PUTATIVE CONTACT CALLS MADE BY HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN SOUTHEASTERN ALASKA

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Résumé

Décrivant les propriétés acoustiques et les habitudes d'utilisation de vocalisations de baleine est essentielle pour documenter leurs fonctions et leur importance biologique. Ici, les auteurs décrivent les caractéristiques acoustiques et les modèles d'occurrence de la vocalisation plus courante de la baleine à bosse (Megaptera novaeangliae) sur son sud-est de l'Alaska été : un simple appel modulés en fréquence appelés les « WHUP ». Les auteurs ont examiné les 59 jours choisis au hasard de données continues enregistrement d'un hydrophone ancré dans le Parc National Glacier Bay, de mai à septembre 2007-2010. À l'aide d'un détecteur automatique de 1326 whups ont été identifiés, et leurs caractéristiques physiques mesurés. On a mesuré les deux composantes distinctes de chaque whup : un grognement de basse fréquence avec un ton fondamental et une large bande upsweep. Le composant de grondement en moyenne 0,47 secondes, dans une plage de fréquence Hz 56-187 et avait une fréquence maximale de 94 Hz. Le composant upsweep moyenne durée de 0,19 secondes sur une gamme de services à large bande de fréquence de 52-743 Hz, avec une fréquence maximale de 93 Hz. De la 1326 whups identifiés, 61 % étaient en garde plusieurs groupements. Whups étaient tout aussi susceptibles de se produire pendant la nuit et pendant la journée (t =-0.5327, df = 103.9, p = 0.5954). En raison de ses modes d'utilisation et de la similitude acoustique d'autres cris de contact de mysticètes, les auteurs pensent que la communication entre les groupes est la fonction principale de cet appel.

Mots clefs : baleine à bosse; whup; wop; communication; cri de contact

Abstract

Describing the acoustic properties and usage patterns of whale vocalizations is essential for documenting their functions and biological importance. Here we describe the acoustic characteristics and patterns of occurrence of one of the most common vocalizations of the humpback whale (*Megaptera novaeangliae*) on its southeastern Alaska summer feeding grounds: a simple frequency-modulated call referred to as the "whup." We examined 59 randomly selected days of continuous data recorded from an anchored hydrophone in Glacier Bay National Park from May through September 2007-2010. Using an automated detector, 1326 whups were identified and their physical characteristics measured. Two distinct components of each whup were measured: a low-frequency growl with a fundamental tone, and a broadband upsweep. The growl component averaged 0.47 sec in duration, within a 56-187 Hz frequency range, and had an amplitude peak at a frequency of 94 Hz. The upsweep component averaged 0.19 sec in duration over a broadband frequency range of 52-743 Hz, with a peak frequency of 93 Hz. Of the 1326 whups identified, 61% were in multiple-call groupings. Whups were equally likely to occur at night and during the day ($t= -0.5327$, $df=103.9$, $p=0.5954$). Due to its patterns of usage and acoustic similarity to other mysticete contact calls, the authors speculate that inter-group communication is the main function of this call.

Keywords: humpback whale; whup; wop; communication; contact call

1 Introduction

Like other baleen whales, humpback whales (*Megaptera novaeangliae*) produce vocalizations in a variety of social contexts. Humpback whales migrate seasonally between high-latitude feeding grounds and low-latitude wintering grounds where mating and calving occur (Dawbin 1966). The importance of the long, complex winter songs made by males to this species' mating system has been a main focus of research in the decades since the songs were first described (Payne and McVay 1971, Winn *et al.* 1981, Mobley *et al.* 1988, Frankel *et al.* 1995, Darling and Berube 2001, Noad *et al.* 2001, Darling *et al.* 2006, Smith *et al.* 2008). Song also occurs in the feeding areas and along migratory routes (Gabriele and Frankel 2001, Smith *et al.* 2008, Charif *et al.* 2001). Non-song "social sounds" in competitive groups of males in the wintering grounds are non-patterned utterances and sounds of physical contact that are thought to convey the aggression and agitation of group members (Tyack 1983, Silber 1986, Frankel *et al.* 1995). Migrating humpback whales produce a variety of social vocalizations that are believed to mediate social interactions and group composition (Dunlop *et al.* 2007, 2008). A variety of humpback whale vocalizations have been documented on their summer feeding grounds (Thompson *et al.* 1986, Cerchio 1996, Stimpert *et al.* 2011, Fournet 2014) only some of which appear to be directly related to feeding (Baker 1985, D'Vincent *et al.* 1985, Cerchio and Dahlheim 2001, Stimpert *et al.* 2007).

