Humpback whales *Megaptera novaeangliae* alter calling behavior in response to natural sounds and vessel noise

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ABSTRACT: Acoustically adept species in the marine environment have to contend with complex and highly variable soundscapes. In the ocean today, sounds from human sources contribute substantially to the underwater acoustic environment. We used a 4-element hydrophone array in Glacier Bay National Park to (1) identify primary drivers of ambient sound in this region, (2) investigate whether humpback whales *Megaptera novaeangliae* exhibit a Lombard response in response to ambient noise, and (3) investigate whether humpback whales adjust their calling activity in response to naturally occurring and vessel-generated sounds. We found that cruise ships and tour boats, roaring harbor seals *Phoca vitulina*, and weather events were primary drivers of ambient sound levels, and that they varied both seasonally and diurnally. As ambient sound levels increased, humpback whales responded by increasing the source levels of their calls (non-song vocalizations) by 0.81 dB (95% CI = 0.79–0.90) for every 1 dB increase in ambient sound. There was no evidence that the magnitude of the observed response differed between natural and man-made sounds. We also found that the probability of a humpback whale calling in the survey area decreased by 9% for every 1 dB increase in ambient sound. Controlling for ambient sound levels, the probability of a humpback whale calling in the survey area was 31–45% lower when vessel noise contributed to the soundscape than when only natural sounds were present.

KEY WORDS: Humpback whale calls · Vessel noise · Anthropogenic noise · Soundscape

INTRODUCTION

Anthropogenic sounds are recognized as a threat to acoustically oriented species across taxa in both the marine and terrestrial realm (Patricelli & Blickley 2006, Popper & Hastings 2009, Kight & Swaddle 2011, Potvin et al. 2011, Finneran 2015, Pacini & Nachtigall 2016, Simpson et al. 2016). Pervasive sound has the potential to limit acoustic communication, elicit changes in foraging behavior, alter preda-

tor–prey dynamics, and have negative physiological impacts (Weilgart 2007, Potvin et al. 2011, Rolland et al. 2012, Richardson et al. 2013, Finneran 2015, Simpson et al. 2016). This threat is particularly pronounced in marine ecosystems, where low frequency sound can travel great distances with little loss of energy and where—in the absence of human activities—many marine species have evolved to rely on sound as their principal sensory modality (Urick 1983, Richardson et al. 2013). The contemporary

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ocean is characterized by global trade, resource extraction, and other maritime activities, all which have an acoustic footprint (Haver et al. 2017, 2018). Sound from large vessels in particular extends over large distances underwater, often overlapping spatially and temporally with ecologically important environmental and biological sounds (Wenz 1962, Hildebrand 2009, Parks et al. 2009, Haver et al. 2017). Sounds emanating from ships worldwide can be characterized as chronic 'noise', i.e. an unwanted acoustic signal that persists for a long duration without stable and predictable intervals (Crutzen & Stoermer 2000, McKenna et al. 2012, 2017, Lewis & Maslin 2015, Haver et al. 2017). Ecologists and managers need to understand the effects of noise on species which rely on sound for vital life functions in order to prevent and mitigate negative interactions between humans and wildlife.

While the threats associated with increasing anthropogenic noise in the ocean are new from an evolutionary perspective, acoustically oriented species have been subjected to natural variation in ocean soundscapes on time scales ranging from seconds to millennia. Environmental noise from wind, waves, and storms can dramatically increase ambient sound levels across a broad range of spatial and temporal scales (Wenz 1962, Hildebrand 2009). Sympatric species contribute vocalizations to shared environments (Wenz 1962, Scheifele & Darre 2005, Erbe et al. 2015). Geological events such as earthquakes and volcanic eruptions have acoustic signatures within the same vocal range as several acoustically oriented marine species (Nishimura & Conlon 1993, Kong et al. 1995, McDonald et al. 1995, Buckingham & Garcés 1996, Garcés et al. 2013). Sounds from these or other sources combine to form an animal's 'acoustic habitat', which we define as the combination of biological, environmental, and anthropogenic sounds present within a given environment in the frequency band used by that animal. For effective communication to occur within a species' acoustic habitat under ambient biological and environmental conditions, an intended signal must be detectable and interpretable by a receiver (Bradbury & Vehrencamp 2011).

Many marine species have developed vocal adaptations that allow them to cope with highly variable ambient sound conditions. In elevated ambient sound conditions, animals may alter their call rate by calling more or less often, alter the frequency (pitch) of their vocalizations, change their acoustic communication strategy from vocal to non-vocal, or adopt a response known as the Lombard Effect whereby the animal alters the amplitude (loudness) of calls in response to

the loudness of their acoustic environment (Brumm & Slabbekoorn 2005). These strategies have been documented for several marine mammal species, e.g. North Atlantic right whales *Eubalaena glacialis* (Parks et al. 2007, 2016), beluga whales *Delphinapterus leucas* (Lesage et al. 1999, Scheifele et al. 2005), and humpback whales *Megaptera novaeangliae* (Dunlop et al. 2010, 2014), indicating that these animals are able to adapt their behavior in response to changing noise conditions in their acoustic habitat.

Humpback whales are a migratory baleen whale species with a cosmopolitan distribution and a diverse acoustic repertoire that includes song (Payne & McVay 1971, Herman 2017), calls (Tyack 1983, Silber 1986, Thompson 1986, Stimpert et al. 2011), and percussive sounds (breaches, flipper slaps, tail lobs; Whitehead 1985, Dunlop et al. 2010, Kavanagh et al. 2017). While the exact function of these sounds is not certain, humpback whales use acoustic communication in concert with vital life functions such as breeding (Herman 2017), foraging (D'Vincent et al. 1985, Thompson 1986, Stimpert et al. 2007), migrating (Dunlop et al. 2007), socializing (Silber 1986, Dunlop et al. 2008, Dunlop 2017), and across age and sex classes (Zoidis et al. 2008, Silber 1986, Dunlop et al. 2008), indicating that acoustic communication is an important aspect of behavior for this species.

Humpback whales overlap spatially and temporally with numerous maritime industries, including shipping, oil and gas extraction, marine transportation, and tourism (Weir 2008, Cerchio et al. 2014, Rosenbaum et al. 2014). Due to their predictable seasonal distributions and propensity for aerial displays, humpback whales are also the centerpiece of many whale-watching operations worldwide (Corkeron 1995, Au & Green 2000, Weinrich & Corbelli 2009). As such, this species is culturally and economically valuable, and also at risk of being disturbed by vessel noise. At high latitudes, humpback whales change their diving behavior in response to vessels transiting within 4 km (Baker & Herman 1989) and significantly alter their foraging behavior in the presence of vessels (Blair et al. 2016); whether they alter their vocal behavior in response to vessels on feeding grounds is unknown. This differentiation may be significant for managers tasked with mitigating negative interactions between vessels and whales. In general, little is known about humpback whale calling behavior at high latitudes (but see Stimpert et al. 2011, Van Opzeeland et al. 2013), or whether this species is resilient to anthropogenic noise while on their foraging grounds.

Glacier Bay National Park and Preserve (GBNPP) is a marine protected area in Southeast Alaska

that hosts a seasonal population of foraging humpback whales and year-round populations of several other marine mammal species. As a wilderness area and national park, GBNPP managers are tasked with balancing the needs of Park resources and values—which includes organisms, physical processes, and cultural systems—with the human user groups that come to the area seeking a recreational experience. A vessel management system has been implemented which limits the number of vessels in the Park and limits human access to sensitive areas. Additionally, GBNPP limits the course and/or speed of vessels in certain places during times of year where whales are usually present (Code of Federal Regulations 2001). Large commercial vessel traffic is scheduled in advance, such that in GBNPP traffic is spatially and temporally predictable during summer months. Cruise ships and smaller tour boats typically enter and exit at a predetermined time of day and follow a prescribed path as they enter the bay. While the schedules of smaller charter and private boats are less regimented, the diurnal preferences of tourists generally follow the same rhythm. This results in punctuated periods of vessel presence followed by longer periods of vessel absence in portions of the Park. The contributions of vessel traffic to the underwater soundscape, including the impact of vessel timing and vessel quotas, have been investigated using a single hydrophone (McKenna et al. 2017, Frankel & Gabriele 2017, Gabriele et al. 2018). However, in the absence of a hydrophone array, quantifying humpback whale responses to vessel noise has previously been unfeasible. By deploying a hydrophone array in a traditional humpback whale foraging ground outside of the direct cruise ship path but well within the acoustic range of the vessels entering Glacier Bay, we aimed to document calling patterns in the presence of natural and man-made noise.

