 8.2% of the sampled hooded seal airborne repertoire) and septum (CII and CIII: 57.4%, septum inflation and deflation: 22.9%) noises produced by male hooded seals were the predominant sounds heard on the ice surface.

Figure 3 shows the sequence of inflation and deflation of the proboscis and septum and corresponding sounds produced in air. Figure 3 also illustrates the sequence of sounds produced both in air and underwater with those structures and mechanisms. See SuppPub2.zip for the corresponding audio files.[1]

2. Underwater signals

From the 3033 signals identified in the recordings, 855 signals were of a sufficient SNR (>6) to be analyzed further. Subjectively based on the classification scheme suggested by Ballard and Kovacs (1995) and complemented with a new classification, 22 underwater sounds were identified, with five of them being proboscis/septum sounds (Fig. 4) and 17 of them being voiced calls (Fig. 5 and Table II). We recorded some sounds like the CVI ("beating") reported by Ballard and Kovacs (1995), but we were not convinced that they were actually produced by hooded seals and excluded them from our dataset (those sequences of pulses were low frequency and extended over several minutes similar to some fish-like sounds).

The moan category was subdivided into two calls, including Moan1 (Fig. 5), a call centered around 560 Hz

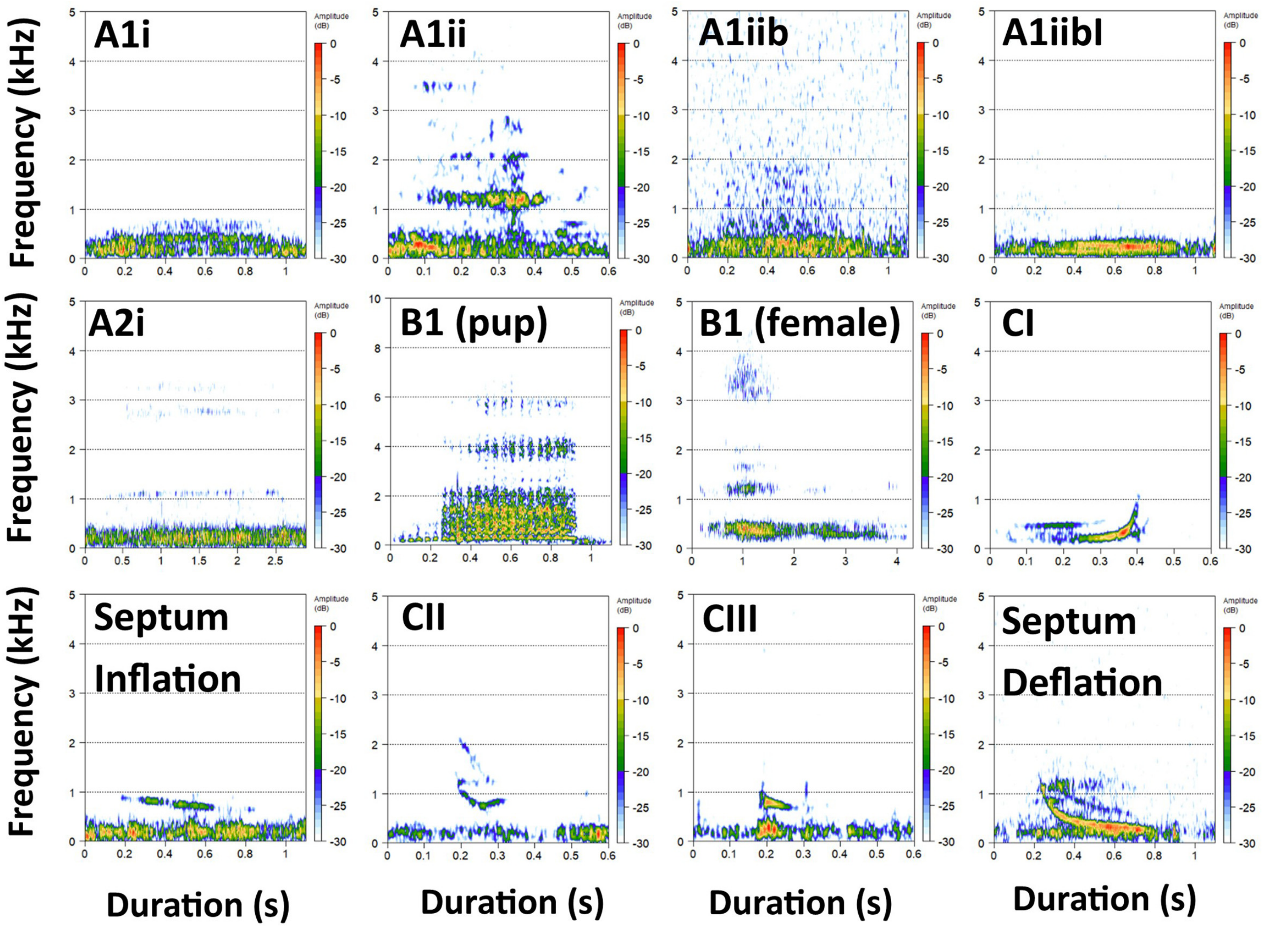

FIG. 2. (Color online) In-air sounds produced by hooded seals *C. cristata* previously described in the literature (Ballard and Kovacs, 1995). Voiced calls: A1i (exhalation by a female), A1ii (guttural growl by a female), A1iib (moaning growl by a female), A1iibI (wailing moan by a pup), A2i (long growl by a female), B1 pup (frequency-modulated growl by a pup), B1 female (frequency-modulated growl by a female). Sounds produced through the inflation and deflation of the proboscis and septum: CI (bloop), septum inflation, CII (wooshes), CIII (ping), and septum deflation. Spectrogram parameters: Hanning window, FFT window size: 1536 pts, 95% overlap. Figures were constructed using *Seewave* (Sueur *et al.*, 2008). For easier viewing, these spectrograms are plotted on different time scales. For easier viewing, B1 (pup) is on a different frequency scale. See SuppPub2.zip[1] for the corresponding audio files.

