

Incorporating tides into the acoustic ecology of humpback whales

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ABSTRACT

North Pacific humpback whales (*Megaptera novaeangliae*) migrate annually to foraging grounds in Southeast Alaska that are characterized by semidiurnal tidal cycles. Tidal activity is an important driver of marine mammal behavior on foraging grounds, but is often omitted in studies of acoustic ecology. To better understand the role of sound in this vocal species we investigated the influence of tidal height and direction on humpback whale nonsong calling behavior in Frederick Sound and described new call types for this population. The likelihood of detecting a call from the low-frequency-harmonic, pulsed, or noisy-complex call classes was independent of tidal activity. The likelihood of detecting a call from the tonal call class, and a feeding call in particular, was 2.1 times higher during flood tides than during ebb tides (95% CI 1.1–4.4). This likely reflects an indirect relationship between humpback whale foraging and tides.

Key words: acoustic ecology, humpback whale, *Megaptera novaeangliae*, tides, repertoire, Southeast Alaska.

The daily tidal cycle is a significant driver of ocean ecology. The interactive effects of seasonality, bathymetry, and tidal currents influence nutrient flux within a system, which in turn impacts primary productivity and subsequent trophic interactions (Wolanski *et al.* 1988, Zamon 2002, Whitney *et al.* 2005, Inazu *et al.* 2009, Benjamins *et al.* 2015). The strong association between tidal phase and energy flow to piscivorous predators, including marine mammals, is particularly pronounced in steep-sided coastal regions characterized by predictable tidal rips and

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jets (Zamon 2003, Benjamins *et al.* 2015). The distributions and behaviors of many marine mammal species have been shaped in response to this strong ecological driver, resulting in a relatively robust body of research that incorporates the role of tidal cycles into distribution modeling, foraging ecology, and movement ecology in marine mammals (see Benjamins *et al.* 2015 for a review). The field of acoustic ecology, however, has less directly incorporated the role of tidal cycles into developing research.

We define acoustic ecology as the branch of science that investigates how biotic organisms use sound to interact with one another and their habitat. Understanding how acoustic behavior relates to various environmental features, including tides, supports investigation into the ecological role of sound (*i.e.*, whether a sound is associated with navigation, foraging, sociality, or a combination), and allows for more nuanced inference pertaining to how marine mammals interact with each other, their prey, and their habitat. All marine mammals use sound to interact with their environments to some degree (Dudzinski *et al.* 2009). Harbor seal (*Phoca vitulina*) vocalizations show clear association with diel and tidal patterns during their breeding season (Van Parijs *et al.* 1999). Odontocete species use echolocation—the process by which an animal produces sounds and uses the echoes to assess physical features—for foraging and navigation (Au 2012). Bowhead whales (*Balaena mysticetus*) may use song to gauge ice thickness and thus avoid areas with heavy ice flow (Ellison *et al.* 1987, George *et al.* 1989). The vocalization rates of sei whales (*Balaenoptera borealis*) in the Gulf of Maine show strong diel variation that closely reflects the vertical migration of their zooplanktonic prey (Baumgartner and Fratantoni 2008). Identifying the relationship between vocalizations and habitat features has revealed, to a degree, potential call functions. We propose that incorporating tidal phase into acoustic ecology studies would be similarly beneficial for identifying drivers of acoustic communication.

Before more complicated ecological questions can be posed about the use of acoustic communication, including drivers of vocal behavior or call function, calls must first be described and attributed to a specific species. Humpback whales (*Megaptera novaeangliae*) are a migratory baleen whale species whose vocal behaviors are seasonally and geographically stratified (Payne and McVay 1971, Silber 1986, Cerchio *et al.* 2001, Garland *et al.* 2011). On breeding grounds, and to a lesser degree on migratory corridors and foraging grounds, humpback whales produce long, highly structured songs that are thought to be associated with mating behaviors (Payne and McVay 1971, Gabriele and Frankel 2002, Cholewiak *et al.* 2018). Humpback whales also produce a suite of lesser described sounds known collectively as social calls, or nonsong vocalizations, throughout their migratory range and across all life stages (Silber 1986; Dunlop *et al.* 2007, 2008; Zoidis *et al.* 2008; Fournet *et al.* 2015). A number of studies have described the acoustic structure and use of nonsong vocalizations across populations (Dunlop *et al.* 2007, 2008; Stimpert *et al.* 2007; Rekdahl *et al.* 2013, 2015, 2016); however, many populations' repertoires remain unknown or incomplete and drivers of calling behavior are only beginning to be described (*e.g.*, Dunlop 2017).