While the vocal repertoire of humpback whales in their feeding grounds has previously been documented, little

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work has quantified signal variation or examined patterns of occurrence and social function. The current study makes the first thorough, quantitative description of one of the most common sounds made by humpback whales in southeastern Alaska - a simple, upsweep call we refer to as a 'whup' in an effort to understand its biological significance and usefulness for passive acoustic monitoring.

This call is similar in description to other calls recorded elsewhere in Alaska, referred to by the name 'whoop' (Thompson *et al.* 1986, Cerchio 1996). It also has similar properties to a call referred to as a 'wop,' described in the east Australian migratory route (Dunlop *et al.* 2007), as well as the North Atlantic feeding grounds (Stimpert *et al.* 2011). Part of our analysis compared measurements of the calls between the different populations, to determine if it was indeed the same call. These previous studies did not attempt to explore behavioral association, patterns of occurrence, or function of the call.

North Pacific humpback whales congregate on a small number of sub-tropical breeding grounds including Hawai'i, Mexico and Japan in winter, and separate into genetically-distinct, maternally-directed feeding grounds, including southeastern Alaska, in the spring, summer and fall (Baker *et al*. 1986, 1990). Humpback whale behavior and population composition are dramatically different in feeding versus breeding areas (Baker and Herman 1984, Baker *et al.* 1998). The southeastern Alaska feeding aggregation is composed of whales that return annually to the same areas to exploit patchy food resources that move and change over the course of the summer (Straley 1994). Feeding whales are mostly solitary or in the company of one other whale with whom they have often associated many times before, although larger coordinated feeding groups also occur (Baker 1985, D'Vincent *et al.* 1985). Wintering humpback whale behavior is centered around calf-rearing and competition for mating, with little site fidelity or repeat associations among whales between days or years (Baker 1985, Craig and Herman 1997).

Every year over 200 North Pacific humpback whales spend the summer months (primarily May through September) feeding in the waters of Glacier Bay National Park (GBNP) in southeastern Alaska (Fig 1) (Neilson and Gabriele 2014). The whales share the bay with many other acoustically active marine mammals including harbor seals, killer whales, and harbor porpoises (Dahlheim *et al.* 2009). Adding to this acoustic soundscape is the motorized vessel traffic that brings hundreds of thousands of visitors to the park each year.

Baleen whale calling behavior has been attributed to a few main functions including breeding displays, facilitation of feeding, contact calling and exploring their physical environment (Clark 1990, Tyack and Clark 2000). Determining the function or functions of a specific call type is challenging but extremely valuable in assessing human impacts to the acoustic environment. Our study aims to describe the physical characteristics and usage patterns of the whup in eastern North Pacific humpback whales, using continuous acoustic recordings from an anchored hydrophone in the mouth of Glacier Bay, southeastern Alaska. It is important to examine the properties and usage of this call to understand its biological significance and the degree to which vessel-generated underwater noise could affect humpback whale communication in high-latitude feeding grounds.

2 Methods

2.1 Acoustic Monitoring System

In 2000, GBNP installed a bottom-mounted (depth = 52m), calibrated ITC 8215A hydrophone with integrated preamplifier (sensitivity -174 dB re 1 V/µPa at 1 to 10,000 Hz), near the mouth of Glacier Bay (Fig 1, Kipple and Gabriele 2003). The hydrophone is mounted 1m from the seafloor on a metal tripod base. A study in 2001 showed current at the site to have a mean speed of 3.34m/sec (±1.97s.d.). The hydrophone and its pre-amp were specifically designed in conjunction with a submersible 9.1 km cable to transmit data to a custom-built computer control unit that powers the hydrophone and serves as the electronic interface between the hydrophone and a computer. The computer is equipped with a 24-bit National Instruments PCI-4461 dynamic signal acquisition card, which performs signal conditioning and 22,050 Hz sample rate digitization of hydrophone signals into digital samples. Using custom software, the samples are saved on a hard drive as 5-minute long 24-bit AIFF files.

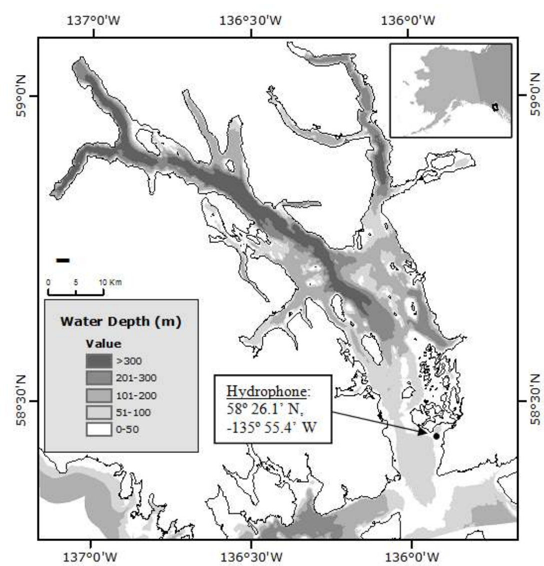

Figure 1: Map of Glacier Bay National Park (GBNP), Alaska, with • showing the location of the hydrophone.