Our specific objectives were to (1) identify primary drivers of ambient sound in this region of GBNPP and describe their seasonal and daily patterns during the humpback whale foraging season, (2) investigate whether humpback whales in GBNPP exhibit a Lombard response to ambient sound conditions and, if identified, investigate whether there is a threshold beyond which humpback whales fail to adjust their source levels to ambient sounds, and (3) investigate whether humpback whales adjust their calling activity in response to naturally occurring and vessel-generated sound sources.

MATERIALS AND METHODS

Visual data collection

In June–August 2015 and June–September 2016, visual scan point surveys of humpback whales and vessels were conducted from an elevated (11 m) viewing platform located on the easternmost point of Strawberry Island (58.5184° N, 135.9867° W; Fig. 1) in the Beardslee Island complex of GBNPP, Southeast Alaska. Between 3 and 12 surveys were conducted d^{-1}. Surveys lasted 15 min, were separated by at least 5 min of rest, and occurred during daylight hours. Whale densities in this region are low (median number of whales within 5 km = 4) and animals generally travel at slow speeds (average swim speed = 5 km h^{-1}); prior knowledge of typical whale dive times, observer training and pilot data collection indicated that 15 min was an adequate amount of time to visually locate all humpback whales within the primary survey area (visual range 5 km where not blocked by land). Survey teams consisted of 2 observers, a theodolite operator, and a data operator. Observer roles were rotated to minimize fatigue and bias.

Whale and vessel locations were documented in real time using a theodolite (DT-5; Sokkia) connected to a laptop computer running the program Pythagoras (Cetacean Ecosystem Research). Every whale and vessel within visual range was fixed with the theodolite once per survey; whale behavior and vessel type and size class were collected for each fix. Theodolite outputs were converted to Cartesian coordinates, and the total number of whales and vessels present along with their locations were aggregated for each 15 min survey. Aggregated counts also included a small subset of whales that were visually identified but could not be fixed by the theodolite. These animals were documented during regular survey effort, and their locations estimated visually according to standardized geographic landmarks. A categorical quality rating was developed based on the visibility of geographic landmarks to describe observing conditions. Surveys were included in the analysis only if visibility was considered 'good' or 'excellent', an indication that visibility extended at least 6 km to the north and south of the observation station. Provided that visibility was rated at least 'good', surveys were not halted on account of rain. Visual data were collected only in Beaufort sea state 2 or less, which is characteristic of wind activity in this region during the summer. Wind speeds in the Beardslee Island complex are typically low (Horel et al. 2002), and only reached 10 knots or higher on 5%
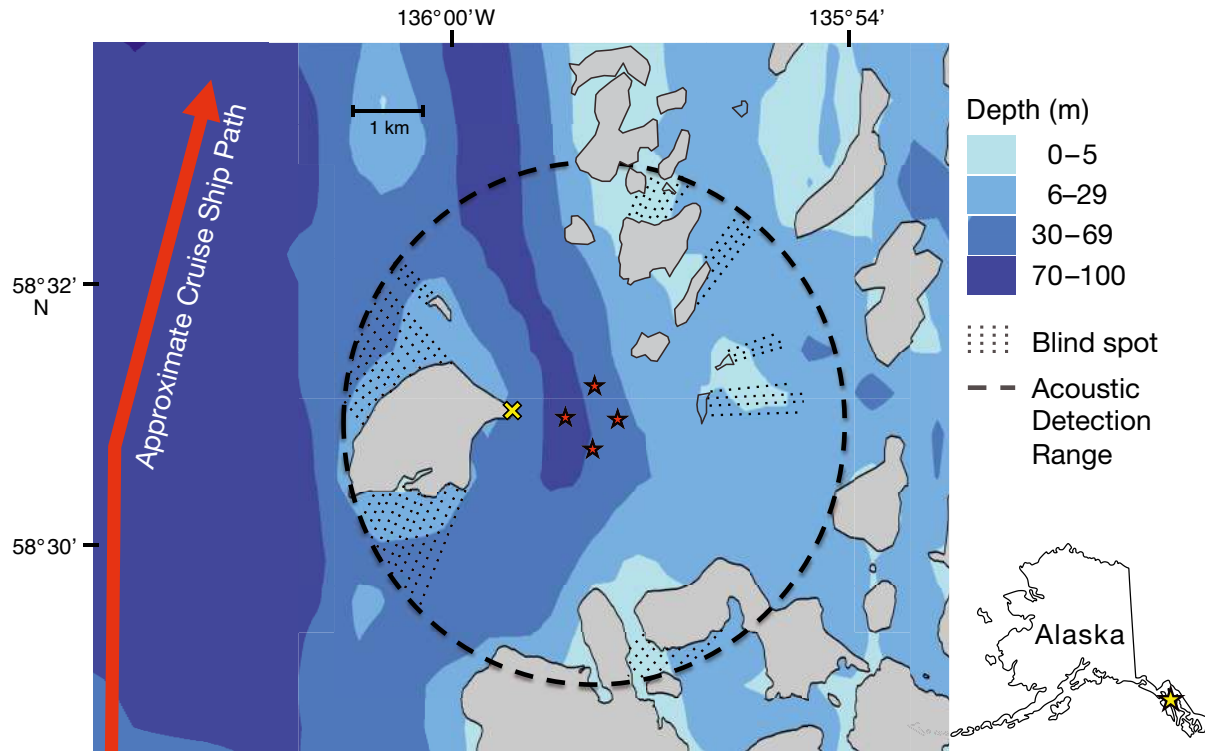
Fig. 1. Survey region in the Beardslee Island Complex, Glacier Bay National Park and Preserve, Southeast Alaska. Dashed line: 3 km acoustic detection range; blue shading: water depth; stippling: area not within visual range of shore-based observers. Yellow 'X': visual observing station; red stars: 2016 hydrophone array; the 2015 array location was 1 km southwest. Red arrow: approximate cruise ship path. Inset: star indicates larger map area within Alaska

(n = 9 d) of the days during which the research team was in the field. Surveys that ended early for any reason, or that experienced sudden weather changes resulting in a change in visibility, were omitted from analyses.

Photographs of humpback whale flukes and dorsal fins were collected opportunistically from shore and by kayak between July and September 2015 and 2016 to identify individual whales (Katona & Whitehead 1981). Photographs were matched to an existing catalog of known humpback whales in Southeast Alaska (Straley & Gabriele 1997) to generate a minimum number of individuals present throughout the study period.

Acoustic data collection

Acoustic data were collected using a 4-element planar array with a 1 km baseline deployed in the Beardslee Island Complex of GBNPP from May to October in 2015 and April to October 2016 (Fig. 1). Each array element consisted of an autonomous underwater hydrophone recorder (AUH, Fox et al.

2001; hydrophone model ITC-1032; International Transducer Corporation) mounted on a weighted aluminum lander and connected to an acoustic release (Edgetech); there was no surface buoy. The landers suspended the 4 AUHs approximately 1 m above the ocean floor at 62–81 m depth and recorded continuously with a 10 kHz sampling rate and 16 bit resolution. Hydrophone sensitivity was −192 dB re 1 V μPa^{-1} with a flat frequency response of ±1 dB over the 15 Hz–4 kHz frequency band. Incoming acoustic signals were low-pass filtered (4 kHz corner frequency) and conditioned (pre-whitened) by a pre-amplifier. The resulting frequency-dependent system sensitivity was −144.1 dB re 1 V μPa^{-1} at 15 Hz and −122.3 dB re 1 V μPa^{-1} at 4 kHz, respectively. Each AUH included a highly accurate internal clock (Q-Tech model 120 number QT-2001, error of approximately 1 s yr^{-1}). Clocks were calibrated to satellite (GPS) time at both deployment and recovery, allowing for clock drift over the deployment to be quantified and for recordings from each AUH to be retroactively time-aligned. Clock drift was assumed to be linear, as water temperatures did not vary widely. Data were recorded as custom-format (.DAT)

sound files and converted to WAVE (.wav) files for analysis using a custom-written MATLAB script. Due to a clock malfunction, the easternmost hydrophone in 2015 could not be precisely time-aligned and was excluded from localization analyses for that year.

