More of the same: Allopatric humpback whale populations share acoustic repertoire (#28037)

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More of the same: Allopatric humpback whale populations share acoustic repertoire

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Background. Humpback whales (*Megaptera novaeangliae*) are a widespread, vocal baleen whale best known for producing song: a complex, repetitive, geographically discrete acoustic signal sung by males, predominantly in a breeding context. Humpback whales worldwide also produce non-song vocalizations (“calls”) throughout their migratory range, some of which are stable across generations.

Methods. We looked for evidence that temporally stable call types are shared by two allopatric humpback whale populations while on their northern hemisphere foraging grounds in order to test the hypothesis that some calls, in strong contrast to song, are fixed within the humpback whale acoustic repertoire.

Results. Despite being geographically and genetically discrete populations, humpback whales in Southeast Alaska (North Pacific Ocean) share at least five call types with humpback whales in Massachusetts Bay (North Atlantic Ocean).

Discussion. This study is the first to identify call types shared by allopatric populations, and provides evidence that some call types may be innate to the humpback whale repertoire.

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Abstract

Background. Humpback whales (*Megaptera novaeangliae*) are a widespread, vocal baleen whale best known for producing song: a complex, repetitive, geographically discrete acoustic signal sung by males, predominantly in a breeding context. Humpback whales worldwide also produce non-song vocalizations ("calls") throughout their migratory range, some of which are stable across generations. **Methods.** We looked for evidence that temporally stable call types are shared by two allopatric humpback whale populations while on their northern hemisphere foraging grounds in order to test the hypothesis that some calls, in strong contrast to song, are fixed within the humpback whale acoustic repertoire. **Results.** Despite being geographically and genetically discrete populations, humpback whales in Southeast Alaska (North Pacific Ocean) share at least five call types with humpback whales in Massachusetts Bay (North Atlantic Ocean). **Discussion.** This study is the first to identify call types shared by allopatric populations, and provides evidence that some call types may be innate to the humpback whale repertoire.

Introduction

The study of acoustic signaling is a valuable tool for investigating animal behavior across a broad range of taxa (Brockelman & Schilling 1984, Gannon 2008, Pijanowski et al. 2011, Clink et al. 2018). Sounds produced by animals can be systematically measured and compared, as can patterns of vocal behavior made in association with critical activities such as breeding, foraging, or socializing. Acoustic monitoring allows for broad-scale observations of animals across space and time and between populations (Mann & Lobel 1998, Cerchio et al. 2001, Risch et al. 2007, Potvin et al. 2011). When coupled with what is known about genetics, population structure, and behavior, acoustic analyses become powerful tools for investigating drivers of communication.

Drivers of acoustic repertoires vary between taxa and species. While anatomy is a restricting force driving sound production, genetic, neurological, and environmental drivers also influence acoustic repertoires and vocal plasticity. For acoustic communication to be effective a sound must be detectable within its acoustic habitat and sufficiently convey information to a receiver. As such, acoustic communicators have evolved adaptations to couple the acoustic properties of sounds to the environment in which they are produced in order to meet their signaling needs and maximize fitness (Slater 1983, Boncoraglio & Saino 2006). As a result, within the repertoire of most, if not all, sound-producing vertebrates are a collection of innate (*i.e.* unlearned) calls that are exercised independently of vocal learning and persist across generations (*e.g.*, Domestic Fowl *Gallus gallus* and other species in the order Galliformes (Konishi 1963, Matsunaga & Okanoya 2009), white-handed gibbons *Hylobates lar* (Brockelman & Schilling 1984), New Zealand fur seals *Arctocephalus forsteri* (Page et al. 2001)). A smaller subset of taxa – most notably passerine songbirds – exhibit a combination of learned and unlearned vocal signals, which persist over time within a population (Baker & Jenkins 1987, Vicario 2004, Matsunaga & Okanoya 2009, Zann 2010). Some mammals including mouse, pinniped, and cetacean species are also capable of vocal learning as indicated by vocal imitation or improvisation (Tyack & Sayigh 1997, Poole et al. 2005, Petkov & Jarvis 2012, Arriaga & Jarvis 2013). What is less common among mammalian vocal learners, however, is the coupling of stable sound types, which may be innate, with a dynamically changing repertoire of sound types whose variation appears to be culturally driven. Cetaceans, and specifically humpback whales (*Megaptera novaeangliae*), may be the best example of a taxon which exhibits this coupling of highly stable calls types and dynamically shifting vocal behaviors (Payne & Payne 1985, Tyack & Sayigh 1997, Rekdahl et al. 2013, Fournet et al. 2015a, Fournet 2018).

Humpback whales are a migratory baleen whale with a cosmopolitan distribution. Generally, humpback whales migrate between low-latitude breeding and calving grounds and high-latitude foraging grounds (Clapham et al. 1999). Their vocal behaviors are geographically and seasonally stratified. Primarily on breeding grounds and migratory corridors, but also to a lesser extent on foraging grounds, male humpback whales produce a long elaborate, and repetitive vocal display known as ‘song’, (Payne & McVay, 1971; Gabriele & Frankel, 2002; Stimpert et al., 2012; Dunlop & Noad, 2016; Herman, 2017). Songs are highly structured and acoustically complex, and are culturally transmitted between males within a single breeding region (Cerchio et al. 2001, Mercado et al. 2005, Herman et al. 2013, Herman 2017). Song structure changes rapidly over time (1-2 years) (Payne & Payne 1985, Noad et al. 2000, Parsonset al. 2008), ~~and~~ Further, geographic variation in song between regions is typical (Winn et al. 1981, Cerchio et al. 2001, Parsons et al. 2008), with song sharing only occurring between regions that share individuals (Cerchio et al. 2001, Mercado et al. 2005, Garland et al. 2015, Herman 2017).

