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Sensitive aerial hearing within a noisy nesting soundscape in a deep-diving seabird, the common murre *Uria aalge*

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ABSTRACT: Diving seabirds face a combination of sound exposure in marine and terrestrial environments due to increasing human encroachment on coastal ecosystems. Yet the sound-sensitivity and sensory ecology of this threatened group of animals is largely unknown, complicating effective management and conservation. Here, we characterize aspects of the acoustic ecology of the common murre *Uria aalge*, one of the deepest diving alcid seabirds. Electrophysiological aerial hearing thresholds were measured for 12 wild, nesting individuals and compared to conspecific vocalizations and short-term aerial soundscape dynamics of their cliff nesting habitat. Auditory responses were measured from 0.5 to 6 kHz, with a lowest mean threshold of 30 dB at 2 kHz and generally sensitive hearing from 1 to 3.5 kHz. The short-term murre nesting soundscape contained biotic sounds from con- and heterospecific avifauna; broadband sounds levels of 56–69 dB re: 20 µPa rms (0.1–10 kHz) were associated with both diel and tidal-cycle factors. Five murre vocalization types showed dominant spectral emphasis at or below the region of best hearing. Common murre hearing appears to be less sensitive than a related alcid, the Atlantic puffin *Fratercula arctica*, but more sensitive than other non-alcid diving birds described to date, suggesting that adaptations for deep diving have not caused a loss of the species' hearing ability above water. Overall, frequencies of common murre hearing and vocalization overlap with many anthropogenic noise sources, indicating that the species is susceptible to disturbance from a range of noise types.

KEY WORDS: Hearing · Noise · Soundscape · Seabird · Sensory ecology · Stress · Wildlife

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1. INTRODUCTION

Seabirds live at the interface of terrestrial and marine environments, nesting and breeding on land but foraging for fish below the ocean surface. This amphibious lifestyle is made possible by the evolution of secondarily adapted traits that enable them to exploit and survive in the marine environment, including adaptations to some aspects of their sensory biology (e.g. Martin & Brooke 1991, Martin 1999, White et al. 2007). However, despite their conspicuous vocalizations, raucous nesting colonies, and the known im-

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portance of sound as a communication channel for seabirds, their encompassing acoustic and auditory biology is poorly understood. For example, there are limited data on seabird hearing across the diversity of some 350 species with different life history, ecology, and evolutionary relationships (Wever et al. 1969, Crowell et al. 2015, Larsen et al. 2020, Mooney et al. 2020).

In particular, pursuit-diving seabirds, which dive and pursue prey at depths of up to and sometimes exceeding 150 m (Piatt & Nettleship 1985, Burger & Simpson 1986, Croll et al. 1992, Putz et al. 1998, Bonnet-Lebrun et al. 2021), are exposed to a significantly different ambient environment than non-diving species due to the property differences between air and water. For instance, they are subjected to significant increases in barometric pressure while diving, which can affect sensitive air-filled spaces related to hearing such as the middle ear and inter-cranial cavities. The acoustic properties between air and water are also significantly different (e.g. Larsen & Wahlberg 2017). These factors have likely shaped aspects of diving seabird auditory anatomy. For example, the middle ear structures of aquatic birds are modified compared to their fully terrestrial counterparts, including reduced input areas of the tympanic membrane as well as reduced volume and interconnectivity of cranial air cavities, among others (Zeyl et al. 2022). These structural changes are most pronounced in deep pursuit-diving seabirds, and may have evolved as an adaptation for baroprotection during dives (Zeyl et al. 2022). Yet it is unknown how such adaptations influence sound reception, in part due to limited auditory data from deep-diving species.

Nonetheless, the importance of hearing as a sensory modality in seabirds, including deep-divers, is implied from their reliance on the detection of acoustic cues for a variety of critical behaviors. Vocal communication can facilitate recognition among adult individuals as well as between parents and their offspring (Mathevon 1997, Jouventin et al. 1999, Humphries et al. 2016, Ligout et al. 2016, Kriesell et al. 2018), and the begging calls of chicks can reflect body condition (Gladbach et al. 2009, Klenova 2015). Biological acoustic cues derived from the surrounding environment may be important as well. For example, brown skuas *Stercorarius antarcticus* localize the advertising calls of their blue petrel *Halobaena caerulea* prey for hunting, while the nesting petrels will call less when they detect brown skua calls (Mougeot & Bretagnolle 2000). Additionally, the breeding calls of the Whenua Hou diving petrel *Pelecanoides georgicus whenuahouensis* have been shown to attract additional seabirds to conservation nesting sites (Fischer et al. 2020). Furthermore, experiments with king penguins *Aptenodytes patagonicus* have shown that chicks will orient towards colony noise in the absence of visual cues, suggesting some level of utility in colony background noise (Nesterova et al. 2013). Thus, like many birds, the detection of soundscape cues also appears to be an important component of seabird sensory ecology. Indeed, habitat-associated soundscapes underpin various ecological processes in a variety of animal taxa and are important for contextualizing characteristics of the auditory and acoustic communication systems that operate within them. However, quantitative measurements of aerial soundscapes in many coastal ecosystems, including seabird nesting habitats, are largely unexplored.

Such baseline acoustic biology and sensory information is increasingly important for conservation and management efforts (Elmer et al. 2021), in no small part due to the growing concern surrounding the potential impacts of anthropogenic noise exposure on animal biology. Key to improvements in the understanding, prediction, and mitigation of noise effects is baseline documentation and characterization of a species' acoustic biology, such as hearing thresholds and levels of sound detectability, characteristics of vocal communication, and important features of the acoustic environment within animal habitats. Together, these areas of investigation provide a vital foundation of data for the subsequent assessment of noise impacts, such as physiological and behavioral effects, damage to hearing from acoustic over-exposure, and masking of important bioacoustics and communication signals (e.g. Dooling & Popper 2016). Of particular concern are species in Arctic and subarctic environments where accelerated environmental warming and greater accessibility is projected to increase human encroachment into sensitive coastal ecosystems. Moreover, diving seabirds face a unique combination of exposures to both marine and terrestrial sensory cues and anthropogenic noise (Mooney et al. 2019b). Thus, there is a need to quantitatively measure the hearing abilities and vocal characteristics of holarctic diving seabirds and document unperturbed acoustic environments within their ecosystems.

One of the deepest diving seabirds in northern environments is the common murre *Uria aalge*, a pursuit-diving alcid that is capable of diving to depths exceeding 150 m (Piatt & Nettleship 1985, Burger & Simpson 1986, Bonnet-Lebrun et al. 2021). Hearing sensitivities of a single common murre exhibited significantly elevated auditory thresholds compared to ecologically similar diving birds (Crowell et al. 2015, Mooney et al. 2019a, Larsen et al. 2020), including a closely related alcid, the Atlantic puffin *Fratercula arctica* (Mooney et al. 2019a, 2020). While this might suggest that common murres do not hear well, perhaps due to adaptations for deep diving, the limited sample size of a single individual prevented assessment of inter-individual variability and firm interpretation of the results in a broader biological context. Here, we examined the aerial hearing sensitivities of multiple common murre individuals using electrophysiological methods. Moreover, as a colonial alcid, individuals nest in high densities along narrow cliff ledges (e.g. Chaney 1924, Birkhead 1977) and are known to be highly vocal. Therefore, we also compared how their hearing sensitivities relate to other aspects of the species' acoustic biology by providing baseline descriptions of adult vocalization characteristics and the short-term soundscape dynamics of a nesting colony at Latrabjarg, Iceland. These data provide a valuable update to initial auditory sensitivities described for a single individual by Mooney et al. (2019a) and also provide preliminary quantitative vocalization and nesting soundscape descriptions for the species.

2. MATERIALS AND METHODS

2.1. Bird capture and sedation

A total of 15 adult common murres were captured in the Westfjords, Iceland (65° 30′ 02″ N, 24° 31′ 42″ W) between 30 May and 5 June 2021, coinciding with the start of the breeding season but prior to chick hatching. Captures occurred at the Latrabjarg sea cliffs, a 14 km long coastline that provides nesting habitat for approximately 1.5 million birds representing at least 7 seabird species, including the common murre (Skarphéðinsson et al. 2016). The individuals were haphazardly selected and ensnared from a ledge 4−5 m below the edge of the ca. 70 m high cliff using a wire noose at the end of a long pole. Once caught, the bird was weighed before being transported in a padded box by car to the hearing test site at Breidavik, 13 km away (~20 min drive). Overall, 12 animals were studied, and all were released safely back into the same habitat at the end of the procedure.

