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2024

Faculty of Science

Faculty Publications

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Original citation:

Molder, Z. A., Halliday, W. D., Reidy, R., Kraemer, C. N., & Juanes, F. (2024). Humpback whale (*megaptera novaeangliae*) social calls in southern British Columbia. *Marine Mammal Science*. <https://doi.org/10.1111/mms.13138>

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# Humpback whale (*Megaptera novaeangliae*) social calls in southern British Columbia

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## Funding information

Western Division of the American Fisheries Society, Grant/Award Number: Eugene Maughan Scholarship; Canadian Network for Research and Innovation in Machining Technology, Natural Sciences and Engineering Research Council of Canada; Liber Ero Foundation; Pacific Whale Watch Association; Shaw Centre for the Salish Sea; Mitacs

## Abstract

Humpback whale (*Megaptera novaeangliae*) nonsong vocalizations, or social calls, are much more poorly understood than humpback song. We examined humpback whale social calls from a foraging ground in southern British Columbia (BC) and developed a catalog for humpback social calls in BC. We tagged four humpback whales on the eastern edge of Swiftsure Bank, BC, in early September 2020, with a passive acoustic and movement tag. We manually classified 32 call types in our data set based on comparisons with published classifications of humpback social calls. Many of the calls identified in our data set had similar characteristics to calls from other locations. We also used two statistical classification methods, a cluster analysis and a random forest. The cluster analysis grouped 20 of these call types into four categories, and the random forest classifier was able to accurately classify all 20 call types 87.6% of the time. This study fills a geographical gap of humpback whale social calls on foraging grounds and is a first step towards categorizing the social calls of humpback whales in BC.

## KEYWORDS

bioacoustics, biologging, passive acoustic monitoring, social call characteristics, social call repertoire, vocalizations

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## 1 | INTRODUCTION

Acoustic communication is vital for many animals, and since sound propagates much further than light underwater, many marine mammals rely on sound more than visual cues for communication and to perform their daily life functions (Richardson et al., 1995). Marine mammals, such as humpback whales (*Megaptera novaeangliae*), have evolved traits to efficiently transmit sound in their environment for meeting their signaling requirements (Richardson et al., 1995). Vocal signaling for the purpose of communication can be used for influencing the behavior of the receiver(s) in a way favorable to the signaler, but also must relay information that is of interest to the receiver(s) (Maynard Smith & Harper, 2003). Humpback whales are highly migratory with an extremely complex vocal repertoire. Their vocalizations often differ among seasons and regions, are associated with behaviors such as breeding and foraging, and play a crucial role in social interactions (Fournet et al., 2015; Payne & McVay, 1971; Richardson et al., 1995; Silber, 1986).

Vocalizations by humpback whales can be categorized into songs, social calls, and repetitive tones (Palanca, 2021). Humpback whale song is well-studied and generally varies among populations and changes annually. Song is predominantly performed by male humpbacks in low-latitude breeding grounds, where they are known to produce a long, continuous, patterned, and repetitive sequence of sounds (Darling, 1983; Medrano et al., 1994; Payne & McVay, 1971; Tyack, 1982). Their song contains nested structured units, phrases, and themes often associated with breeding behavior (Darling, 1983; Medrano et al., 1994; Mobley et al., 1988; Payne & McVay, 1971; Tyack, 1981). Humpback whales also produce lesser studied “social sounds” that include social vocalizations, hereafter referred to as social calls, and surface percussive social sounds, such as those produced from breaching and tail-slapping (Silber, 1986; Tyack, 1982, 1983). Social calls are short, separated by silence, occur outside the patterned and repetitive structure of song, and are more unpredictable than song (Silber, 1986; Tyack, 1982, 1983). Social calls can be heard across the migratory ranges of humpback whales and are produced by males and females at all life stages (Dunlop et al., 2007; Mobley et al., 1988; Silber, 1986; Thompson et al., 1977; Tyack, 1983; Winn et al., 1979; Zoidis et al., 2008). Also, unlike humpback song, certain social calls appear to remain stable across years (Epp et al., 2021; Fournet et al., 2018a; Rekdahl et al., 2013). Over 40 humpback whale social call types have been classified from populations globally (Dunlop et al., 2007; Fournet et al., 2015; Rekdahl et al., 2017). Humpback whale social calls have a wide range of frequencies (50 Hz to >10 kHz) and durations (0.09–5 s), although the majority of social calls are <3 kHz and <1 s (Recalde-Salas et al., 2020; Stimpert et al. 2011; Zoidis et al., 2008).

Humpback whale social calls can be linked to social interactions (Dunlop et al., 2008; Silber, 1986; Tyack, 1983; Wild & Gabriele, 2014) and foraging activities (D'Vincent et al., 1985; Fournet et al., 2018b; Sharpe, 2001). For example, the whup call type, produced by humpbacks around the world, appears to have a communication function, and is used as a contact call between conspecifics (Dunlop et al., 2008; Wild & Gabriele, 2014). The same function has been proposed for other identified social calls, including droplet, swop, teepee, and growl (Dunlop et al., 2008; Fournet, 2014; Wild & Gabriele, 2014). In the Gulf of Maine, Parks et al. (2014) determined that paired burst sounds were associated with bottom feeding behavior in low-light conditions, predominantly with close-by conspecifics. This result suggests that the paired burst call may function as a communication signal to conspecifics and/or to manipulate the behavior of prey (sand lance, *Ammodytes* spp.) to improve feeding success (Parks et al., 2014). Humpback whales on foraging grounds exhibit loose social associations that vary from no association to short- or long-term interactions among groups of related or unrelated individuals (Ramp et al., 2010; Weinrich et al., 2006). Humpback whale acoustic repertoires (Garland et al., 2011) and behaviors such as novel feeding strategies can spread within populations (Allen et al., 2013; McMillan et al., 2019). Humpbacks also exhibit complex feeding and call behaviors that appear to depend both on prey type and social scenario, including solitary surface or bottom feeding and coordinated feeding events as pairs or groups (Cerchio & Dahlheim, 2001; D'Vincent et al., 1985; Fournet et al., 2018b; Mastick et al., 2022; Parks et al., 2014; Sharpe, 2001; Ware et al., 2014). For example, feeding calls made by humpback whales in southeast Alaska have been related to bubble net feeding on Pacific herring (*Clupea pallasii*; Sharpe, 2001).

Humpback whales have a cosmopolitan distribution where nearly all populations migrate seasonally from low-latitude winter calving and breeding grounds to high latitude summer foraging grounds (Bettridge et al., 2015; Mobley et al., 1988). North Pacific humpback whales that feed off the coast of southern British Columbia (BC), Canada, may migrate to breeding grounds off Hawaii, Central America, and/or Mexico (Bettridge et al., 2015; Darling et al., 2022). However, the population structure and migration patterns of North Pacific humpback whales are complex, where there are varying degrees of mixing and interchange between the feeding and breeding populations (Baker et al., 2013; Calambokidis et al., 2001; Calambokidis et al., 2008; Darling et al., 2022). Humpback whales in geographically isolated feeding aggregations typically disperse in the boreal fall to one or more separate breeding grounds, although recent work analyzing photo-identification data of humpbacks shows that some individuals move between breeding grounds in a single season (Darling et al., 2022). There have also been several humpback whale movements documented between northern BC and southeast Alaska (Calambokidis et al., 2008; Palacios et al., 2019), which encompasses a large regional feeding group that is isotopically distinct from the whales feeding in southern BC and Washington State (Witteveen et al., 2011). All these complex movements are likely driving the large degree of overlap of social call types for humpback whales in the North Pacific. Furthermore, humpback whales in the North Pacific and North Atlantic (southeast Alaska and Massachusetts Bay) share at least five call types (Fournet et al., 2018c). These same five call types have also been observed on a foraging ground in Newfoundland in 2015–2016 and on a breeding ground in Hawaii in 1981–1982 (Epp et al., 2021). Similarly, several common call types have been found among humpback whales in Hawaii, Mexico, Australia, and Alaska (Seger et al., 2015) and around the Vema Seamount, southeast Atlantic Ocean and off the west coast of South Africa (Ross-Marsh et al., 2022). Furthermore, 16 call types identified in southeast Alaska have been conserved through generations of humpback whales over decades (Fournet et al., 2018a). Such temporal and spatial stability in specific call types suggests that certain social calls in the humpback whale call repertoire may be inherent, improve fitness in some way, and have essential functions in humpback communication and behavior (Epp et al., 2021; Fournet et al., 2015, 2018c).