Data analyses

Three separate but interrelated analyses were conducted to meet project objectives. We conducted (1) an acoustic habitat analysis to investigate sources of ambient noise and identify diel, seasonal, and inter-annual trends in ambient noise levels; (2) a Lombard Effect analysis, to assess whether or not humpback whales increase source levels in response to ambient noise; and (3) a call probability analysis, to test the hypothesis that the probability of a humpback whale calling in the survey area changes as ambient sound levels increase.

Soundscape level analysis and sound level extraction

Long-term spectral averages (LTSA) in the 15 Hz–4 kHz range (1 Hz, 5 min bins) were calculated for both deployment years from raw .DAT files of the easternmost hydrophone using a custom MATLAB algorithm. Information from individual hydrophone pre-amp frequency response curves was applied to the data retrospectively to obtain absolute received level values for each 1 Hz/5 min bin. All measurements are made in dB_{RMS} re 1 µPa @ 1 m (for source levels) or dB_{RMS} re 1 µPa (for ambient levels) unless otherwise stated. The easternmost hydrophone was selected for ambient sound level analyses because water currents were slowest at this location and recordings contained less flow noise, which creates artefacts in ambient sound measurements. For each 5 min bin, we used LTSA values to calculate broadband ambient sound levels in dB_{RMS} re 1 µPa in the 50 Hz–3 kHz band (hereafter 'broadband levels'). Sound levels in the 50 Hz–3 kHz bandwidth are driven by biological and vessel noise as well as environmental noise (wind and waves) (Wenz 1962, Cato 1976, Kipple & Gabriele 2003); this band was used to assess and describe cumulative ambient sound levels for given time periods. Seasonal and inter-annual patterns in the acoustic data were investigated by analyzing daily medians, 5th percentiles, and 95th percentiles of broadband ambient sound levels by year and month. Long-term spectrogram figures were generated by plotting broadband bin values

according to time of day and date to identify diel and seasonal noise trends. A selection of high-noise periods identified through LTSA figures were manually reviewed in Raven Pro 1.5 (Cornell Lab of Ornithology) and sound sources were aurally and visually identified and annotated.

Lombard analysis

We used stratified random sampling to generate a subset of data for manual review that accounted for a broad range of vessel conditions. A total of 90 acoustic files of 1 h duration were randomly selected from the 2015–2016 data set; based on theodolite-tracked vessels, we chose 30 h corresponding to low vessel periods, which were determined by the absence of vessels operating within visual range of the observation tower (1–11 km for vessels), 30 h corresponding to moderate vessel periods, when small vessels were adjacent to but not operating within 3 km of the hydrophone array and cruise ships were absent, and 30 h corresponding to high vessel periods, which included at least one cruise ship transiting through the main channel adjacent to the survey area (Fig. 1). Recordings were manually reviewed in 1 min intervals (Hann window, discrete Fourier transform [DFT] size 2048, analysis resolution 4.8 Hz and 0.09 s, 50% overlap) in Raven Pro by a single observer (M.E.H.F.). The start time, end time, lowest frequency, and highest frequency of every detectable humpback whale call was logged. We took a calibrated 2 s *in situ* ambient noise measurement in the frequency range of the call (dB_{RMS} re 1 µPa, inband power feature, Raven Pro; hereafter RMS_{inband}) immediately preceding each vocalization, and for each call also categorically annotated the simultaneous presence or absence of any type of aurally discernible vessel noise within the 15 Hz–3 kHz band.

Calls were localized using the near-field beamforming method described in detail by Matthews et al. (2017b) and Fournet et al. (2018b), which searches for the set of time-of-arrival delays that give maximum power from the beamformer output (Hawthorn et al. 2018). The variance of the energy output from the beamformer was estimated using Bartlett's formula, which resulted in error values in meters for the northern and eastern bearings for each call. A sound speed of 1481 m s^{-1} was selected for localization based on a temperature of 8.3°C from a CTD cast collected by the National Park Service in the survey area in 2015 and 2016 (Shar-

man 2017). Localization methods were ground-truthed by comparing GPS locations and theodolite fixes of known sound sources to acoustic localization estimates.

Using the 'earth.dist' function in the 'fossil' package in R (Vavrek 2011), the distance between the vocalizing animal and nearest hydrophone was calculated for each call with an error of <100 m. Source levels were estimated based on the formula SL = RL + TL, where SL is the estimated source level of the call (dB_{RMS} re 1 μPa @ 1 m in the bandwidth of the call), RL is the RMS received level in the bandwidth of the call measured using the in-band power measurement in Raven Pro, and TL (transmission loss) is estimated using a 15 log(range) dependency. This transmission loss coefficient was empirically derived for this region during extensive acoustic characterization of GBNPP and reconfirmed by semi-empirical modeling (Malme et al. 1982, Frankel & Gabriele 2017). RMS_{inband} sound values were used to calculate signal-to-noise ratios (SNRs). Initial data exploration indicated there was no change in model results when distant (localized to >2 km) calls or calls with low SNR values were included in analysis; therefore, all humpback whale calls with a localization error estimate within 100 m that were localized to within 5 km of the hydrophone array were included in the analysis. For more detailed methods on source level calculations, see Fournet et al. (2018b).

A linear regression model was built to test for the effect of RMS_{inband} levels in the bandwidth of the respective call, file ID (a proxy for the individual assemblage of animals present on a given recording), day of the year, and year on humpback whale source levels. A quadratic term was built into the model to assess whether humpback whales failed to adjust source levels beyond a certain ambient noise threshold. Visual inspection of residual plots and histograms indicated that assumptions of linearity, equal variance, and normality were met. Akaike's information criterion (AIC) was used to assess which variables should be conserved in the final model. Analysis of covariance (ANCOVA) was used to test for differences in the magnitude of change in source level (change in regression line slope) between vessel treatments (vessel noise present vs. vessel noise absent). Observations were treated as independent because data were randomly subset across 36 unique days in 2 separate years; however, there is potential for single animals to have produced multiple calls. Including file ID as a model variable allowed us to assess the impact of potential oversampling. Recording periods included in the analysis were separated

by a minimum of 12 h, and calls detected during one period were assumed to be independent of calls detected in other periods. Additionally, to demonstrate the robustness of this data set to potential violations in independence, we used non-parametric bootstrapping with replacement ('boot' function in R; Canty & Ripley 2012) to iterate linear regression and ANCOVA analyses on smaller random subsets of calls. For each iteration, one call from each file was randomly selected for analysis (n = 54); this process was iterated 1000 times to generate model coefficients, 95% confidence intervals, and p-values. Humpback whale residency time in the survey region was generally limited to 1–4 h during the study.

Calling probability modeling

A total of 50 h of visual survey effort corresponding to the logged acoustic recordings were subset across the 2 yr to investigate the hypothesis that the probability of a humpback whale calling changed as ambient sound levels increased. The following data were aggregated into 5 min bins: presence or absence of a call with a SNR of 6 dB or greater, presence or absence of a call with a SNR of 10 dB or greater, the number of humpback whales located within 2 km of the hydrophone array, the presence or absence of vessel noise in the 15–1500 Hz band, and broadband ambient sound levels. For this analysis, we measured the likelihood of sampling a call more than 6 dB above noise levels in every 5 min time bin, and subsequently measured the likelihood of sampling a call more than 10 dB above ambient noise levels in every time bin as a function of these variables. We selected 5 min as an appropriate bin size because data exploration indicated that (1) averaged over 5 min periods, hydrophones recorded equivalent received levels from transiting vessels, indicating that sound exposure is approximately equal in the survey region throughout that time period; and (2) humpback whales produce calls in short bouts, so aggregating over 5 min periods increases the probability of detecting one or several calls from an individual, while reducing the probability of treating calls by the same individual as independent.