At the time of capture or after hearing tests, a blood sample was collected from the ulnar vein and placed into a heparinized vacutainer™. After centrifugation (~2−3 h post-collection), the (nucleated) red blood cell fraction was saved for genetic analysis and frozen at ≤−20°C. DNA was extracted using the DNeasy Blood and Tissue mini spin-column kit (Qiagen), following the manufacturer's protocols for avian blood. DNA concentrations were measured using a fluorometer (Qubit 4, Thermo Fisher), and samples were sent to the HealthGene, Molecular Diagnostic and Research Center for molecular sexing following Griffiths et al. (1996, 1998).

At the testing site, birds received intranasal or intramuscular doses of Midazolam (2.5–5 mg kg^{-1}) followed by an intramuscular combination of Ketamine (5 mg kg^{-1}) and Xylazine (2 mg kg^{-1}). Body temperatures were continuously monitored with a digital anal monitor and probe (DataTherm II), while heart rates were manually checked with a stethoscope continuously after injections until fully sedated and thereafter approximately every 20 min. Respiratory rate was continuously monitored. Animals were ready for the hearing tests approximately 40 min after initial sedation, as noted by a stable temperature, heart rate, respiration rate, minimal movement, and closure of the eyes. Supplementary doses of Midazolam were given as needed after that time. Reversal agents (Atipamezole 0.25 mg kg^{-1} and Flumazenil 0.1 mg kg^{-1}) were kept on hand to be administered either upon completion of the auditory tests or if parameters fell outside nominal criteria and it was determined that auditory testing should be discontinued (which occurred in 2 individuals). In either of these cases, once the reversal agent was administered, a bird was placed back in the padded box for continued observation until sedation was appropriately reversed and the birds were awake and prepared for flight. To ensure that the same individuals were not captured again on subsequent days, birds were then banded and marked before being released back at the capture site.

2.2. Hearing test setup and procedure

Auditory thresholds were assessed via the recording of auditory evoked potentials (AEPs), an electrophysiological response generated in response to the presentation of acoustic stimuli. The hearing tests occurred in a portable anechoic chamber built from a wire-frame dog kennel (118 × 84 × 77 cm) padded with 4 cm thick sound-absorbing foam on all sides (Mooney et al. 2019a). The kennel, along with all electronic equipment, was housed inside a large geodesic tent to protect equipment from the elements. The generation of acoustic stimuli and collection of concurrent electrophysiological data was controlled with a custom-made LabView program from a laptop computer connected to a NI PCMCI-6062E analog–digital data acquisition (DAQ) board (National Instruments).

AEPs were elicited using various acoustic stimuli. Narrowband tone pips were used to explore auditory sensitivity at specific frequencies between 0.5 and 8 kHz. Tone pips above 0.5 kHz were 10 ms in duration with a symmetrical rise and fall time of 5 ms. Tone pips at 0.5 kHz were 20 ms long with a 10 ms symmetrical ramp up and down to compensate for the frequency-dependent reduction in the number of complete wave cycles per pip. Additionally, a more broadband 'click' stimulus consisted of 6 cycles of a 2 kHz sine wave (3 ms duration) with a 1.5 ms symmetrical ramp up and ramp down. All stimuli were projected at a rate of 15 Hz from a speaker (Nagra DSM) placed within the sound chamber approximately 60 cm from each bird's auditory meatus. The projector exhibited a flat frequency response between 0.25 and 10 kHz. Prior to projection, stimuli were amplified by a constant factor via the speaker's on-board amplifier (−6 dB with respect to the speaker's maximum amplification). Stimulus output levels were controlled in 1–10 dB steps via an HP 350D 5 W, 600 Ω DC attenuator placed along the signal pathway between the DAQ board and speaker.

We recorded 40 ms epochs of AEP signals concurrently with the production of each pip via 3 subdermal needle electrodes. The active electrode was placed just above the meatus, a reference electrode was placed just beyond the vertex of the head, on the side opposite the active electrode (just off the midline), and a common grounding electrode was placed dorsally along the lower back. Bio-potential signals from the electrodes were differentially amplified (10 000×) and bandpass-filtered (0.3–3 kHz) with a custom-made biopotential amplifier (Aarhus University) before being bandpass-filtered a second time at the same cutoff frequencies with an 8 pole Krohn-Hite DC-powered single channel filter (FMB300). Data were then digitized at a rate of 16 kHz on the DAQ board.

An AEP record was generated by projecting between 750 and 1000 pips of each stimulus at a certain output level and then averaging the corresponding AEP epochs together to extract the AEP waveform from noise. Each AEP recording was displayed in real time on the computer before being saved to the laptop hard drive for analysis offline. Examinations started with the presentation of the click stimulus as a quick assessment of successful electrode placement and preliminary indication of a subject's auditory receptivity. Frequency-specific thresholds were then explored using the narrowband tone pips. For a given frequency, each threshold test began by recording an AEP to a high stimulus level (80–90 dB referenced to [re:] 20 µPa rms), which was then reduced in 5 or 10 dB steps until no response was discernable for 2–3 consecutive trials. An additional 1–2 trials were conducted at increased, but untested, levels to confirm a response was still present. Stimulus frequencies were generally tested in a prioritized order, starting with 2 kHz and increasing in 1 kHz steps until no response could be detected above approximately 90–95 dB re: 20 µPa rms (the output limit of the system) at the tested frequency. Lower frequencies of 1, 0.75, and 0.5 kHz were then tested, followed by the interspersed 'higher' frequencies of 1.5, 2.5, 3.5, and 4.5 kHz, dependent on the anesthesia time and bird health status. If conditions allowed, full threshold trials were also conducted for the broadband click stimulus.

Acoustic recordings were made of the ambient background noise and the projected test tones during each trial within the chamber via a Type-4189 microphone attached to a Type-2250 hand-held analyzer (Brüel & Kjær) placed adjacent to the birds' auditory meatus. Recordings were digitized by an Olympus LS-12 Linear PCM recorder attached to the line output of the analyzer. All recordings were calibrated against a 94 dB sound pressure level (SPL) tone at 1 kHz from a calibrated piston phone that was recorded prior to the start of data collection with each bird.

2.3. Auditory threshold estimation and analysis

Final threshold calculations were made offline in Matlab (Mathworks). For each stimulus frequency, the peak amplitudes of the AEPs were measured and plotted as a function of the stimulus received level at the position of the bird's auditory meatus. A linear regression was fit over points corresponding to waveforms with clearly visible responses. The threshold estimate was taken as the intersection of the linear regression with the zero-magnitude level. In cases where responses were too few to allow regression-based estimation (near the projection limit of the system), the threshold was estimated as the lowest stimulus level that elicited a discernable response.

To explore potential sources of inter-individual variation in audiograms, we first looked for threshold differences between male and female individuals, using a linear mixed effects regression model

(LMER) with Gaussian error structure, with sex and stimulus frequency treated as categorical fixed main effects and individual ID as a random effect. We used a mixed model to account for the repeated measures on individual birds, which would otherwise violate the independence assumption of an ordinary linear regression model. We examined the fitted model using diagnostic tests and plots implemented using the package DHARMa (Hartig 2022) to ensure that all pertinent assumptions were met. These assumptions included normality of residuals (checked with Q–Q plot and a Kolmogorov-Smirnov test) and homoscedasticity (tested by examining a plot of residuals vs. model prediction for departures from uniformity). We also checked for outliers. The model passed all tests, and no problematic outliers were detected.