Humpback whales of both sexes and across the migratory range also produce a series of vocalizations ("calls") independently of song (Silber 1986, Dunlop et al. 2008, Stimpert et al. 2011). Calls occur in isolation or in short bouts and occasionally appear as song units (Rekdahl et al. 2013, 2015). Call use varies based on social and behavioral context; some calls facilitate intra-group interactions, while other calls are specific to foraging contexts (Stimpert et al. 2007, Dunlop et al. 2008, Wild & Gabriele 2014, Fournet et al. 2018). Unlike song, many calls are stable over time. The most commonly produced call types in the east Australian migratory corridor, making up 64% of the call detected in one study, are stable over 7-11 year time periods (Rekdahl et al. 2013), while in Southeast Alaska, at least 16 call types, including all described call types to date, persist in the call repertoire for decades and across generations (Fournet et al. 2015a, Fournet 2018).

Call longevity across generations is an indication that some call types may be fixed within the humpback whale repertoire. Identifying the same stable call types in other, unrelated populations would provide further evidence that humpback whales may be anatomically or behaviorally predisposed toward the production of certain sounds. Qualitative comparisons have been made of calls produced in the North Pacific (Southeast Alaska), South Pacific (East Australia), North Atlantic (Massachusetts Bay) and South Atlantic (Coastal Angola, Africa) with the general agreement that global humpback whale populations produce some similar call types (Dunlop et al. 2007, Stimpert et al. 2011, Fournet, et al. 2015, Rekdahl et al. 2016), but no formal comparison of call types between populations has been thus far attempted.

To test the hypothesis that some calls types are inherent to humpback whales, we looked for evidence of shared call types in the calling repertoire of two allopatric humpback whale populations on their northern latitude foraging grounds, one in the North Atlantic and one in the North Pacific. Based on genetic analyses it is estimated that global humpback whale populations last shared a maternal ancestor in the Miocene, approximately 5 Mya, and that discrete lineages split 2-3 Mya (Baker et al. 1993). In the northern hemisphere, humpback whales in the Atlantic and Pacific Ocean are geographically separated by the North American continent and are genetically isolated from one another (Valsecchi et al. 1997, McComb et al. 2003). Cultural exchange of acoustic signals between the two populations is extremely unlikely based on this geographic barrier and known migratory patterns. Thus, a shared acoustic repertoire would indicate that individual signals may be fixed within the species and conserved with time, rather than socially learned. We hypothesized that call types that are stable across multiple generations on a North Pacific foraging ground would also be present in the humpback whale calling repertoire on a North Atlantic foraging ground.

Methods

Data collection

We compiled acoustic datasets from two humpback whale foraging grounds in the North Pacific and North Atlantic. Acoustic data were collected using passive acoustic recording devices during summer months (June-August) in Southeast Alaska (SEAK; North Pacific) in 1976, 2007, and 2008, and Massachusetts Bay (MB; North Atlantic) in 2008 (Figure 1, Table 1). Acoustic recordings from Frederick Sound, SEAK were opportunistically collected with a dip hydrophone from a drifting vessel and were of variable duration (32-94 minutes). Acoustic recordings from Glacier Bay National Park and Preserve (GBNPP) made in 2007 and 2008 were collected from a cabled hydrophone in Bartlett Cove (Figure 4) with a 30-seconds-per-hour recording cycle (Wild & Gabriele 2014). Data from GBNPP were reviewed by U.S. Navy acousticians to characterize the content of each sound sample. Data from MB were collected as part of a long-term monitoring project in that region (see also Hatch et al. 2012). Recordings were made using an array of marine autonomous recording units (MARUs (Calupca, et al.,2000), Table 1). Technicians from the Cornell Lab of Ornithology reviewed array recordings and noted the presence or absence of humpback whale calls on each element. We randomly subset 60 hours of two channel acoustic data from the array for analysis (Figure 1). Sound samples from both regions were analyzed only if they were known to contain humpback whale calls.

Data Processing and Analysis

Recordings from SEAK were originally sampled at 44.1 kHz and were resampled at a rate of 2 kHz for consistency with data from MB (Table 1). Spectrograms of acoustic recordings were created with Raven Pro 1.5 (Cornell Lab of Ornithology, Ithaca, NY) using an FFT length of 1046, a 30 s window length, Hann window, 75% overlap, and constrained to the 10 Hz to 1 kHz frequency range to facilitate analysis. Recordings were manually reviewed by experienced observers familiar with the humpback whale calling repertoire. All calls were annotated in the time and frequency domain and salient acoustic features were extracted for quantitative classification in Raven Pro (Table 1). Start and end frequency measurements were made on the fundamental frequency for harmonic sounds. For amplitude-modulated sounds containing a broadband component, measurements were made on the lowest-frequency component of the call (Dunlop et al. 2007, Rekdahl et al. 2013). Frequency parameters were log-transformed to account for the mammalian perception of pitch, which is approximately logarithmic rather than linear (Table 2) (Richardson et al., 1995; Dunlop et al., 2007; Fournet et al., 2015b). Time-frequency parameters were input into a Principal Component Analysis (PCA) in order to aggregate variables for classification and comparative analyses (R, *psych* package). A varimax rotation was applied to maximize loading and facilitate variable interpretation (Table 2) (Cerchio & Dahlheim 2001, Dunlop et al. 2007).