[that was the third (11.3% of total signals) most common signal], and Moan2 (Fig. 5), a call centered around 255 Hz (2.3% of total signals). The trill category was subdivided into three calls, including Trill1 (2.5% of total signals; Fig. 5), Trill2 (< 2% of total signals; Fig. 5), and Trill3 (2.8% of total signals; Fig. 5). The CVIII (paired pulsed signal; Fig. 5) was the most frequent underwater call (21.6% of all the sampled hooded seal underwater repertoire—in this paper, the call is described as only one of the pulsed signals) and has the shortest duration (0.47 ± 0.01 s). The A1iibII (a repetitive "whooping" noise; Fig. 5) call represented 17.5% of hooded seal underwater repertoire and has the highest minimum frequency (514 ± 13.9 Hz). A1iibIII (a metallic "blaat"; Fig. 5) represented 9.6% of the total signals. Roar (Fig. 5), CIII (underwater ping similar to the one produced in air; Fig. 4), "Ouwah" noise (Fig. 5), Howl (Fig. 5), and Moo (Fig. 5) were the fifth to ninth most common signals (5.3%, 4.6%, 4.2%, 3.8% and 3.2% of total signals, respectively). This was closely followed by Inflation2 (sound possibly due to the inflation of the proboscis) (2.3% of total signals; Fig. 4) and Deflation (sound possibly due to the deflation of the proboscis/inflation of the septum) (2.2% of total signals; Fig. 4). Inflation1 (sound produced by the proboscis or septum; Fig. 4), Pong (short duration, single pulse produced by the proboscis or septum; Fig. 4), CIV (pulsed call; Fig. 5), Boing (Fig. 5), A1iibIV (low-frequency "metallic moan"; Fig. 5), Groan (Fig. 5), and Downsweep (Fig. 5) were less common, with <2% of the total number of signals per signal. Groan was produced when both male and female hooded seals were in water. See SuppPub2.zip for the audio files corresponding to each signal type.[1]

B. CART

All underwater voiced calls were included in a single analysis with all 29 measured variables. All variables from Table I were available for tree construction; the variables CART utilized in tree construction (in decreasing order of use for splitting the tree) were BW (two splits), Freq25 (two splits), MedFreq (two splits), Max (one split), Min (one