Any variability in threshold estimates between individuals could also be reflective of experimental factors, including variation in each bird's baseline electrophysiological noise or the background acoustic noise. To assess the impact of these factors on the resulting individual audiograms, we tested a null hypothesis that neither the electrical noise nor the background audio noise affected an automatic calculation of the threshold. We first modeled the response as a constant background signal (m) below the threshold (T) that linearly increased above the threshold with gradient (g): $f(L;m;g;T) = m + g \max(0, T - L)$, where L is the stimulus level (dB). T was taken to be a function only of the frequency and constant for each bird, whereas the strength of the responses m and g was chosen independently for each bird. The least squares deviation (see Eq. 1 below with $\alpha = 0$) was then found for the $2N + 1$ parameters, where N is the number of birds with successful measurements at this frequency. This approach resulted in similar audiograms, indicating the automatically calculated thresholds were suitable for assessing the influence of noise on threshold variability. Background acoustic noise was assessed by extracting 20 ms of acoustic data between successive stimuli projections within the chamber for each trial and bird. Similarly, baseline electrophysiological noise was assessed using the last 20 ms of each averaged AEP record from each trial and bird. We tested the influence of each noise level separately. Our hypothesis was that the threshold depends linearly on the noise level through an additional parameter, α. We did not want to make any assumptions about the underlying probability distributions of the noise, so we used a bootstrap technique where we randomly permuted the noise measurements. For a given set of measurements, we let X_{jk} be the measured noise (electrical or audio) for bird k with stimulus level j. Then we found the best-fit parameters by minimizing the statistic:

$$S = \frac{1}{N} \sum_{k=1}^{N} \sum_{j=1}^{n_k} \left[M_{jk} - \mathrm{f}\left(L_{jk}; m_k; g_k T + \mathrm{a} X_{jk} \right) \right]^2 \qquad (1)$$

with respect to $\{\alpha, T, m_1, m_2, \ldots, m_N, g_1, g_2 \ldots, g_N\}$, where n_k is the number of frequencies tested for bird k. To generate the distribution for this statistic, we reordered the noises $\{X_{jk}\}$ with a random permutation p_i and again found the best-fit parameters to generate a new statistic, Si. We performed this 10 000 times and then compared S to the set $\{Si\}$ to determine whether it was smaller. We also examined the confidence intervals for the α fit to the data; if these included zero, then we concluded that the influence of the noise (either acoustic or electrophysiological) was not significant.

2.4. Short-term soundscape recording

Passive acoustic recordings were made to document the environmental acoustic conditions experienced by the nesting common murre individuals studied here and to provide an initial baseline description of the soundscape at Latrabjarg in general. A dual-channel Song Meter (SM4) acoustic recorder (Wildlife Acoustics) was placed at the top of the cliff directly above the short rock ledge where murres were captured for the auditory tests (65° 30′ 02″ N, 24° 31′ 42″ W). Sounds were recorded continuously from 6–8 June 2021 (following completion of the hearing tests) via 2 omni-directional A2 microphones positioned 10 cm out from the cliff edge and approximately 4.6 m vertically above the targeted murre nest ledge. Signals were amplified by 0 or 16 dB and digitized at a sample rate of 24 kHz. Recordings were saved as dual-channel .wav files on SD cards for offline analysis. The A2 microphones were manually calibrated before and after deployment with a 94 dB SPL 1 kHz tone from a calibrated pistonphone.

2.5. Soundscape analysis

Sound levels were measured from the recordings in 1 s intervals, and mean (±SD) sound levels were then calculated for multiple spectral bands across 5 min bins of the data. Geophonic contributions to the soundscape were explored by comparing mean A-weighted sound levels to environmental parameters of interest using publicly available data sets from the closest available location to the study site. Parameters included wind speed (6–8 June 2021, Latrabjarg weather station, Icelandic Meteorological Office Database, delivery no. 2021-09-10/01), offshore wave height (Blakknesdufl buoy, 4–10 June 2021, Vegagerðin Icelandic Road and Coastal Administration), tidal level (6–8 June 2021, Olafsvik, Veðurstofa Íslands [Icelandic Meteorological Office]), and solar radiation on the ground as a proxy for ambient light levels (6–8 June 2021, Gufuskála weather station, Veðurstofa Íslands [Icelandic Meteorological Office]).

To statistically compare sound levels (5 min intervals) to the available environmental data (10 or 60 min intervals), we first interpolated the environmental data to match the sound level data using cubic splines (Forsythe et al. 1977) implemented using the 'splinefun' function in R. The sound level data are characterized by high-frequency variation around a lower frequency mean trend of interest. This high-frequency variation was eliminated by taking a rolling arithmetic mean along the time series with a window of 65 min. The efficacy of this window to adequately characterize the observed trends was checked visually (see Section S2 in the Supplement at www.int-res.com/articles/suppl/m714p087_supp.pdf). Next, to avoid well-known issues of spurious correlations among non-stationary time series (Shumway & Stoffer 2017), the stationarity of all 5 time series was first assessed using Dickey-Fuller tests. The non-stationary time series were detrended by differencing. Finally, using these stationary time series, Pearson correlation coefficients between the A-weighted sound level and the environmental time series were calculated first with no lag and then, to investigate the potential for lagged relationships, with lags from −120 to +120 min. For clarity, the code for the soundscape analysis is provided in the Supplement. We also looked at the periodicity of the sound level and environmental parameters via fast-Fourier transform of each full time series.

The occurrence of anthrophonic and biophonic contributions to the soundscape was investigated via a combination of viewing spectrograms and listening to the complete recordings via Raven Pro software. Given the large number of vocal bird species at the site, the dominant biophonic sound sources were assessed qualitatively and identified by comparison to online databases (www.xeno-canto.org and Macauley Library, Cornell Lab of Ornithology) and confirmed by an expert of the local avifauna (author Y.K.). No effort was made to assess call rates or behavioral acoustic patterns of any specific species.

2.6. Vocalization analysis

Although the behavioral contexts around common murre vocalizations have been studied to some degree, published descriptions are largely limited to qualitative descriptions of adult vocalizations (e.g. Tschanz 1968, Birkhead 1978, Gaston & Jones 1998, Walsh 2001). A few studies have also provided more quantitative analysis of vocalizations from a closely related species, the thick-billed murre *Uria lomvia* (Lefevre et al. 2001). A comparison of vocal recordings from both common murres and thick-billed murres available via the aforementioned online databases indicates that the calls of both species are similar, complicating species-specific vocal identification via a passive acoustic platform. Thus, it was possible to initially identify calls within the soundscape recordings as being produced by murres, but not which species. To identify potential calls from common murres, any murre calls that were subjectively identified as being of high quality and received level in the soundscape recordings were extracted and analyzed using Matlab. Received levels were calculated for all calls, which were then separated according to call types based on previous descriptions by Lefevre et al. (2001) for thick-billed murres. Individual calls that fell above the 90% percentile received level for each call type were reasonably assumed to have been produced by murre individuals on the closest nesting ledge, which was repeatedly observed to only include common murres. Basic parameters of spectral emphasis were then calculated for each call type using only this 90th percentile call subset as well as estimates of call source levels by correcting for a sound attenuation distance of 4.6 m.

By combining data on vocalization characteristics, environment noise, and auditory sensitivity measurements, we also calculated a simplified estimate of common murre acoustic communication distances under assumptions of both noise- and threshold-limited conditions using the equation $\mathrm{DT} = \mathrm{SL} - 20\log(r) - ar$. In this equation, the detection threshold (DT) is either the measured hearing threshold at the nearest audiogram frequency ('threshold-limited') or the level of the background noise power spectral density (PSD) plus an auditory critical ratio (CR) constant ('noise-limited'); SL is the vocalization source level within the 1/3-octave band containing the peak frequency; r is the sound source distance, $20\log(r)$ is an estimate of spreading loss; and ar is the frequency-dependent attenuation coefficient of air. Given that common murre auditory CRs are unknown, the mean of known CRs from 14 species of birds was used in the calculations instead (Dooling 2002). The threshold-limited condition assumes a quiet environment where acoustic detection is limited solely by the auditory threshold and a propagating vocalization is unmasked by background noise. In contrast, the 'noise-limited' scenarios assume that the auditory thresholds of a receiver are below the environmental noise PSD + CR level and result in an estimate of how far away the murre vocalization can be detected before it may become masked by the soundscape noise.