The nonsong repertoire of the Eastern Australian humpback whale population is the best known to-date with a catalog of over 40 call types (Dunlop *et al.* 2007, Rekdahl *et al.* 2013). Humpback whale nonsong vocalizations have also been classified off the coast of northern Angola, Africa (Rekdahl *et al.* 2016), on North Atlantic foraging grounds (Stimpert *et al.* 2007, 2011), and in Southeast Alaska (Thompson *et al.* 1986, Fournet *et al.* 2015).

The Southeast Alaskan foraging grounds are characterized by a semi-diurnal tidal system (two high tides and two low tides daily) with broad tidal ranges (up to 7 m of change over a 6 h period). The distribution of foraging humpback whales around headlands has been linked to tidal current direction in Southeast Alaska (Chenoweth *et al.* 2011), and the distribution and increased foraging activity of several humpback whale prey species (*i.e.*, Pacific herring, *Clupea pallasii*, sand lance, *Ammodytidae* spp.) have also been linked to tidal phase (Zamon 2003). Whether tides are also an important ecological driver of calling behavior is unknown. In Southeast Alaska, 16 nonsong call types have been described, with the caveat that additional call types may be documented over time (Fournet *et al.* 2015). In this study, we investigated the relationship between the vocal repertoire of Southeast Alaskan humpback whales, tide height, and tide direction to test the hypothesis that humpback whales adjust their calling behavior in response to tidal activity. To achieve this objective, we documented the use of known call types and classified previously undescribed call types in this population.

METHODS

This study was conducted in the waters surrounding Five Finger Lighthouse, at the confluence of Frederick Sound and Stephens Passage, Southeast Alaska (57°16'13"N, 133°37'53"W; Fig. 1). Acoustic recordings were obtained between 14 June and 15 August 2015, from an omnidirectional hydrophone (SQ26-08, Cetacean Research Technology, Seattle, WA) attached to an anchored surface buoy at a fixed location, approximately 260 m from shore (~57°16'19"N, 133°38'4"W). The water depth at the location of the hydrophone was approximately 60 m. The hydrophone was deployed to 7.5 m depth (limited by equipment length), attached to a negatively buoyant lead line and 2.26 kg weight to facilitate sinking; the hydrophone was only deployed during a Beaufort sea state 2 or less. The SQ36-08 hydrophone has a built-in +25 dB preamplifier with an effective sensitivity of -169 dB, re 1 V/ μ Pa and an effective frequency range of 10 Hz to 50 kHz. Hydrophone output was sent *via* a wireless FM transmitter (model WM, Lectrosanics, Rio Rancho, NM) with a high-pass filter of 35 Hz at the surface of the water to a wireless receiver (Lectrosanics UCR401) stationed in the lighthouse tower approximately 260 m away. The receiver was positioned 16 m above the median tide height with unobstructed line-of-sight between instruments. Recordings were made with a Zoom H4N Handy digital audio recorder (44.1 kHz sampling rate, 16-bit sample resolution) that recorded continuously for 12–48 h, contingent on battery life.