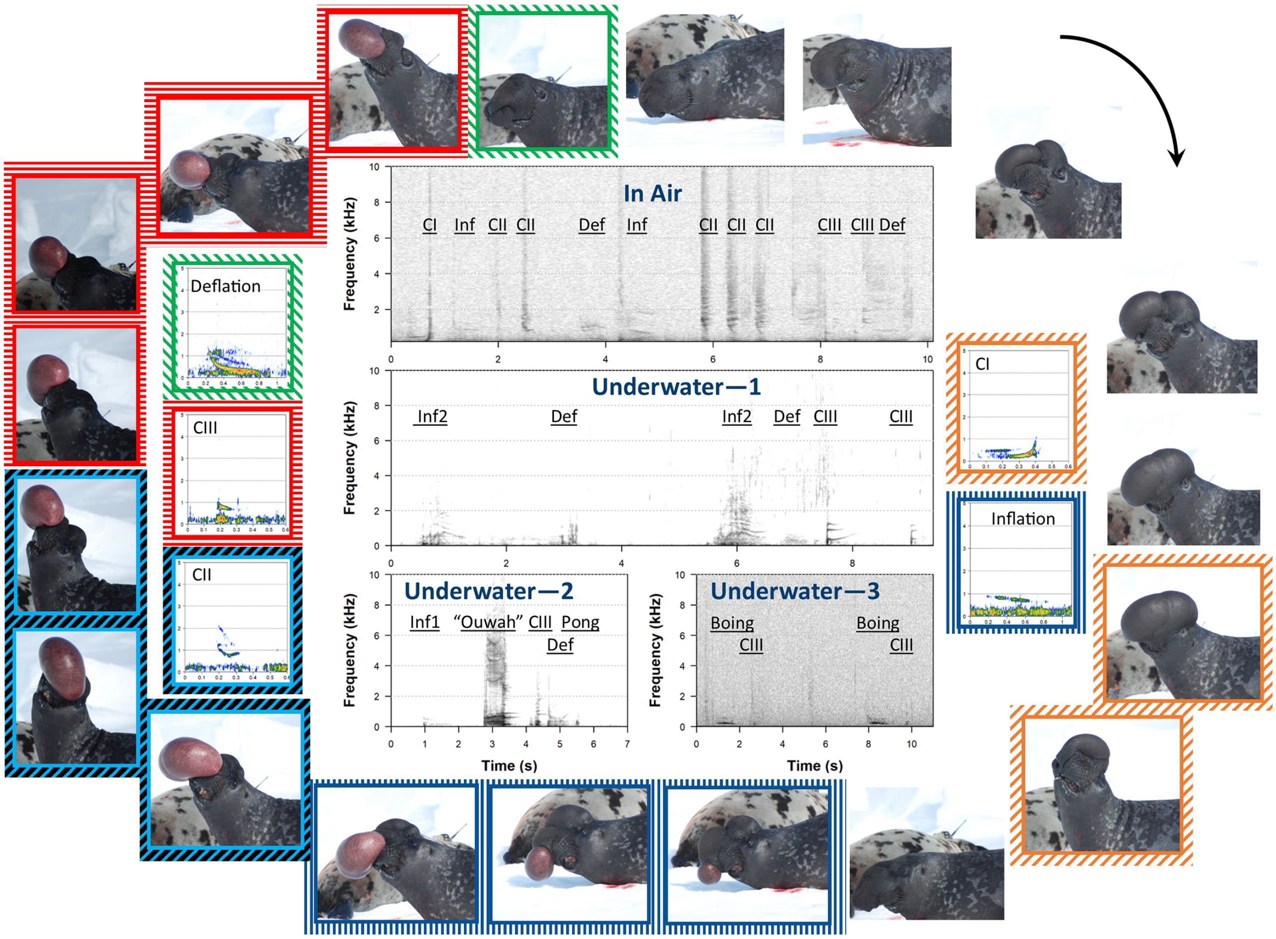

FIG. 3. (Color online) Male hooded seal showing the sequence of proboscis, inflated proboscis (hood), extruded nasal septum, and the sounds (CI in orange, Inflation in dark blue, CII in light blue, CIII in red, and Deflation in green) corresponding to the different structures and mechanisms (highlighted by the corresponding colors and patterns). In the middle, four spectrograms show some examples of in-air sounds (one sequence) and of underwater sounds (three sequences). Ouwah and Boing sounds are considered to be voiced calls. In-air spectrogram parameters: Hanning window, FFT window size: 1536 pts, 95% overlap. Underwater spectrogram parameters: Hamming window, FFT window size: 512 pts, 95% overlap. The figure was constructed using *Seewave* (Sueur *et al.*, 2008). See SuppPub2.zip[1] for the corresponding audio files.

split), TimeIQR (one split), FreqIQR (one split), and Skew (one split). These variables provided the analysis with 85.3% classification of call types (root node error) and correctly classified over 77% of calls. Twelve terminal nodes (Fig. 6) were created from the 12 call types included in the analysis (as explained previously, only voiced calls with a sample size larger than 10 have been included, and terminal nodes were set to have a minimum final size of 10). The moan calls (Moan1 and Moan2) resulted in a different branch based on the median frequency, whereas the trill calls (Trill1 and Trill2) resulted in a different branch based on the bandwidth.

C. Random forest analysis

The random forest analysis correctly classified (see SuppPub1.pdf for Table S3, providing random forest confusion matrix and classification error for each underwater voiced call)[1] most hooded seal underwater calls (OOB error rate = 12.18%). The most important variables (see SuppPub1.pdf for Table S4, providing the Gini index for the random forest analysis of the hooded seal underwater voiced call classification)[1] were Freq25 (mean decrease in Gini index = 41.5), timeIQR (mean decrease in Gini index = 40.9), BW (mean decrease in Gini index = 36.1), and MedFreq (mean decrease in Gini index = 34.8). Call types with a small number (<10) of examples (A1iibIV, CIV, Downsweep, Groan) had a high misclassification rate that increased the measure of error. Overall, the random forest analysis was able to discriminate 13 call types, the same 12 call types identified with the CART analysis plus one additional, "Boing," suggesting a high level of agreement in classification between both analyses.

IV. DISCUSSION

In-air and underwater acoustic signals from the Northwest Atlantic hooded seal population recorded during their breeding period in the Gulf of St. Lawrence were classified in 12 and 22 signal types, respectively. Five of the 22 underwater signals were produced by male hooded seals through the inflation and deflation of the proboscis and