The main goal of this study is to develop a catalog of social calls produced by humpback whales from a foraging area in southern BC. To do this, we used data from a multisensor tag fitted with a hydrophone. We quantified the acoustic parameters of the calls and classified them into different call types using aural/visual (AV) characteristics and paired this manual analysis with statistical classifications of call types. This study adds to the call catalog of the known call types produced by humpback whales on their foraging grounds, both in the northeast Pacific and worldwide. Humpback whale vocalizations have been detected in the offshore waters of the west coast of Vancouver Island, BC via deployments of submersible, autonomous recording devices (Ford et al., 2010) and off the Washington coast with acoustic recorders (Emmons et al., 2020). They have also been detected in the Kitimat Fjord System of northern BC using a towed hydrophone array, an over-the-side hydrophone, a single autonomous recorder (Keen, 2017), and from a hydrophone network (Hendricks et al., 2019; Keen et al., 2018). However, none of these studies have published a catalog of social calls produced by humpback whales in BC. Our study is the first to assess humpback whale social calls in BC using passive acoustic tags and to publish a catalog.

## 2 | METHODS

### 2.1 | Data collection

We collected passive acoustic data from humpback whales using an animal-borne, multisensor, suction-cup tag (Customized Animal Tracking Solutions, CATS, Moffat Beach, Australia) fitted with an HTI-96-min hydrophone (sensitivity =  $-201$  dB re:  $1$  V/ $\mu$ Pa; High Tech, Inc., Long Beach, MA) set to record continuously at a 96 kHz sample rate and no gain. The hydrophone recorded ambient sounds in the underwater environment, including vocalizations from the tagged whale and other whales nearby, while inertial sensors in the tag sampled the tagged whale's

**TABLE 1** Deployment details for four tagged humpback whales (*Megaptera novaeangliae*), showing the tag deployment ID, date, whale ID, duration of tag attachment, maximum whale foraging depth, the number of whales present near the tagged whale, and the number of social calls classified from each deployment.

Deployment ID	Date	Whale ID	Duration (hr)	Maximum depth (m)	No. of whales	No. of social calls
HB-1	September 3, 2020	OSUWTG-MnWA-220 <sup>a</sup>	8.92	216	20	287
HB-2	September 5, 2020	CRC-17890 <sup>a</sup>	3.32	156	40	414
HB-3	September 7, 2020	BCX1899 <sup>b</sup>	3.78	268	30	719
HB-4	September 8, 2020	Unknown	0.90	210	15	175

<sup>a</sup>Cheeseman et al., 2021.

<sup>b</sup>Malleson & Shaw, 2018.

underwater movements (pitch, roll, heading) at 20 Hz, and depth at 10 Hz. We deployed this tag on four different adult-size humpback whales (~12 m in length) in early September 2020, in an area located between the western entrance to Juan de Fuca Strait and Swiftsure Bank, British Columbia, as part of a larger tagging study in southern BC (R.R., unpublished data). The area is consistently used by humpback whales for feeding (Calambokidis et al., 2004; McMillan et al., 2022; Nichol et al., 2017), and overlaps with inbound and outbound shipping lanes at the western entrance to the Strait of Juan de Fuca (Nichol et al., 2017). Deployment information is shown in Table 1.

## 2.2 | Manual classification of humpback whale social calls

A total of 16.23 hr of passive acoustic data was recorded across all four tag deployments. We examined the acoustic data aurally and visually using Raven Pro 1.6.1 (Center for Conservation Bioacoustics, 2019) set with window size at 4,000 samples using a Hann window with 50% overlap. We set the scale of the viewing window to 15 s and 0–4,000 Hz, and the analyst zoomed in and out as needed. We drew feature boxes (selection boxes) around individual social calls and measured a suite of quantitative parameters using Raven Pro (Table 2). We selected the lowest frequency component of the calls (the fundamental frequency,  $f_0$ ) when there were harmonics and when  $f_0$  was clearly visible. For calls with harmonics where the lower frequencies were not clearly visible, we selected bands of the lower frequency harmonics. If selecting the  $f_0$  was not possible, we selected the next lowest measurable harmonic. For broadband sounds, we selected the whole call. We noted whether calls had clipping (periods of time where the hydrophone in the tag was overloaded and did not collect any acoustic data) and/or overlap with other high amplitude noise, such as boat, water, or tag noise, but still identified these calls when possible. We only measured calls with a signal to noise ratio (SNR) greater than 9 dB. The majority of calls had pure bouts (calling events with multiple repetitions of the same call, as opposed to mixed bouts, which include more than one call type), and we selected all calls in each bout; however, a few pure bouts had many repeating calls, and in these cases, we only selected one representative call but counted the number of total calls per bout. We manually measured five additional parameters in Raven Pro for each call: the number of harmonics, number of inflections in the call, frequency of the start of the fundamental frequency, frequency of the end of the fundamental frequency, and change in frequency from the start to the end of the fundamental frequency. Number of inflections in the call refers to the number of times that the call switched from an upsweep, downsweep, or flat shape to one of the other shapes. Effectively, a flat call or a pure upsweep or downsweep would have no inflections, a call that switched from an upsweep to a downsweep (“N” shape) or vice-versa (“U” shape) would have one inflection, and calls with multiple switches in direction of frequency change (like a sine wave) would have multiple inflections.

We manually classified humpback whale social calls based on comparisons to published spectrograms and quantitative parameters of call types from southeast Alaska (Barlow et al., 2019; Fournet et al., 2015, 2018a,c) because

**TABLE 2** Description of acoustic parameters measured for the classification of humpback whale social calls.

Measurement	Description
Minimum frequency (Hz)	Lower frequency limit of the selected call
Maximum frequency (Hz)	Upper frequency limit of the selected call
Peak frequency (Hz)	Frequency of the spectral peak or the frequency with the greatest amplitude
Frequency range (Hz)	The difference between the maximum and minimum frequency limits of the selection
Call duration (s)	Length of the call or the difference between the start and end time of the selected call
Calls per pure bout (n)	Number of repetitions of the same call within one calling event, or “pure bout”; $n = 1$ for nonrepetitive calls
Start frequency (Hz)	The frequency of the fundamental frequency at the start of the call
End frequency (Hz)	The frequency of the fundamental frequency at the end of the call
Change in frequency (Hz)	The change in frequency of the fundamental frequency between the start and end of the call
Number of harmonics (n)	Number of harmonics within a call
Number of inflections (n)	Number of inflections of the fundamental frequency of the call

there were no published papers that we could find which classified humpback whale social calls in BC. The humpback whales in our study off southern BC and the humpbacks in southeast Alaska most likely overlap in their migratory range, and could even be from the same breeding population, leading to intermixing of whales and call repertoires. Thus, the humpback whale call types off southeast Alaska most likely have similar acoustic characteristics to those in our study. However, because previous work did not include some of the social calls observed in our data set, we used a global social call catalog in development<sup>1</sup> that contains spectrograms of calls that have been published for each call type. We also used papers that documented quantitative parameters of social calls from humpback populations in the waters off western and eastern Australia, in the northwest Atlantic, and off northern Angola, Africa (Dunlop et al., 2007; Recalde-Salas et al., 2020; Rekdahl et al., 2017; Stimpert et al., 2011) to effectively classify the social calls in our acoustic data set. Certain call types remain stable across humpback whale populations (Epp et al., 2021; Fournet et al., 2018c), allowing comparison of our call parameters with these other humpback whale populations. In all these comparisons across studies, we focused on the shape of the vocalization, duration, and frequency characteristics when determining whether social calls that we identified matched the classification from a previous study. We classified three social calls that did not match any of the social calls from these sources, and labeled these as unknown\_1, unknown\_2, and unknown\_3.