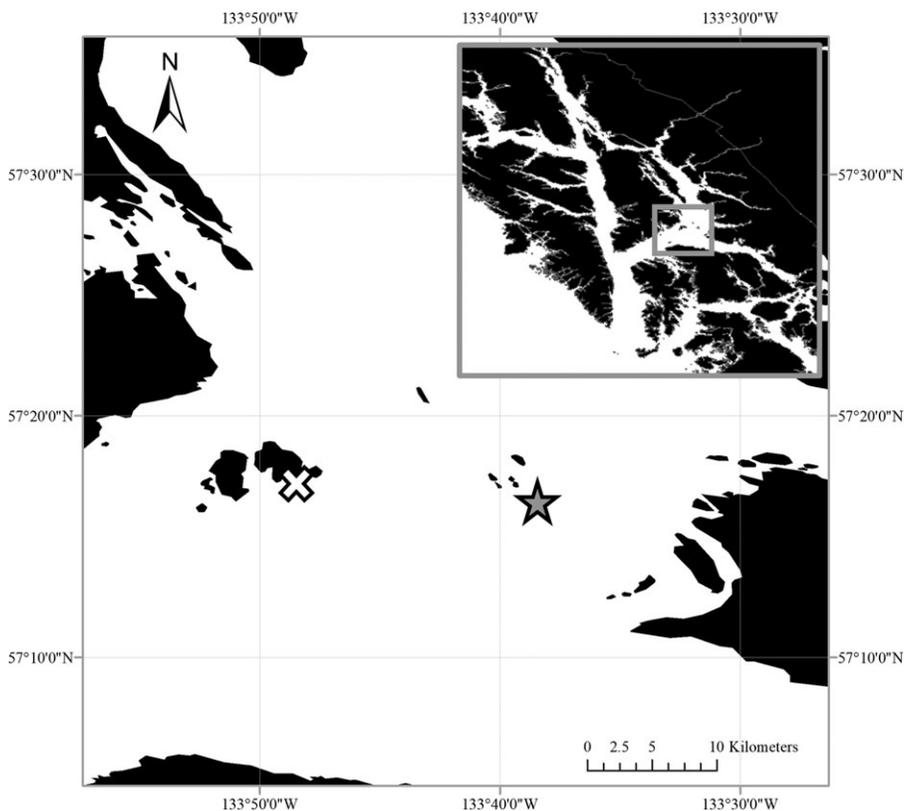


Figure 1. Map of the study area in Frederick Sound, Southeast Alaska. The research station at Five Finger Lighthouse is marked with a gray star (57°16'13"N, 133°37'53"W). NOAA buoy #9451785 at Brothers Islands is marked with a white X (57°17.7'N, 133°47.8'W).

Data in this study were grouped according to 30 min “tidal periods,” which categorically described tide height and direction. Tidal periods were designated as either high ebb (HE), mid ebb (ME), low ebb (LE), low flood (LF), mid flood (MF), or high flood (HF) (Table 1). Mid is defined as the time midway between peak high and peak low tides. We randomly selected 10 periods from each tidal state for acoustic analysis (60 periods total). Tidal periods were separated by a minimum of 1.5 h and included all possible combinations of time of day and tidal cycle. For each tidal period the tide height at the median time (*i.e.*, at the 15 min mark within the 30 min period) was extrapolated using the *rtides* package in R 3.3.3 (Thorley *et al.* 2017). Tidal data were obtained from a NOAA buoy positioned at the Brothers Islands, Stephens Passage (Station ID 9451785; 57°17.7'N, 133°47.8'W; Fig. 1), 10.3 km west of the hydrophone at Five Finger Lighthouse. The movement of water around the Five Finger Islands is generally in a northeastward direction during flood tides, and westward during ebb tides (NOAA 2013).

Table 1. Start and end time calculations for the six periods of the tidal cycle included in this study; high ebb (HE), mid ebb (ME), low ebb (LE), low flood (LF), mid flood (MF), and high flood (HF).

Tidal period	Start time	End time
High ebb	High tide + 1 h	High tide + 1 h 30 min
Mid ebb	Mid (low-high) – 15 min	Mid (low-high) + 15 min
Low ebb	Low tide – 1 h 30 min	Low tide – 1 h
Low flood	Low tide + 1 h	Low tide + 1 h 30 min
Mid flood	Mid (high-low) – 15 min	Mid (high-low) + 15 min
High flood	High tide – 1 h 30 min	High tide – 1 h

Recordings were analyzed using the MATLAB-based acoustic analysis program Osprey (Mellinger 2014). Each sound file was examined in its entirety, in 45 s windows (4,096-point fast Fourier transform, Hamming window, 5.4 Hz resolution). Calls were visually and aurally identified and manually annotated. Acoustic features were extracted using Osprey's Noise Resistant Feature Set (NRFS; Mellinger and Bradbury 2007; Table 2). The NRFS was developed for identifying and analyzing marine animal sounds in a noisy environment (Mellinger and Bradbury 2007) and is therefore well-suited for this analysis given that the hydrophone was subject to flow and vessel noise. The output of the NRFS is comparable to traditional acoustic feature extraction, however, the terminology and measurement method for parameters is altered slightly. Rather than taking measurements from an annotation region drawn by an observer, the NRFS employs a "feature box." The feature box is a subset of a human drawn annotation box that has been denoised and includes time and frequency parameters calculated based on an algorithm that ranks summed energy within a sound relative to the background noise. As a result, the loudest parts of the spectrogram have the greatest influence on calculated feature values (Mellinger and Bradbury 2007). Frequency parameters used in analysis were log-transformed to minimize skew and to better approximate the mammalian perception of pitch (Parks and Tyack 2005, Dunlop *et al.* 2008, Stimpert *et al.* 2011, Fournet *et al.* 2015; Table 2). Start and end frequencies for each call were obtained manually by marking the beginning and end of the fundamental frequency on the spectrogram in RavenPro 1.5 (Cornell Lab of Ornithology, Ithaca, NY).