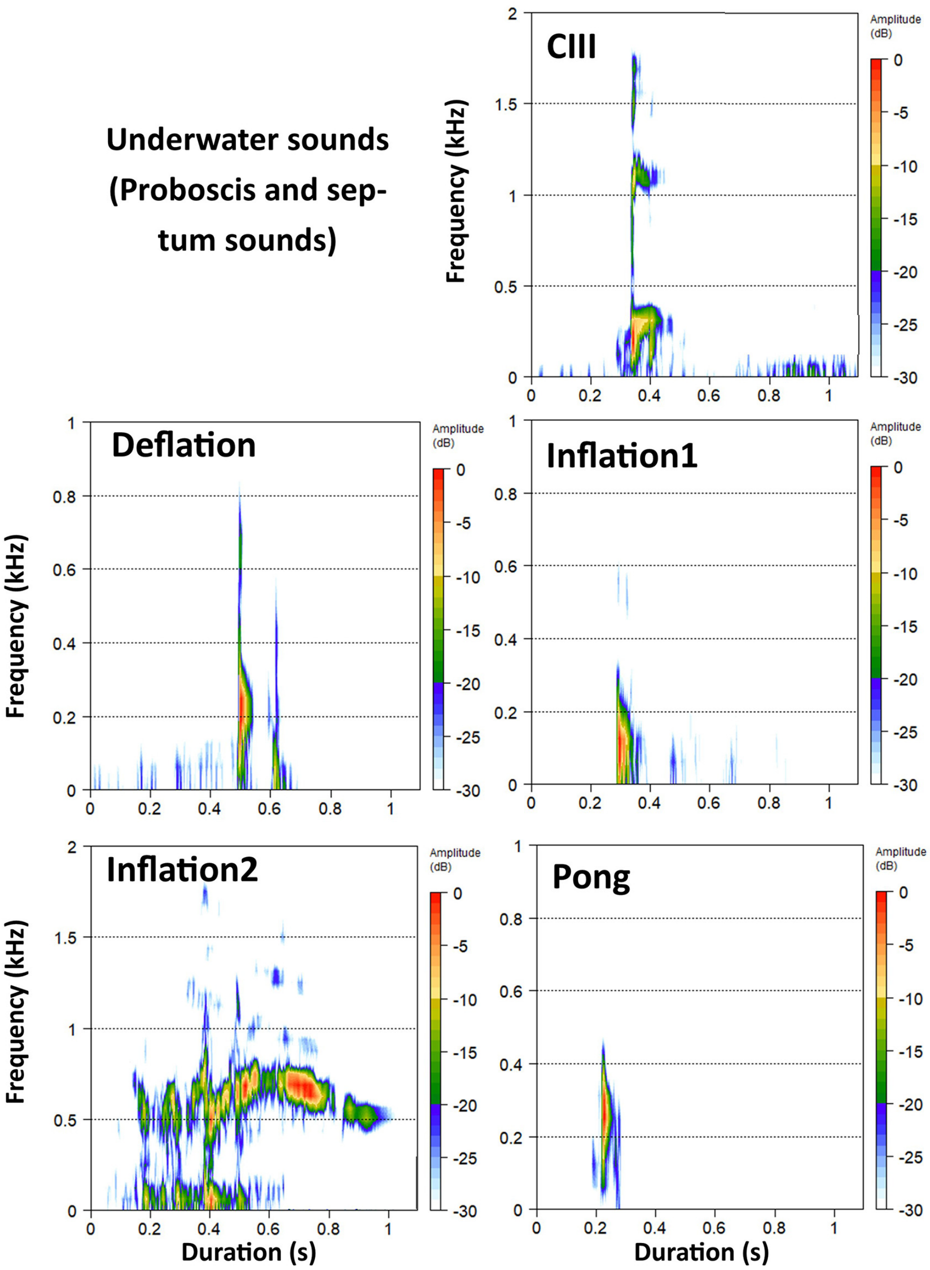

FIG. 4. (Color online) Underwater sounds produced by male hooded seals *C. cristata* through the inflation and deflation of the proboscis and septum: CIII [underwater ping, previously described in the literature (Ballard and Kovacs, 1995)], Deflation, Inflation1, Inflation2, and Pong. Spectrogram parameters: Hanning window, FFT window size: 512 pts, 95% overlap. The figure was constructed using *Seewave* (Sueur *et al.*, 2008). For easier viewing, these spectrograms are plotted on different frequency scales. See SuppPub2.zip[1] for the corresponding audio files.

septum. The remaining underwater signals (17) were categorized as voiced calls. This study provides a detailed description of the underwater call repertoire for this population and builds on the initial descriptions by Terhune and Ronald (1973) and Ballard and Kovacs (1995).

Ballard and Kovacs (1995) described a large variety of in-air signals (growl, moan, airy exhalation, roar, bloop, woosh, and ping), and most of them are also reported in the present study. Female hooded seals do not leave their pup during the brief lactation period and produced different calls (A1i, A1ii, A1iib, and A2i) during low-threat situations (e.g., males that were nearby and displaying with their proboscis and septum). However, during high-threat situations (e.g., in response to males that approached closely and when the pup was located between the mother and the approaching male), females produced a B1 call. Weaners emitted A1iibI while lying idle or moving around and emitted B1 in agonistic situations.

Sounds produced through the inflation and deflation of the proboscis and septum by male hooded seals were the predominant sounds heard on the ice surface. Those sounds and visual display (of the proboscis and septum) were emitted in the presence of other males and when adult females (with or without pups) were nearby. Male hooded seals that attended females were predominantly large (Kovacs, 1990) and displayed frequently. We observed that hooded seal males challenge each other to gain and maintain proximity to a female mainly using visual and acoustic display by repeating a sequence composed of CI, septum inflation, CII, CIII, and septum deflation until one male leaves (displaced from the female). Combat between males was observed on rare occasions.