We produced summary statistics to summarize all manually classified social call characteristics defined in Table 2. We analyzed all social calls picked up by the hydrophone; however, calls with clipping or overlap with other signals were included in the count but excluded from the summary statistics of call characteristics.

### 2.3 | Statistical classification of humpback whale social calls

We used statistical methods to classify manual annotations of humpback whale social calls in R (R Core Team, 2023). First, we used a cluster analysis (function: `kmeans`; package: `cluster`) to examine natural groupings in the social calls. We filtered the data to include only calls with no overlap or clipping, and only included call types with  $n \geq 10$  calls. Data were scaled such that each parameter had a mean of 0 and a standard deviation of 1. We included all call parameters in Table 2 for the cluster analysis. We used the gap statistic method (function: `clusGap`; package: `cluster`) with 1,000 bootstrap samples to estimate the number of clusters within the data. We compared manual

<sup>1</sup>Kerri Seger, Biological Oceanography Senior Scientist, Applied Ocean Sciences, LLC (unpublished data, December 2020).

classifications of calls to the groupings identified in the cluster analysis and examined how different call parameters varied among the clusters.

The second statistical classification method that we used was a random forest (function: `randomForest`; package: `randomForest`) with 10,000 trees, which uses a machine learning algorithm to train the forest based on the manual classifications of the calls, and then tests whether the random forest model can successfully predict the classifications of calls. We split the annotations into a training data set, which was a random selection of 80% of the annotations within each call type, and a test data set with the remaining 20% of the annotations. Various studies use different splits between the training and test sets, often ranging between 70:30 and 90:10. For our study, we chose 80:20 because some call types only had  $n = 10$ , therefore an 80:20 split allowing for more than one call to be included in the test set, while still allowing for a relatively large number to go into the training set. We used the same subset of the data for the random forest as in the cluster analysis, except that we used the raw data (i.e., not scaled) for the random forest.

## 3 | RESULTS

### 3.1 | General results

In total, we manually identified 32 social call types across the four tag deployments (refer to the Supplemental Material for example spectrograms of each call type; example WAV files can be listened to and downloaded at <http://wdhalliday.weebly.com/humpback-whale-calls.html>). There was a wide range of variation in acoustic parameters among call types. The lowest average minimum frequency per call type was  $75 \pm 20$  Hz (mean  $\pm$  SD) and the highest average maximum frequency per call type was  $8,532 \pm 2,358$  Hz (Table 3). Call durations among call types ranged from  $0.08 \pm 0.02$  s to  $2.20 \pm 1.62$  s (Table 3). Most social calls had peak frequencies below 1,000 Hz and durations of  $\leq 1$  s (Table 3). Frequency ranges among call types varied from being narrowband ( $148 \pm 53$  Hz) to broadband ( $7,616 \pm 2,692$  Hz) (Table 3). The total number of social calls across all deployments was 1,595, with a minimum of 175 (HB-4) and maximum of 719 (HB-3) social calls classified per deployment (Table 1; Figure 1). Each tagged whale had many other conspecifics nearby, with 20, >40, >30, and 10–15 conspecifics nearby for deployments HB-1, HB-2, HB-3, and HB-4, respectively (Table 1).

### 3.2 | Most common social call types and summary statistics

There was wide variation in the social call types observed for each tag deployment in the same feeding area (Figure 1, Table 1). Moan calls occurred in all deployments and were the most frequent across all deployments at 210 calls (Table 3). In the literature, moans were often split into modulated moans, ascending moans, descending moans, and short moans (Dunlop et al., 2007; Fournet et al., 2015). However, moans in our acoustic data were similar (average peak frequency of the fundamental frequency =  $240 \pm 79$  Hz), had harmonics, and were tonal/narrowband (average frequency range of  $202 \pm 123$  Hz), with few exceptions. Thus, all moans other than short moans were grouped into the general moan call type (Table 3, Figure 2a). Short moans had similar frequency measurements compared to the regular moans but were much shorter in duration ( $0.38 \pm 0.09$  s) compared to regular moans ( $1.5 \pm 0.8$  s); short moans were also much less common (Table 3). The second most common social call was the horse call, with 166 calls (Table 3), although this was driven by the large number of horse calls for deployments HB-2 and HB-3 (Figure 1). Horse calls were short ( $0.16 \pm 0.02$  s), broadband (frequency range =  $1,705 \pm 1,011$  Hz), and intermediate in peak frequency ( $575 \pm 358$  Hz) but were characteristic in that they had multiple repeating calls per pure bout ( $4 \pm 2$  calls per bout; Table 3, Figure 2b). Grunts were the third most common call type with 152 calls (Table 3), but this was again driven by the large number of grunts observed in deployments HB-2 and HB-3 (Figure 1). Grunts

**TABLE 3** Summary statistics (mean  $\pm$  SD) of social call types recorded during four tag deployments on humpback whales as described in Table 2. Social calls that had overlap with other noises and clipping were omitted from calculations of the call parameters for each call type, leaving only the “Clean calls” for those calculations (n). “N” is the total number of calls per call type (including calls with clipping and overlap). “Change in freq” is the change in frequency from the start to the end of the call, “N harm” is the number of harmonics, and “N infect” is the number of inflections.

Call type	Total calls (N)	Clean calls (n)	Min freq (Hz)	Max freq (Hz)	Peak freq (Hz)	Freq range (Hz)	Duration (s)
bark	84	47	102 $\pm$ 42	1,498 $\pm$ 586	283 $\pm$ 171	1,395 $\pm$ 583	0.48 $\pm$ 0.12
bellow	10	9	780 $\pm$ 261	1,489 $\pm$ 220	1,060 $\pm$ 233	709 $\pm$ 420	1.03 $\pm$ 0.27
bop	126	72	102 $\pm$ 41	734 $\pm$ 297	239 $\pm$ 136	631 $\pm$ 290	0.13 $\pm$ 0.02
compound call	40	29	91 $\pm$ 32	1,018 $\pm$ 526	324 $\pm$ 460	140 $\pm$ 341	1.54 $\pm$ 1.58
cry	32	26	351 $\pm$ 103	583 $\pm$ 109	469 $\pm$ 91	232 $\pm$ 83	2.20 $\pm$ 1.62
droplet	62	43	185 $\pm$ 110	643 $\pm$ 146	312 $\pm$ 143	458 $\pm$ 184	0.27 $\pm$ 0.06
growl	87	63	77 $\pm$ 18	311 $\pm$ 101	110 $\pm$ 35	234 $\pm$ 96	0.87 $\pm$ 0.3
grunt	152	127	76 $\pm$ 17	504 $\pm$ 129	116 $\pm$ 46	429 $\pm$ 127	0.28 $\pm$ 0.06
gunshot	13	10	916 $\pm$ 860	8,532 $\pm$ 2,358	2,468 $\pm$ 1,778	7,616 $\pm$ 2,692	0.23 $\pm$ 0.07
hiccup	3	3	240 $\pm$ 42	883 $\pm$ 277	477 $\pm$ 14	643 $\pm$ 318	0.31 $\pm$ 0.03
horse	166	24	199 $\pm$ 96	1,903 $\pm$ 1,055	575 $\pm$ 358	1,705 $\pm$ 1,011	0.16 $\pm$ 0.02
knock	42	38	169 $\pm$ 95	1,128 $\pm$ 806	453 $\pm$ 439	959 $\pm$ 745	0.08 $\pm$ 0.02
moan	210	135	160 $\pm$ 62	361 $\pm$ 125	240 $\pm$ 79	202 $\pm$ 123	1.5 $\pm$ 0.8
modulated cry	63	45	382 $\pm$ 213	1,240 $\pm$ 488	697 $\pm$ 310	858 $\pm$ 494	1 $\pm$ 0.64
purr	70	52	143 $\pm$ 35	388 $\pm$ 77	254 $\pm$ 41	246 $\pm$ 77	0.8 $\pm$ 0.36
roar	8	7	164 $\pm$ 79	1,087 $\pm$ 411	362 $\pm$ 242	923 $\pm$ 448	2.45 $\pm$ 1.21
scream	4	4	471 $\pm$ 87	764 $\pm$ 60	557 $\pm$ 112	293 $\pm$ 28	0.72 $\pm$ 0.1
short moan	44	37	169 $\pm$ 76	317 $\pm$ 96	243 $\pm$ 87	148 $\pm$ 53	0.38 $\pm$ 0.09
shriek	6	4	1579 $\pm$ 910	4,700 $\pm$ 4,865	3,557 $\pm$ 3,667	3,121 $\pm$ 4,322	1.49 $\pm$ 0.8
squeak	100	79	1951 $\pm$ 747	4,109 $\pm$ 798	2,791 $\pm$ 865	2,158 $\pm$ 907	0.12 $\pm$ 0.03
squeegie	5	5	341 $\pm$ 221	2,037 $\pm$ 1,213	773 $\pm$ 380	1,696 $\pm$ 1,201	1.78 $\pm$ 0.88
swops	34	12	145 $\pm$ 70	772 $\pm$ 416	234 $\pm$ 73	627 $\pm$ 357	0.29 $\pm$ 0.08
teepee	17	9	92 $\pm$ 18	554 $\pm$ 134	240 $\pm$ 91	462 $\pm$ 136	0.43 $\pm$ 0.1