2.2 Acoustic Detection

Humpback whales are known to occur in Glacier Bay, with peak abundance generally from May through September (Neilson and Gabriele 2014). Using samples from May-September over four years from 2007-2010 (612 days possible) we randomly selected four days from each month in which to detect whup calls from a list of eight days randomly generated for each month. If on a chosen date there were no acoustic data available or just a partial day's data, due to system outages or hydrophone maintenance, the next random date generated was used. Thus, a total of 59 days, over 20 months, were used to automatically detect whups, out of a possible 80 days.

Examples of whups from Glacier Bay recordings were examined to determine the frequency range of the call, which was from 40-1000Hz. Because the general frequency range of calls similar to the whup calls recorded in this experiment were also within 40-1000Hz (Cerchio 1996, Dunlop *et al.* 2007, Stimpert *et al.* 2011), a low-pass filter was applied and the AIFF files were decimated by a factor of 10 (sampling rate 2,205Hz) to reduce file size and computation time. All files for each day were loaded into XBAT (eXtensible BioAcoustic Tool, Cornell Lab of Ornithology 2002) and a template created from example whups from each month was used to automatically detect whups. Whups can be variable in their frequency range as well as their duration, so to minimize the number of whups the detector missed, multiple whup templates were used each month for various frequency ranges and durations. XBAT first scanned the entire day's audio files, during which time whups were detected and logged. Each detection was then manually checked to confirm reliability of the detector. If additional whups were found by the analyst during manual checks, they were also logged. If whup-like upsweeps were part of a song, we discarded them. We also discarded repetitive broadband upsweeps that occurred during a period of a variety of other social sounds. These were higher frequency upsweeps with an inter-call interval of <1 sec and duration <0.2 sec that occurred in conjunction with other sounds such as grunts, cries, or moans, (Silber 1986, Cerchio 1996). While sharing similar qualities with whups, the upsweeps accompanied by other sounds did not contain a growl component to the call, were higher in frequency, and always occurred in sets of 2 or more repetitions. They have been differentiated from whups [wops] by other authors (Dunlop *et al.* 2007, Stimpert *et al.* 2011), and referred to as pulse trains in this context (Stimpert *et al.* 2011). Thus, in concurrence with other studies which examined this vocalization, we created a library of stand-alone whups, that occurred without the presence of other social sounds or song units.

A clip of each whup was saved, and measurement parameters of each call were logged in a table. Parameters included were an individual ID number for each whup, start/end time, min/max frequency over a broadband frequency up to 1000Hz, and quality rating. Ambient noise samples were taken just after each whup to aid in quality coding with respect to signal-to-noise ratio (SNR). This signal-to-noise ratio measurement allowed the analyst to exclude calls that were not of high quality. Since the goal of this portion of the study was to accurately measure the acoustic properties of the whup, these noisy calls were excluded from analysis.

2.3 Whup measurement and analysis

All whups were loaded into Raven Pro 1.4 acoustic analysis software (Cornell Lab of Ornithology © 2003); a Hanning window was applied to the data, with a 512-point FFT, 80% overlap, and 30sec time window. The analyst coded each whup in the library with a quality rating of 1 to 5, based on the categories very poor, poor, fair, good, and excellent, with 1 being very poor and 5 being excellent. Selection of high quality whups was based primarily on the clarity of the call due to low ambient noise, high frequency range of between 40-700Hz, absence of other marine mammal vocalizations, and lack of interfering knocks and bumps on the hydrophone. A simple received signal-to-noise ratio (SNR) was also calculated using Raven Pro 1.4, and all high quality whups had an SNR ratio of 6dB or greater, similar to detection threshold values of between 6-10dB in bioacoustics literature (Jacobsen 1976, Dabelsteen *et al.* 1993, Good 1996, Stafford *et al.* 2007). Whups with all quality ratings were retained (n = 1326), but physical measurements were made only on the high quality calls (rated 4 or 5, SNR≥6dB). Based on these ratings, the 20 highest quality whups of each month were chosen, resulting in a total of 248 total high quality whups spread out amongst all months.