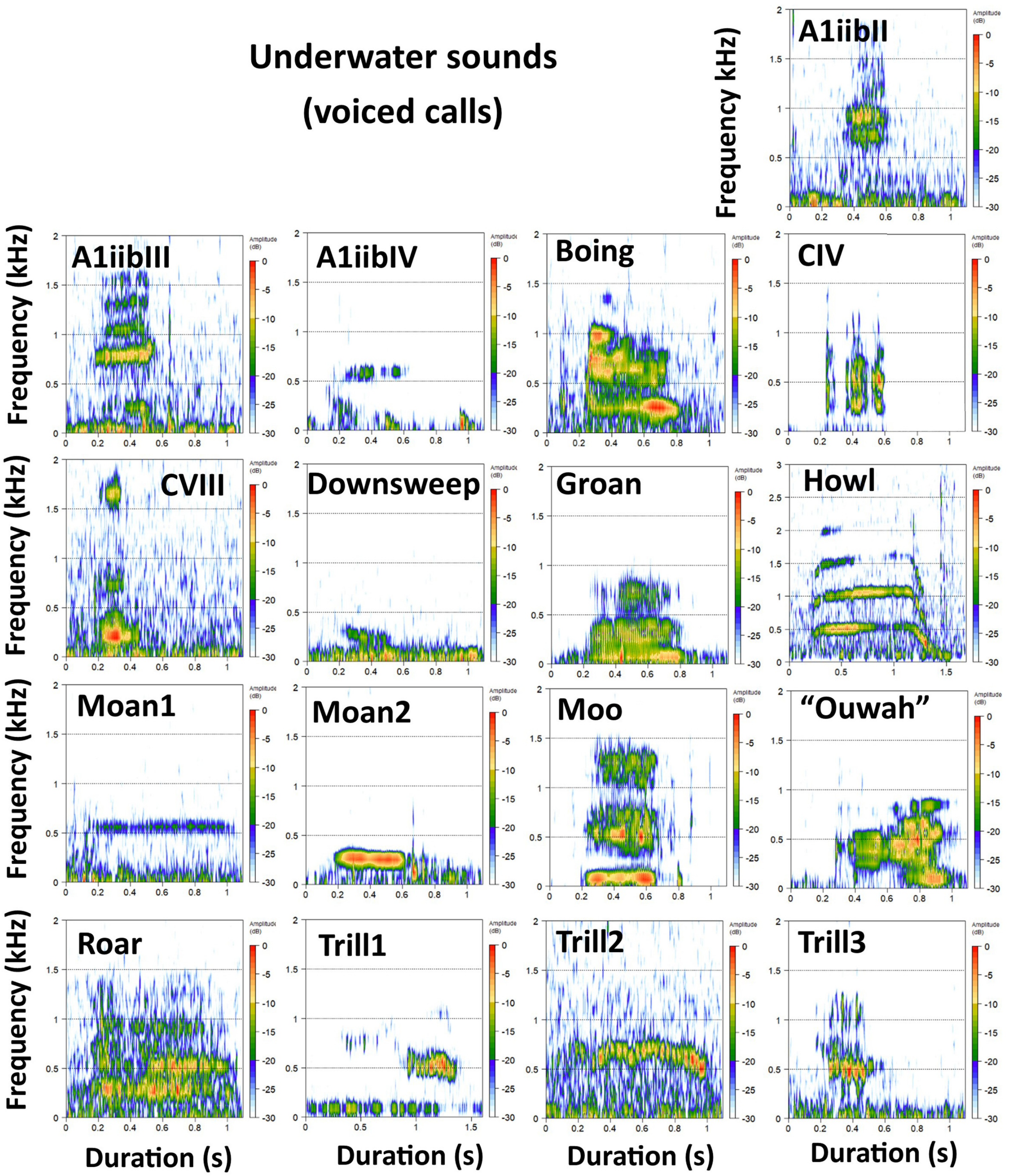

FIG. 5. (Color online) Underwater voiced calls produced by hooded seals *C. cristata* described in this study, including A1iibII ("whooping" noise), A1iibIII (metallic "blaat"), A1iibIV ("metallic moan"), CIV (underwater "clicks"), and CVIII (paired pulsed signals), were previously described in the literature (Ballard and Kovacs, 1995). Boing, Downsweep, Groan, Howl, Ouwah, Moan1, Moan2, Moo, Trill1, Trill2, Trill3, and Roar were not previously reported. Spectrogram parameters: Hanning window, FFT window size: 512 pts, 95% overlap. The figure was constructed using *Seewave* (Sueur *et al.*, 2008). For easier viewing, Howl is on a different frequency scale and duration scale, and Trill1 is on a different duration scale. See SuppPub2.zip[1] for the corresponding audio files.

In this study, through spectrographic analysis, 17 candidate call types for voiced calls were suggested. Two powerful non-parametric classification methods, CART and random forests, were applied on voiced calls. Agreement with the initial subjective classification of calls was high (77% for CART and 88% for random forests), showing that 12–13 call types separated well, depending on the analysis. The main features separating the proposed call types were

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TABLE II. Mean ± SE values of the measured acoustic variables (most important variables for CART and random forest analyses) for the hooded seal underwater signals with a sufficient SNR (>6). Percent total usage (%) of each signal (voiced calls and proboscis/septum sounds) was calculated as number of observations of each signal over total number (3033) of underwater signals identified.