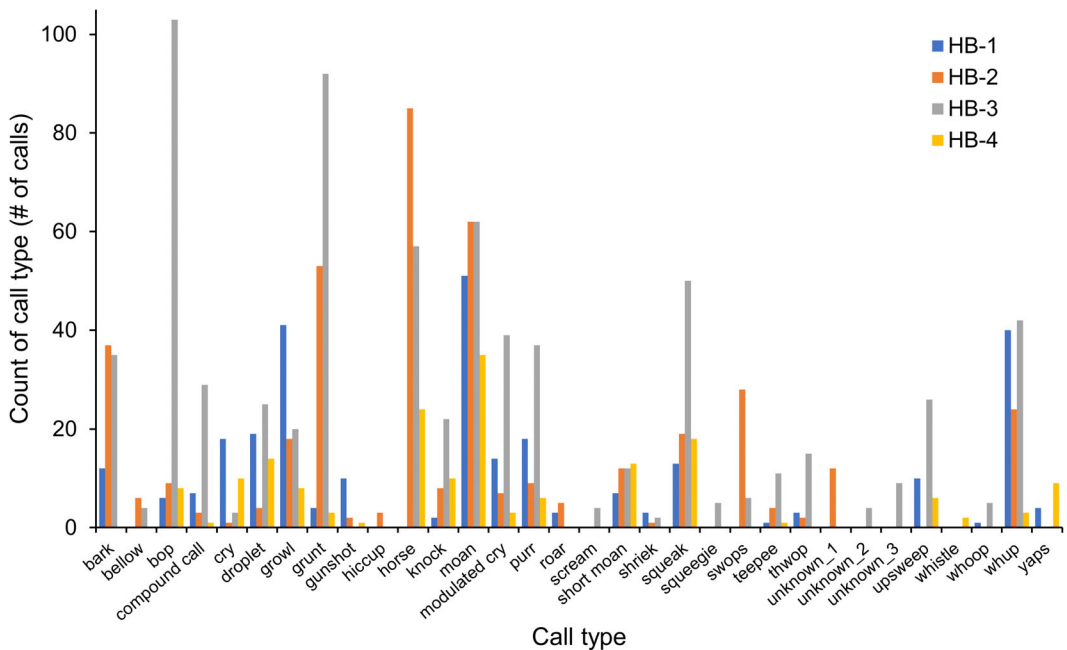
(Continues)

TABLE 3 (Continued)

Call type	Total calls (N)	Clean calls (n)	Min freq (Hz)	Max freq (Hz)	Peak freq (Hz)	Freq range (Hz)	Duration (s)
thwop	20	19	75 ± 20	707 ± 289	126 ± 60	632 ± 289	0.86 ± 0.3
unknown 1	12	11	1044 ± 421	2,318 ± 240	1,877 ± 317	1,274 ± 374	0.81 ± 0.27
unknown 2	4	4	374 ± 59	712 ± 115	551 ± 104	339 ± 63	0.55 ± 0.25
unknown 3	9	9	117 ± 77	790 ± 158	380 ± 173	674 ± 185	0.94 ± 0.23
upsweep	42	28	119 ± 46	487 ± 110	206 ± 77	369 ± 117	0.3 ± 0.09
whistle	2	2	692 ± 9	1,118 ± 309	773 ± 0	426 ± 300	0.85 ± 0.18
whoop	6	5	254 ± 79	648 ± 163	478 ± 178	394 ± 132	0.57 ± 0.12
whup	109	78	89 ± 30	600 ± 182	139 ± 72	510 ± 184	0.8 ± 0.24
yaps	13	6	163 ± 64	467 ± 136	297 ± 107	304 ± 131	0.28 ± 0.04
Call type	Start freq (Hz)	End freq (Hz)	Change in freq (Hz)		Calls per pure bout	N Harm	N Infect
bark	131 ± 51	414 ± 204	283 ± 184		1 ± 1	3 ± 2	0 ± 0
bellow	876 ± 328	845 ± 327	-31 ± 90		1 ± 0	12 ± 7	0 ± 0
bop	125 ± 53	125 ± 53	0 ± 0		1 ± 1	0 ± 0	0 ± 0
compound call	159 ± 109	427 ± 351	268 ± 308		1 ± 0	8 ± 6	1 ± 1
cry	485 ± 126	423 ± 141	-62 ± 131		1 ± 0	2 ± 3	1 ± 1
droplet	179 ± 113	629 ± 156	450 ± 192		1 ± 1	0 ± 0	0 ± 0
growl	113 ± 50	110 ± 57	-3 ± 66		1 ± 0	3 ± 2	0 ± 1
grunt	96 ± 20	97 ± 22	1 ± 13		1 ± 0	5 ± 3	0 ± 0
gunshot	1008 ± 932	1008 ± 932	0 ± 0		1 ± 0	0 ± 0	0 ± 0
hiccup	302 ± 59	302 ± 59	0 ± 0		1 ± 0	0 ± 0	0 ± 0
horse	239 ± 101	239 ± 101	0 ± 0		4 ± 2	0 ± 0	0 ± 0
knock	188 ± 118	188 ± 118	0 ± 0		1 ± 0	0 ± 0	0 ± 0
moan	208 ± 89	229 ± 132	21 ± 131		1 ± 0	4 ± 4	1 ± 1
modulated cry	409 ± 231	931 ± 462	522 ± 446		1 ± 0	4 ± 4	1 ± 1
purr	193 ± 61	186 ± 80	-6 ± 82		1 ± 0	3 ± 3	0 ± 0
roar	260 ± 128	275 ± 154	15 ± 138		1 ± 0	7 ± 5	1 ± 1

TABLE 3 (Continued)

Call type	Start freq (Hz)	End freq (Hz)	Change in freq (Hz)	Calls per pure bout	N Harm	N Infect
scream	527 ± 111	559 ± 125	32 ± 74	1 ± 0	3 ± 1	1 ± 1
short moan	215 ± 95	248 ± 96	32 ± 75	1 ± 0	1 ± 1	0 ± 0
shriek	1460 ± 1202	4055 ± 4880	2,595 ± 4,161	1 ± 0	3 ± 1	1 ± 1
squeak	2068 ± 821	2068 ± 821	0 ± 0	1 ± 1	0 ± 0	0 ± 0
squeegie	403 ± 253	536 ± 244	133 ± 330	1 ± 0	3 ± 1	9 ± 5
swops	145 ± 49	188 ± 58	43 ± 24	3 ± 2	7 ± 3	0 ± 0
teepee	109 ± 18	143 ± 40	34 ± 40	2 ± 2	6 ± 3	1 ± 1
thwop	486 ± 149	684 ± 220	198 ± 210	1 ± 0	1 ± 1	1 ± 0
unknown_1	1104 ± 424	1108 ± 413	4 ± 29	1 ± 0	19 ± 8	0 ± 0
unknown_2	541 ± 205	605 ± 187	65 ± 212	1 ± 0	2 ± 0	1 ± 1
unknown_3	176 ± 75	655 ± 216	478 ± 201	1 ± 0	2 ± 1	0 ± 0
psweep	125 ± 48	468 ± 173	343 ± 185	1 ± 1	0 ± 1	0 ± 0
whistle	1165 ± 217	709 ± 35	-456 ± 182	1 ± 0	0 ± 0	1 ± 1
whoop	239 ± 56	610 ± 167	372 ± 137	1 ± 0	1 ± 1	0 ± 0
whup	145 ± 50	621 ± 258	476 ± 253	1 ± 0	1 ± 1	1 ± 0
yaps	228 ± 95	246 ± 133	18 ± 115	1 ± 0	3 ± 3	0 ± 0