We used the detection of a call within a 5 min bin to measure the probability of a humpback whale producing a call within our survey area. We created conservative inclusion criteria in order to (1) include all bins where a humpback whale call would have been detectable if it were produced from within 2 km of the hydrophone array, and (2) exclude any bin that

had a humpback whale call produced within 2 km of the hydrophone array but not be detected because of acoustic masking. Humpback whales in this region of GBNPP maintain an average signal excess (dB loudness of a call above ambient noise levels) of 52 dB (Fournet et al. 2018b). There is some evidence that at in-band noise levels above 105 dB, signal excess decreases by approximately 1.5 dB (see Results), but within the bounds of this study this should not significantly affect detection probability of animals vocalizing within 2 km of a hydrophone. Approximating transmission loss as a 15 $\log_{10}$(range) dependency (Malme et al. 1982, Frankel & Gabriele 2017), we estimate the detection range of a calling humpback in this area to be 2.91 km. Accordingly, 2 km was selected as an appropriate inclusion range, given the variability associated with signal excess and the dynamic movement patterns of the whales; this is consistent with other studies investigating the impact of ambient noise on humpback whale vocal behavior (Dunlop et al. 2014). For a bin to be included in the analysis, at least one humpback whale had to be visually present within 2 km of the hydrophone array. Additionally, for a given bin to be included in analysis, the broadband ambient sound value had to be less than or equal to 108 dB (Dunlop et al. 2014). Most of the energy contained in humpback whale calls in Southeast Alaska falls within the 50 Hz–3 kHz band (Cerchio & Dahlheim 2001, Wild & Gabriele 2014, Fournet et al. 2015), and several studies of baleen whale calling behavior in noise have investigated responses to noise under similar ambient sound conditions (Di Iorio & Clark 2010, Cerchio et al. 2014, Dunlop et al. 2014, Dunlop 2016). Based on visual review of a random selection of spectrograms from this region, 112 dB in this band was not loud enough to mask vocalizations (Fig. 2). However, to be consistent with other studies and to minimize the probability of attributing masked vocalizations to a lack of calling whales, we limited our analysis periods to lower ambient noise conditions (≤108 dB). Furthermore, to be included in modeling, any bins fitting

the inclusion criteria with broadband ambient sound value >105 dB were manually re-reviewed. Any bins that contained excessive flow noise from currents, tides, or mechanical noise associated with recording equipment were omitted from analysis regardless of broadband sound level.

Lastly, to ensure that a lack of humpback whale call detections represented a true absence of humpback whale calling and was not merely an artefact of acoustic masking, we also used harbor seal *Phoca vitulina* roars as a detection proxy for humpback whale calls. Harbor seals are sympatric with humpback whales throughout GBNPP, and have been the focus of study using the same recording equipment and time periods (Matthews et al. 2017a). During the breeding season, male harbor seals in GBNPP roar approximately once min^{-1} (Matthews 2017). Harbor
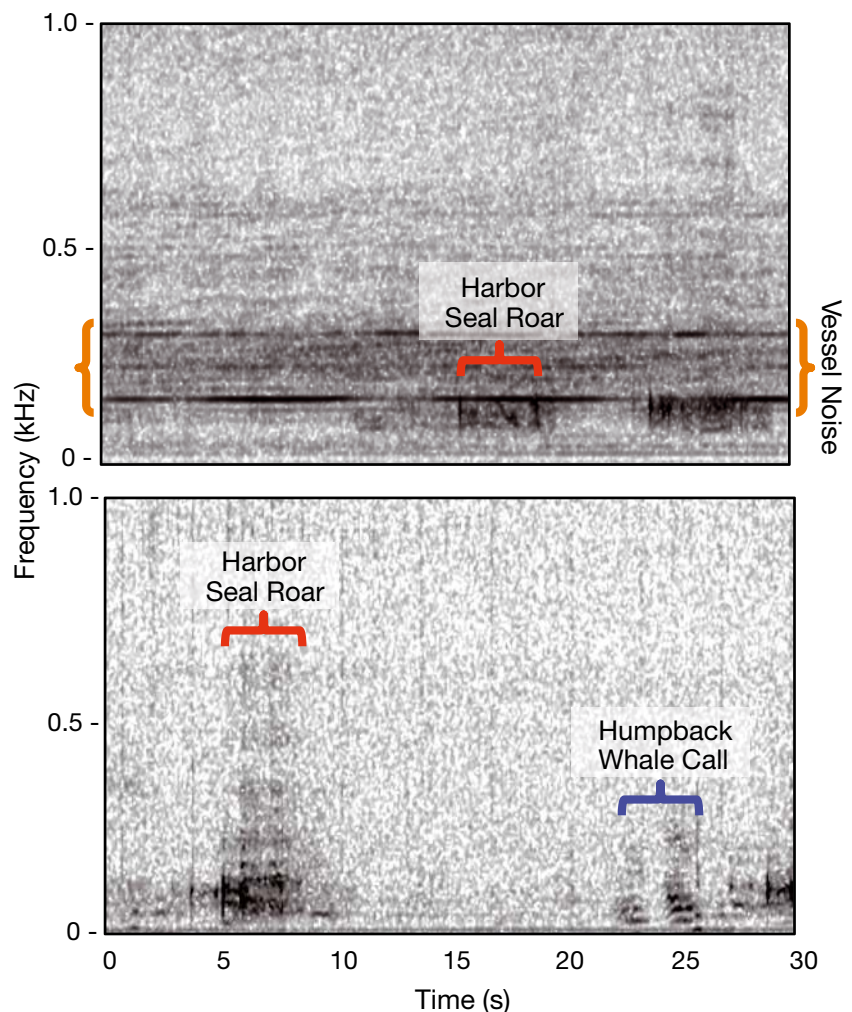

Fig. 2. Spectrogram of (top) harbor seal *Phoca vitulina* roar vocalizations in high noise (122 dB RMS re 1 μPa in the 50–3000 Hz band) and (bottom) harbor seal roar and humpback whale *Megaptera novaeangliae* call in moderate noise (112 dB re 1 μPa RMS, 50–3000 Hz)

seal roars overlap in frequency with humpback whale calls and share similar source levels (Fournet et al. 2015, 2018b, Matthews et al. 2017b) (Fig. 2). Moreover, harbor seals do not appear to adjust their call rates in response to noise in the study area, exhibit a maximum observed source level of 155 dB in the presence of vessel noise (Matthews 2017), and lack the ability to maintain signal excess as ambient noise levels increase (L.P.M. pers. obs.). We examined 6 h of recordings containing cruise ship passages for visual/acoustic evidence of harbor seal *P. vitulina* roars. Harbor seal vocalizations with a SNR of at least 6 dB were detected in every 5 min bin examined, regardless of noise level (max. broadband ambient sound level: 122 dB, seal source level at that time: 155 dB). Out of the 360 samples reviewed for evidence of roars, 39 contained broadband ambient sound values in excess of 108 dB. At no point in the manually reviewed data were harbor seal roars spectrographically obscured by ambient vessel sound (Fig. 2). By demonstrating that it is possible to detect a harbor seal roar in this region in a given noise regime, we assert that it would also be possible to detect a calling humpback whale in this region in the same noise regime. Based on this assumption, bins were excluded from modeling if noise levels were high enough to prevent the visual identification of harbor seals roars at any point within the 5 min period.

Generalized linear mixed effect models with a logit link function were built to test the relationship between the probability of a humpback whale call occurring, whale abundance within 2 km, broadband ambient sound levels, the presence or absence of vessel noise, and a random effect of survey period encompassing the variability associated with the unique combination of individuals present at any given moment (Table 1; R Development Core Team 2013). We built a full model based on explanatory variables and the presence or absence of a humpback whale call with a SNR of 6 dB or higher, and a more conservative full model using the presence or absence of a humpback whale call with an SNR of 10 dB or higher as the response variable (Table 1). The significance of each variable was assessed using AIC model selection. Initial data exploration did not identify any temporal correlation structure within the data. Visual inspection of residual plots and a goodness-of-fit test (p > 0.05) indicated that logistic regression models were appropriate. From the linear model output, predictions were made to generate a trend line and 95% confidence intervals. Model output from the 6 dB model and the more conservative 10 dB model are compared.