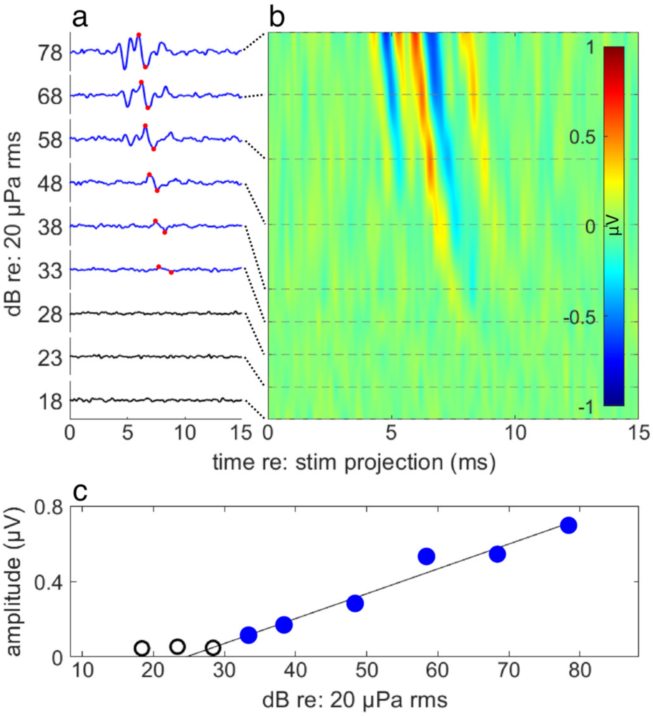

Fig. 1. Common murre auditory evoked potential (AEP) characteristics in response to presentation of click stimuli centered at 2 kHz across stimulus levels (re: referenced to). (a) Example AEP waveforms elicited by the stimulus presented at decreasing received levels. Blue waveforms contain visually discernable AEP responses, while black waveforms contained no discernable responses. Red dots in the blue waveforms denote the peak-to-peak magnitudes used for subsequent threshold calculation. (b) Interpolated heat map of individual response waves showing wave latencies increased as the stimulus received level was decreased. (c) Example threshold calculation from the AEP amplitudes in (a) using linear regression. Thresholds were estimated as the point where the linear regression fit to detected response magnitudes (blue dots) crossed the zero value of the *y*-axis

3. RESULTS

3.1. AEP characteristics

Of the 15 common murres captured for this study, we measured full or partial audiograms from 11 individuals, with a single threshold at 2 kHz from a 12th individual. Hearing measurements were not successful from 3 individuals due to either insufficient sedation or vital signs being outside nominal range during sedation. Sex was identified via blood tests for 9 individuals, which included 4 females and 5 males. Like other birds, the typical murre AEP response was a series of positive and negative wave deflections lasting 5.25–5.5 ms in duration (Fig. 1a). There was some variability between birds in the number of waves visible and their relative amplitudes to one another, which is likely explained by variability in electrode placements from bird to bird. Response amplitudes decreased and wave latencies increased as a function of decreasing stimulus intensity (Fig. 1b,c). When accounting for stimulus propagation delays according to the bird–speaker distance, there was a lag time of 2.25 ms from the approximate time stimuli reached the birds' ears to the peak of the first positive wave deflection in the AEP.

3.2. Audiograms and threshold variability

Fig. 2a shows the overlapping audiogram thresholds measured from all birds. The most sensitive frequency for all individuals occurred between 1 and 3.5 kHz, while the lowest threshold from any bird was 13 dB re: 20 µPa rms at 2 kHz. Thresholds generally increased with increasing frequency above 3.5 kHz. Above 4 kHz, most individuals were unresponsive to stimuli below approximately 105 dB re: 20 µPa rms, indicating a high-frequency auditory cutoff between 4 and 5 kHz. Similarly, thresholds increased with decreasing frequency below 1.5 kHz. At 0.75 kHz, thresholds were obtained for 7 of 10 tested birds. Stimulus artefacts often contaminated the generally lower AEP response levels when projecting sounds at 0.5 kHz or below. As a result, only 4 individuals could be adequately tested at 0.5 kHz, and only 2 of those exhibited a sufficiently clear response to estimate a threshold visually.

Composite audiograms calculated across all birds using measures of central tendency (median, mean ± SD) showed a lower threshold of 30 dB at 2 kHz (Fig. 2b). The dominant bandwidth as measured by thresholds within 30 dB of the lowest threshold was 3.25 kHz, extending from 0.75 to 4 kHz. There was variation in auditory threshold estimates between individuals for a given stimulus frequency. Within the dominant bandwidth, thresholds differed by be-

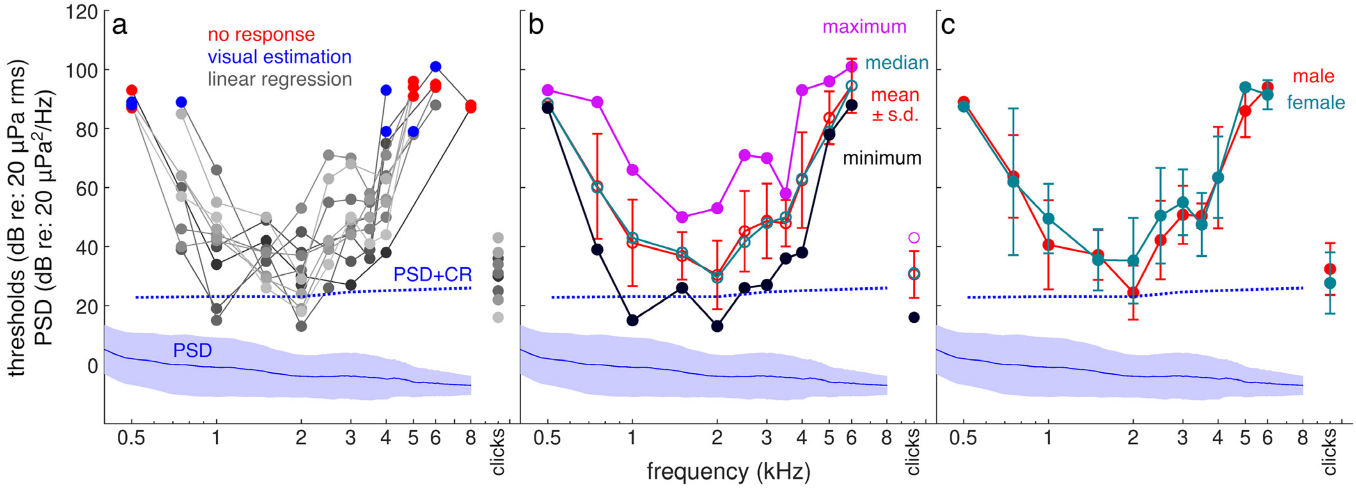

Fig. 2. Hearing threshold curves for the common murre (re: referenced to). (a) Audiograms of 11 individuals. Dark grey/black points: thresholds calculated with linear regression; blue points: thresholds where linear regression was not possible and the threshold was estimated as the lowest stimulus level that elicited a discernable AEP. If no response was detected at a stimulus frequency, the highest stimulus level tested is plotted in red. (b) Maximum, minimum, mean, and median audiograms of all birds, and (c) mean audiograms of male and female birds. All audiogram data is plotted against the mean (solid blue line) and standard deviation (blue shaded area) of the background noise power spectral density (PSD) in the experimental acoustic chamber. Dotted blue line: estimated level of masking by adding mean avian critical ratios (CR) (Dooling 2002) to the mean chamber PSD

tween 22 and 55 dB, which was the maximum inter-individual difference observed (Fig. 2c). Overall, not including the 2 thresholds at 0.5 kHz, threshold variability decreased with increasing frequency when measured by standard deviations or by maximum difference between individuals (Fig. 3). Regarding sex differences in threshold, the LMER had substantial explanatory power (conditional $R^2 = 0.73$, marginal R^2 for the fixed effects alone = 0.69). The model showed that although the threshold varied significantly across frequencies (likelihood ratio test: 106.968, number of parameters: 10, $p < 0.001$), sex did not explain a significant amount of variation in threshold, i.e. there was no sex difference in threshold (likelihood ratio test: 0.791, number of parameters: 1, $p = 0.374$). The model's intercept, corresponding to sex = female and frequency = 0.5, was at 89.83 (95% CI [75.65, 104.00]). The effect of sex = male was ($\beta = -3.13$, 95% CI [−10.99, 4.72]). Although we found no significant sex differences, we acknowledge that sex differences may have been undetected due to the small sample size, which results in fairly low statistical power.

