



The environmental limitations on marine animal acoustic communication and sensing and their strategies to deal with them

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ABSTRACT

Marine animals make extensive use of sound in an environment where vision and the effectiveness of the sense of smell are limited. Sound travels much further in water than in air for the same loss but the complexities of the environment limit the effectiveness of the ocean as a communication channel. Propagation of sound is very variable, especially in shallow water and there can be a wide variation in propagation loss to any range. Ambient noise varies over a wide range and together with the variation in propagation loss, results in signal detection ranges commonly varying by more than a factor of 10. Reverberation from multipath arrivals distorts the signals, increasing the difficulty of deciphering them. This paper briefly examines how some of these factors affect marine animal communication and sensing and considers strategies that animals appear to use to deal with these limitations, assuming that the signals have evolved to optimise the intended biological function under the constraints of the ocean environment. Some examples are presented of the use of sound by whales.

1 INTRODUCTION

Those who work in underwater acoustics are well aware of the limitations imposed by the ocean environment (Urick, 1983). Marine animals are subject to the same limitations and it is reasonable to expect that they have evolved to optimise the way they use sound. This paper considers some of these limitations and infers possible strategies for optimising the transmission of signals to achieve the intended biological function. It deals mainly with the acoustics involved, recognising that a full analysis would also require consideration of the auditory capability of animals including their hearing frequency ranges (audiograms) and their ability to detect signals against noise (critical ratios). In the ocean, the audibility of signals will depend more on the ability to detect signals in ambient noise than on absolute hearing sensitivity.

2 SENDING AND RECEIVING INFORMATION

The value of sound to marine animals may be assessed in terms of the information that is transmitted by the sender and received and perceived by the listener. This may be the information in a communication signal from a conspecific, or in the returning echo in echolocation, or the sound indicating the presence of a vocalising predator. Adapting Shannon's theory of communication (Shannon, 1949), we can consider a source of sound (the vocalising animal) transmitting a signal through a noisy channel (the ocean environment) to the receiver (the listener). Noise is considered to be an input to the channel so that the received signal is a combination of the transmitted signal and the noise. The channel itself may degrade, distort or perturb the signal through the variable propagation which may be frequency dependent and provide multiple arrivals of the same signal, reducing the intelligibility of the information at the receiver. On the other hand, changes to the signal as it propagates injects information about the ocean environment which may be useful. Vocalising animals other than the ones of interest to the receiver can be considered as other sources (senders) or as part of the noise. From an evolutionary point of view, it may be expected that sounds produced by marine animals have been optimised to carry the most useful information to the receiver which may not necessarily be the maximum amount of information that could be sent and received by the signal.

3 DIFFERENCES BETWEEN TOOTHED WHALE AND BALEEN WHALE SOUNDS POSES

Toothed whales (odontocetes) and baleen whales (mysticetes) produce significantly different types of sounds (Au and Hastings, 2008; Erbe et al., 2025). Toothed whale sounds are generally higher frequency, shorter duration compared with the lower frequency, longer duration baleen whale sounds, although there is some overlap. The

functions of sounds produced by toothed whales are far better known than they are for baleen whales, largely because many species of toothed whales are small enough to be studied in captivity whereas no such experiments seem to be possible for baleen whales because of their size. The higher frequency, shorter duration sounds of toothed whales are suited for their use in high resolution echo-location and short range communication (Au, 1993). The lower frequency longer duration sounds of baleen whale whales imply that they are used for longer range communication, partly because absorption attenuation decreases with decreasing frequency (Urick, 1983). Reliable studies of baleen whale behaviour in relation to sound production are very difficult because of the logistical challenges of working at sea with such large whales and the likely distances of their communication. Hence, inferences from the nature of their sounds may be useful in helping to understand the biological functions of the sound.

4 THE EFFECTS OF PROPAGATION AND AMBIENT NOISE

The range at which a signal can be detected depends on the propagation loss, which reduces the level of the signal, and the ambient noise, which masks the received signal. Propagation and ambient noise are very variable, depending on ocean conditions and the contribution of other sources of sound and this leads to substantial variation in detection ranges for a specific signal. It is not unusual for ambient noise levels to vary by 20 dB as wind speed changes or biological choruses rise or fall (Cato, 2012) and this would cause a variation of a factor of 10 if propagation is by spherical spreading. Propagation loss is also very variable, so actual detection ranges can vary by large amounts.