Table 1. Variable descriptions for logistic model testing the hypothesis that humpback whale calling behavior is altered in response to ambient noise conditions. SNR: signal-to-noise ratio

Response	Explanatory variables
Presence of humpback whale call (+6 dB SNR)	Ambient sound (dB_{RMS} 50–3000 Hz) Vessel noise present/absent Number of whales (3 km) Number of whales (5 km) Time of day
Presence of humpback whale call (+10 dB SNR)	Ambient sound (dB_{RMS} 50–3000 Hz) Vessel noise present/absent Number of whales (3 km) Number of whales (5 km) Time of day

RESULTS

General

A total of 885 scan point surveys were conducted over 66 sampling days between July–August 2015 and June–September 2016. Approximately 8188 h of acoustic array recordings were made spanning May–October 2015 and April–October 2016. For the purpose of this analysis, the acoustic dataset was limited to the May–September months. A total of 36 individual humpback whales *Megaptera novaeangliae* were identified over the 2 summer seasons: 25 individuals were identified in 2015 and 21 in 2016, with 10 of these identified in both years. Photo ID effort was not comprehensive and likely underrepresents the number of individuals present during the study.

Soundscape analysis

Overall daily median broadband ambient sound levels (dB_{RMS} in the 50 Hz–3 kHz band) over both summers combined was 96 dB (range 86–107 dB; Fig. 3). There was moderate variability in daily median broadband levels within years and between months (2015 ambient sound range = 18 dB, 2016 ambient sound range = 19 dB; Table 2); however the data revealed little inter-annual variability. Daily median broadband levels were slightly higher in 2016 than in 2015 (2015 = 96 dB, 2016 = 97 dB).

Broadband ambient sound levels varied on seasonal and diel cycles (Fig. 4). Aural and visual spectrogram inspection revealed that seasonal variation in broadband levels was driven primarily by roaring harbor seals during the late June–early August
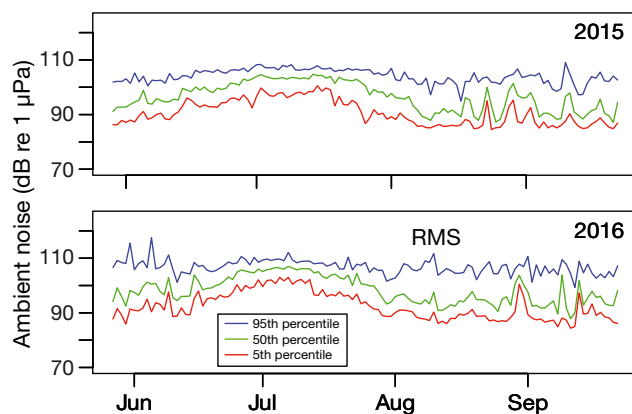
Fig. 3. Daily median, 95th percentile, and 5th percentile of broadband ambient sound levels (dB_{RMS} re 1 µPa) in the 50–3000 Hz range over the summers of (top) 2015 and (bottom) 2016 in the Beardslee Island Complex of Glacier Bay National Park, Southeast Alaska

Table 2. Daily median, 5th percentile, and 95th percentile ambient sound levels (dB_{RMS} re 1 µPa in the 50–3000 Hz bandwidth) by month

Month	dB_{RMS}		
	5th	Median	95th
May	88	95	105
June	90	99	107
July	93	103	108
August	86	94	105
September	86	92	105
Overall	87	97	107

breeding season in both 2015 and 2016 (Table 2, Fig. 4). Diel variation in broadband levels was attributed to cruise ship vessel passages. Anomalously high broadband ambient sound periods on the scale of hours to days (e.g. 21 August 2016; Fig. 4) were associated with storms accompanied by high winds (15–27 knots) and rain. Anomalously high broadband ambient sound periods on the scales of minutes (e.g. 10 August 2016, 10:30 h; Fig. 4) were associated with small vessel passages through the survey area. Flow noise associated with spring tides, appearing as diagonal stripes in Fig. 4, also left a moderate acoustic signature, although it is unknown how much of this noise is an artefact of flow noise over the hydrophone element versus actual ambient noise from flow over rocks and other environmental features.

Lombard Effect analyses

In total, 90 h of acoustic recordings were subset from 49 d in June–August of 2015 and 2016. A total of 2260 humpback whale calls were detected; 711

vocalizations spanning 36 d in the months of June, July, and August in 2015 (n = 17 d) and 2016 (n = 19 d) met inclusion criteria for the Lombard Effect analysis (error <100 m, localized to within 5 km of the hydrophone array). Histograms and quantile–quantile plots (qqplots) of source levels were generated for the low (RMS_{inband} < 90 dB), mid (RMS_{inband} = 90–97 dB), and high (RMS_{inband} > 98 dB) noise levels (Dunlop et al. 2014); histograms and qqplots indicated that source levels were normally distributed across noise levels. A skewed distribution at higher noise levels, which may have indicated masking of quieter calls as noise increased, was not observed in this study. The median source level of calls was 131 dB_{RMS} re 1 µPa @ 1 m in the bandwidth of the call (range 100–163 dB; Fig. 5). Median RMS_{inband} sound levels were 81 dB (range 60–106 dB; Fig. 5). AIC model selection indicated that year, day of the year and file ID did not substantially contribute to the model, and these terms were dropped (Table 2). Additionally, there was no evidence of a quadratic relationship between source level and ambient sound (Table 2). There was strong evidence that call source level was associated with RMS_{inband} ($F_{1,709}$ = 323, p < 0.00001). For every 1 dB increase in the RMS_{inband} sound level, the mean source level increased by 0.81 dB (95% CI = 0.79–0.90; Fig. 5). There was no evidence that the relationship between estimated source level and RMS_{inband} significantly differed based on the absence or presence of vessel noise (ANCOVA, F_{707} = 0.08, p = 0.78; Fig. 5). On average, humpback whale call source levels were 50 dB (±0.3 dB SE) greater than RMS_{inband} sound levels (range 20–79 dB). There was evidence of a positive relationship between signal excess and RMS_{inband} ambient sound ($F_{1,709}$ = 8.20, p < 0.0001). However, the estimated magnitude of the response indicated a 0.18 dB change in signal excess for every 1 dB change in ambient noise (95% CI = 0.1–0.27), which is within the range of equipment and analysis error for source level calculations, and therefore is not statistically significant. In this study, average signal excess in high noise was 49 ± 0.2 dB, in mid noise was 50 ± 0.05 dB, and in low noise was 51 ± 0.2 dB. Source levels of calls in low-noise periods averaged 1.5 dB (95% CI = 0.75–2.25 dB) higher than calls in high-noise periods.