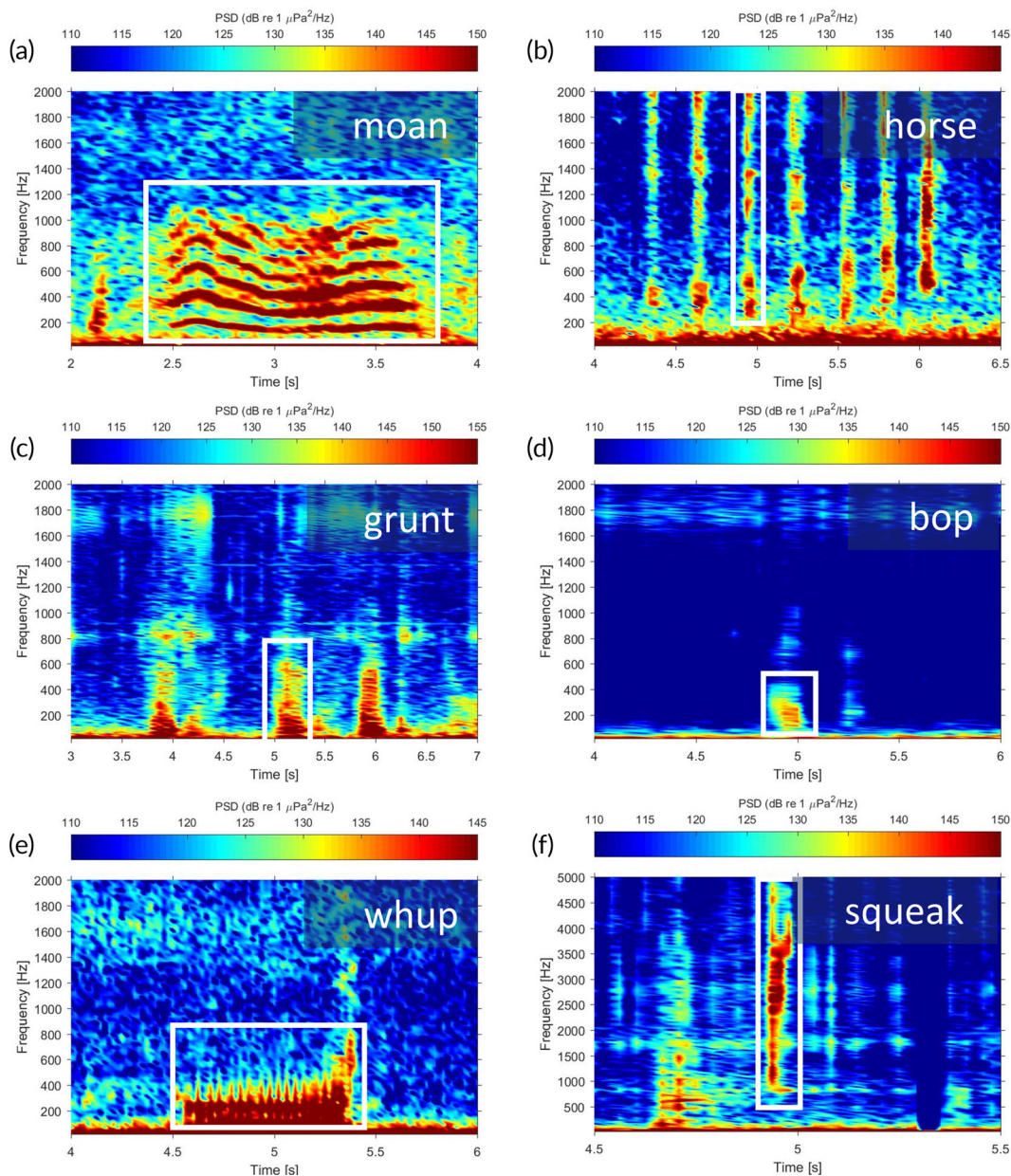


**FIGURE 1** Counts of calls for each social call type recorded during four tag deployments on humpback whales HB-1 to HB-4. All calls were included (with clipping and overlap) if they were identifiable. All calls for pure bouts with greater than one call were also included.  $N = 1,595$  calls.

had low peak frequencies ( $116 \pm 46$  Hz) and were short in duration ( $0.28 \pm 0.06$  s; Table 3, Figure 2c). Bops were the fourth most common call with 126 bops across all deployments (Table 3) and were extremely common for deployment HB-3 but were uncommon for the other deployments (Figure 1). Bops were generally low in frequency (peak frequency =  $239 \pm 136$  Hz), broadband ( $631 \pm 290$  Hz), and very short in duration ( $0.13 \pm 0.02$  s; Table 3, Figure 2d). The fifth most common call was whup, with a count of 109 calls (Table 3) and was particularly common in the first three deployments (Figure 1). Whups were intermediate in duration ( $0.8 \pm 0.24$  s) and low in peak frequency ( $139 \pm 72$  Hz; Table 3). Whups were highly stereotyped calls that began with a growl but ended in an upswipe, which is why there was a greater frequency range and maximum frequency for whups compared to growls (Table 3, Figure 2e). The sixth most common call was squeak with 100 total calls detected (Table 3). Squeaks were very short with an average duration of  $0.12 \pm 0.03$  s, broadband (frequency range =  $2,158 \pm 907$  Hz) and were high in peak frequency ( $2,791 \pm 865$  Hz; Table 3, Figure 2f).

### 3.3 | Statistical classification of humpback whale social calls

A total of 20 manually classified social call types were included in the automated analyses, with a minimum of 10 and maximum of 135 calls within a class (Table 4). The total sample size for the cluster analysis was 966 calls. The cluster analysis identified four dominant clusters of the humpback social calls (Table 4, Figure 3), which were driven mostly by call duration, low frequency, high frequency, and end frequency (Figure 4). Cluster 1 grouped most of the longer duration calls together, with an interquartile range of delta time between 1.3 and 2.6 s, mean of 2.0 s, and median of 1.9 s. The third quartile of the remaining three clusters was  $<1$  s, although cluster 4 had a very small interquartile range for delta time between 0.12 and 0.15 s. Clusters 2 and 3 had similar ranges of values for delta time and low frequency, but cluster 3 tended to have higher values than cluster 2 for both high frequency and end