Signal-to-noise ratios (SNR) were calculated for each acoustic sample by measuring the in-band power contained in a one second sound sample directly preceding each call; this value was then subtracted from the in-band power measured of the call of interest to get a SNR value. Calls in this study were only included if they had a SNR of 10 dB or higher (Dunlop et al. 2007, Rekdahl et al. 2016).

Using the existing SEAK call catalogue as a base reference, each acoustic sample was assigned an *a priori* call type based on aural and visual call features. Because the goal of this study was to investigate the potential for calls to be fixed within this species, only calls that persist across generational timescales that could be detected given a 2 kHz sampling rate were included in this study; this included triplet, growl, feed, swop, teepee, and whup calls (Fournet et al. 2015a, Fournet 2018). Calls that were qualitatively different than previously described call types were classified as 'unknown' and no further attempts for classification were made.

Quantitative classification methods were identical to those used by Fournet (2018), with the exception that all predictor variables were extracted in RavenPro. Calls were classified through the use of a Classification and Regression Tree (CART) analysis and a random forest analysis. The Gini index was used to assess the "goodness-of-split" for each node in the tree (Rekdahl et al. 2013, 2016). A total of 1,000 trees were grown for the random forest analysis. Predictor variables included salient acoustic features as well as two rotated principal components (PC) that aggregated correlated acoustic variables (Dunlop et al. 2007); a detailed description of predictor variables can be found in Table 2. Quantitative classification assignments were compared to *a priori* call type assignments to validate observer classification. Major discrepancies in call type assignment were re-reviewed by at least two observers. Calls were excluded if observers were not in agreement. If observers were in agreement about call type assignment than the *a priori* classification was deemed ‘correct’.

To assess differences in acoustic parameters between calls from MB and SEAK populations, we compared PC values for all call types that exhibited stability between regions. Comparative analyses were made based on *a priori* classification. A Bartlett’s test with a significance level (α) of 0.05 indicated that the assumption of equal variance between locations was not met. To account for this and for non-normally distributed data, we used a non-parametric Kruskal-Wallis test to test for significant differences in median PC values between locations (α=0.05). All analyses were conducted in R version 3.3.3 (R, 2013).

Results

In SEAK there are six call types that are stable over generational time (Fournet 2015b) that have ~~with~~ average bandwidths between 10 - 1000 Hz: droplet, growl, feeding call, swop, teepee, and whups. A total of 411 sounds fitting the inclusion criteria were classified to one of these known call types; 191 calls were collected across 10 recording days from MB, and 220 calls were collected across 76 sample days from SEAK (Table 1, Table 3). Drops, growls, swops, teepees, and whups were found in both populations (Figure 2, Table 3); feeding calls were detected only in SEAK. PCA output indicated that the use of two principal components was adequate to encompass the variability of the data (χ^2= 683.29, p < 0.00001). The first rotated component (PC1) corresponded most closely to entropy, bandwidth, and upper frequency, meaning that as PC1 increases, the calls grow more complex, grow broader-band, and extend to higher frequencies. The second rotated component (PC2) corresponded most closely to lower frequency, start frequency, and peak frequency, meaning that as PC2 increases, calls grow higher in pitch overall, but not necessarily more broadband or complex. Neither component was strongly affiliated with duration or bout in this analysis, meaning that the PC variables in this analysis do not represent temporal variability.

CART call type assignment and *a priori* call type assignment were in agreement 82% of the time (n=335/411, Table 4). Bandwidth, bout, center frequency, duration, end frequency, entropy, lower frequency, and PC1 were all important splitting variables. The random forest analysis correctly classified most of the calls (out-of-bag error rate = 23%). The variables most important for splitting decisions in the random forest analysis were bout, end frequency, duration, entropy, lower frequency, PC1, PC2, and frequency trend. Whups were the most commonly misclassified calls (Table 4); in the CART analysis whups were mistaken for growls 38% of the time (n=22). Observers validated call type assignment for most whup calls (95%, n=57); three calls were omitted due to classification incongruity.

PC1 values were significantly higher in SEAK than MB for all call types except for growls, indicating that calls from SEAK were generally broader band and exhibited higher levels of complexity (Table 3, Figure 3). PC2 values were significantly higher in SEAK than MB for droplet and teepee calls (Table 3, Figure 4), indicating that calls from SEAK were generally higher pitch than calls from MB.

Discussion

This is the first study to describe call types shared by allopatric humpback whale populations. Evidence that temporally stable call types are shared between SEAK and MB humpback whale populations supports the hypothesis that a portion of the calling repertoire may be fixed in this species.

Misclassification was low for all call types, except for whups, which were commonly classified as growls. Misclassification of these call types is unsurprising, as the only distinguishing acoustic feature between growls and whups is a terminal upsweep, which attenuates with distance and is not adequately encompassed by traditional acoustic parameters (Figure 2) (Fournet et al., 2015b). The humpback whale calling repertoire has been described as an acoustic continuum, where graded signals are common (Rekdahl et al. 2013, Fournet et al. 2015b). The delineation between growls and whups is not discrete, and it is currently unknown whether whups and growls are functionally interchangeable. Graded signals within the humpback whale calling repertoire deserve dedicated study, and methods for either classifying graded signals or more broadly aggregating them according to their functional roles merits future investigation.