To be selected for analysis, acoustic samples needed to have a signal-to-noise ratio (SNR) of 10 dB or greater (Dunlop *et al.* 2007, 2008; Stimpert *et al.* 2011; Rekdahl *et al.* 2013) as measured by the NRFS. To ensure accurate parameter measurements, vocalizations were only included if they had clearly aurally and visually distinguishable start and end points. Any overlapping vocalizations or vocalizations with excessive flow noise were excluded from analysis.

Acoustic samples fitting the inclusion criteria were extracted from the recordings in Raven Pro 1.5 with a 2.5 s buffer preceding and following each call. Samples were randomly ordered for observer analysis. Each sample was assigned to a vocal class based on aural-visual (AV) analysis

Table 2. Description of acoustic variables used for analysis for classifications of humpback whale nonsong calls. Variables are all calculated in the noise resistant feature set (NRFS; Mellinger and Bradbury 2007).

Measurement	Description
Duration (s) ^a	Length of feature box
Vocalizations per bout	Number of repetitions of the same unit of sound within a single calling event
Lower frequency (Hz) ^{a,b}	Lowest frequency limit of feature box
Upper frequency (Hz) ^{a,b}	Highest frequency limit of feature box
Start frequency (Hz) ^b	The fundamental frequency at the start of the call
End frequency (Hz) ^b	The fundamental frequency at the end of the call
Peak frequency (Hz) ^b	Frequency of the spectral peak
Bandwidth (Hz) ^b	Height of the feature box
Median frequency (Hz) ^{a,b}	Frequency where cumulative sum of cell values reach 50% of the total energy
Frequency quartile (Hz) ^{a,b}	Frequency where cumulative sum of energies is 25% of total energy in feature box
Amplitude modulation rate ^a	Dominant rate of amplitude modulation
Frequency modulation rate ^a	Dominant rate of frequency modulation
Upsweep fraction ^a	Fraction of time in which median frequency in one block is greater than in the preceding block, weighted by total energy in each block
Frequency trend ^a	Start F ₀ /End F ₀
Aggregate entropy ^a	A measure of total disorder in the call

^aFeature from the noise resistant feature set (NRFS).

^bVariables that were log-transformed for analysis (see text).

following the classification system developed by Fournet *et al.* (2015) (low-frequency harmonic, noisy/complex, pulsed, or tonal). Once assigned to a vocal class the AV classification process was repeated; each acoustic sample within a vocal class was then assigned to a vocal subclass and vocal type (“call”). In order to merit classification as a new vocal type, calls fitting the inclusion criteria had to occur a minimum of three times on nonconsecutive days to reduce the chance that the calls were all made by a single individual. All classifications were made by a single observer (DRB).

Following AV classification, discriminant function analyses (DFA) with cross validation using the parameters in Table 2 were conducted to confirm qualitative classification assignments (JMP Pro 12, SAS Institute, Cary, NC). All acoustic samples were pooled and a DFA was run to assess agreement between AV class assignment and supervised (DFA) classification. DFA were run within each vocal class to assess classification agreement at the vocal subclass and vocal type levels. DFA has been

used in previous studies classifying humpback whale social sounds (Dunlop *et al.* 2008, Fournet *et al.* 2015), as well as southern right whale (*Eubalaena australis*) (Clark 1982) and dolphin vocalizations (Boisseau 2005). For this study the human classification was considered the “correct” classification. All statistical analyses were done according to AV classification. We used Kruskal-Wallis tests to assess differences in median acoustic parameters between newly classified call types. We used Dunn’s tests with a Bonferroni correction for all *post hoc* multiple comparisons of acoustic parameters between newly classified vocal types (JMP Pro 12).

Once acoustic samples were classified, repertoire data were aggregated as counts (number of calls per vocal class) within each 30 min tidal period and converted to proportions (number of calls per vocal class/total number of calls) for analysis. We fit a quasi-binomial general linear model with a logit link to test whether the probability of detecting a call from a given vocal class varied as a function of tide height (median tide height within each 30 min tidal period) in meters and tide direction (ebb *vs.* flood; $\alpha = 0.05$); an overdispersion parameter was calculated using the sum of the square of the Pearson residuals divided by the residual degrees of freedom for each model. Drop-in-deviance tests were used to test for evidence of a relationship between tide height, tide direction, and call proportion for each vocal class. Where significant relationships between tide direction (ebb *vs.* flood) and vocal class were identified, Mann-Whitney *U* tests were run to assess whether the proportion of each call type varied by tide direction. All analyses were done with R version 3.3.3 (2017); models were run using the `glm` function in package MASS.