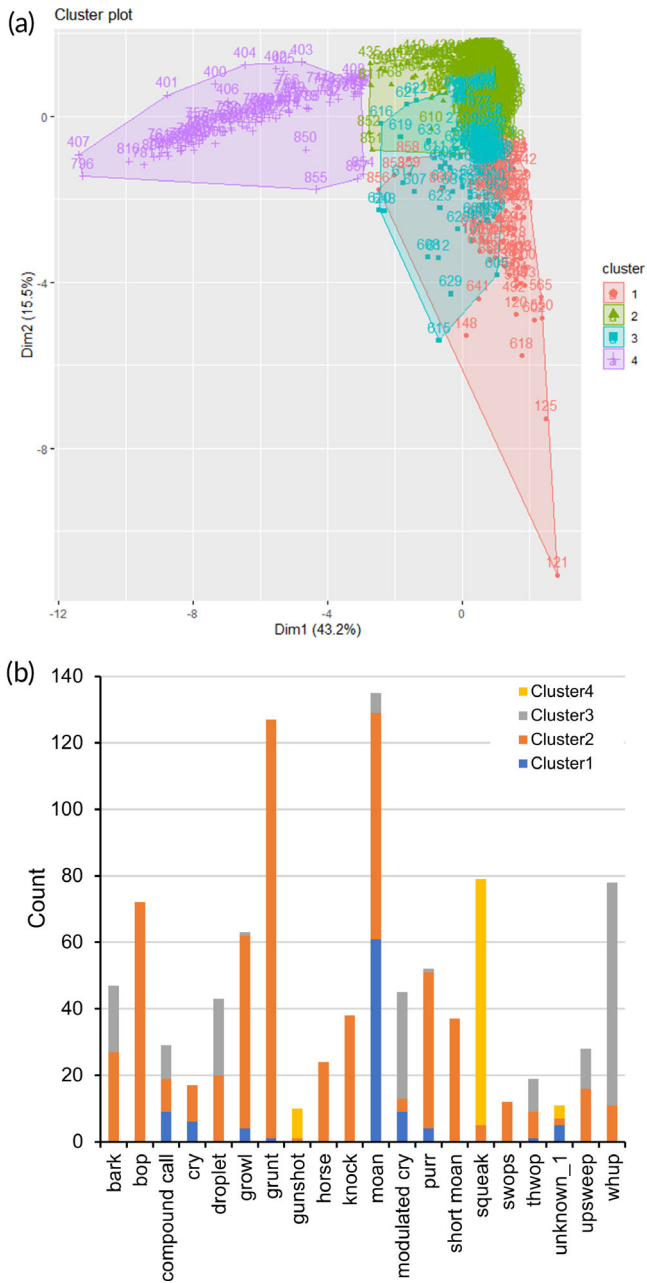
**FIGURE 2** Representative spectrograms of common humpback whale social call types (outlined with white boxes) determined by aural-visual classification in Raven Pro 1.6.1. Social calls were recorded during four tag deployments on humpback whales. Moan (a), horse (b), grunt (c), bop (d), whup (e), and squeak (f). Spectrograms were built with a window size of 4,000 samples and a Hann window with 50% overlap. Note that the frequency, time, and amplitude scales vary among panels.

frequency. Cluster 4 had the lowest range of delta time among all the clusters but had much higher values than all other clusters for low frequency, high frequency, and end frequency.

Cluster 4 had the strongest groupings of manually classified call types, with gunshots and squeaks being the main calls within this cluster. No other clusters had such a clear grouping of calls, although some individual call types

**TABLE 4** Classification statistics for the 20 social call types used in the cluster analysis and random forest classifier, including the sample size for each call type, the percentage of each call type classified to each cluster (with the highest percentage bolded), and the percent accuracy of the classification by the random forest.

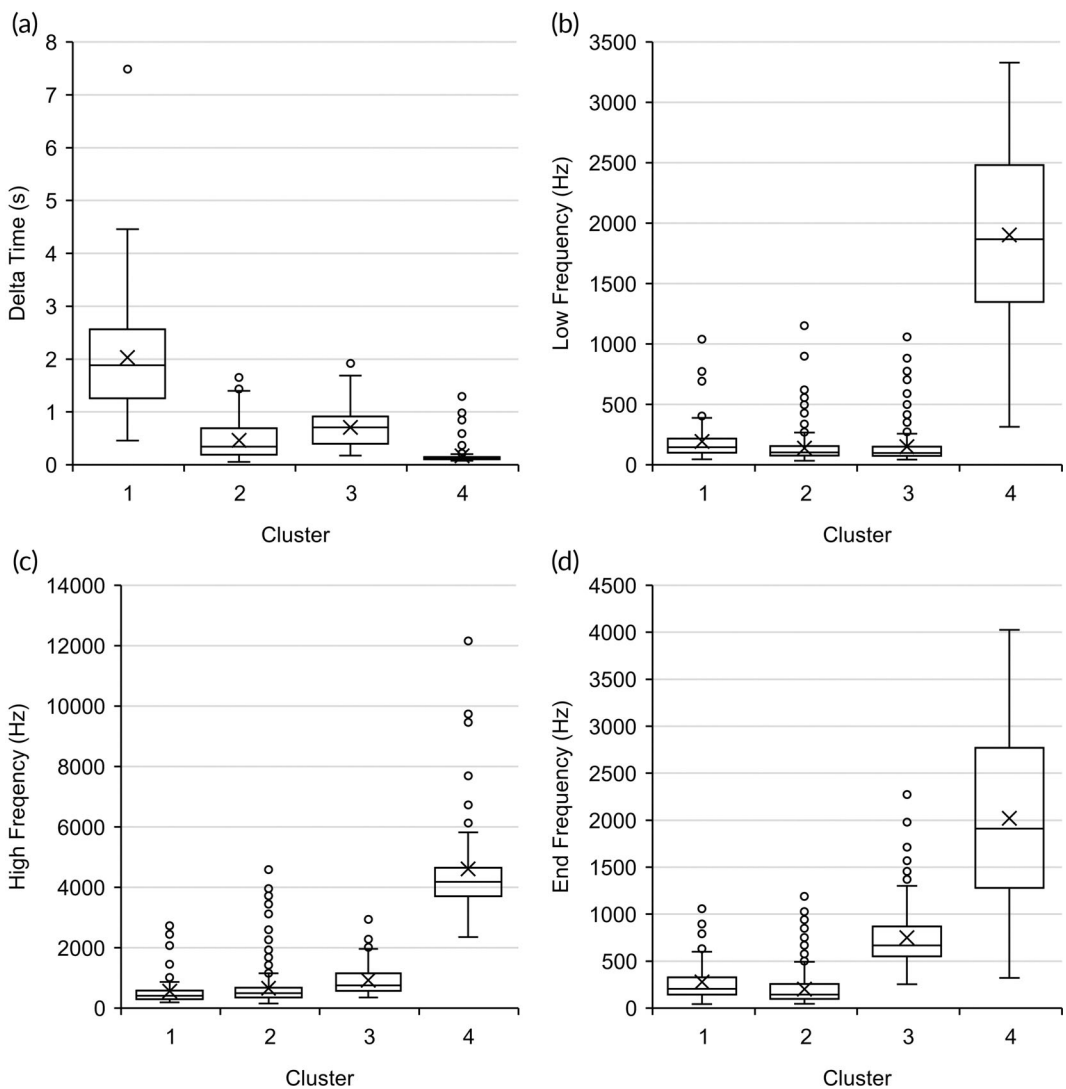
Call type	Total calls (n)	Cluster percentage	Random forest accuracy
bark	47	<b>57% Cluster 2</b> 43% Cluster 3	100%
bop	72	<b>100% Cluster 2</b>	93%
compound call	29	31% Cluster 1 <b>34% Cluster 2</b> <b>34% Cluster 3</b>	40%
cry	17	35% Cluster 1 <b>65% Cluster 2</b>	33%
droplet	43	47% Cluster 2 <b>53% Cluster 3</b>	100%
growl	63	6% Cluster 1 <b>92% Cluster 2</b> 2% Cluster 3	69%
grunt	127	1% Cluster 1 <b>99% Cluster 2</b>	100%
gunshot	10	10% Cluster 2 <b>90% Cluster 4</b>	50%
horse	24	<b>100% Cluster 2</b>	60%
knock	38	<b>100% Cluster 2</b>	100%
moan	135	45% Cluster 1 <b>50% Cluster 2</b> 5% Cluster 3	81%
modulated cry	45	20% Cluster 1 9% Cluster 2 <b>71% Cluster 3</b>	89%
purr	52	8% Cluster 1 <b>90% Cluster 2</b> 2% Cluster 3	90%
short moan	37	<b>100% Cluster 2</b>	100%
squeak	79	6% Cluster 2 <b>94% Cluster 4</b>	94%
swop	12	<b>100% Cluster 2</b>	100%
thwop	19	5% Cluster 1 42% Cluster 2 <b>53% Cluster 3</b>	75%
unknown 1	11	<b>46% Cluster 1</b> 18% Cluster 2 36% Cluster 4	100%
upsweep	28	<b>57% Cluster 2</b> 43% Cluster 3	83%
whup	78	14% Cluster 2 <b>86% Cluster 3</b>	94%



**FIGURE 3** Four clusters identified in the cluster analysis (a) and the groupings of humpback whale social call types among the clusters (b).

were only found predominantly in one cluster, specifically all bops, horses, knocks, short moans, and swops were 100% within cluster 2, and the majority of growls, grunts, and purrs were also in cluster 2. Longer calls, like compound calls, cries, and moans made up a high proportion of cluster 1, but those calls were also categorized in other clusters. Whups and modulated cries were predominantly classified in cluster 3.