Results of bootstrap analyses conducted on random data subsets were consistent with results from linear regression analyses conducted on the data set as a whole. For every 1 dB increase in RMS_{inband} sound levels, bootstrapping produced an estimated 0.79 dB increase in call source level (95% CI = 0.67–0.87).
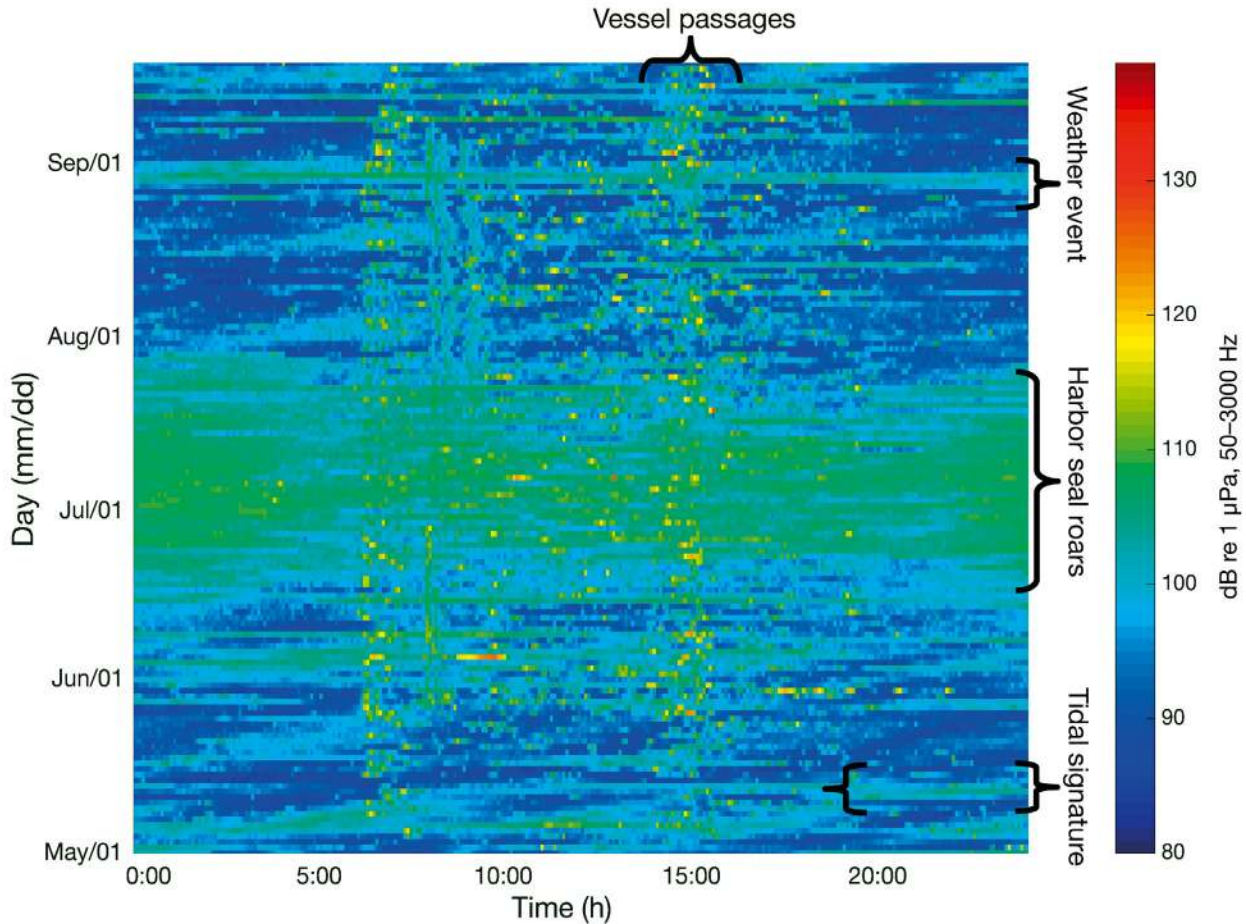
Fig. 4. Long-term spectral average of broadband ambient noise levels (dB$_{RMS}$ re 1 μPa in 50 Hz–3 kHz band) recorded from the easternmost hydrophone in the Bearsdlee Island Complex, Glacier Bay National Park and Preserve, Southeast Alaska in the summer of 2016. Primary sound sources annotated with black brackets

There was no evidence that the magnitude of the Lombard Effect differed between periods of vessel presence and absence (p = 0.48).

Call probability analysis

A total of 102 scan point surveys spanning 29 d from June–August 2015 and June–September 2016 fit the inclusion criteria for call probability modeling. Within this sample, 191 of the 5 min bins met the analysis inclusion criteria by having whales within 2 km of the hydrophone array and broadband ambient sound values ≤108 dB. Two bins contained broadband ambient sound values in excess of 105 dB; harbor seal roars were spectrographically evident in both of these samples. Although not included in the analysis, humpback whale calls were aurally and visually distinguishable in 19 bins containing broadband ambient
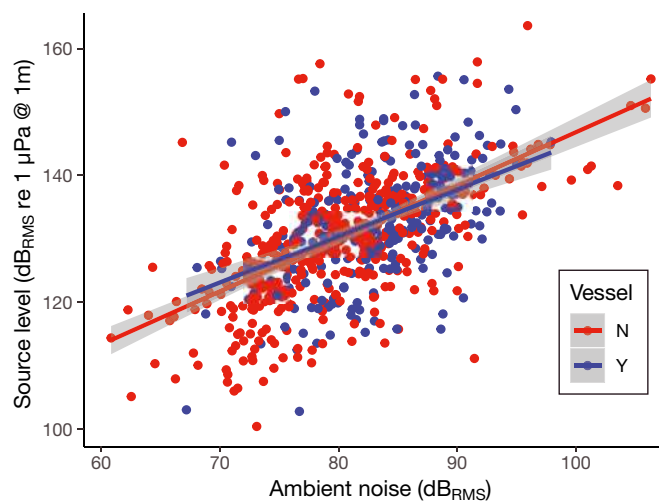

Fig. 5. Ambient noise levels (dB RMS re 1 μPa in the bandwidth of the call) versus estimated source levels of humpback whale calls. Shaded area: 95% CI. The presence (Vessel = Y) and absence (Vessel = N) of vessel noise is indicated by color

noise levels in excess of 108 dB (max. = 124 dB). Seventy bins (36%) contained at least one humpback whale vocalization with a SNR of 6 dB or higher; 51 bins (26%) contained at least one humpback whale vocalization with a SNR of 10 dB or higher. Vessel noise was present in 85 bins (45%) and absent in 106 bins (55%). Because visual observations were only made when Beaufort sea state conditions were 2 or less, ambient sound levels in this analysis were independent of anomalous weather events or ambient noise associated with high wind in this area.

AIC model selection indicated that the appropriate model included only ambient sound levels and the presence/absence of vessel noise (Table 3); the number of whales within 2 km of the hydrophone array and sampling period were dropped from the model. There was strong evidence of a relationship between the likelihood of a call occurring with an SNR of 6 dB or higher and broadband ambient sound levels (p = 0.001, $Z_{190,188} = -3.2$). There was strong evidence of a relationship between the likelihood of a call occurring with an SNR of 6 dB or higher and the presence or absence of vessel noise (p = 0.0005, $Z_{190,188} = -3.46$; see Fig. 7, Table 4). For every 1 dB increase in broadband ambient sound levels, the probability of detecting a humpback whale call of SNR 6 or higher decreased by 9% (95% CI = 8.3–9.6%; Fig. 6). After

controlling for ambient noise levels, the probability of detecting a call with an SNR of at least 6 dB was 31% lower (95% CI = 16–60%) when vessel noise was present than when vessel noise was absent. That is to say, the probability of detecting a call when vessels are present and ambient sound levels are 99 dB was 31% lower than when vessels were absent and ambient sound levels were 99 dB (Fig. 7).

Using the more conservative call inclusion criteria (SNR ≥ 10 dB) produced functionally identical model results (Table 4). AIC model selection indicated that ambient sound levels and vessel noise should be conserved within the model; the number of whales within 2 km of the hydrophone array and sampling period were dropped. There was strong evidence of a relationship between the likelihood of a call occurring with an SNR of 10 dB or higher and broadband sound levels (p = 0.005, $Z_{190,188} = -2.78$; Fig. 6). There was strong evidence of a difference in the likelihood of detecting a call with an SNR of 10 dB or higher and the presence or absence of vessel noise (p = 0.02, $Z_{190,188} = -2.24$). For every 1 dB increase in broadband ambient sound levels, the probability of a call occurring decreased by 9% (95% CI = 8.5–9.7%, Fig. 6). At equal ambient noise levels, the probability of a call occurring with an SNR 10 dB or higher when vessel noise was present was 45% (95% CI = 22–89%) lower than when vessel noise was absent (Fig. 7).