Call type	*N*	Min (kHz)	Max (kHz)	BW (kHz)	Dur (s)	Freq25 (kHz)	MedFreq (kHz)	FreqIQR (kHz)	Time IQR (s)	Skew	Percent total usage (%)
Proboscis/septum sounds											
CIII	48	0.04 ± 0.01	4.60 ± 0.68	4.56 ± 0.69	0.51 ± 0.02	0.19 ± 0.02	0.32 ± 0.02	0.47 ± 0.05	0.10 ± 0.01	5.28 ± 0.48	4.55
Deflation	16	0.08 ± 0.02	1.31 ± 0.14	1.23 ± 0.15	1.02 ± 0.08	0.23 ± 0.02	0.38 ± 0.03	0.35 ± 0.04	0.35 ± 0.04	2.24 ± 0.23	2.18
Inflation1	18	0.09 ± 0.04	3.85 ± 0.74	3.76 ± 0.76	1.02 ± 0.06	0.23 ± 0.04	0.37 ± 0.04	0.40 ± 0.06	0.42 ± 0.05	4.81 ± 0.73	1.71
Inflation2	27	0.05 ± 0.02	3.02 ± 0.30	2.97 ± 0.30	1.13 ± 0.07	0.25 ± 0.04	0.50 ± 0.05	0.65 ± 0.07	0.34 ± 0.02	5.34 ± 0.45	2.27
Pong	15	0.12 ± 0.03	1.28 ± 0.15	1.16 ± 0.15	0.49 ± 0.04	0.31 ± 0.03	0.42 ± 0.04	0.30 ± 0.04	0.11 ± 0.01	2.19 ± 0.19	1.65
Voiced calls											
A1iibII	112	0.48 ± 0.02	1.64 ± 0.04	1.16 ± 0.05	0.56 ± 0.01	0.76 ± 0.01	0.92 ± 0.01	0.39 ± 0.02	0.17 ± 0.00	2.92 ± 0.10	17.5
A1iibIII	92	0.15 ± 0.01	1.81 ± 0.02	1.66 ± 0.02	0.73 ± 0.01	0.50 ± 0.01	0.80 ± 0.00	0.60 ± 0.01	0.25 ± 0.00	5.24 ± 0.18	9.63
A1iibIV	1	0.42	0.66	0.24	0.66	0.55	0.58	0.05	0.23	2.66	0.43
Boing	15	0.1 ± 0.01	1.62 ± 0.33	1.52 ± 0.33	0.94 ± 0.06	0.29 ± 0.02	0.51 ± 0.04	0.43 ± 0.06	0.33 ± 0.02	4.77 ± 0.60	0.63
CIV	2	0.17 ± 0.02	1.17 ± 0.62	1.00 ± 0.60	0.77 ± 0.05	0.32 ± 0.07	0.43 ± 0.10	0.23 ± 0.08	0.29 ± 0.12	1.93 ± 0.80	0.66
CVIII	29	0.11 ± 0.01	2.00 ± 0.06	1.89 ± 0.06	0.45 ± 0.01	0.27 ± 0.02	0.63 ± 0.04	0.95 ± 0.06	0.14 ± 0.01	7.31 ± 0.45	21.6
Downsweep	2	0.11 ± 0.05	0.53 ± 0.14	0.42 ± 0.19	0.71 ± 0.17	0.21 ± 0.03	0.24 ± 0.01	0.12 ± 0.07	0.29 ± 0.12	1.83 ± 0.46	0.23
Groan	3	0.02 ± 0.02	1.02 ± 0.33	1.00 ± 0.34	0.98 ± 0.21	0.16 ± 0.04	0.30 ± 0.02	0.35 ± 0.11	0.32 ± 0.09	4.98 ± 2.23	0.33
Howl	86	0.13 ± 0.01	4.92 ± 0.46	4.79 ± 0.46	1.30 ± 0.02	0.48 ± 0.01	0.65 ± 0.02	0.62 ± 0.05	0.50 ± 0.01	11.8 ± 0.67	3.79
Moan1	69	0.48 ± 0.01	0.64 ± 0.00	0.16 ± 0.01	0.98 ± 0.03	0.54 ± 0.01	0.56 ± 0.00	0.03 ± 0.00	0.40 ± 0.02	2.54 ± 0.10	11.3
Moan2	21	0.18 ± 0.01	0.34 ± 0.01	0.16 ± 0.02	0.68 ± 0.04	0.23 ± 0.01	0.25 ± 0.01	0.04 ± 0.01	0.23 ± 0.02	2.84 ± 0.18	2.27
Moo	75	0.01 ± 0.03	10.6 ± 4.50	10.6 ± 4.51	1.04 ± 0.22	0.47 ± 0.13	0.81 ± 0.21	0.95 ± 0.34	0.22 ± 0.04	10.5 ± 5.94	3.17
"Ouwah"	82	0.04 ± 0.01	6.11 ± 0.53	6.07 ± 0.53	1.27 ± 0.02	0.32 ± 0.01	0.48 ± 0.02	0.55 ± 0.06	0.39 ± 0.01	5.75 ± 0.20	4.19
Roar	31	0.13 ± 0.01	1.00 ± 0.05	0.87 ± 0.05	0.59 ± 0.04	0.29 ± 0.02	0.41 ± 0.02	0.27 ± 0.03	0.17 ± 0.02	2.63 ± 0.18	5.28
Trill1	46	0.29 ± 0.02	2.24 ± 0.23	1.95 ± 0.24	1.38 ± 0.08	0.59 ± 0.02	0.77 ± 0.04	0.53 ± 0.06	0.55 ± 0.04	2.87 ± 0.15	2.47
Trill2	30	0.33 ± 0.11	0.87 ± 0.23	0.54 ± 0.24	1.09 ± 0.37	0.47 ± 0.10	0.55 ± 0.09	0.18 ± 0.08	0.47 ± 0.23	2.04 ± 0.77	1.42
Trill3	35	0.34 ± 0.02	1.03 ± 0.12	0.69 ± 0.12	0.67 ± 0.03	0.48 ± 0.02	0.55 ± 0.02	0.17 ± 0.02	0.23 ± 0.02	2.06 ± 0.13	2.80