RESULTS

A total of 507.9 h of total acoustic recordings were made over 29 d between 13 June and 15 August 2015; 30 h corresponding to 60 tidal periods were subsampled for analysis. A total of 809 calls were detected within the 60 tidal periods of interest. Of these, 380 calls (47%) were classified by AV analysis as being in the low-frequency harmonic (LFH) vocal class, 65 calls (8%) were in the noisy/complex (NC) vocal class, 227 calls (28%) were classified within the pulsed vocal class (P), and 137 calls (17%) fell into the tonal (T) vocal class. DFA results showed 80% agreement with AV classification to the vocal class level ($n = 648$, Table 3). A total of 41 calls were identified that could be classified to the vocal class level but could not be matched to the existing call catalog nor fit the criteria to merit a new call type classification (*i.e.*, not identified on multiple days or in large enough sample sizes). These call types are included in analyses conducted at the vocal class level but are excluded from finer scale analyses.

Results of the within-class DFA showed between 78% and 96% agreement at the vocal subclass level, and between 60% and 87% agreement at the vocal type level (Table 4). Classification to the call type level revealed that all 16 call types previously described in the vocal

Table 3. Confusion matrix illustrating level of agreement between aural visual classification (AV) and discriminant function analysis (DFA) in bold. “Actual” call classes were determined through AV analysis. “Predicted” call classification indicate classification placement according to the DFA. Call classes include: low-frequency harmonic (LFH), noisy/complex (NC), pulsed (P), and tonal (T).

Actual	Predicted			
	LFH	NC	P	T
Vocal class				
LFH	326 (86%)	10	39	5
NC	4	44 (68%)	8	9
P	52	7	168 (74%)	0
T	12	13	2	110 (80%)

repertoire for Southeast Alaska (Fournet *et al.* 2015) were present in this data set. Additionally, this study proposes an expansion of the T vocal class to include a new “arched” subclass, which contains two new call types: “simple arches” and “hoots” (Fig. 2; Table 5). The T vocal class is characterized by narrow bandwidth calls with low peak fundamental frequencies of approximately 500 Hz (Fournet *et al.* 2015), and previously only contained one call type, the feeding call (Fig. 2A).

The two new vocal types described here, simple arches and hoots, possess similar acoustic properties to feeding calls, but are distinct enough to warrant their own vocal type. Simple arches usually occur in short bouts (1–2 sounds per call) and are significantly shorter in duration than either hoots (Dunn’s test: $z = -4.57$, $P < 0.0001$; Table 5) or feeding calls (Dunn’s test: $z = -4.41$, $P < 0.0001$; Table 5, Fig. 2). Like all vocal types in the T vocal class, simple arches are narrowband and tonal without noticeable harmonics or broadband components. Hoots are characteristically long in duration, tonal, and narrowband with a significantly higher number of bouts per call than either simple arches or feeding calls (Dunn’s test: $z = -4.89$, $P < 0.0001$; $z = -1.70$, $P < 0.001$,

Table 4. Results of within class discriminant function analysis (DFA) illustrating agreement between aural-visual (AV) classification and a DFA. Within class DFA was run on acoustic samples within a single vocal class (low frequency harmonic, LFH; noisy/complex, NC; pulsed, P; and tonal, T). “Classified” indicates the number of calls classified with DFA. “Excluded” indicates calls not included in DFA analysis. “Subclass” indicates level of agreement between DFA and AV at the vocal subclass level. “Type” indicates level of agreement between DFA and AV at the vocal type level.

Class	<i>n</i>	Classified	Excluded	Subclass	Type
LFH	380	371	9	235 (78%)	252 (68%)
P	227	220	7	186 (85%)	132 (60%)
NC	65	46	19	44 (96%)	40 (87%)
T	137	131	6	118 (90%)	112 (85%)
Total	809	768	41		

Table 5. Summary statistics and results of a Kruskal-Wallis test for equality of median call parameters for feeding calls and newly described vocal types within the tonal vocal class and the arched vocal subclass. Values represent mean \pm standard deviation.

Subclass	Call type	Duration (s)	Bandwidth (Hz) ^a	Peak (Hz)	Entropy (bits)	Bout
Feed	Feeding call ($n = 102$)	8.3 \pm 7.0	2.4 \pm 0.4	471.0 \pm 136.7	29.0 \pm 33.2	2.9 \pm 3.0
	Hoot ($n = 12$)	13.7 \pm 9.7	2.4 \pm 0.3	416.8 \pm 128.5	37.1 \pm 29.4	10.8 \pm 7.6
Arched	Simple arch ($n = 17$)	2.7 \pm 2.1	2.4 \pm 0.3	403.8 \pm 206.9	42.1 \pm 32.6	1.6 \pm 0.8
	P	<0.0001	0.0403	0.006	0.0045	<0.0001
	χ^2	24.40	6.42	5.7	10.8	26.07

^aBandwidth has been log-transformed.