The individual growl and upsweep components of each whup were measured separately (Fig. 2). The two components are continuous in time but so distinctive that it was necessary to measure them individually. A 1-second ambient noise profile taken for each whup was measured for the SNR measurement (Fig. 2).

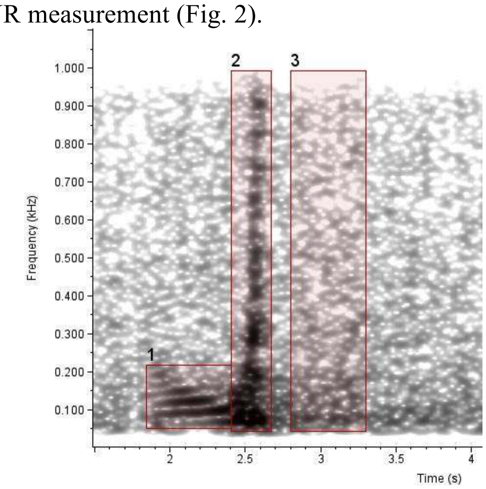

Figure 2: A spectrogram view of a single complete whup call. Three selections were taken for each whup, (1) the growl, (2) the upsweep, and (3) an ambient noise profile. Hanning window, window size 256 samples, DFT 512, 80% overlap.

For each growl and upsweep we used Raven Pro 1.4 to measure the following characteristics (Table 1): start/end time, duration, minimum and maximum frequency, peak frequency, bandwidth, and SNR. Minimum and maximum frequencies were the lowest and highest frequencies measured for each component of the call respectively. Peak frequency refers to the frequency of the spectral peak, where the most power spectral density of the call is found. Bandwidth was defined in Raven as the difference between the 5% and 95% frequencies of the signal. These measurement data were saved in text format and imported into a spreadsheet where summary statistics were calculated.

Table 1. Description of measurements taken of whups, as stated in Raven Pro 1.4 user manual. Selection boxes were created by the analyst, and measurements calculated by the program.

Measurement	Abbreviation	Description
Duration (sec)	Dur	Length of vocalization
Bandwidth	Bw	Difference between 5% and 95% frequencies
Min Frequency (Hz)	Fmin	Minimum Frequency
Max Frequency (Hz)	Fmax	Maximum Frequency
Peak Frequency (Hz)	Fp	Frequency of the spectral peak
Frequency Range	Fr	Max Frequency - Min Frequency

2.4 Whup measurement and analysis

To examine the usage patterns of whups, we used all 1326 detected whups, not just the highest quality calls. The separation time between consecutive whups was calculated and cumulative distribution charts of these measurements were generated using MATLAB. Our goal was to describe how whups are used, so the characteristics of multiple-call groupings of whups were examined.

To examine the relationship between whale presence and the number of whups, we used sighting data from a limited number of photo-identification surveys that occurred on the same days as our randomly selected whup analysis dates (n=16). We conservatively defined the area over which we presume that whups would be audible as those within line of sight (unobstructed by land) within 10 km of the hydrophone (Munger *et al.* 2011). Data were analyzed using a hypothesis correlation test against the null hypothesis that whup occurrence was not correlated with the number of whales in the area.

To determine whether calling behavior showed diurnal variability, we counted the number of whups that occurred during each hour of all 53 days on which whups occurred. Whups were coded based on whether they were between sunrise and sunset ("Day") or between sunset and sunrise ("Night"), based on the time of local sunrise and sunset on that day. Using the number of hours of daylight for each day, we calculated a rate of whups during the day and at night. We used a t-test to test the null hypothesis that whup rates were no different between day and night hours. A previous study of ambient noise in Glacier Bay found a diurnal rhythm of vessel traffic, with late night and early morning noise samples (between 21:00 and 05:00) much less likely to contain vessel noise compared to samples collected at other times of the day (Kipple and Gabriele 2003). This time period roughly corresponds with night in the study area in May through September. Thus, to quantify the difference in ambient noise between day and night, we used available ambient noise data samples from May through September 2007-2008 (GBNP unpublished data, after Kipple and Gabriele 2003), to sum the acoustic energy in the 40 to 1000 Hz one-third-octave bands. We also examined the signal to noise ratios (SNR) for whup samples from day vs. night.

3 Results

No whups were detected for six of the 59 randomly selected days, leaving 53 days of data for whup analysis. In total, 1326 whups were detected; 813 were found with automated detectors and 513 were found manually by the analyst. The number of whups detected over each day varied widely (range = 0 to 111; Fig. 3).