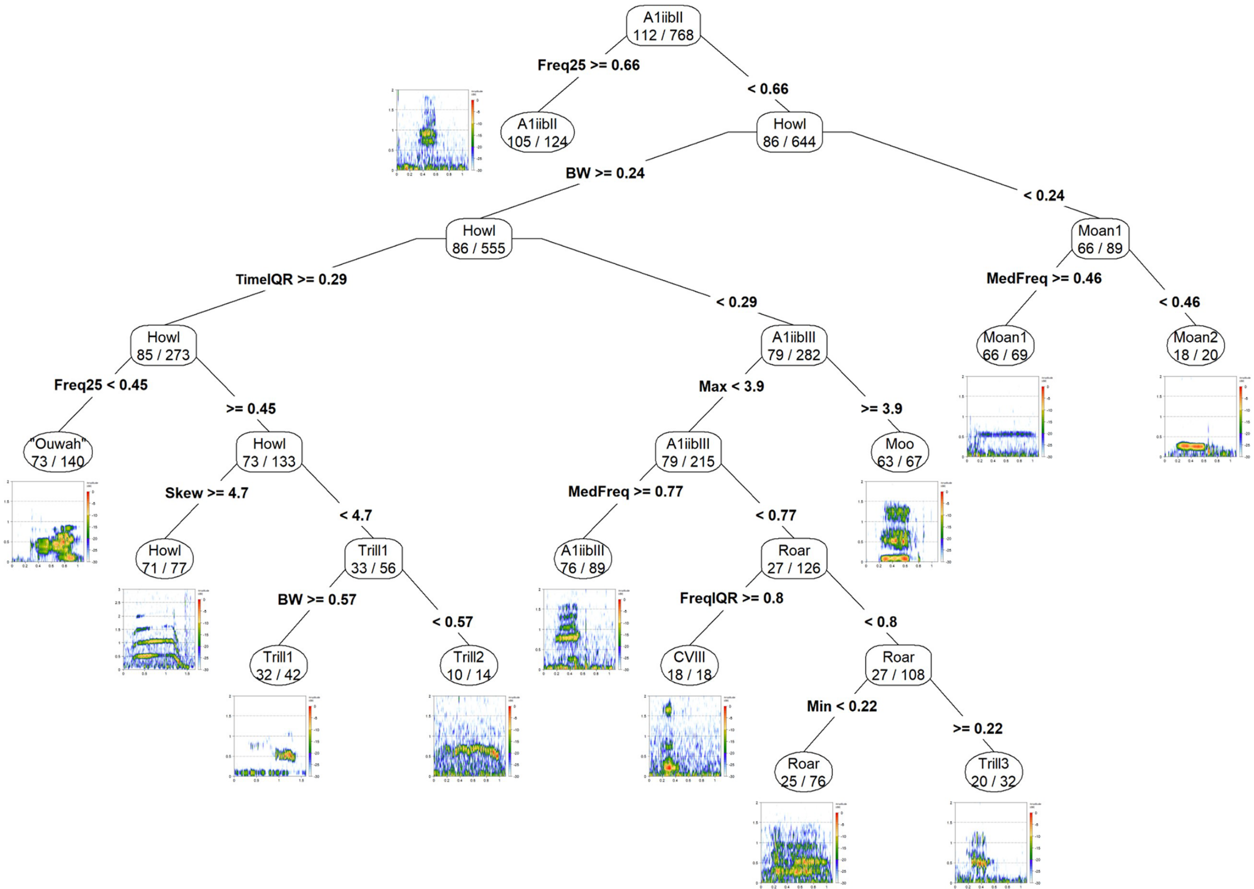

FIG. 6. (Color online) An 11-node classification tree (CART) showing how hooded seal underwater voiced calls split, based on data of eight measured acoustic parameters. The variables used at each split in the tree are listed, along with the criteria (<, >, or =). Rounded rectangle nodes display the number of calls to be split (right) and the number (left) and name of the call type with the highest number of calls. The round terminal boxes display the call type along with the number of correctly classified calls out of the total number of calls. An example spectrogram is provided below. The round terminal boxes display the total number of correct classifications (below the call type) and the call type (example) below the box. Spectrogram parameters: Hamming window, FFT window size: 512 pts, 95% overlap.

the Freq25, TimeIQR, BW, and MedFreq. Classification showed that two call categories (the trill and the moan) separated well. Trills recorded in this study did not match the trill (CV) description provided by Ballard and Kovacs (1995), so they were classified as new calls. Ballard and Kovacs (1995) described ten underwater calls; six of them matched our findings (A1iibII, A1iibIII, A1iibIV, CIII, CIV, and CVIII).