The random forest classification was able to successfully converge for all 20 manually classified call types (Figure 5) and was able to predict the test data with 87.6% accuracy (Table 4). Fourteen of the call types in the test

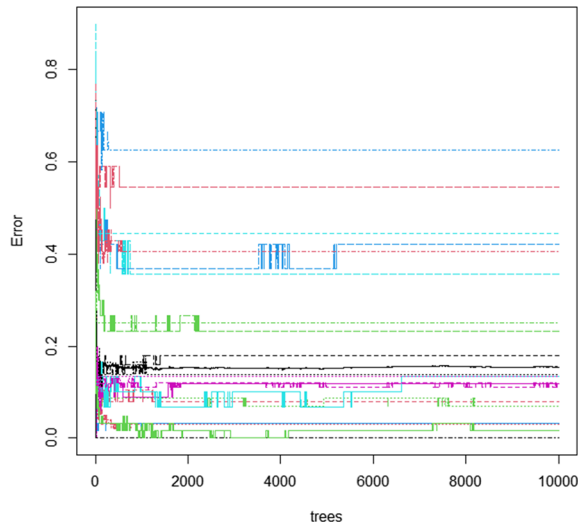


**FIGURE 4** Top four important humpback whale social call parameters for grouping four clusters of call types, including delta time (a), low frequency (b), high frequency (c), and end frequency (d).

data set were classified correctly 80% of the time, with seven being correct 100% of the time. Only three call types were classified correctly <50% of the time, specifically gunshots, compound calls, and cries. These incorrectly classified call types also had low sample sizes of 10 for gunshots, 29 for compound calls, and 17 for cries, although other call types with low sample size (e.g., unknown call 1,  $n = 11$ ; swop,  $n = 12$ ) were correctly classified 100% of the time.

### 3.4 | Comparisons of common social calls across studies

We compared the peak frequency and duration of five common social call types identified in our study and in two other studies in both the Atlantic and Pacific Oceans (Epp et al., 2021; Fournet et al., 2018c), representing multiple



**FIGURE 5** Random forest error plot showing error rates for the 20 humpback whale social call types as the number of trees in the forest increases.

**TABLE 5** Summary statistics for humpback whale call parameters per call type and location. First value for each call type is mean peak frequency (Hz)  $\pm$  SD for British Columbia (BC), southeast Alaska (SEAK), and Massachusetts Bay (MB) and  $\pm$  SE for Newfoundland (NL) and Hawaii (HI). Second value for each call type is mean duration (s)  $\pm$  SD for BC, SEAK, and MB and  $\pm$  SE for HI and NL. Duration is the length of the call for BC, HI, and NL and 90% of the duration of the selected call for SEAK and MB. Data in the table for SEAK and MB are taken from Table 3 in Fournet et al. (2018c). Data for NL and HI are taken from Table 2 in Epp et al. (2021).

Call type	BC	SEAK	MB	NL	HI
Growl	110 $\pm$ 35	116 $\pm$ 62.6	87.4 $\pm$ 15.1	120.31 $\pm$ 3.32	202.37 $\pm$ 30.93
	0.87 $\pm$ 0.3	0.7 $\pm$ 0.3	0.8 $\pm$ 0.24	0.69 $\pm$ 0.01	0.79 $\pm$ 0.07
Whup	139 $\pm$ 72	128 $\pm$ 70.3	94.9 $\pm$ 26.2	108.27 $\pm$ 3.41	249.1 $\pm$ 60.48
	0.8 $\pm$ 0.24	0.7 $\pm$ 0.2	0.6 $\pm$ 0.18	0.67 $\pm$ 0.02	0.71 $\pm$ 0.06
Droplet	312 $\pm$ 143	252 $\pm$ 120	187 $\pm$ 62.6	269.93 $\pm$ 12.82	266.27 $\pm$ 5.72
	0.27 $\pm$ 0.06	0.3 $\pm$ 0.16	0.4 $\pm$ 0.2	0.24 $\pm$ 0	0.34 $\pm$ 0
Swops	234 $\pm$ 73	214 $\pm$ 85.6	159 $\pm$ 54.3	215.97 $\pm$ 5.38	420.71 $\pm$ 33.96
	0.29 $\pm$ 0.08	0.3 $\pm$ 0.2	3.9 $\pm$ 4.2	0.25 $\pm$ 0	0.26 $\pm$ 0.01
Teepee	240 $\pm$ 91	154 $\pm$ 70.3	79.2 $\pm$ 28.8	152.14 $\pm$ 7.66	269.62 $\pm$ 42.43
	0.43 $\pm$ 0.1	0.4 $\pm$ 0.23	1.1 $\pm$ 1.77	0.35 $\pm$ 0.01	0.29 $\pm$ 0.01

humpback whale populations (Table 5). These five common social call types were growl, whup, droplet, swop, and teepee. Duration was relatively consistent within call types across studies, other than Massachusetts Bay having much longer durations of swops (with high, overlapping error with measurements from other studies) than in the other studies. Peak frequency was a bit more variable within call types across studies. Droplet was relatively consistent and overlapping across studies, although lowest values were recorded in Massachusetts Bay for peak frequency. Growl, whup, and swop peak frequencies were relatively consistent across all locations except Hawaii, which had higher peak frequency than all other sites for all three of these call types. Teepee had the most variable peak frequency across studies with Massachusetts Bay having the lowest peak frequency, southeast Alaska and Newfoundland having intermediate peak frequency, and BC and Hawaii having the highest peak frequency.



Variation in call parameters among regions could be due to a variety of reasons. The studies by Fournet et al. (2015, 2018a, 2018c) and Epp et al. (2021) used either moored or dip hydrophones deployed from a drifting vessel whereas our study used a whale-borne tag fitted with a hydrophone. Tags capture quieter and higher frequency sounds that could be attenuated or distorted while traveling long distances to a hydrophone (Stimpert et al., 2011), and thus could explain some of the variation in acoustic parameters among studies. Further, individual differences among animals such as body size, sex, and motivational state due to social and behavioral contexts could cause differences in the acoustic characteristics of calls among populations and individuals (August & Anderson, 1987; Dunlop, 2017; Owings & Morton, 1998). However, this within-category/call variation occurs in most vertebrates that vocalize and does not inhibit classifying the calls into various call types and comparing them among populations (Ford, 1991; Fournet et al., 2018c; Rekdahl et al., 2013; Riesch et al., 2006). Differences in the environmental surroundings during recording such as sound levels from, for example, vessel noise or wind and waves could also explain some of the among-population variation in the acoustic properties of the social calls (Fournet et al., 2018d; Parks et al., 2016), as could flow noise recorded on the animal-borne tag used in our study. Finally, whales from different populations could have had a different dialect of social calls due to vertical (mother to offspring) and cultural transmission, resulting in slightly different call parameters for the same social calls.

