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Individual right whales call louder in increased environmental noise

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The ability to modify vocalizations to compensate for environmental noise is critical for successful communication in a dynamic acoustic environment. Many marine species rely on sound for vital life functions including communication, navigation and feeding. The impacts of significant increases in ocean noise levels from human activities are a current area of concern for the conservation of marine mammals. Here, we document changes in calling behaviour by individual endangered North Atlantic right whales (Eubalaena glacialis) in increased background noise. Right whales, like several bird and primate species, respond to periods of increased noise by increasing the amplitude of their calls. This behaviour may help maintain the communication range with conspecifics during periods of increased noise. These call modifications have implications for conservation efforts for right whales, affecting both the way whales use sound to communicate and our ability to detect them with passive acoustic monitoring systems.

Keywords: animal signals; noise; acoustic communication; right whale

1. INTRODUCTION

Social communication requires the detection and recognition of a signal from a sender by a receiver. Sources of noise in the environment can limit the range for successful detection of signals [1]. Animals producing acoustic signals use a number of shortterm compensation mechanisms to improve the probability of signal detection during periods of increased noise. Common compensation mechanisms increase the signal-to-noise ratio of the signal, either through modification of the signal (e.g. increased amplitude or shifted frequency), or adjustment of the timing of production (e.g. increased call rate, call repetition or waiting until noise decreases) [2]. These mechanisms have been demonstrated over a broad range of taxa, ranging from frogs to marine mammals [3,4]. Changes to calling behaviour are potentially costly to the signalling individual, through increased energy expenditure, modification of the original information content of the signal, or increased risk of detection by predators [5].

This study investigates short-term modifications in calling behaviour of individual endangered North Atlantic right whales (Eubalaena glacialis) under varying noise conditions. Right whales use low frequency (approx. 50-400 Hz) sounds for social communication, most notably stereotyped upcalls that are used as contact calls and other tonal sounds that are used for mate attraction [6,7]. The primary habitat for North Atlantic right whales is in coastal waters of the eastern United States, an area with high levels of commercial, naval and recreational ship traffic [8]. The predominant source of human generated noise in right whale habitats is from commercial shipping, resulting in a chronic noise source that overlaps the frequency range of right whale communication signals [9]. Potential impacts of increased environmental noise on this species range from a reduced communication range for critical behaviours including mating and feeding, to chronic increases in stress levels that could indirectly affect individual fitness [10].

Previous studies of noise effects on marine mammal calling behaviour have focused on signal modifications by groups of animals [11-13] or assessed changes in call rate or song length by individuals [14,15]. Here, we investigate whether individual right whales modify their call intensity, duration and frequency in increased background noise.

2. MATERIAL AND METHODS

(a) Data collection and analysis

An archival acoustic recording suction cup tag (DTAG) [16] was attached to North Atlantic right whales in the Bay of Fundy, Canada ($44^{\circ}40'$ N, $66^{\circ}35'$ W) during the summers of 2001, 2002 and 2005. Individual identity, age and sex were determined through comparing photographs of the tagged whales to individuals in the North Atlantic right whale consortium catalogue by the New England Aquarium [17].

Calls produced by tagged whales, as opposed to other nearby animals, were identified by a combination of high received levels with a signal-to-noise ratio greater than 10 dB (range: 10-41 dB) and visual observations confirming that the whale was alone at the time of the call. Tags were attached to the back of whales behind the sound source where the sound level and spectra may be quite different from the far field sound in front of the whale [18]. For this reason, we restricted call measurements to robust signal parameters: received level, duration, and fundamental frequency within individual records. Call recordings that included splashing, detectable flow noise from whale movement, other whale calls, or were produced after a tag changed position on a whale were removed from the analysis. The correlation between fluke stroke rate (a proxy for flow noise) for 1 min before the call and the measured noise level was tested to confirm the independence of these two parameters for the remaining calls.

All acoustic records were low-pass filtered and re-sampled at 16 kHz for analysis. Background noise (NL) and call received level (RL) measurements were made in dB_{rms} re 1 µPa over a 20 Hz-8 kHz frequency band in MATLAB (Mathworks Inc.). A single-pole emphasis filter was applied to signals to compensate for a 400 Hz single-pole high-pass filter on the tag. Noise power was measured in 500 ms intervals throughout the 10 sec prior to each call and the NL was taken as the lowest of these noise measurements. Call duration (dur), and minimum and maximum frequency (f_{min} and f_{max}) were measured using RAVEN PRO 1.3.1 (Cornell Bioacoustics Research Programme) with spectrogram resolutions of 32 ms and 4 Hz. Measurements were made of NL and RL for all calls including variable tonal and upcalls and dur and f_{min} and f_{max} only for upcalls.