The hooded seal is distinguished from most other phocid seals by the possession of an inflatable proboscis. Male elephant seals (*Mirounga* Gray, 1827), which share several characteristics with hooded seals (for example, similar diving ability; Folkow and Blix, 1999; McIntyre *et al.*, 2010), also have a proboscis that is used as an agonistic display organ (Sandegren, 1976). Vocalizations are a main component of elephant seal agnostic behavior (Sandegren, 1976; Sanvito and Galimberti, 2000), and vocalizations are always emitted with the proboscis expanded (Sanvito *et al.*, 2007a). The acoustic features determined by the main part of the southern elephant seal vocal tract are related to body size, but sound characteristics are also influenced by the proboscis, which acts as an extension of the vocal tract (Sanvito *et al.*, 2007b). As mentioned earlier and described in Fig. 3, male hooded seals have a specialized inflatable nasal hood (proboscis) and septum (not extruded by elephant seals) that are used for a combined visual and acoustic display. Part of the nasal septum is highly elastic and can be extruded through one nostril as a large red air-filled bladder (Kovacs and Lavigne, 1986). Tyack and Miller (2002) described a possible mechanism of septum ("balloon") extrusion: "beginning from a relaxed position, one nostril is closed and the internal air pressure forces the anterior elastic nasal septum to bulge outward, until it is extruded through one nostril as a large balloon." Ping (CIII) sounds are produced underwater similarly to those emitted at the ice surface (Ballard and Kovacs, 1995). Interestingly, Ouwah sound (as illustrated in Fig. 3) is produced underwater in sequence with inflation and deflation sounds as well as CIII (ping sound) and Pong sound. Moreover, the Boing sound (as illustrated in Fig. 3) is sometimes produced underwater with CIII. It could be hypothesized that Ouwah and Boing sounds are produced by the male hooded seal and that the proboscis and/or septum has a role in their production and sound amplification or at least could be responsible for resonance phenomena. Underwater competition between males has been described previously, with proboscis inflation expected to play a viable role in underwater agonistic behavior (Frank and Ronald, 1982).

The functions of the underwater sounds recorded during this study are still unknown. Whether both males and females produce some of these calls is unclear, but in most cases, only males were observed in the water, and it is assumed that the female is predominantly on the ice tending her pup, and thus, the underwater calls would come from males. After the pups are weaned, females leave the ice, mate, and then leave the area to move off to the Laurentian Channel for feeding (Bajzak *et al.*, 2009). Adult males either patrol among the floes in the ice pack, "spy-hopping" to look over the surface, or move across the ice in search of females that have given birth to pups and are nursing them. We hypothesize that these sounds are used by male hooded seals for intra-specific agonistic behavior, defense of territories, or access to females. The Groan was recorded when both male and female (after her pup has been weaned) were in the water, possibly to advertise his breeding condition, because mating takes place in the water (Kovacs and Lavigne, 1986).

Male hooded seals are serially monogamous, with an adult male defending a female and her pup from other males until the pup is weaned, after which the male mates with the female and then seeks another female to defend and mate with (Stirling and Thomas, 2003). Those authors found a positive relationship in phocid seals between vocal repertoire size and mating system (serial monogamy, promiscuous, and polygamous in that order) and a negative relationship between repertoire size and risk of predation. These findings are similar to those of Terhune (2019), whose results suggested that the lowest vocal complexity is found in species that engage in serial monogamy; the females are well spaced on breeding beaches or pack ice with a significant predation risk. The lowest complexity group use low-frequency, burst pulse, or irregular waveforms and have small repertoires. Terhune (2019) found an association between hooded and gray (*Halichoerus grypus*) seals and their low underwater vocal complexity. Similarly, Rogers (2003) grouped the hooded seal with the gray and the crabeater (*Lobodon carcinophagus*) seals as seal species that produce mainly smaller repertoires of agnostic broadband noisy pulsed sounds. Based on the current study, the underwater acoustic repertoire of the hooded seal is larger and more complex than was previously described.

Little is known about the seasonal distribution of hooded seals outside the spring breeding areas. Knowledge of seal movements is essential, not only for understanding the basic ecology of hooded seals and their habitat preference, but for implementing accurate conservation and management programs for this species. Autonomous acoustic recorders are an economical tool for long-term monitoring and studying the spatiotemporal distribution of vocalizing marine species, such as seals (e.g., ribbon seal, *Histriophoca fasciata*; Frouin-Mouy *et al.*, 2019), particularly in restricted locations and when ship-based or on-ice studies are unfeasible. But PAM is not without its limitations, the major one being that animals must be vocalizing to be detected. Hence, understanding not only their acoustic repertoires, but also their calling behavior (i.e., call rates and behavioral context), is important for monitoring species using passive acoustics. It is not known whether hooded seals produce underwater signals during the non-breeding season. Moreover, hooded seals may have developed geographic variation in their underwater acoustic repertoire. Therefore, it would be interesting to compare the signals described in this study to signals recorded near Jan Mayen Island, in the Davis Strait, off the northeastern Newfoundland coast (the Front) during the breeding season and at other locations during the non-breeding season. Furthermore, acoustic data would ideally be collected from different groups and individuals, displaying a multitude of varying behaviors, to capture the potentially broad acoustic repertoire of the subject.

In summary, we have presented a detailed description of the underwater acoustic repertoire of the Northwest Atlantic hooded seal during its breeding season (March) in the Gulf, which provides a baseline against which the acoustic repertoire of other hooded seal populations can be compared to investigate possible population-specific dialects in an underwater acoustic repertoire. This information offers valuable knowledge of the underwater acoustic repertoire of hooded seals in the Northwest Atlantic Ocean and provides important baseline information necessary for monitoring hooded seals using PAM.

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[1]See supplementary material at https://www.scitation.org/doi/suppl/10.1121/10.0005478 for files mm1.mp4, SuppPub1.pdf (containing Figs. S1 and S2 and Tables S1–S4) and SuppPub2.pdf (containing sound files corresponding to Figs. 2–5).

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