The five social calls common across populations (droplets, swops, teepees, growls, and whups) may facilitate social interactions (Dunlop et al., 2008; Fournet, 2014; Wild & Gabriele, 2014). It has been proposed that pulsed, repeated social calls such as swops, teepees, and droplets are used to communicate with closely associated conspecifics on foraging grounds (Fournet, 2014). Rates of pulsed social calls increase when humpbacks aggregate and vocalizations in general get increasingly complex as social interactions intensify (Fournet, 2014). In our study, the large number of whales present in the vicinity of the tagged whales could explain why other short, pulsed social calls such as horses, bops, grunts, and barks were common (Table 3) and thus likely serve a social function. This was especially true for two deployments that had >30 whales in the vicinity of the tagged whale. These deployments (HB-2 and HB-3) had the highest counts of pulsed social calls, as well as the highest diversity of call types and counts of total social calls in this study (Figure 1). The whup and growl call types specifically are used by many humpback populations and have been documented on breeding and foraging grounds as well as along migration routes, indicating persistence over space and time (Dunlop et al., 2008; Epp et al., 2021; Fournet et al., 2015, 2018a; Recalde-Salas et al., 2020). Many studies have related these call types to serving a contact function (e.g., Dunlop et al., 2008; Wild & Gabriele, 2014). These low frequency social calls can travel for several kilometers and thus can play an important role in long-range communication. Wild & Gabriele (2014) found that whups often had “counter-calling” properties where the signal-to-noise ratios (SNRs) alternated back and forth, suggesting that two whales were repeating the call to each other. Whups and growls are among the most common call types in southeast Alaska (Fournet, 2014) and Hawaii (Epp et al., 2021), as they were in our data (Table 3), and most likely serve as an important communication signal. Future studies could take a more experimental approach and provide playbacks of these contact social calls to determine if and how conspecifics in the surrounding area respond. Responses to the playbacks could help resolve the context of the social calls. Analysis of future and archived tagging data from across years and migratory regions could examine where these proposed communicative social calls occur in the water column over time. This analysis could be especially useful for the highly stereotyped, widely distributed, and well-studied whup call to delineate how this call type relates to the diving behavior of humpback whales.

In our study, cries had a peak frequency of  $469 \pm 91$  Hz and a duration of  $2.20 \pm 1.62$  s and were acoustically similar to feeding calls in southeast Alaska. Feeding calls in southeast Alaska are reported at peak frequencies of around 500 Hz and  $3.6 \pm 2.8$  s to  $16.6 \pm 23.1$  s in duration, and occasionally may occur in multiple bouts (Barlow et al., 2019; Fournet et al., 2015, 2018a). The southeast Alaska feeding calls are persistent through time and are associated with feeding on Pacific herring (Fournet et al., 2018a; Sharpe, 2001). Herring have a hearing range most sensitive between 200 and 500 Hz and will “flee and clump” in response to the humpback feeding calls, aiding in effective foraging for the whales (Cerchio & Dalheim, 2001; Mann et al., 2005; Sharpe, 2001). Feeding calls mostly occur in groups of whales to facilitate cooperative group foraging (Cerchio & Dalheim, 2001; D’Vincent et al., 1985;

Sharpe, 2001), but are also produced by solitary whales, indicating a function for manipulating prey (Fournet et al., 2018b). Foraging strategies associated with feeding calls have largely involved the production of bubble nets with surface lunges by humpbacks (Sharpe, 2001), and occasionally subsurface lunges without bubble nets (Fournet et al., 2018b). For example, Huang et al. (2016) found that humpback cries on northeastern Georges Bank (northwest Atlantic) were ~ 5 s long and had frequencies around 500 Hz. They found that cries occurred at time periods and locations that overlapped with areas of dense Atlantic herring (*Clupea harengus*) shoals located at depths of 80–200 m, indicating that these vocalizations served a foraging function. The authors relate the feeding cries observed on northeastern Georges Bank to serving a similar purpose as those produced in southeast Alaska for bubble net feeding. During the tag deployments from which the hydrophone data for this study were obtained, subsurface prey sampling with a scientific echo sounder was conducted (67, 125, and 200 kHz frequencies). Echo sounder data showed a dense prey layer above the seafloor between 100 and 180 m, consistent with dense aggregations of fish and zooplankton. In addition, a molecular and visual analysis of humpback whale fecal samples obtained during the tagging and acoustic prey sampling revealed fish, euphausiids, and bottom-dwelling crustaceans (Reidy et al., 2022). Also, no surface foraging activity was observed during any of the deployments (R.R., personal observation). As a result of the similar depths of prey between our study and the study by Huang et al. (2016), and the similarities in acoustic parameters of cries in our study compared to cries and feeding calls in the studies mentioned above, we can hypothesize that cries serve a foraging function rather than a socializing function for humpback whales. Further tagging studies on foraging grounds in BC would be useful for determining if cries are associated with foraging behavior at depth. Cries could be used in coordinating closely associated whales while foraging, recruiting more whales for group foraging activities, or to manipulate the prey in some way.

Although our study adds to the knowledge of call types produced by humpback whales on foraging grounds, there were limitations and other factors to be considered and addressed by future studies. First, the main obstacle for studies that use tags is the difficulty in obtaining robust sample sizes due to high field costs and inherent challenges involved in accessing the deeply foraging whales, often in harsh conditions (Godwin et al., 2016). This was a factor in our study with only four whales being tagged. Future studies could record more humpbacks in this area and in other BC feeding areas to add to the knowledge of the call repertoire of humpbacks in this region. In all studies that involve aurally and visually classifying call types and then comparing those call types to those in published studies, there is some measure of human error, as comparing whale sounds from published spectrograms and quantitative call parameters from other regions poses a challenge (Stimpert et al., 2011). This was the case in our study where there were no call types from humpback whales in BC with which to compare. To alleviate this issue, future studies should incorporate spectrograms, quantitative parameters of social calls, recording information, and sound files of the call types to effectively compare call types among regions and even among different species (Fournet et al., 2015; Stimpert et al., 2011). There were also discrepancies among studies for the names of social calls and thus there is a need for broader, detailed call type classifications agreed upon by researchers around the world. Furthermore, there were differences in the lengths of hydrophone deployments with HB-4 being by far the shortest (54 min). This should be considered when interpreting the low number of social calls observed for this deployment (Table 1, Figure 1). Also, some call types were less common than others with lower sample sizes, causing call parameters measured for rare call types to be less robust and more variable than common call types (Table 3).

This study provides the first quantification of call types made by foraging humpback whales in southern British Columbia and adds to the global call catalog of humpback whale social calls. Humpback calls are socially and behaviorally context-specific, where some are used to facilitate foraging activities and others are used for social interactions. Many pulsed social calls such as droplets and swops, as well as low frequency social calls such as whups, thwops, and growls have been related to a communication function. Conversely, cries in BC likely serve a foraging function similar to cries and feeding calls in southeast Alaska and on northeastern Georges Bank. Recently repopulated foraging areas in southern BC are highly productive waters for humpbacks that result in dense aggregations of whales with complex social, foraging, and vocal behaviors. The vocal and diving behaviors of humpbacks in this area are relatively unknown and future studies need to focus on these aspects to gain insight into the ecology of

humpbacks and how they are using their environment to perform vital life functions like communicating and foraging. This is especially important given the overlap of shipping traffic in key foraging areas, where vessel noise can mask ecologically important vocalizations by humpbacks (Erbe et al., 2012; Parks et al., 2016), and where the whales are physically vulnerable to ship strikes (Nichol et al., 2017).

## ACKNOWLEDGMENTS

We sincerely thank Simon Pidcock and Jared Towers for their fieldwork support and Juliet Rowe for her analytical assistance, as well as helpful reviews by two anonymous reviewers. Funding was provided by grants from the NSERC Discovery program and the Liber Ero Foundation (to F.J.) and through a MITACS Accelerate fellowship in partnership with the Pacific Whale Watch Association and Shaw Centre for the Salish Sea, and the Eugene Maughan Scholarship from the Western Division of the American Fisheries Society (to R.R.). Data were collected under DFO permit MML-45 and University of Victoria animal use protocol 2017-009.

## AUTHOR CONTRIBUTIONS

**Zoe A. Molder:** Conceptualization; formal analysis; visualization; writing – original draft. **William D. Halliday:** Conceptualization; data curation; formal analysis; methodology; project administration; resources; software; supervision; validation; visualization; writing – original draft; writing – review and editing. **Rhonda Reidy:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; validation; visualization; writing – review and editing. **Chloe N. Kraemer:** Formal analysis; writing – review and editing. **Francis Juanes:** Conceptualization; funding acquisition; project administration; resources; supervision; validation; writing – review and editing.

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## SUPPORTING INFORMATION

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**How to cite this article:** Molder, Z. A., Halliday, W. D., Reidy, R., Kraemer, C. N., & Juanes, F. (2024). Humpback whale (*Megaptera novaeangliae*) social calls in southern British Columbia. *Marine Mammal Science*, e13138. <https://doi.org/10.1111/mms.13138>