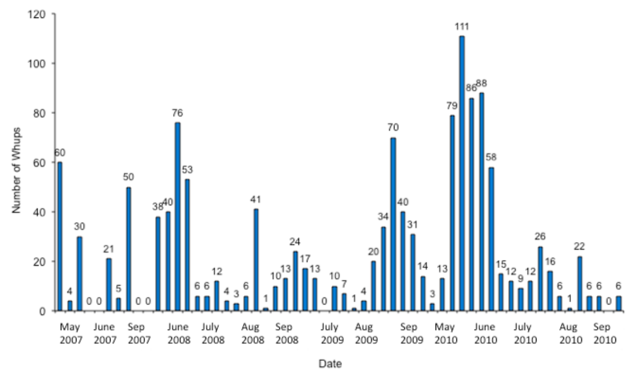

Figure 3. Number of whups detected per day May-September, 2007-2010.

3.1 Whup Characteristics

A whup consists of two parts, a growl and an upsweep (Table 2, 3, Fig. 2). The growl duration averaged 0.5s (s.d =0.2), with minimum frequency of $\bar{x}$ = 55.7Hz (±13Hz), maximum frequency $\bar{x}$ = 187Hz (±51Hz), and peak frequency 93.5Hz. Bandwidth of growls ranged from 39-380Hz ($\bar{x}$ =131±54). The duration of the upsweep averaged 0.2s (±0.1), with a minimum frequency of $\bar{x}$ = 52Hz (±13Hz), maximum frequency $\bar{x}$ = 743.4Hz (±169Hz), and peak frequency at 92.7Hz. Bandwidth of the upsweep was generally much larger than for the growl, from 292-977Hz ($\bar{x}$ =691±172). On average, good whups had a signal to noise ratio of 17dB (n=248). The spectrogram of a complete whup had a frequency range 52.1-743.4Hz, with a peak frequency at 93.1Hz, and average duration of 0.7±0.23sec (Fig 2).

Table 2. Measurements of the growl portion of a humpback whale whup (n=248).

	Duration (s)	Min Freq (Hz)	Max Freq (Hz)	Bandwidth (Hz)	Peak Freq (Hz)	SNR
Average	0.467	55.692	186.919	131.265	93.454	16.760
St. Dev.	0.178	13.145	51.164	54.199	19.090	4.357
Min	0.143	16.500	111.200	38.700	21.500	6.000
Median	0.448	54.700	172.500	120.550	90.400	16.350
Max	1.090	95.900	426.200	379.900	168.000	28.400

Table 3. Measurements of the upsweep portion of a humpback whale whup (n=248).

	Duration (s)	Min Freq (Hz)	Max Freq (Hz)	Bandwidth (Hz)	Peak Freq (Hz)	SNR
Average	0.185	52.142	743.439	691.302	92.719	16.760
St. Dev.	0.047	12.783	168.563	171.542	32.085	4.357
Min	0.076	20.500	335.500	292.000	34.500	6.000
Median	0.181	51.150	751.450	692.200	86.100	16.350
Max	0.353	104.100	1032.800	977.400	340.200	28.400

3.2 Patterns of call occurrence

Whups occurred throughout our analysis period of May through September (Fig. 3) the period of peak whale abundance in the study area. They have been observed in other months of the year when humpback whales are present (Glacier Bay National Park, unpublished data). The six days with no whups occurred in June, July and September of 2007, 2009, and 2010 with no detectable pattern. No significant difference in whup production per month was found (ANOVA, p>0.05 for all months). The days with the highest numbers of whups were found in May, June and September, with a mean of 12.3 whups per day (range 0 to 111, Fig. 3). A hypothesis test of correlation revealed no statistically significant correlation between the number of whups and the number of whales sighted in 16 same-day photo-identification surveys (r=0.489, F=2.922, p = 0.497) . Whups were detected during all hours of the day. Within the entire dataset, 869 whups occurred during the day, while 467 occurred at night, as defined by sunrise and sunset on each respective day. However, because this was a summer dataset in a high-latitude study site, daylight hours outnumbered nighttime hours with the maximum difference occurring on the summer solstice (around June 21) each year at 18:16:41 hours of daylight. To correct for this inequality between daylight and nighttime hours, whups during daytime were divided by daylight hours for that specific day, with the same method applied to nighttime whups. A paired t-test showed no significant difference between the rate of whups per hour during daytime and nighttime (t= -0.5327, df=103.9, p=0.5954).