Despite otherwise high classification agreement, there were some significant differences in call type parameters between populations. The increased PC1 values found in SEAK versus MB may be recording artifacts. The ambient sound conditions in SEAK are significantly different than MB (Kipple & Gabriel 2003, Hatch et al. 2008, Haver et al. 2018). Recordings from Frederick Sound were made in the absence of vessel noise, and recordings made in GBNPP were made in the presence of limited vessel traffic. By contrast the hydrophones in MB were located within a shipping lane that services Boston Harbor, which is among the busiest harbors on the North American east coast. For this reason, vessel noise was recorded simultaneously with almost all calls recorded in MB (Figure 2). Overlapping ambient sounds – including vessel noise, which is common throughout the 10 – 1000 Hz range (Wenz 1962) – may have masked fine scale acoustic features, resulting in decreased entropy measurements in MB calls. Similarly, vessel noise in MB may have masked upper frequency portions of calls, which contain less energy, attenuate faster, and are thus more easily obscured by overlapping ambient sound.

Droplet and teepee calls appear to be generally higher frequency in SEAK than in MB, although calls from both populations fall within previously described parameters for these call types (Fournet et al. 2015b). There are many factors that drive changes in pitch in cetacean vocalizations (e.g., motivational state (Rehn et al. 2011, Dunlop 2017), caller body size (May-Collado et al. 2007), ambient noise (Parks et al. 2007)). With an unknown number of individuals in our samples, and in the absence of body size or motivational state observations to accompany acoustic recordings any inferences made to describe the differences observed here are speculative. However, it seems plausible that the comparatively noisy environment in MB may have shaped the use of particular frequency bands of these stereotyped calls, as documented in right whales and blue whales. (Parks et al. 2007, DiOrio & Clark 2010). Dedicated future effort may confirm fine-scale differences in call types between regions as well as potential drivers of geographic variation between population repertoires.

With one exception, call types of interest from SEAK were also found in MB. The notable exception was the SEAK feeding call. Feeding calls are highly stereotyped, tonal calls, with a fundamental frequency of ~500 Hz that occur when humpback whales in Southeast Alaska forage on Pacific herring (*Clupea palisii*) (D'Vincent et al. 1985, Sharpe 2001, Fournet et al. 2018). Herring are a primary food source for humpback whales in Southeast Alaska (Krieger & Wing 1984, D'Vincent et al. 1985, Dolphin 1988), whereas in MB humpback whales feed primarily on sand lance (*Ammodytes spp*), a calorie-dense prey species that burrows in the sandy substrate (Overholtz & Nicolas 1979, Hain et al. 1995, Friedlaender et al. 2009). The absence of feeding calls in MB may be attributed to their focus on forage species other than herring.

Droplets, growls, swops, teepees, and whups were present in the call repertoire of both humpback whale populations. Evidence of the same calls in allopatric populations supports the hypothesis that a portion of the humpback whale calling repertoire is innate in this species. Non-passerine bird species, like doves (*Streptopelia sp.*), produce highly stereotyped calls instinctively (Lade & Thorpe 1964), and as a result allopatric dove populations of the same species, even those separated by great distances, show no significant difference in call types (de Kort et al. 2002). Ornate chorus frogs (*Microhyla fissipes*) produce advertisement calls independently of vocal learning that are aurally indistinguishable between geographic regions, and that vary only minutely with genetic distance (Lee et al. 2016). Genetic predetermination of calls is common across taxa, including zebra finches (*Taeniopygia guttata*; Forstmeier et al. 2009), fur seals (Antarctic, *Arctocephalus gazella*, subantarctic, *A. tropicalis*, and New Zealand, *A. forsteri*; Page et al. 2001), and *Spheniscus* penguins (Thumser & Ficken 1998). Call type longevity in these species is generally multi-generational and geographically widespread. In humpback whales, similarly identifying call types that are multi-generational, and persist in geographically and genetically discrete populations provides strong evidence that these call types are innate.

For calls to be conserved within the calling repertoire of genetically and geographically discrete populations is an indication that they play an important role in humpback whale life history by increasing individual fitness in some capacity. It has been proposed that in Southeast Alaska the whup call serves a contact function (Wild & Gabriele 2014), and the analogous “wop” call of east Australia may facilitate communication between cows and calves (Dunlop et al. 2008). There is also evidence that droplets, swops, and teepees are used for close range communication on foraging grounds (Fournet 2014), and similar pulsed calls may facilitate affiliation or disaffiliation in groups during migration (Dunlop et al, 2008). These contextual descriptions, while broad, indicate that these calls serve a vital function or functions. The fixed nature of calls stands in marked contrast to humpback whale song, which is geographically discrete, changes rapidly, and is culturally transmitted rather than innate (Payne & Payne 1985, Noad et al. 2000, Cerchio et al. 2001). Thus, it seems that the humpback whale vocal repertoire is composed of both fixed and adaptable calls, which likely serve different roles. Dedicated research pairing the call types described in this study with behaviors and social context will be important for understanding role of calls in the acoustic ecology of humpback whales and what drives their persistence.