(b) Statistics

Descriptive statistics and a Kolmogorov–Smirnov test of normality were performed using SYSTAT 12 (Systat Software, Inc.). Mixed model analysis was performed using PROC MIXED in SAS v 9.1 (SAS Institute Inc.) with individual identification as a random effect for the measured call parameters. The RL, dur, f_{min} and f_{max} were the dependent variables tested. Independent variables included

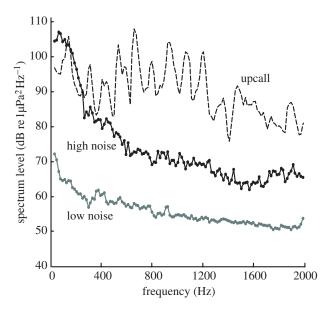


Figure 1. Maximum (black line) and minimum spectral (grey line) noise levels from a single tag record in 2005. Dashed line indicates spectrum level of an upcall from the same whale.

NL as well as age class (adult > 9 years of age) and sex as potential confounding effects related to body size for all call types.

3. RESULTS

Fourteen tag recordings contained multiple calls from the tagged whales that were suitable for measurement (n = 107 total calls, range: 2-18 calls per tag,mean \pm s.d.: 7.6 ± 5.6). These recordings included seven males and seven females, ranging from eight months to 23 years of age. Upcalls were the predominant call type (85 out of 107) produced by 11 whales. The background noise in the 20 Hz-8 kHz band measured from the tags ranged from 92-143 dB re 1 μ Pa and was dominated by noise below 400 Hz, which overlaps with the fundamental frequency of right whale upcalls (figure 1).

NL affected RL (mixed model, $F_{1,13} = 29.12$, p = 0.0001) for all call types (figure 2). For upcalls, RL increased in increased NL (mixed model, $F_{1,10} = 24.93$, p = 0.0005) but f_{min} (mixed model, $F_{1,10} = 2.82$, p = 0.12), f_{max} (mixed model, $F_{1,10} = 1.30$, p = 0.28) and dur (mixed model, $F_{1,10} = 2.97$, p = 0.16) were not significantly different in increased noise. Age class and sex were not significant factors in any of the models (p > 0.2).

4. DISCUSSION

These results provide, to our knowledge, the first evidence for noise-dependent amplitude modification of calls produced by a baleen whale. The impacts of increased noise on communication depend on whether receivers are able to detect and respond to relevant signals above the local noise level. Right whales increased their call amplitude linearly as background noise levels rose, indicating that the whales were able to maintain the signal-to-noise ratio of their signals in the moderate noise levels measured in this study. Whether these modifications are sufficient to maintain their

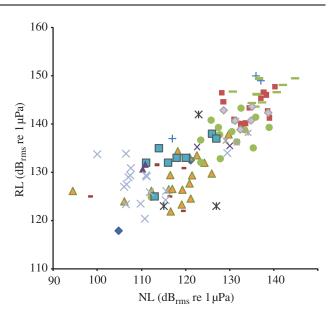


Figure 2. Call RL versus NL for all 107 calls recorded from the tagged right whales. Data from each whale are presented with unique symbols.

communication range in higher noise situations remains to be tested.

The modifications to the frequency of stereotyped upcalls produced by individual whales were not significant over short time periods. A previous study described a gradual increase in the mean frequency of stereotyped right whale upcalls through time [19], which was hypothesized to be in response to increases in low frequency ambient ocean noise [4]. These results suggest that increased call amplitude may be an immediate short-term response to moderate noise levels, while frequency changes may be a more gradual change, tracking long-term changes in both the spectrum and level of low frequency ambient noise.

Evidence that right whales regularly modify the intensity of their calls in changing background noise has implications for descriptive studies of acoustic repertoires for all species. When reporting measurements of important call parameters, a description of the noise conditions should be included, as call parameters probably vary with the background noise. Right whale upcalls are used extensively for passive acoustic monitoring in conservation efforts to protect this endangered species [20]. Variability of call parameters can reduce the effectiveness of detection algorithms and should be taken into account when calculating the probability of detection in different habitats [21].

Ocean sound levels will probably continue to increase owing to human activities and there is a physical limit to the maximum source level that an animal can produce. When background noise levels exceed the compensation abilities of right whales, either the whales' communication range will be reduced or animals will have to wait until the noise levels are lower to call. Social calls are used to mediate vital social interactions in right whales; therefore a reduction in time or space for acoustic communication could have serious implications for survival and reproduction in a species located in a highly urbanized marine environment.

Tag recordings were collected under NOAA NMFS Permit No. 1040 issued to Scott Kraus and Canadian DFO permits 2001–599, 2002–258 and SA-2005-03 and were approved by the Woods Hole Oceanographic Institution Animal Care and Use Committees.

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