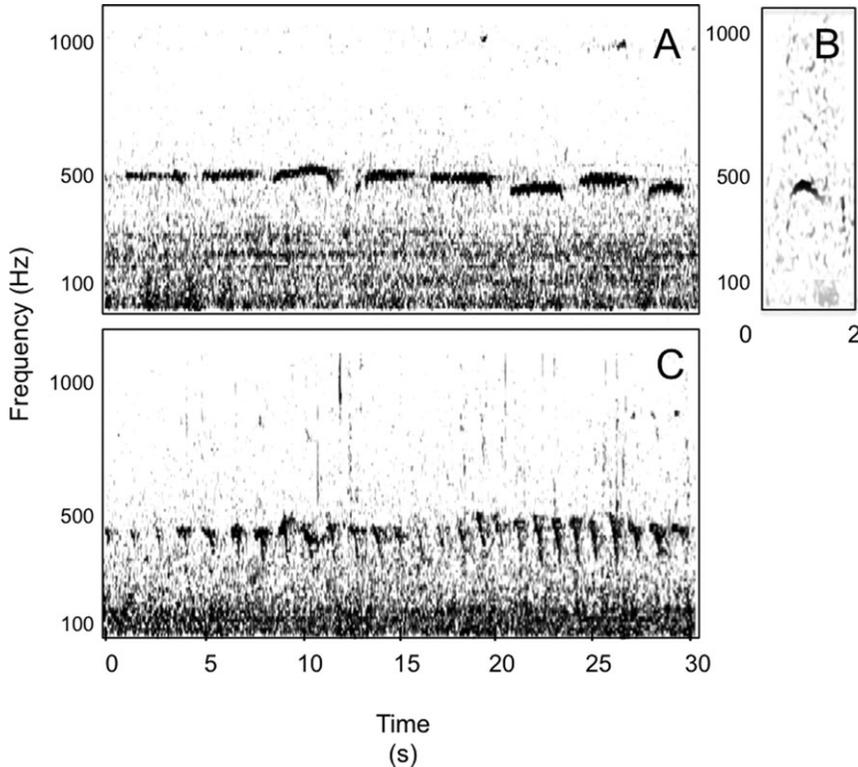


Figure 2. Spectrograms of the three call types within the tonal (T) call class, (A) the previously described feeding call, (B) the newly described simple arch, and (C) the newly described hoot.

respectively; Table 5, Fig. 2). Hoots also lack noticeable harmonics or nonlinear acoustic features (*i.e.*, biphonation, deterministic chaos, amplitude modulation).

No difference was detected in the median abundance of calls between the six tidal periods (Kruskal-Wallis test, $\chi^2 = 8.79$, $df = 5$, $P = 0.12$, minimum number of calls/period = 0, maximum number of calls/period = 71). In all tidal periods, the LFH class was the most abundant, followed by the P class, then the T class, with the NC class being least abundant (Fig. 3, Table 6).

Visual inspection of residuals *vs.* deviance for all the models included in this study found that the use of a quasi-binomial linear regression with a logit link was an appropriate fit for the data. There was no evidence of a significant relationship between either tide height or tidal direction and the proportion of LFH calls, NC calls, or P calls (Table 7). There was no evidence of a significant relationship between tide height and proportion of T calls (Table 7) so tide height was removed from the model and a resulting model was fit that included only the probability of detecting a T call (response variable) and tide direction (explanatory

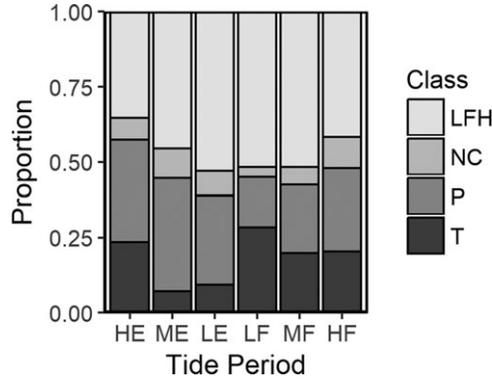


Figure 3. Proportion of the total calls observed during the study from each vocal class by tidal periods ($n = 10$ per tidal period).

variable). There was significant evidence that the probability of detecting T calls was associated with tide direction ($F = 0.029$, $P = 0.03$). There was an 11% likelihood of detecting T calls during ebb tides (95% CI 6%–19%) and a 21% likelihood of detecting T calls during flood tides

Table 6. Mean number of calls detected from each call class (low frequency harmonic (LFH), noisy/complex (NC), pulsed (P), and tonal (T) per 30 min survey period \pm standard deviation, and the number of calls for each vocal type detected during this study.