A SNR comparison between daytime and nighttime whups (all whups, n=1326) showed nighttime whups to have a significantly higher SNR (paired t-test, t=3.762, df=693.2, p=0.0018). Similarly, the median ambient sound level in the 40-1000 Hz band was 99.5 dB re 1 μPa at night (n=1633) and 101.7 dB re 1 μPa (n=3845) in the day. This difference of 2.2 dB re 1 μPa was statistically significant (Mann-Whitney U(1) = 2311312, Z=-15.467, df=1, p <0.0001). The median difference in sound levels for samples that did not contain vessel noise in the day (97.9 dB re 1 μPa, n=618) and night (97.7 dB re 1 μPa, n=1104) was not statistically significant (Mann-Whitney U(1) = 336005, Z=-.518, p <0.6042). These contrasting results suggest that vessel noise and not sea conditions were responsible for the diurnal difference in ambient noise.

Of the 1326 whups detected, 815 (61%) were in multiple-call groupings. Examination of the data indicated that additional calls would occur within 60 seconds at least 50% of the time if they were going to occur (Fig 4). This formed the basis of our definition of multiple-call events, in which we assumed that inter-whup intervals greater than 60 seconds were unrelated events. In total, 223 multiple-call events were detected. Groups of calls contained 2-34 whups ($\bar{x}$ =4 ± 3.4), with durations varying between 1 and 380 seconds ($\bar{x}$ =67±0.001). Calls were separated by 1 to 60 seconds ($\bar{x}$ =17±16) as constrained by our 60-second criterion.

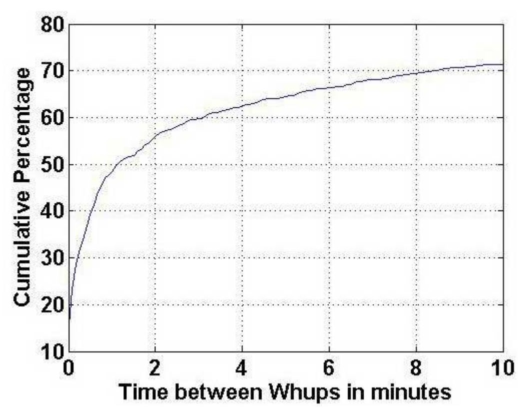

Figure 4. Cumulative distribution of time between whups, showing 50% of whups occur within 60 seconds of the last whup.

4 Discussion

Whups occurred often in May through September, the peak months of whale presence in GBNP; they were detected on 53 of our 59 randomly selected days over 4 years (Fig 3). Anecdotal observations show occurrence of whups in most or all months that humpback whales have been documented in the study area (GBNP unpublished data). Our study is an important first step in measuring the acoustic properties and patterns of occurrence of this call, enabling a better understanding of its functions, susceptibility to vessel-generated noise and potential for use in passive acoustic monitoring in the Southeastern Alaska feeding grounds of humpback whales.

4.1 Whup characteristics

Separating the whup into its component parts allowed us a closer look at the similarities and differences between them. Growls were longer and more variable in duration ($\bar{x}$ =0.5sec ±0.2) than upsweeps ($\bar{x}$ =0.2sec ±0.05). On the other hand, upsweeps were more broadband than growls with a 700 Hz bandwidth versus 130 Hz, and maximum frequency measured of 1 kHz versus 426 Hz. It should be noted that the maximum frequency of the call was at the upper limit of the frequency range of the decimated data, making it possible that some of the energy of the call was contained in a higher frequency, which would have been eliminated by filtering prior to data decimation. It is possible that each unit of the whup may have different social relevance to listening whales. We speculate that ambient noise and heading of the whale with respect to the hydrophone (Pack *et al.* 2003, Au *et al.* 2006) affected the projection of the upper frequencies of the call. This makes sense given assertions that humpback whales have directionality with their calls (Pack *et al*. 2004).

The peak frequency of the growl and the upsweep averaged 93.5Hz and 92.7Hz respectively, a striking similarity considering that the call bandwidth varied drastically, (131Hz in growls versus 691Hz in upsweeps). We speculate that the 92-93Hz peak frequency is an important feature of this call for long-range communication. Alternatively, the size of the vocalizing whale may play a role in the characteristics of a whup. Sound production mechanisms in humpback whales are poorly understood, but their vocal folds (Adam *et al.* 2013) likely influence the resonant frequencies of various calls. While it is known that the peak frequency of calls varies between different species of baleen whales, little is known about variation within a species. Humpbacks produce a wide range of calls and vocalizations in varying bandwidths, making it possible that certain calls may be produced at specific spectral peaks depending on function, rather than simply being a byproduct of body size.