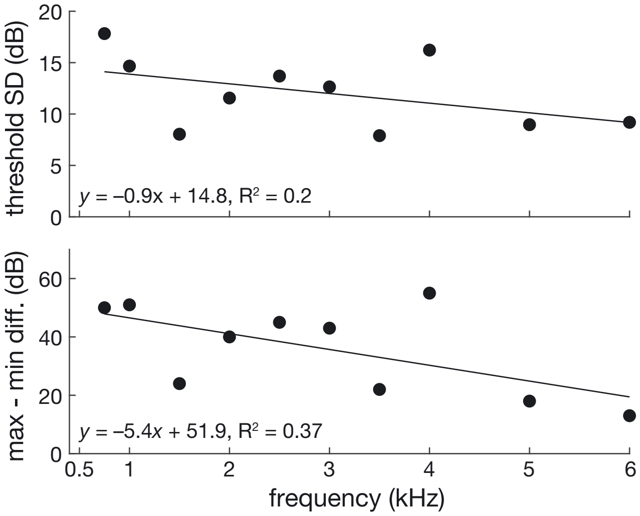

Fig. 3. Threshold variability between common murre individuals. The standard deviation (top panel) and maximum–minimum threshold difference (bottom panel) of thresholds between individuals tended to decrease with increasing stimulus frequency

We explored other potential sources of the inter-individual threshold variability, including background acoustic levels within the chamber and baseline electrophysiological noise levels from each bird in the absence of acoustic stimuli. Baseline electrophysiological noise levels were low for all birds (mean ± SD: 0.07 ± 0.01 µV), although there were significant differences between individuals (Kruskal-Wallis 1-way ANOVA; $\chi^2 = 196$, df = 10, $p < 0.001$). Similarly, background acoustic noise within the test chamber was also quiet across the bandwidths tested for the hearing measurements (0.5–8 kHz). Mean PSDs of the chamber noise were low and ranged from 2 to −7 dB re: 20 $\mu Pa^2\,Hz^{-1}$ (see Fig. 2). Results of the bootstrap analysis indicated that neither background electrophysiological nor acoustic noise levels significantly affected threshold measurements. Therefore, the threshold variation between individuals most likely reflects real individual differences in auditory sensitivity, although it does not exclude the possibility that the lowest thresholds measured were limited by masking from the acoustic noise floor of the chamber.

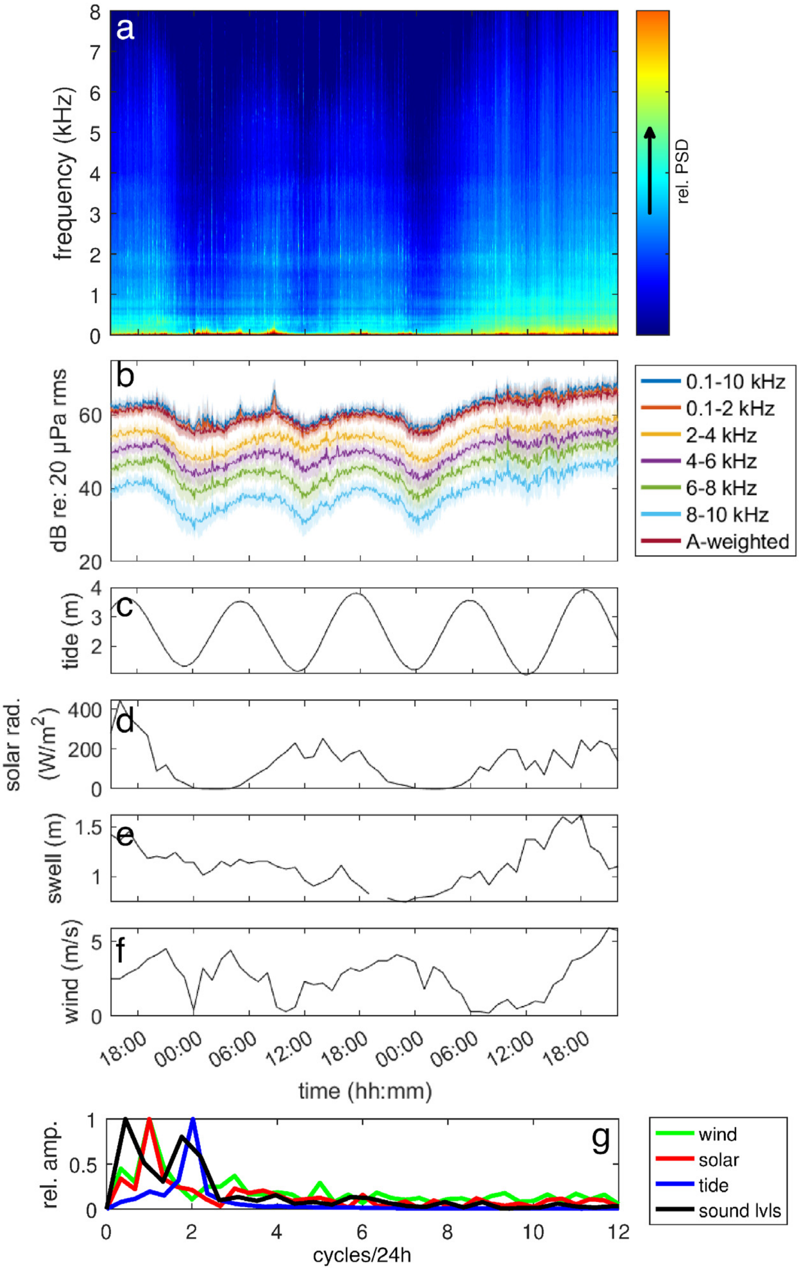

Fig. 4. Comparison of short-term soundscape and environmental patterns of the common murre rookery. (a) Long-term spectral average of the nesting soundscape; (b) comparison of environmental sound level dynamics (re: referenced to) across multiple frequency bandwidths temporally aligned with data on (c) tidal height, (d) solar radiation as a proxy for daylight levels, (e) offshore swell height, and (f) wind speed. (g) Periodogram showing the dominant cyclical patterns of the environmental parameters with significant correlations to the sound levels

3.3. Soundscape and vocalization characteristics

A long-term spectral average of the aerial soundscape at the capture site was calculated from 54 h of recordings (Fig. 4a). Sound levels encompassing frequencies from 0.1 to 10 kHz varied temporally at the recording site during this short timeframe (Fig. 4b). The maximum and minimum mean levels across any 5 min epoch were 69 and 56 re: 20 µPa rms, respectively. The maximum and minimum A-weighted sound levels were 67 and 54 A-weighted decibels (dBA). Rhythmic patterns of the sound level time series showed cyclical peaks at 0.44 and 1.8 cycles d^{-1}, with the latter closely corresponding to a typical 12.5 h tidal period. The sound levels were significantly correlated ($p < 0.001$) with solar radiation ($r = 0.533$) and tidal height ($r = 0.365$). The correlation with wind speed was markedly lower, though still statistically significant ($r = 0.154$), and the correlation with offshore swell height was non-significant ($r = -0.047$, $p = 0.230$). The cross-correlation analysis showed that the peak correlation was at ~0 lag for solar radiation, but that there was a marked lag in the peak correlation for tidal height, with the strongest correlation occurring approximately 1 h after high tide.

Anthropogenic noise was rarely detected in the short-term soundscape, with less than 10 s of anthropogenic sound (human conversation) documented across the entire 52 h, although the soundscape recording duration is too short to speculate if such low human noise is the norm. Latrabjarg is a well-known tourist attraction in Iceland, but in the absence of precise attendance data for our recording days, it cannot be determined if human presence was low or perhaps visitors were simply quiet. In contrast, the soundscape contained the frequent presence of biophonic sound sources which were exclusively birds, dominated by black-legged kittiwakes *Rissa tridactyla* (e.g Mulard et al. 2009), at a nearby section of the sea cliff, and murres (Lefevre et al. 2001). Calls from other bird species were also present, although much more infrequent; they included Atlantic puffins (Mooney et al. 2019a), northern fulmars *Fulmarus glacialis*, and ravens *Corvus corax* (Conner 1985). No calls were identified as being produced by razorbills *Alca torda*.

A total of 2578 individual murre vocalizations were of high spectral clarity above the background noise, did not overlap with other biophonic sounds, and were extracted for further analysis. This included 4 of the 6 call types previously described for the thick-billed murre (Lefevre et al 2001), including 'nods' (n = 246), 'crows' (n = 108), 'growls' (n = 192), and 'adows' (n = 44) (see Fig. 5a). It also included an additional short-duration call type that was not previously described for the thick-billed murre, which we refer to here as a 'coo' (n = 1988). Another call type previously documented for the thick-billed murre, the 'laugh', was also often observed in the recordings; however, it always contained overlapping calls from con- or heterospecifics and was not suitable for subsequent acoustic analysis. Estimated mean call source levels ranged between 94 dB re: 20 µPa rms for the adow and 85 dB re: 20 µPa rms for the growl (Fig. 5b). All calls exhibited at least some acoustic energy from approximately 100 Hz up to 10 kHz, but dominant energy occurred at low frequencies (below ~3 kHz) as indicated by measures of the peak frequency, centroid frequency, and −3 dB bandwidth (Fig. 5b).