Lastly, humpback whales are notoriously difficult to monitor acoustically due to their broad and changeable repertoire. It has been suggested that calls rather than song, which is not prevalent throughout the entire migratory range, may play an important role in passive acoustic monitoring of this species (Stimpert et al. 2011). The ability to confidently credit particular vocalizations to humpback whales in the absence of visual confirmation allows for broader spatial and temporal monitoring with significantly lower effort and cost. If the call types described in this study are innate as we hypothesize, then theoretically it would be possible to build an automated acoustic detector that could be run on datasets from across ocean basins and years to confirm the presence of humpback whales at previously unknown regions or times.

Conclusions

This study demonstrates that temporally stable humpback whale call types on northern latitude foraging grounds are not geographically distinct. These two features, geographic and temporal stability, lend strong support to the hypothesis that some calls, in strong contrast to song, are not culturally transmitted, and may be innate. Natural next steps include a global comparison of call repertoires between allopatric populations and across the migratory range, with particular attention paid to change or stability at various temporal and geographic scales.

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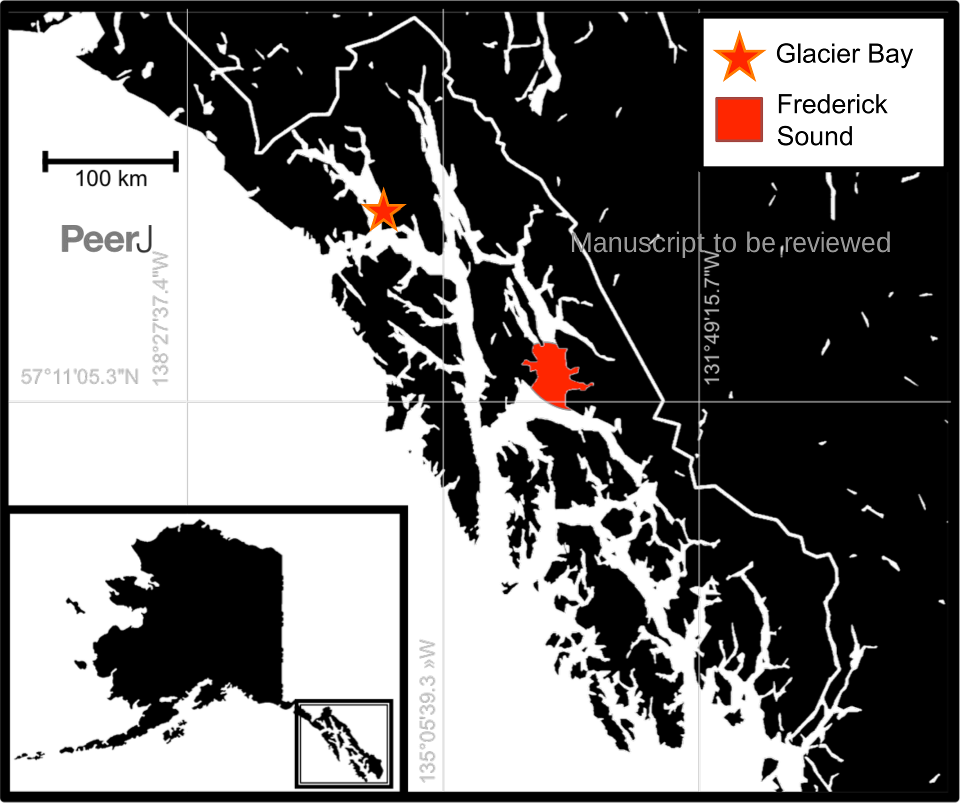
Figure 1(on next page)

Map of (top) Southeast Alaska, North Pacific recording locations and (bottom) Massachusetts Bay, North Atlantic recording locations. Red area indicates sampling region for hydrophone recordings made in 1976. Stars in both maps indicate moored hydrophone l

Red area indicates sampling region for hydrophone recordings made in 1976. Stars in both maps indicate moored hydrophone locations.


Glacier Bay
🟥 Frederick Sound
100 km
57°11'05.3"N
138°27'37.4"W
131°49'15.7"W
135°05'39.3 »W