Table 3. Models tested for Lombard analysis including Akaike's information criterion (AIC) values. The selected model is annotated in **bold**

Response variables	df	AIC
Ambient noise (RMS$_{inband}$)	**3**	**5019.46**
Ambient noise (RMS$_{inband}$) + vessel presence/absence	5	5031.5
Ambient noise (RMS$_{inband}$) + vessel presence/absence + file ID	62	5237.5
Ambient noise (RMS$_{inband}$) + vessel presence/absence + quadratic	4	5023.4
Ambient noise (RMS$_{inband}$) + vessel presence/absence + file ID	61	5230.8

Table 4. Akaike's information criterion (AIC) model selection for logistic modeling with one of 2 response variables: humpback whale calls with a signal-to-noise ratio (SNR) of 6 dB or higher or calls with a SNR of 10 dB or higher. The selected model is in **bold**

Response variables	df	AIC SNR6	AIC SNR10
Ambient noise dB$_{RMS}$ (50–3000 Hz) + vessel noise present/absent	**3**	**234.08**	**214.7**
Ambient noise dB$_{RMS}$ (50–3000 Hz) + vessel noise present/absent + (n) whales 2 km + group number	5	236.02	216.67
Ambient noise dB$_{RMS}$ (50–3000 Hz) + vessel noise present/absent + group number	4	236.07	216.69
Ambient noise dB$_{RMS}$ (50–3000 Hz)	2	244.9	218
Ambient noise dB$_{RMS}$ (50–3000 Hz) + (n) whales 2 km	3	246.83	219.98

DISCUSSION

This study documented 2 strategies that calling humpback whales *Megaptera novaeangliae* on a North Pacific feeding ground employ to compensate for natural and man-made noise sources in their acoustic habitat. By quanti-
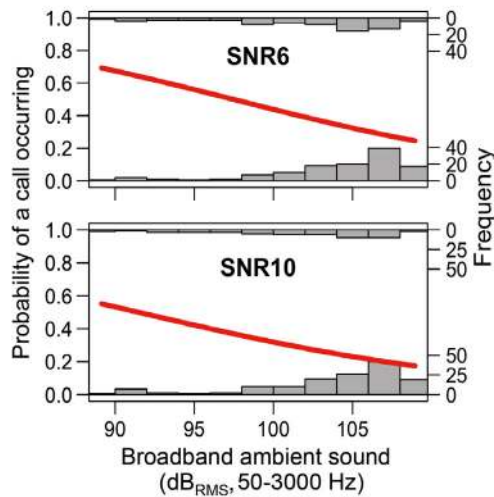
Fig. 6. Probability of a humpback whale call occurring with (top) a signal-to-noise ratio (SNR) of 6 dB or higher, or (bottom) a SNR of 10 dB or higher as a function of broadband ambient sound, overlaid on histograms of call occurrence (top of plots) or absence (bottom of plots)

fying the contributions of natural and man-made ambient sounds in this area of GBNPP and quantifying humpback whale calling behavior within each of these ambient sound regimes, we were able to investigate how humpback whales respond to natural sounds versus vessel noise. We identified some strategies that are used equivalently regardless of the noise source, and other strategies that differed based on sound sources. This study also systematically documented humpback whale calling behavior in the absence of human activities. Such baselines are rare and arguably obtainable only within the bounds of marine protected areas like GBNPP where human activities are limited.

There are 3 primary drivers of ambient sound levels in the Beardslee Island complex of GBNPP, each operating at a different temporal scale: (1) harbor seal *Phoca vitulina* roars, (2) cruise ship and tour boat passages, and (3) weather events. Seal roars are seasonally predictable in early summer months and between years; roars occurred at all hours of the day without significant interruption throughout the breeding season in both 2015 and 2016. Daily passages of cruise ships and tour vessels are predictable at the scale of hours (1–4 h twice daily) under predetermined tourism schedules. Because medium-sized daily tour vessels and large cruise ships operate on similar schedules, we were not able to discriminate between noise emanating from these 2 vessel types; their contributions to the acoustic habitat were considered jointly. Weather events are sporadic, can be acousti-

cally extreme, and occur on the scale of minutes, hours, or days. Elevated ambient noise associated with storm events involving wind and rain persisted for the duration of the storm and manifested as moderate (2–36 h) periods of loud continuous sound. Noise associated with small vessels in this region did not leave an obvious persistent signature on the acoustic habitat; this is likely due to the absence of small vessels in the area, and should not be misconstrued as small vessels being negligible producers of ambient sound. The study region is bounded by an area off-limits to motorized vessels, and is otherwise not along the direct path travelled by vessels en route to glacier viewing. Additionally, independent small ves-
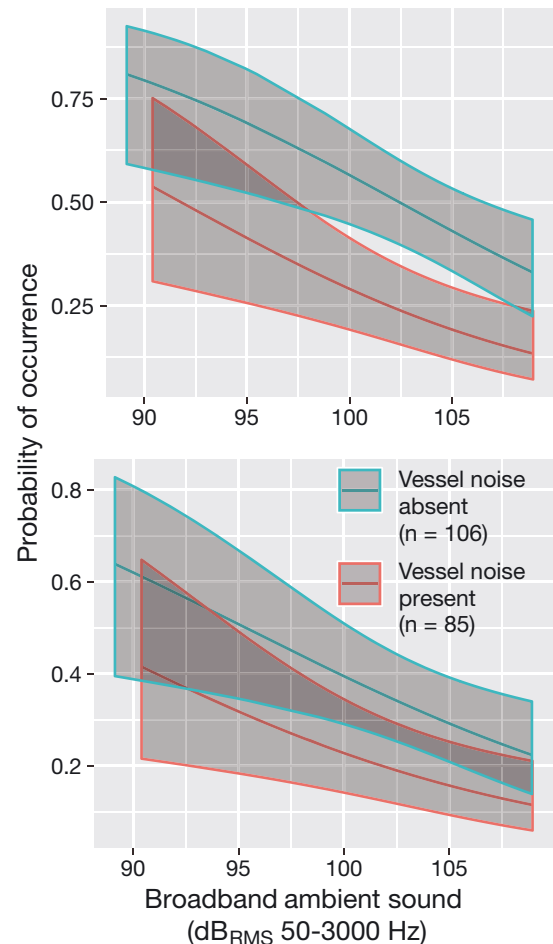

Fig. 7. Probability of a humpback whale call occurring with a signal-to-noise ratio (SNR) of (top) 6 dB or higher, or (bottom) 10 dB or higher as a function of ambient sound levels. Shaded areas: 95% confidence intervals. Green indicates the probability of a humpback whale call occurring when biological or environmental noise is the primary driver of ambient sound and vessel noise is absent; red indicates the probability of a humpback whale call occurring when vessel noise also contributes to ambient sound levels

sel signatures may be indistinguishable due to the combined effect of concurrent large-vessel noise. Therefore, while small vessels resulted in punctuated periods of isolated sound at high levels when they actively traversed the region, and distant noise from small vessels was frequently present at low levels, small vessel activity could not be identified as a primary driver of ambient sound in the study area. Caution should be exercised in extrapolating these results to other regions of GBNPP or elsewhere. Harbor seal breeding activities, including roaring, are spatially localized, and it is unknown if roars contribute the same acoustic energy ubiquitously throughout GBNPP. Similarly, in other regions small vessels may be present longer, travel faster, and overlap more directly with important acoustic habitats. Comparisons of acoustic habitats both within GBNPP and between other regions in Southeast Alaska are suggested.

Our results demonstrate that humpback whales increase the source levels of their calls equally to compensate for both environmental and anthropogenic sounds. While it seems almost certain that humpback whales have a maximum ambient sound threshold beyond which they can no longer increase their call amplitude, there was no evidence that this threshold was met under the conditions of this study. Evidence of a quadratic relationship, not observed here, would have implied a maximum ambient sound level beyond which compensation remained steady. Furthermore, the maximum observed estimated call source levels documented in this study (163 dB$_{RMS}$ re 1 µPa @ 1 m) were below the maximum plausible source levels of 175–183 dB$_{RMS}$ (Cato et al. 2001, Au et al. 2006, Dunlop et al. 2013) documented for this species, and lower than maximum source levels (183 dB) documented for non-song calls specifically (Dunlop et al. 2013).

The trend for humpback whales to increase call source levels as ambient noise from natural sound sources rose is consistent with the Lombard Effect observed in migrating humpback whales in response to wind noise (Dunlop et al. 2014), although both source levels and signal excess observed in this study were lower than those documented along the migratory corridor, which likely reflects differences in social context. In this study we also demonstrated that humpback whales increased source levels to compensate for moderate levels of vessel noise. This is contrary to what Dunlop (2016) observed along migration. Humpback whales in the east Australian population did not increase call source levels according to expected trends. The most notable difference

between the 2 studies is the proximity to vessels. In this study, vessels were between 3 and 10 km away from animals in the survey region, while the distance between vessels and animals observed by Dunlop (2016) ranged from 500 m to 5.5 km. It is reasonable to assume that the presence of a moving vessel at close proximity combined with elevated noise levels, like the observations from Australia, will elicit a different behavioral response than noise in isolation or from distant vessels. These dissimilar circumstances appear to have elicited different behavioral responses between the 2 populations.