Using these measured call parameters, we estimated detection ranges for each vocalization under both threshold and noise-limited scenarios (Fig. 6). Maximum estimated acoustic detection ranges for threshold-limited conditions were 112 m for the adow, 83 m for the crow, and only 1 m for the growl, coo, and nod. Under a noise-limited scenario corresponding to a period of low tide, estimated vocalization detection limits were 33 m (adow), 22 m (crow), 9 m (growl), 8 m (nod), and 6 m (coo). Similar calculations using the maximum recorded soundscape levels during a period of high swell and wind resulted in range estimates of 12 m (adow), 8 m (crow), 3 m (growl), 3 m (nod), and 2 m (coo).

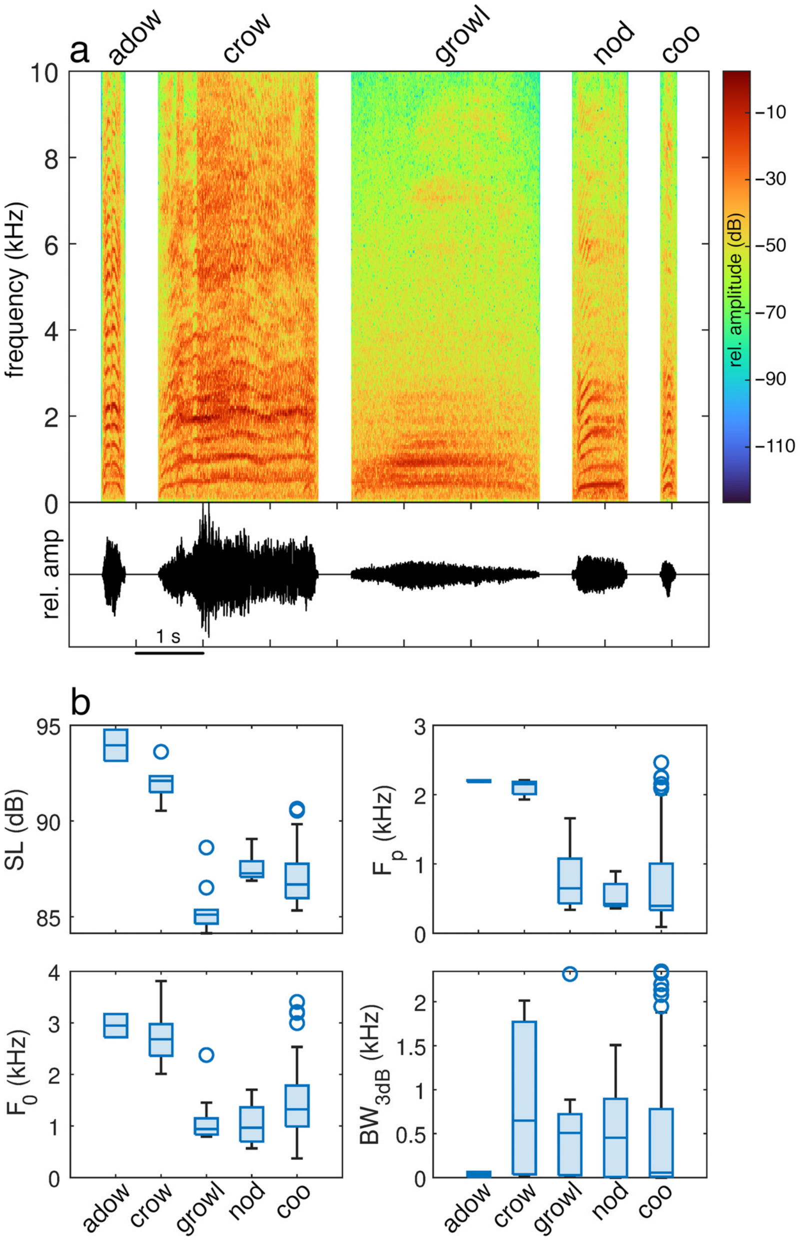

Fig. 5. Characteristics of recorded common murre vocalizations. (a) Example spectrograms and pressure waveforms of 5 vocalization types identified in the soundscape recordings. (b) Comparison of maximum estimated vocal source parameters of the call types shown in (a) with standard boxplot format. Parameters include source level (SL), peak frequency (F_p), centroid frequency (F_0), and −3 dB bandwidth (BW_{3dB})

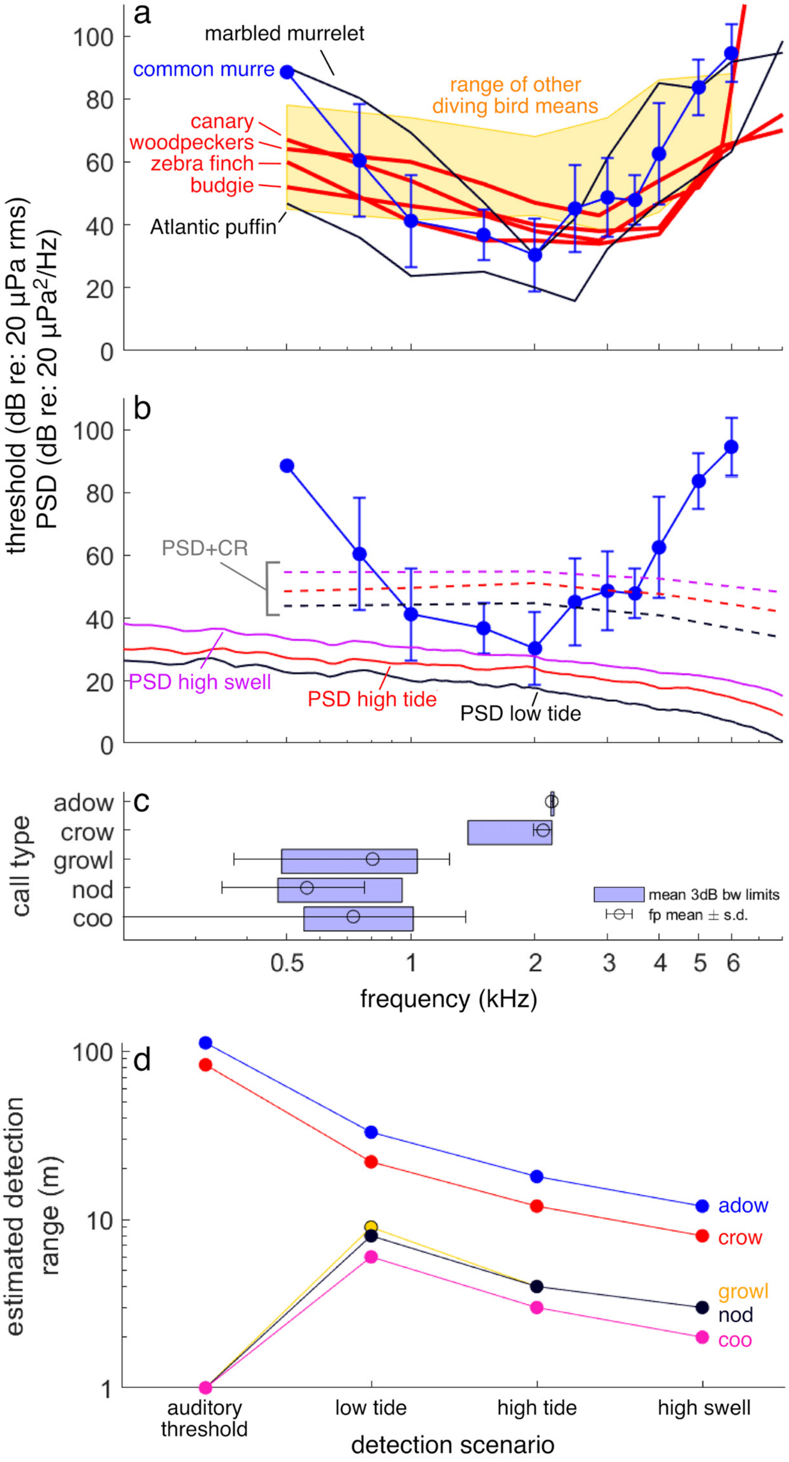

Fig. 6. (a) Mean auditory evoked potential (AEP) audiogram comparison between the common murre and other birds, including representative terrestrial species in red (canary *Serinus canaria*, Brittan-Powell et al. 2010; woodpeckers [average of multiple species], Lohr et al. 2013; budgerigar *Melopsittacus undulatus*, Brittan-Powell et al. 2002, zebra finch *Taeniopygia guttata*, DeAngelo 2008) and other Alcids in black (Atlantic puffin, Mooney et al. 2020; marbled murrelet, Smith et al. 2023). The tan-shaded region encompasses the mean AEP audiograms of other non-Alcid diving birds measured to date (Crowell et al. 2015). (b) Comparison of mean common murre auditory sensitivity (blue, mean ± SD) with the soundscape power spectral density (PSD) across different noise conditions and (c) with the dominant spectral bandwidths of conspecific vocalizations. The dotted lines in (b) denote estimated onset levels of auditory masking in the environment by adding mean avian critical ratios (CR) to the soundscape PSD. (d) Estimates of the detection ranges of common murre vocalizations under different detection threshold conditions