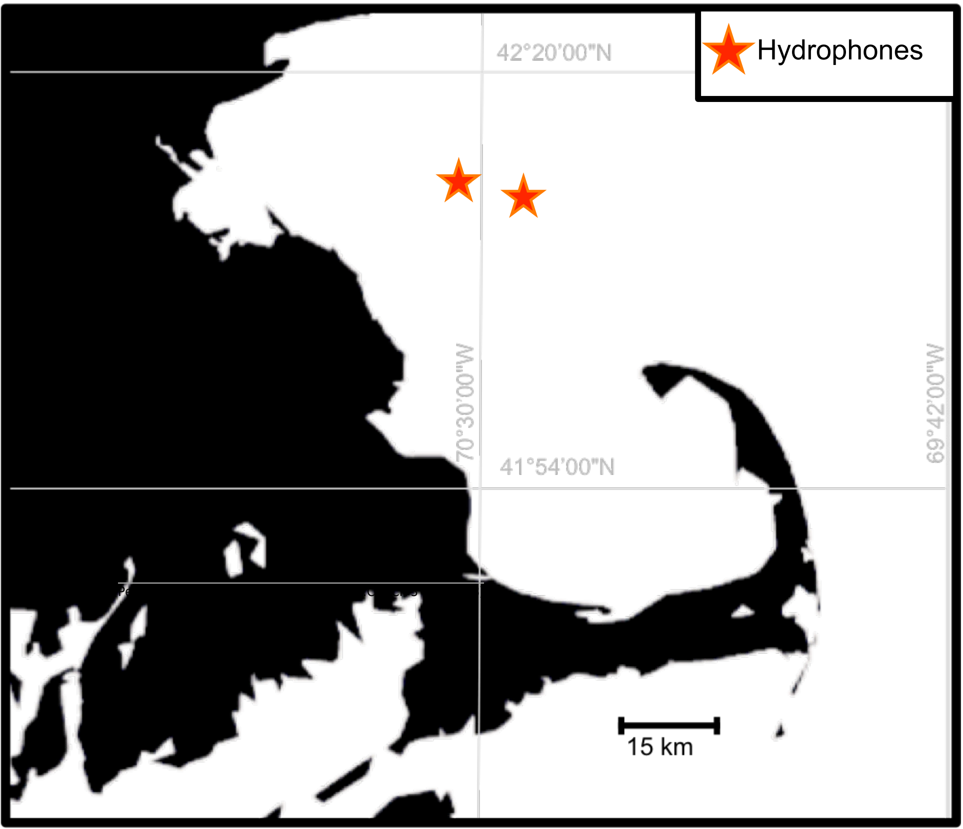
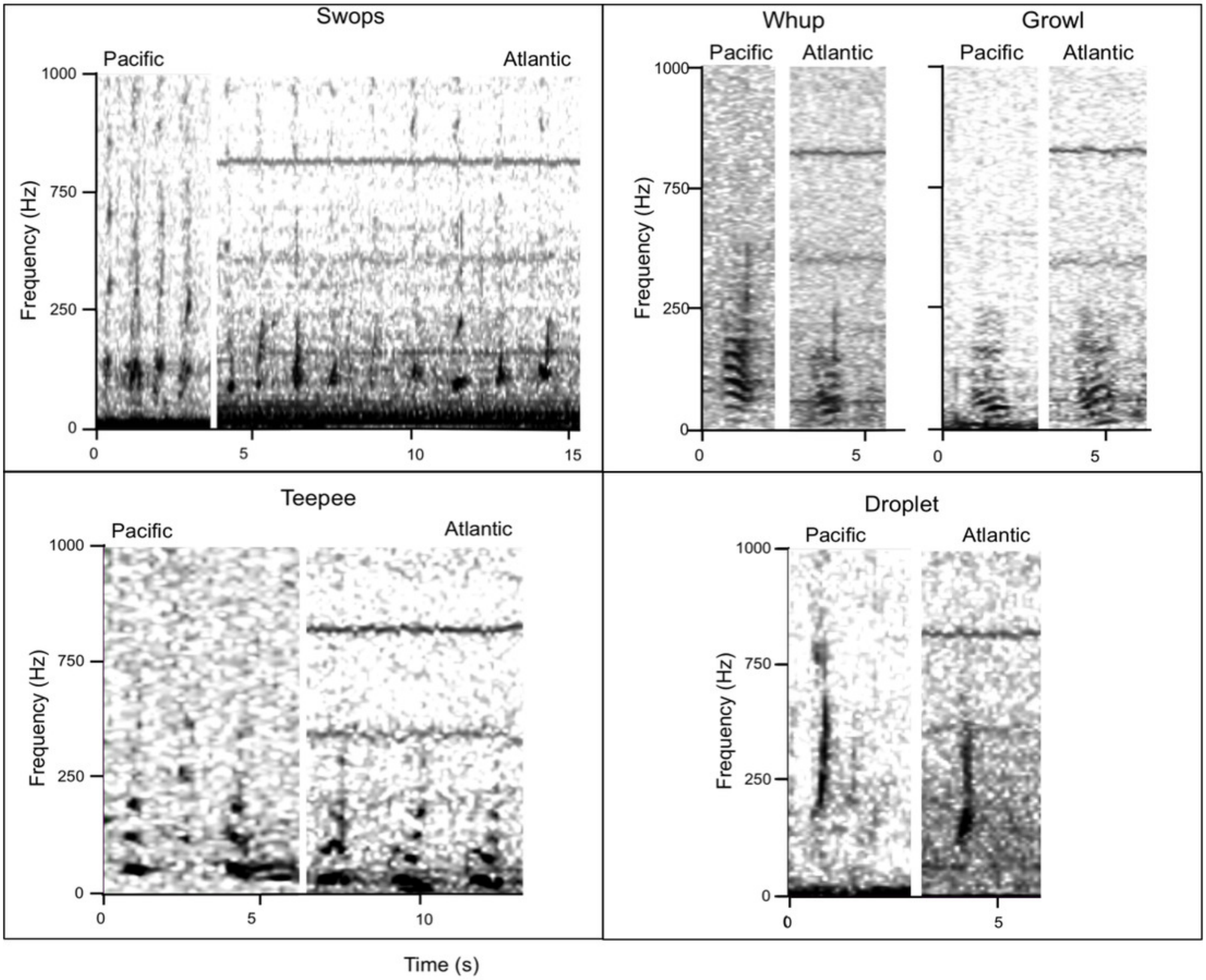

Hydrophones
42°20'00"N
41°54'00"N
70°30'00"W
69°42'00"W
15 km

Figure 9

Spectrograms of call types by ocean basin (FFT 256, Hann window, 90% overlap).

Call types: (top left) swops, (top right) whups and growls, (bottom left) teepees, (bottom right) droplets. The horizontal lines at ~500 and 800 Hz in spectrograms from the Atlantic indicate vessel noise.



gure 3(on next page)

Boxplots of PC1 values (indicative of entropy, bandwidth, and upper frequency components) between call types and ocean basins.