Call class	Mean calls/survey	Type	Number of calls
LFH ($n = 380$)	6.33 \pm 7.98	Descending moan	17
		Groan	23
		Growl	195
		Modulated moan	28
		Variable moan	11
		Whup	95
		Unknown	11
		Unknown	11
NC ($n = 65$)	1.08 \pm 1.99	Ahooga	4
		Ascending shriek	15
		Descending shriek	3
		Squeegee	10
		Trumpet	14
		Unknown	19
		Unknown	19
P ($n = 227$)	3.78 \pm 6.01	Droplet	34
		Horse	21
		Swop	127
		Teepee	39
		Unknown	8
		Unknown	8
T ($n = 137$)	2.28 \pm 3.89	Feeding call	101
		Simple arch	17
		Hoot	12
		Unknown	7

Table 7. Results of drop-in-deviance tests assessing a relationship between the probability of detecting calls from each vocal class and tide direction (Direction) and tide height (Height).

Class	Variable	<i>F</i>	df	<i>P</i>
Low frequency harmonic	Direction	0.2	1	0.66
	Height	2.82	1	0.1
Noisy/complex	Direction	0.01	1	0.91
	Height	3.26	1	0.08
Pulsed	Direction	2.33	1	0.13
	Height	0.38	1	0.54
Tonal	Direction	0.29	1	0.03 ^a
	Height	5.16	1	0.59

^aSignificant.

(95% CI 15%–29%). The likelihood of detecting T calls during flood tides was 2.1 times greater than the likelihood of detecting T calls during ebb tides (95% CI 1.1–4.4). The proportion of feeding calls produced was higher on flood tides than on ebb tide (Mann-Whitney *U* test, $\chi^2 = 5.01$, $P = 0.02$; Fig. 4); there was no relationship between the proportion of arched calls (Mann-Whitney *U* test, $\chi^2 = 0.5$, $P = 0.47$), or hoot calls (Mann-Whitney *U* test, $\chi^2 = 0.47$, $P = 0.5$), and tide direction (Fig. 4).

DISCUSSION

In this study, we expanded the known vocal repertoire of humpback whales and were subsequently able to quantify the relationship, and lack thereof, between vocal classes and the tidal cycle in humpback whales foraging in Southeast Alaska. The classification results indicated that all 16 vocal types previously described in the Southeast Alaskan nonsong catalog, which was developed from data collected at the same survey location 3 yr prior (Fournet *et al.* 2015), were preserved within the nonsong repertoire in 2015. Additionally, the proportions of calls detected from each vocal class were nearly identical between the two years. This is consistent with findings that the humpback whale nonsong repertoire is stable across several temporal scales (years to decades) on both migratory corridors and foraging grounds (Rekdahl *et al.* 2013, Fournet 2018). The results of this study may further indicate that call use (*i.e.*, more frequent use of certain call types over others) is also stable over time; expanded work on calling behavior over time would help answer this question.

We identified two new vocal types belonging to the T vocal class, nested in the “arched” subclass: simple arches and hoots (Fig. 2, Table 5). Additionally, several acoustic samples were identified in this data set that did not meet the criteria necessary to be classified as unique call types, but that were confidently classified to the vocal class level. Investigators in the North Pacific, Australia, and southern Africa have converged on the understanding that humpback whale nonsong vocalizations occupy an acoustic continuum (Stimpert *et al.* 2011, Fournet

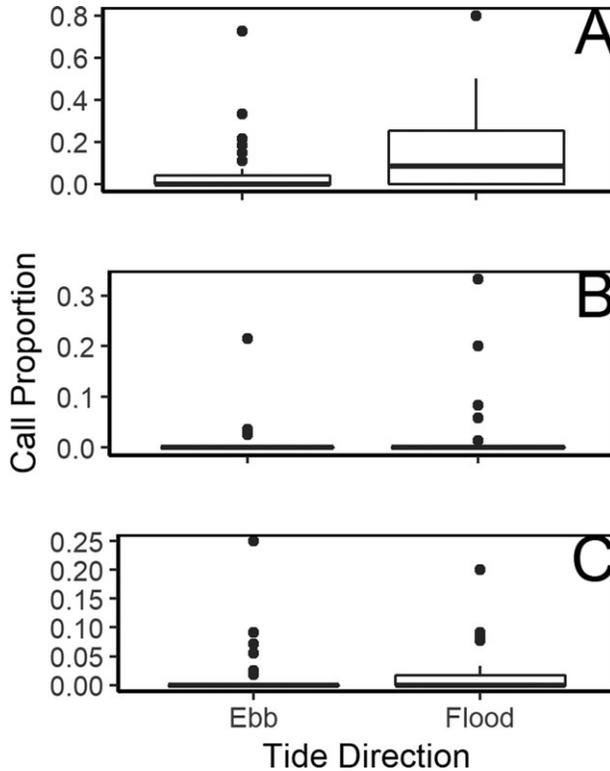


Figure 4. Proportion of (A) feeding calls, (B) hoots, and (C) simple arches to all other call types on ebb vs. flood tide.