4. DISCUSSION

In this paper, we report electrophysiological auditory thresholds from 12 wild common murres measured in a field setting, as well as baseline soundscape levels and vocalization characteristics for nesting individuals of the species. The hearing data from a relatively large number of wild birds provide a generally robust estimation of in-air auditory sensitivity and variability for the species. They also provide a valuable update to data published for a single murre by Mooney et al. (2019b). The tested individual in that previous study exhibited elevated thresholds of between 65 and 90 dB at frequencies between 1 and 4 kHz. In contrast, our results show common murres have significantly more sensitive hearing than previously documented despite their noisy nesting environment and the evolution of peripheral auditory adaptations that likely relate to baroprotection during deep diving (Zeyl et al. 2022). Indeed, the lowest threshold of 13 dB at 2 kHz from one individual is quite sensitive considering that AEP thresholds are generally elevated compared to thresholds determined via psychophysical tests (Brittan-Powell et al. 2002, Yuen et al. 2005, Houser & Finneran 2006). Thus, the absolute auditory thresholds for the common murre may even be lower than determined here.

4.1. Audiogram comparison to other birds

The common murre is the third alcid for which aerial hearing thresholds have now been measured, in addition to the Atlantic puffin and marbled murrelet *Brachyramphus marmoratus* (Smith et al. 2023), and provide a valuable comparison species within the same family (Mooney et al. 2019a, 2020). Mean audiograms of the alcids showed similarly typical U-shapes and frequency regions of best sensitivity (~1–3 kHz; see Fig. 6a). However, like the marbled murrelet, the murre audiogram exhibited a steeper increase in thresholds at the audiogram tails and was less sensitive than the puffin by between 10 and 42 dB across the entire hearing bandwidth. Notably, the large low-frequency threshold difference from the puffin (42 dB at 0.5 kHz) could suggest the murre has significantly poorer low-frequency hearing, although it may also be related to experimental or situational variation between the studies. For example, AEP data collection was not possible from most murres at 0.5 kHz (all but 4) due to significant stimulus artefacts within the low-frequency electrophysiological record. Lower amplitude responses in the murres may thus have been masked by the stimulus at this low frequency.

In-air audiograms have also been collected from 11 additional species of diving birds using the same electrophysiological methodology (Crowell et al. 2015, Larsen et al. 2020). Mean thresholds at the best frequency for these species ranged between 38 dB at 3 kHz for the lesser scaup *Aythya affinis* and ca. 68 dB at 1.7 kHz for the northern gannet *Morus bassanus*. By comparison, lowest mean thresholds are 30 and 16 dB for the common murre and puffin (Mooney et al. 2020), respectively. Thus, the 2 alcids exhibit more sensitive in-air hearing at their best frequency than other (often shallower) diving bird species tested to date. There is also growing interest in how the auditory biology of deep-diving bird species compares to that of fully terrestrial birds, but it is difficult to compare audiograms across the full breadth of species due to methodological differences and variations. Most avian audiograms have been collected using behavioral experiments, which typically estimate lower thresholds than AEP audiograms (Brittan-Powell et al. 2002, 2005, Yuen et al. 2005, Crowell et al. 2016). Yet there is a smaller but growing number of terrestrial avian AEP audiograms for comparison. In general, the lowest thresholds of diving birds vary compared to those of terrestrial birds that are not auditory specialists (Fig. 6a). Notably, the 2 alcid species exhibit lowest thresholds comparable to non-auditory specialist terrestrial birds despite being among the deepest diving seabirds tested so far (up to 150 m; e.g. Piatt & Nettleship 1985, Burger & Simpson 1986, Bonnet-Lebrun et al. 2021). This suggests that auditory adaptations to a life of deep-diving have not significantly reduced in-air hearing in the common murre or puffin (Mooney et al. 2020). The broader collection and comparison of auditory and acoustic data across additional alcids and diving seabird species in general might help elucidate the driving factors of the auditory differences discussed here. In particular, since acoustic behavior is comparatively well documented in penguins (e.g. Aubin & Jouventin 1998, 2002, Jouventin et al. 1999, Kriesell et al. 2018, 2021), documentation of penguin auditory thresholds using similar methodology for comparison would be broadly valuable.

4.2. Nesting soundscape

Habitat-associated soundscapes underpin various ecological processes in a variety of animal taxa. However, there are few studies on aerial soundscape dynamics of many coastal habitats, including seabird colonies. As humans increasingly utilize these areas, it is essential to characterize these soundscapes with little to no human noise as a baseline for understanding seabird acoustic biology and thus quantifying the effects of human activity on their acoustic ecology over time. Notably, the Latrabjarg soundscape recorded here contained minimal human noise despite being a well-known tourist attraction in Iceland. Although it cannot be determined if this is the result of low human presence during our limited recording days or if visitors were simply quiet, it suggests an acoustic environment with minimal overall encroachment by anthropogenic noise.

The murre nesting site studied here exhibited a naturally complex and noisy acoustic environment, with baseline sound levels ranging from 56–69 dB SPL, or 54–67 dBA (0.1–10 kHz). Although the short recording window precludes conclusion of how representative these sound levels are of the full nesting season, they occurred during a period of calm regional weather and thus may be a conservative portrayal. Sound levels are likely higher during inclement weather due to precipitation, higher winds, and increases in wave height and energy. Notably, these naturally occurring levels are akin to anthropogenic noise levels which can have deleterious effects on a variety of terrestrial bird species (circa 55–60 dBA; e.g. McClure et al. 2013, McClure et al. 2017, Injaian et al. 2018). Noise disturbance thresholds identified for terrestrial birds may therefore not be applicable to common murres or other seabirds that similarly nest on sea cliffs or other areas exposed to consistent wave noise. This underscores the potential importance of incorporating species and niche diversity into avian noise-impact criteria, a need identified in other taxa (Popper et al. 2014).

Temporal dynamics of the soundscape were significantly correlated with multiple environmental parameters and exhibited a diurnal-cycle association. While diurnal cycles are well known in terrestrial soundscapes due to light-associated patterns in sound production by many taxa (Rodriguez et al. 2014, Farina & Ceraulo 2017), the diurnal association found here is perhaps notable due to the continuous 24 h of daylight at the site and thus a minimal dawn–dusk light cue. Although vocalization patterns were not investigated here, it is conceivable that light-related changes in vocal activity from common murres and other birds could underlie the observed diel sound level pattern, since common murre hormonal levels can provide a time-of-day signal despite continuous light (Huffeldt et al. 2021). Also notable is the soundscape's association with the tidal cycle. This clear periodicity was present across all spectral bandwidths, which suggests that it resulted from changes in the broadband sounds of ocean waves (Hildebrand 2009). Yet common murre colony attendance can follow a tidal rhythm (Slater 1976), and this tidal soundscape pattern could have been influenced by murre vocalization patterns as well. To our knowledge, the influence of tidal cycles and continuous daylight in arctic or near-arctic environments on bird vocalization patterns is little studied and would constitute a valuable direction for future research.

4.3. Masking considerations and detection range

Localized environmental noise can limit the detection of important acoustic signals (Klump 1996, Brumm & Slabbekoorn 2005), and there is growing evidence that signal detection constraints can be an evolutionary driver of animal communication systems (Brumm 2013, Wiley 2015). Therefore, the quantification of natural acoustic habitats can be valuable for contextualizing auditory measurements, as high-noise environments can influence species' acoustic biology (e.g. Aubin & Jouventin 2002, Arch & Narins 2008). A comparison of the soundscape spectral profile and murre audiogram suggests that the high background noise levels may interfere with common murre hearing. Across most birds studied to date, tonal signals must be from 18 dB (0.25 kHz) to 38 dB (8 kHz) above the background noise PSD at the same frequency to be detected (the auditory CR; see Dooling et al. 2000, Dooling 2002, Dooling & Popper 2016). Assuming similar frequency-dependent CRs for murres, the species' auditory thresholds across the most sensitive audiogram bandwidth fall below the soundscape PSD + CR level (Fig. 6a). Thus, nesting individuals may experience auditory masking of acoustic cues within this bandwidth under the noise conditions documented here.