Calls recorded in the Atlantic Ocean are indicated by coral, and the Pacific ocean by teal.

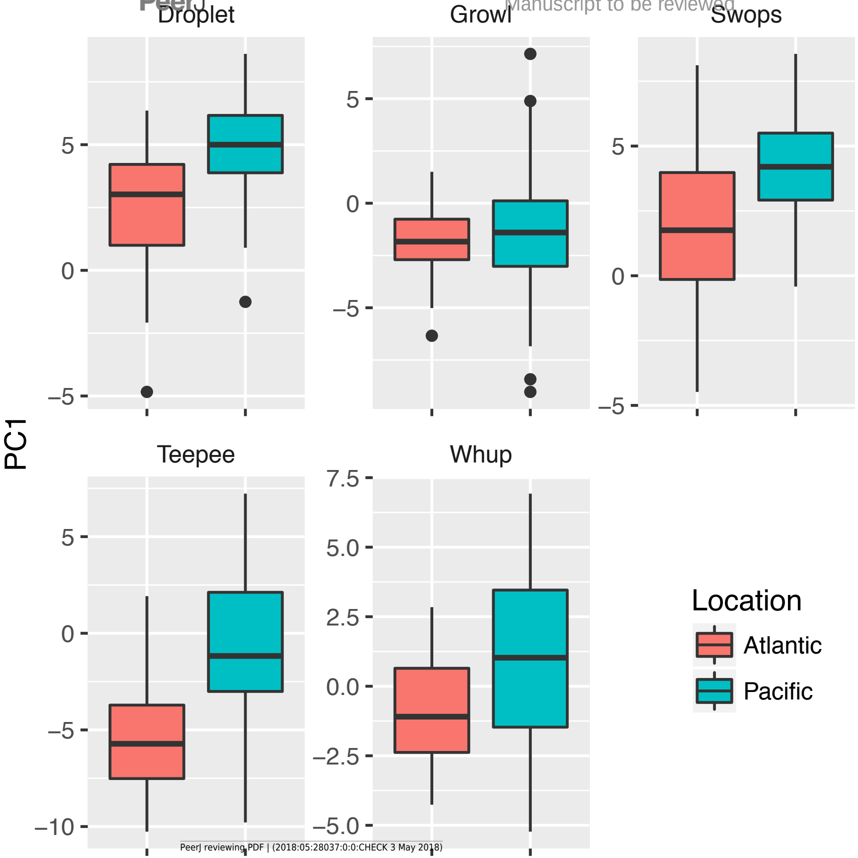

Droplet
Growl
Swops
Teepee
Whup
PC1
5
0
−5
−10
7.5
5.0
2.5
0.0
−2.5
−5.0
Location
Atlantic
Pacific

Figure 4 (on next page)

Boxplot of PC2 values (indicative of lower frequency, start frequency, and peak frequency components) between call types and ocean basins.

Calls from the Atlantic are indicated by coral, calls from the Pacific are indicated by teal.

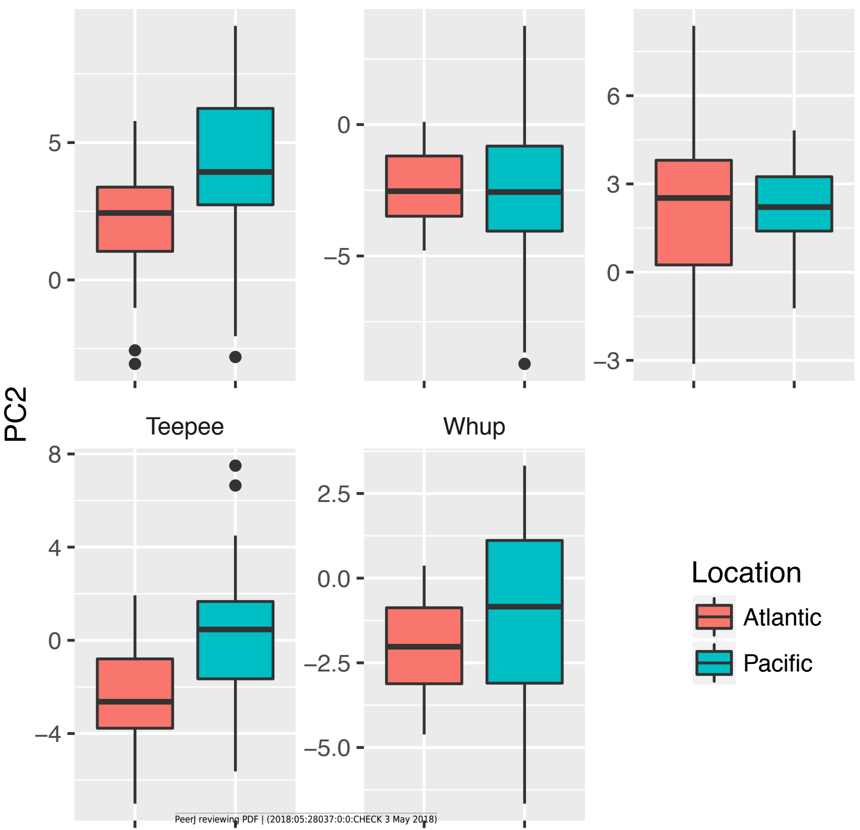

Droplet
Growl
Swops
Teepee
Whup
PC2
5
0
0
−5
6
3
0
−3
8
4
0
−4
2.5
0.0
−2.5
−5.0
Location
Atlantic
Pacific

Table 1(on next page)

Recordings specifications for data collection protocols from North Pacific and North Atlantic foraging grounds.