Note that each of the separate components were sometimes found separately when running the automated detector. These were most commonly a growl-only event, or sometimes a quick upsweep that was not associated with a growl. However, the detector searched for calls based on cross correlation from the entire call, thus eliminating most of the false positive detections of a single portion. False positive detections were discarded by the analyst and not counted, but they were relatively infrequent. It should be noted that more work would be necessary to optimize automated detection and eliminate the need for multiple detectors. With future use of more complex analysis tool capabilities, it is likely that detectors can be made to simplify the process, making automated analysis a robust method.

The 'whup' is likely the same call first referred to as a frequency modulated grunt (Thompson *et al.* 1986) in southeastern Alaska and later as a 'whoop' (Cerchio 1996) in the Aleutian Islands of Alaska. Because we were not successful at obtaining previous Alaska recordings to confirm that they match the calls we are describing, we did not adopt the names used by previous Alaska studies (Thompson *et al*. 1986, Cerchio 1996). It is visually similar to the 'wop' described in the Gulf of Maine (Stimpert *et al*. 2011) and the 'wop' and 'thwop' described in migrating east Australian humpback whales (Dunlop *et al*. 2007). We provide an example of the whup in the online supplementary material for this article, because, as noted by other investigators (Stimpert *et al.* 2011), naming sounds based solely on spectral images is problematic.

We attempted to compare call parameters between the wop from Dunlop *et al.* (2007) and Stimpert *et al.* (2011), and our whup, and found that measurements were taken differently between the three studies and recording systems. The wop recorded by Dunlop *et al*. (2007) was described to have a more narrow-band frequency range (43Hz-73Hz) than the whup (52Hz-743Hz). Stimpert *et al.*'s (2011) Gulf of Maine wop did not specify a minimum frequency, but a maximum frequency of 229Hz. However upon examining the spectrograms of the calls, Dunlop's wop appeared to reach 700Hz or more in the upsweep portion of the call, similar to our whup, while Stimpert et al.'s wop appears to reach upwards of 2000Hz in spectrogram images. These differences in call parameters, measurements and descriptions, along with the different social contexts of the calls with the Dunlop et al. study (migration versus feeding) dissuaded us from assuming that these calls should be given the same name. However, we concur with the idea that, like the wop, the whup functions in inter group communication (Dunlop *et al.* 2008).

4.2 Patterns of occurrence

We found no apparent relationship between whup production and month or year; whups occurred throughout all summer months every year in GBNP (Fig 3). On days when they occurred, there was nearly always more than one whup (Fig 3). Days with no calls also seemed to occur at random times throughout the study period, irrespective of month, ambient noise conditions, or the presence or absence of calls on the previous day. Whales appeared to call under a variety of sea and noise conditions, judging by the range of SNR measurements we encountered and other marine mammal vocalizations documented in the area (Kipple and Gabriele 2003), current and high wind.

Whup call counts were not correlated with the number of whales seen on photo-identification surveys within 10km of the hydrophone. Though we had a limited number of survey days for this comparison (n=16), the lack of correlation was so clear that no statistical power analysis was done. However future studies using additional data would be valuable in confirming these findings.

A lack of diurnal variability in whup occurrences differs from findings in other baleen whales (Au *et al*. 2000, Stafford *et al.* 2005, Wiggins *et al*. 2005, Munger *et al.*

2008). This disparity may reflect a difference in call function. Median nighttime ambient noise conditions in the 40-1000 Hz band were 2.2 dB lower at night, due to a decrease in vessel noise, suggesting that quieter ambient conditions may have made it easier for us to detect calls at a greater distance. Indeed a SNR comparison between daytime and nighttime whups showed nighttime whups to have a significantly higher SNR. While this suggests that daytime whups may be more prevalent but simply masked, we consistently found that we were able to detect whups when the noise was greater than the signal during both day and night. Due to our confidence in the detections when the signal was quieter than the noise, we do not feel that higher ambient noise during the daytime affected our ability to detect whups.

4.3 Putative functions and implications

Humpback whales use whup-like upsweeps repetitively in their social sounds (Silber 1986, Dunlop *et al*. 2007), and as song units (Payne and McVay 1971, Glacier Bay National Park unpublished data). However, the whup-like upsweeps within social sounds have no growl component, and thus have a higher minimum frequency. Moreover, the predominance of frequency-modulated upsweeps in humpback whale calls in different geographic and social contexts may indicate their broad utility as a contact call. A focused comparison of these vocalizations is warranted.