The coevolution of spectrally matched auditory and vocal systems can help maximize the detection and discrimination of important acoustic signals within noise (Endler 1992), and examples of both matched and unmatched systems have been documented in birds (Konishi 1970, Dooling et al. 1978, Henry & Lucas 2008, Crowell et al. 2015). A simple comparison here shows that dominant murre vocal frequencies only partially match their frequency of best auditory sensitivity (Fig. 6b), which impacted the acoustic detection range estimates. For example, a vocal mismatch contributed to short detection range estimates (1 m) for 3 murre vocalizations under the threshold-limited scenario due to the common murre's elevated thresholds below 1 kHz (Fig. 6). Notably, the auditory threshold of 88.5 dB at 0.5 kHz is above the corresponding third-octave source level of the peak frequency of 'nod' vocalization (62 dB at 0.56 kHz), which would make it undetectable to other conspecifics. This situation is biologically unlikely and suggests that (1) the few murre ABR thresholds estimated at 0.5 and 0.75 kHz may be artificially elevated and (2) the threshold-limited detection ranges for the lower-frequency vocalizations (growl, coo, nod) are likely underestimates.

Nonetheless, acoustic masking by background noise may limit the range at which individuals can detect acoustic cues from conspecifics. In the case of the adow, estimated detection distances were 33 m during low tide, 18 m during high tide (+6 dB re: low tide), and 12 m during the high swell period (+9 dB re: low tide). This corresponds to noise-induced range decreases of 71, 84, and 89% below the overall maximum (112 m). These estimated murre communication ranges are lower than typical estimates for many terrestrial birds (Dooling & Popper 2016) but are similar to penguins (Aubin & Jouventin 1998), another colonial diving seabird that experiences a noisy nesting environment. Multiple penguin species are also able to overcome noisy conditions and the so-called 'cocktail party effect' resulting from a cacophony of vocalizations to detect particular conspecific calls beyond the range where the vocal energy falls to the ambient noise level (e.g. Aubin & Jouventin 1998, Jouventin et al. 1999, Lengagne et al. 1999, Aubin 2004). The common murres studied here also communicate in a complex environment and may have similar capabilities. Certainly, the distance values calculated here represent a simplified estimate that does not account for a variety of additional factors relevant to masking. For example, short-term amplitude fluctuations in the non-continuous environmental noise may lead to comodulation masking release and improved signal detection by communicating individuals (e.g. Klump & Langemann 1995). Other relevant factors include the tonal versus broadband character of the projected signal (e.g. Dooling et al. 2000, Dooling 2002), how the environment shapes the propagating signal (e.g. Dabelsteen et al. 1993), or the directionality of both the vocal signal and the receiver's auditory system (e.g. Dent et al. 1997), all of which can influence the detection range of an acoustic signal but were not accounted for here. Nonetheless, if the background noise fluctuations in our recordings are representative of the general nesting season, common murres may face significant variations in communication range on a nearly daily basis. Future research might investigate if and how common murre acoustic ecology is adapted to these soundscape dynamics.

4.4. Estimates for underwater hearing

There is growing interest in understanding if, and how, the acoustic biology of diving birds may be adapted for use underwater, yet it is currently unknown if they utilize sound underwater. Detection of underwater sound has been documented in 4 species of seabird, including the common murre (Therrien 2014, Hansen et al. 2020, Larsen et al. 2020, Sørensen et al. 2020), and from these, underwater auditory thresholds have been measured from 2: the long-tailed duck *Clangula hyemalis* (Therrien 2014) and great cormorant (Larsen et al. 2020). Only the study by Larsen et al. (2020) has provided a robust comparison of in-air and underwater hearing thresholds in a diving bird. That study utilized AEP methodologies to measure both in-air and underwater thresholds from fledgling cormorants. Their results indicated that mean hearing thresholds across all individuals were similar between the 2 media when compared in terms of the stimulus acoustic pressure. If this aerial–underwater threshold relationship is similar across other diving seabirds, common murres are predicted to have a pressure-equivalent mean underwater threshold of 56 dB re: 1 µPa at 2 kHz. This is in line with the lowest sensitivities found in some pinnipeds (Reichmuth et al. 2013) and would suggest that common murres may have sensitive hearing underwater. Importantly, this prediction represents an oversimplified extrapolation and would benefit from direct underwater threshold measurements in the future.

4.5. Considerations of potential anthropogenic noise impacts

Alcids such as the common murre are influential components of many arctic and subarctic coastal ecosystems (e.g. González-Bergonzoni et al. 2017, Cusset et al. 2019, Hentati-Sundberg et al. 2020) and are sensitive to environmental disturbance (Piatt et al. 2020). Individuals spend their adult life on the open sea and only return to land for breeding. They also exhibit a number of life history and breeding traits that may result in increased vulnerability to the consequences of anthropogenic disturbance, such as late sexual maturity (i.e. several years; Lee et al. 2008), high nest site fidelity (e.g. Hatch et al. 2000), monogamous breeding at localized colonies (Hudson 1985), and they typically lay only a single egg per yearly breeding cycle (Bent 1919, Tuck 1961). Thus, there is growing concern about the potentially negative impacts of exposure to anthropogenic noise on the biology and behavior of alcids, and multiple studies have provided evidence of seabird susceptibility to even low-level anthropogenic noise. For instance, gunshots, passing aircraft, and vessels are known to elicit varying degrees of behavioral changes or flushing in nesting murres at distances ranging from 50 m to 5 km (Rojek et al. 2007, Labansen et al. 2021). Additionally, anthropogenic noise such as off-road vehicles and pedestrians decrease adult attendance at nests and hatchling survival in American oystercatchers and Brandt's cormorants (Borneman et al. 2016, Buxton et al. 2017). Notably, establishing hearing thresholds and levels of sound detectability can further underpin all subsequent assessments of acoustic disturbance, potential hearing loss, estimates of auditory masking, and other noise-impact criteria (Southall et al. 2019).

From the results presented in this study, it can be concluded that frequencies of sensitive hearing in the common murre spectrally overlap with a variety of anthropogenic sounds (for examples and a more thorough discussion of anthropogenic sound characteristics, see Erbe et al. 2018, Halfwerk et al. 2018, Hawkins & Popper 2018, Simmons & Narins 2018, Slabbekoorn et al. 2018). To varying degrees, this overlap includes sound sources in air, such as traffic noise, human speech, and airplanes flying overhead. Only a few studies have directly investigated the impacts of in-air anthropogenic noise on seabirds, including the great cormorant (Buxton et al. 2017). Thus, with more sensitive aerial hearing than the cormorant, the common murre may face similar disturbance at even lower noise level exposure (although behavioral sensitivity and ambient noise conditions will certainly play a role). Moreover, spectral overlap with the murre's vocalizations indicates that at sufficient sound levels, anthropogenic sounds may mask conspecific or inter-specific acoustic cues that are potentially important to these birds. As most anthropogenic noise is heavily weighted towards low frequencies, such concerns may be even more pertinent if the low-frequency auditory thresholds are lower than currently estimated in this study. Direct underwater hearing sensitivities are not yet available for the common murre, but it is known that the species can detect underwater sound (Hansen et al. 2020), and their underwater hearing is likely sensitive to similar frequencies as those determined by their in-air audiograms here. The underwater hearing of common murres, therefore, likely overlaps with multiple anthropogenic sound sources underwater as well, including dredging operations, oil and gas operations, underwater explosions, and large ships and small boats. Anthropogenic encroachment is predicted to significantly increase in and around the Arctic and subarctic due to continued loss of sea ice and the opening of previously unexploited areas of the ocean for trade routes and resource extraction, making noise impacts an important consideration for maintaining the future health of murre populations (AMAP 2017).

5. CONCLUSION

These results provide new data on the airborne hearing of the common murre, a deep-diving alcid seabird. While the audible frequency ranges across individuals are typical of other birds, the lowest auditory thresholds of these murres are among the lowest of diving birds tested. They also appear vocally active in a relatively noisy soundscape. Given these data, the emerging evidence of seabird sound sensitivity and acoustic ecology, and their overall imperiled populations, the results underscore further awareness of, and caution for, acoustic encroachments and disturbances into the habitats of murres and other seabird species for which auditory sensitivities have yet to be studied.

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