Table 1-Recordings specifications for data collection protocols from North Pacific and North Atlantic foraging grounds.

Year	1976	2007 & 2008	2008
Hydrophone model	~~u~~nknown	ITC 8215A	HTI-94-SSQ
Sampling rate	44.1 kHz	44.1 kHz	2 kHz
System sensitivity	~~u~~navailable	-174 dB ± 2 dB re 1 V/µPa	-168 dB ± 1 dB re 1 V/µPa
Deployment method	Dipping (20 m)	Bottom-mounted (52 m)	Bottom-mounted (~60 m)
Location	Frederick Sound	Glacier Bay	Stellwagen Bank National Marine Sanctuary
Recording cycle	Non-standardized	30 seconds from every hour	Continuous
Data format	Continuous	30-second recordings	5-minute recordings
Recording Days	4	72	10

Table 2(on next page)

Acoustic parameters used in Classification and Regression Tree (CART) analysis. Log transformed parameters are indicated with an asterisk (*).

Table 1- Acoustic parameters used in Classification and Regression Tree (CART) analysis. Log transformed parameters are indicated with an asterisk (*).

Duration (90%) (s)	90% of the duration of the annotated call
Bout	Number of repetitions of the same call type
Low Frequency (Hz)*	Lowest frequency component of the call
High Frequency (Hz)*	Highest frequency component of the call
Bandwidth (90%) (Hz)	90% of the difference in frequency between high and low frequency
Start Frequency (Hz)*	Starting frequency of fundamental
End Frequency (Hz)*	Ending frequency of fundamental
Peak Frequency (Hz)*	Frequency of the spectral peak
Center Frequency (Hz)*	The frequency that divides the sound equally into two intervals of equal energy
Frequency Trend*	Start F_0 / End F_0
Aggregate Entropy (bits)	A measure of total disorder in the call (RavenPro, 1.5)
PC1	Rotated principal component most closely associated with entropy bandwidth, and upper frequency; as PC1 increases calls grow broader band, extend into higher frequencies and grow more complex
PC2	Rotate principal component most closely associated with lower frequency, start frequency, and peak frequency; as PC2 increases calls grow generally higher in pitch, but not necessarily more broadband

Table 3(on next page)

Summary statistics (mean in bold, standard deviation) for call parameters by call type and location. Test results for a Kruskal-Wallis test for median rank differences in rotated principal component (PC) scores. PC descriptions can be found in Table 2.

Table 3- Summary statistics (mean in bold, standard deviation) for call parameters by call type and location. Test results for a Kruskal-Wallis test for median rank differences in rotated principal component (PC) scores. PC descriptions can be found in Table 2.

							PC1		PC2	
Type		Variable	Atlantic		Pacific		χ^2	P	χ^2	P
Low Frequen[illegible] Harmonic	Growl	N	**41**		**78**		**1**	**0.3**	**0.15**	**0.69**
		Low Freq (Hz)	**41.5**	12.2	**35.8**	21.8				
		Peak Freq (Hz)	**87.4**	15.1	**116**	62.6				
		Duration (s)	**0. 8**	0.24	**0.7**	0.3				
	Whup	N	**21**		**36**		**4.2**	**0.04**	**1.9**	**0.15**
		Low Freq (Hz)	**49.9**	15.8	**47.4**	25.1				
		Peak Freq (Hz)	**94.9**	26.2	**128**	70.3				
		Duration (s)	**0.6**	0.18	**0.7**	0.2				
Pulsed	Droplet	N	**44**		**29**		**16.9**	**>0.001**	**11.4**	**>0.001**
		Low Freq (Hz)	**99.4**	49	**148**	99.8				
		Peak Freq (Hz)	**187**	62.6	**252**	120				
		Duration (s)	**0.4**	0.2	**0.3**	0.16				
	Swop	N	**45**		**16**		**8.9**	**0.002**	**0.007**	**0.93**
		Low Freq (Hz)	**76.5**	31.4	**70**	30				
		Peak Freq (Hz)	**159**	54.3	**214**	85.6				
		Duration (s)	**3.9**	4.2	**0.3**	0.2				
	Teepee	N	**40**		**51**		**33.05**	**>0.001**	**23.2**	**>0.001**
		Low Freq (Hz)	**40**	17	**214**	25.1				
		Peak Freq (Hz)	**79.2**	28.8	**154**	70.3				
		Duration (s)	**1.1**	1.77	**0.4**	0.23				

Table 4(on next page)

Confusion matrix indicating agreement between (vertical) Classification and regression tree call type assignment versus (horizontal) human call type assignment.

Table 4- Confusion matrix indicating agreement between (vertical) Classification and regression tree call type assignment versus (horizontal) human call type assignment.

	Droplet	**Feed**	**Growl**	**Swops**	**Teepee**	**Whup**	**Agreement**
Droplet	58	0	3	5	4	3	79%
Feed	0	10	0	0	0	0	100%
Growl	0	0	111	1	3	4	93%
Swops	5	0	1	44	9	2	72%
Teepee	3	0	3	4	81	0	89%
Whup	2	0	22	2	0	31	54%
					Total Agreement		**82%**