The high ambient noise levels and significant decreases in signal excess observed in eastern Australia associated with close vessel passages (~127 dB) were not observed in this region of GBNPP. There was only a minimal decrease in signal excess associated with elevated noise observed in this study, but at the ambient noise levels documented here it is uncertain whether this statistic is biologically relevant. Deeper investigation into the loss of signal excess at elevated noise may prove to be a relevant feature for predicting acoustic masking potential. Future investigation into the calling behavior of humpback whales on feeding grounds at higher ambient noise levels would enable assessment of whether there is a peak ambient sound level beyond which humpback whales are either incapable or unwilling to call louder to communicate in noise. Generally, however, the results of our analysis indicate that within the scope of our observations, humpback whales in GBNPP are capable of increasing source levels as an effective strategy for reducing acoustic masking of their vocalizations in moderate noise.

We assert that periods where humpback whale calls were not detected likely reflect an absence of calling. Signal excess of calls at 108 dB re 1 µPa (our maximum observation level included in behavioral modeling) was within 1.5 dB of signal excess at 86 dB re 1 µPa (minimum daily median ambient sound level for this study), so the area over which a call can be detected, while reduced, should not have significantly affected detectability in this study. Further, we implemented several measures to ensure that the lack of call detection reflected a true absence of humpback whale calling rather than a consequence of masking. Using harbor seal roars as a proxy, we demonstrated that a seal calling in the same frequency range and approximate source levels of a humpback whale was detectable given our chosen parameters. We limited our analysis to relatively low noise periods, consistent with other studies of humpback whale calling behavior in noise (Dunlop et al.

2016); although whale calls were visually and aurally distinguishable in periods with ambient noise well above this cutoff (max. = 124 dB). As an additional measure of caution, we manually reviewed all high-noise periods and omitted any periods that would have masked humpback whale calls, and we built several models to account for variability in detections, ultimately producing functionally identical results. Furthermore, we aggregated detections within biologically relevant time bins to increase the likelihood of identifying signals. Humpback whales in this region and elsewhere produce calls in short bouts (Rekdahl et al. 2015). In this study, when calls were detected, the average number of calls within a 5 min bin was 4.0 (±0.2 SE). Ambient noise conditions varied over each 5 min bin, and while there is a possibility of masking distant or quiet calls, it is less probable that all of the calls in a bout would be undetectable given our choice of inclusion parameters. Based on this effort, it is robust to assume that periods in which a humpback whale calls were not detected reflect a true absence of calling. It is important, however, to include the caveat that the effects of masking can not be completely ruled out, and may have impacted detection probability to some degree.

This study demonstrates that humpback whale vocal activity diminishes as ambient sound levels increase. While not exact, these results are a good proxy for a reduction in call rates. Our results are consistent with other cetaceans that alter their calling rates, either positively or negatively, in response to noise. Blue whales *Balaenoptera musculus* call consistently more on days containing seismic survey noise (Di Iorio & Clark 2010), presumably to compensate for a reduction in call detectability associated with acoustic masking, while both beluga whales *Delphinapterus leucas* and North Atlantic right whales *Eubalaena glacialis* decrease their call rates in response to elevated vessel noise (Lesage et al. 1999, Parks et al. 2007). Similarly, humpback whales in this study were less likely to call as ambient noise levels increased. This reduction in calling may be partially due to the increased effort associated with calling more loudly; alternatively, humpback whales may be waiting to call until there is a reduction in ambient sound levels. Both are consistent with our results and would explain the difference in calling probability observed during periods containing naturally occurring sounds, which were dominated by harbor seals, versus periods containing vessel noise.

Ambient noise associated with seals in this region of GBNPP is pervasive, while vessel noise temporally acute. Both substantially raise ambient noise levels, but humpback whales react differently to harbor seal roars than they do to vessel noise. During peak harbor seal breeding season, the broadband sound levels of some time bins containing seal roars but absent vessel noise were as high as bins containing cruise ship passages (Fig. 4). Harbor seals use the Beardslee Island region of GBNPP as a breeding ground from June through early August, and males roar approximately once min^{-1} throughout the 24 h day (Matthews 2017, Matthews et al. 2017a). Because multiple male harbor seals use this area, as many as 15 to 25 roars with an average source level of 144 dB (Matthews et al. 2017b) could be detected in a 5 min time period, contributing substantially to the acoustic environment. Cruise ship noise, by contrast, is louder at the source than harbor seal roars (approximate source level: 171–188 dB; Kipple & Gabriele 2003, Frankel & Gabriele 2017) and is continuous for as long as the vessel is within acoustic range (up to 40 min). Acoustic energy dissipates with distance, and the diurnal cycles associated with tourism in the Park result in 2 discrete times of day, a morning entry and an evening departure, characterized by elevated ambient sound levels. In the presence of vessel noise, humpback whales stop calling more often than they do in the presence of seals alone; therefore, while in this study the ambient sound values associated with each source appear equivalent, they are quite different in terms of their effect on the acoustic ecology of calling humpback whales and the potential for strategies that would result in a release from acoustic masking.

It is possible that the reduction in calling effort observed in this study is linked more directly to the temporal characteristics of the signals (e.g. periodic versus continuous). Qualitatively, humpback whale calls were often detected in between harbor seal roars, and only rarely overlapped them. This may be an indication that whales adjust the timing of their vocalizations as an anti-masking strategy, by calling in between periodic sounds like harbor seal roars, rather than calling over them. If humpback whales consistently wait for a break in noise levels prior to vocalizing, then continuous noise sources like vessels may result in much longer periods between calling bouts.

Humpback whales demonstrate high degrees of acoustic plasticity (Payne & Payne 1985, Garland et al. 2011) and exhibit behavioral responses to changing sound conditions that occur as a result of natural or human activities (Baker & Herman 1989, Miller et al. 2000, Dunlop 2016). In the case of the Lombard Effect, vocal plasticity appears to increase resilience

to changing ambient sound conditions by allowing whales to maintain signal excess and thus communication space, which presumably increases the likelihood of an animal communicating with their intended receivers across ambient sound conditions.

It remains to be seen whether the adjustments in calling behavior observed in this study are indicative of a compensatory strategy to overcome masking, or whether the reduction in calling effort is a result of missed cues from other vocalizing whales. In the absence of vocal compensation, increased ambient noise levels substantially reduce the active communication space of a calling animal (Cholewiak et al. 2018, Gabriele et al. 2018). Even relatively short periods of high noise, like those observed during the twice-daily cruise ship passages, may 'halt the conversation' to unknown effect. In GBNPP, where quiet periods tend to occur between vessel noise events, the behavioral strategy of waiting for relative quiet to communicate with conspecifics may result in effective communication with less effort expended. However, in the many parts of the ocean characterized by chronic anthropogenic noise, this same strategy may not allow a sufficient number of opportunities to communicate over distances comparable to 'quiet' conditions (Clark et al. 2009, Hatch et al. 2012), with potential negative impacts to individuals that may have cascading effects. While the functions of feeding ground vocalizations are not well understood, it is known that humpback whales use vocalizations at high latitudes in concert with critical life functions including foraging (D'Vincent et al. 1985, Stimpert et al. 2007, Fournet et al. 2018a), social interactions (Wild & Gabriele 2014, Fournet 2014), and potentially as a precursor to breeding activities (Gabriele & Frankel 2002). A deeper understanding of the role of acoustic communication from a behavioral ecology perspective holds high conservation value.

Vessel behavior in GBNPP allowed us to acoustically and visually document humpback whale behavior during periods of relative 'quiet'. Quiet ocean conditions in which to study unaltered behavior are increasingly rare, and yet are critically important both for understanding natural animal behavior and potentially providing an acoustic respite for sound-sensitive species. Although humpback whale calling behavior documented here may be specific to southeastern Alaska, it will serve as a useful metric against which to assess the 'normal' range of acoustic behavior in this widespread and dynamic species.

Our findings highlight the importance of framing behavioral research in the context of broader acoustic ecology. It is our hope that future studies will adopt this trend and that as a scientific community we will generate a body of work that investigates the impact of anthropogenic noise from a broader, ecosystem-based perspective. Moreover, incorporating ambient noise metrics such as the number and duration of noise-free intervals in various humpback whale acoustic habitats may allow a better assessment of the biological ramifications of the strategies used by humpback whales in response to anthropogenic noise.

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