et al. 2015, Rekdahl *et al.* 2016, Dunlop 2017). Continued vigilance on the part of humpback whale acousticians will reveal whether the unidentified call types present in this study are discrete calls that appear sporadically within the vocal repertoire, or whether these samples are variations along a vocal spectrum.

In this study we found that, with one exception, calls from most nonsong vocal classes were produced independently of tidal activity. Without dedicated observations of behavior or prey definitively interpreting the absence of a relationship is spurious; however, the decoupling of calling behavior and tidal state is consistent with other studies that have found that nonsong vocalizations serve a social function (Dunlop *et al.* 2008, Wild and Gabriele 2014). There is increasing evidence of complex sociality among humpback whales on foraging grounds (Weinrich 1991, Weinrich and Kuhlberg 1991, Ramp *et al.* 2010), some of which is likely facilitated by the use of nonsong vocalizations (Wild and Gabriele 2014). Future investigations of calling behavior coupled with fine scale behavioral observations, oceanographic parameters, and prey distribution would be extremely valuable for identifying drivers of calling behavior on foraging grounds. Currently, however, we assert that tides are not

independently a strong driver of calls in the LFH, NC, or P vocal classes, and we hypothesize that this is due to the social nature of these vocalizations.

The probability of detecting feeding calls, however, is significantly related to flood tides; this is likely an indirect effect associated with foraging. The feeding call is the only nonsong vocalization worldwide that has been definitively correlated with a behavioral context (D'Vincent *et al.* 1985, Sharpe 2001, Fournet *et al.* 2018). While feeding calls likely serve multiple functions, there is ample evidence to suggest that a primary function of this call is the manipulation of Pacific herring (Sharpe 2001, Fournet *et al.* 2018). Foraging humpback whales, alone or in groups, often pair the use of feeding calls with the production of bubble nets to concentrate schools of herring, driving them toward the surface of the water and ultimately engulfing them in a coordinated surface lunge (Jurasz and Jurasz 1979, D'Vincent *et al.* 1985, Fournet *et al.* 2018). Humpback whales in Icy Straits, Southeast Alaska, also use feeding calls when subsurface foraging as a group on Pacific herring, without bubble nets (Doyle *et al.* 2008). Based on these studies, the assumption that feeding calls serves a prey manipulation function is robust. An alternative hypothesis, that feeding calls are used to coordinate groups of individuals as they forage on Pacific Herring (D'Vincent *et al.* 1985, Cerchio and Dahlheim 2001), also relates this call to feeding activities. That feeding calls are linked to foraging, however, does not directly relate the use of this call to tidal phenomena. More likely the availability of prey—and Pacific herring in particular—is related to the nutrient fluxes associated with incoming tides, and the presence of the call is driven by foraging opportunities. In our study region primary productivity is directly linked to tidal cycles (Weingartner *et al.* 2009). Biological aggregations, including aggregations of herring, develop partially in response to interactions between tidal currents, wind and topography (Wolanski and Hamner 1988, Zamon 2003). As such the relationship between tides and feeding call production observed in this study is likely driven more by larger scale ecological processes (*i.e.*, nutrient cycling, prey behavior, oceanographic interactions) than by tide direction alone.

The results of this study do offer some isolated insight into the relationship between foraging behavior and tides in this region. We are able to identify a relationship between foraging and tide direction by using feeding calls as a proxy for foraging activity. The relationship between tide direction and foraging found in this study is consistent with the findings of Chenoweth *et al.* (2011) that link humpback whale distribution with the direction of tidal currents and tidal amplitude in Icy Straits and Glacier Bay, Alaska. Broadly, the work presented here supports Chenoweth *et al.*'s hypothesis that tidal activity may be a significant environmental feature driving humpback whale foraging in Southeast Alaska. Expanding this study into other regions of Southeast Alaska, including Icy Straits, where feeding calls are frequently documented (Doyle *et al.* 2008), and coupling passive acoustics with prey sampling would greatly enhance our understanding of the interaction between oceanography, prey, and calling behavior in this species.

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