Determining the function of these calls is not possible with the existing dataset, but it is worth noting that the overall characteristics of the humpback whale whup, as well as the wop and thwop, are similar to published descriptions of the North Atlantic right whale (*Eubalaena glacialis*) "upcall", which whales are believed to use to maintain contact with one another (Clark 1983, Parks and Tyack 2005, Parks *et al*. 2009). Right whale upcalls are short (1 sec) upsweeps that rise from 50 Hz to 440 Hz with a peak frequency at 118-129 Hz, and are also the most common call recorded by the species in the North Atlantic Ocean (Parks *et al.* 2009). Southern right whale (*Eubalaena australis*) "up calls" have very similar physical characteristics and were also the most common call type off Argentina (Clark 1983). Behavioral observations that accompanied acoustic recordings indicated that in approximately half the cases when a right whale made an "up call", another whale called back and the two whales called back and forth as they swam toward each other, and stopped calling when they joined (Clark 1983).

Although there was variability within whup calls, they appeared to be stereotyped and showed similar acoustic properties as upcalls. In the absence of behavioral observations to accompany the acoustic data that we recorded remotely from a single hydrophone element, we can only speculate that the whup functions as a contact call. However, two factors suggest that whup calls and upcalls serve a similar function: 1) our finding that 61% of humpback whale whups were multiple-call events, and 2) that additional whups would occur within 60 seconds at least 50% of the time if they were going to occur at all (Fig 4). Whups that occurred within 60 seconds of each other were assumed to be either the same whale repeating the call to contact others, or a conspecific responding to the call in return. SNRs of calls within bouts appeared to vary back and forth between calls, indicating counter-calling, which should be explored further in future studies to assess this theory. Whups not produced in multiple-call sequences may indicate a lack of other animals in the area to hear and respond to the call. Groups of whups were clustered in time, and we speculate that counter-calling between two or more whales is the most likely explanation for multiple-call events. Future work should examine patterns of call amplitude, bandwidth and latency in putative counter-calling bouts. An ideal study design would ensure simultaneous acoustic localization and visual observations near the hydrophones to investigate the behavior of calling whales relative to one another and to non-calling whales. Trends in the number of whups per hour or per day could be monitored concurrently with changes in vessel traffic and numbers of whales, in light of the increasing number of humpback whales in the North Pacific and in Glacier Bay (Neilson and Gabriele 2010, Barlow *et al*. 2011). This approach would also allow determination of the source levels of these calls, which is an important information gap that stands in the way of understanding the functions and propagation of this call.

The whup call was common in the study area and fairly stereotyped, making it a good candidate for passive acoustic monitoring, although additional development of automated detectors would be need to improve their performance. While the presence of whups indicates the presence of humpback whales, it may not necessarily be a good indicator of whale abundance. Further information on the social context of the whup will be necessary to determine whether it is reasonable to expect that the number of whups to correlate with the number of whales in the area. For example, one can just as easily surmise that whales 'whup' when other whales are around (i.e. more calls means more whales), or that whales produce a 'whup' to inquire about the presence of other whales, such that whups may be more common when whale densities are low. Similarly, days with many whups may indicate that there are just two whales having a long exchange of calls, or a number of different calling whales. Humpback whales are long-lived (Gabriele *et al*. 2010) and have very high site fidelity to feeding grounds (Neilson and Gabriele 2014) where they live amongst kin and other familiar individuals. Thus, it is conceivable that calling behavior is not random: certain individuals may be prone to exchange more calls with familiar associates than with just any other whale. Future studies that can determine individual calling rates and the behavioral correlates of calling will be needed to assess the usefulness of the whup as a passive acoustic monitoring tool.

The simplicity and low frequency of humpback whale whups may make them well-suited to communication over at least several kilometers, but these qualities also make them vulnerable to acoustic masking (Clark *et al*. 2009), especially in environments with broad band low frequency noise such as that produced by ships (e.g., Andrew *et al*.

2002, Kipple and Gabriele 2003, McDonald *et al*. 2008). Loss of acoustic habitat due to man-made underwater noise is an issue that nearly every marine mammal in today's oceans may face several times per day as vessels come and go. Fortunately, GBNP is relatively quiet in comparison to industrialized parts of the ocean (Hatch *et al*. 2008, Clark *et al*. 2009) where there is concern that chronic noise may exert population level effects.

Whups are among the most common call types recorded in southeastern Alaska (Fournet 2014, GBNP unpublished data), and are therefore an important communication signal for humpback whales during the feeding season. Their prevalence makes them a good candidate for assessing the impact of vessel traffic on humpback whale communication relative to the seasonal and diel changes in ambient noise levels in GBNP. By characterizing the physical properties of the whup and the patterns of its occurrence we have made a vital first step toward understanding humpback whale use of available acoustic habitat, and the impact that changes in the acoustic habitat could have on these whales in their feeding grounds.

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