With such wide variation in the range of audibility, effective communication requires signal source levels high enough to ensure that the required ranges of audibility are achieved under most conditions. Many whale species produce sounds with high source levels. For example, sperm whale echo-location clicks have mean square source levels up to 236 dB re 1 μ Pa at 1 m and energy per unit area up to 196 dB re 1 μ P².s (Møhl et al., 2003). Baleen whale sounds have lower mean square source levels but are much longer in duration. For example, blue whale source levels are as high as 188 dB re 1 μ Pa at 1 m (Cummings and Thompson, 1971) and 179 dB re 1 μ Pa at 1 m (pygmy blue whales, Gavrilov et al., 2011) with durations of around 20 s compared to the sperm whale sounds of less than a millisecond. Energies per unit area for the blue whale sounds turn out to be similar to those of the sperm whale sounds because of dependence on duration of the sounds. Some calculations have found that baleen whale sounds may be detectable for hundreds of kilometres under the most favourable conditions (e.g. for fin whales, Payne and Webb, 1971). Such conditions are very rare and unlikely to be of use in whale communication. Detection ranges are much less for typical propagation loss and ambient noise levels. The high source levels of baleen whale vocalisations are likely to have evolved to provide reliable communication over modest distances for most of the time rather than over large distances under rare conditions. High source levels for toothed whale echo-location are needed to deal with the losses on reflection from the target and the two way propagation loss.

Propagation loss and ambient noise vary significantly with frequency. Signals may have several components with different source levels and covering different frequency bands, so that the detection range of the components may vary significantly. If there is significant redundancy in a signal, the loss of some components may still allow the required information to be received (see section 5). The frequencies that are most favourable for sending information vary as the propagation loss and ambient noise vary, so that the components of a signal that are most likely to be detected would have components with differing frequency bands, so at least some will be detected.

4.1 Multipath Propagation

Multipath propagation splits a signal into multiple arrivals. The first arrival is by direct path between source and receiver and a surface reflected path, followed by four arrivals involving one bottom reflection, which in turn are followed by four more involving two bottom reflections etc. With negligible energy lost from reflection from the surface, but significant loss from bottom reflection, each set of reflected arrivals is received at a lower level than the preceding one. Each set of arrivals may overlap the ones before or be separated in time, depending on the duration of the emitted signal, the separation of components of the signal and the separation of arrivals, which depends on water depth and transmission range. A strategy to avoid overlap would be to separate successive sound units in sequence or song by enough time to ensure that the significant reflections of one unit arrive before the direct arrival of the following unit. For example, blue whale song units are separated by around 20 s (Gavrilov et al., 2011) suited to their deep water habitat where echoes may arrive several seconds after the direct arrival. On the other hand, humpback whale song units are separated by around 1 s with some variation (Cato, 1991), more suited to shallow water. Sounds generated in the surface duct can be split into multiple arrivals by duct "leakage," with different arrivals having different frequency content (Cato, 1972).

5 AN EXAMPLE: HUMPBACK WHALE SONG

The humpback whale song is very elaborate, containing typically 12 to 15 distinct sound types repeated in sequences of phrases and themes. Song durations are variable but typically around 10 min, so that there are many repetitions of sound types in the hundreds of units in a song. There is, therefore, the potential for the song to carry much information. However, because the song structure is very stereotyped, and whales of a population sing almost the same song, very little information is actually contained in the song (Cato, 1991; Miksis-Olds et al., 2008). Information is carried in the small departure from the stereotype, but it is not known whether this is used by the singer or the listener. Only males sing and the song appears to be a breeding display, so the main information may be to indicate the presence of and some information about the singer. Because the song is so stereotyped there is substantial redundancy, so that only part of the song needs to be heard to receive the message. On the other hand, the song changes with time, usually gradually but sometimes rapidly (Noad et al., 2000) and all singers copy the changes. This requires that the complete song is heard with all harmonics, if a faithful copy is to be made of individual sounds. Higher harmonics extend beyond 24 kHz (Au et al., 2006) and may be lost in shallow water if the propagation loss increases with frequency, so faithful copying of the sounds requires the copier to be relatively close to the sender.

6 DISCUSSION

This paper has discussed some of the limitations on the use of sound by marine animals imposed by the ocean environment and suggested ways in which the signals appear to have been optimised to achieve their purpose within the constraints imposed by the environment. Examples are given for whales, based on what is known about whale the sounds that they use and the biological function. This is a brief outline of a broad subject which extends well beyond the examples given and a full study would also include the extensive use of sounds by invertebrates and fish. It would also consider the wide spread biological choruses that are produced by invertebrates, fish and whales when large numbers of individuals of a species are producing sound *en masse* (Cato, 1978; McCauley and Cato, 2000; Erbe et al., 2025). For animals within the chorus, the main limiting factor may be the sounds of their conspecifics. Choruses substantially increase the ambient noise, typically by around 20 dB, significantly limiting the use of sound by animals outside the chorus.

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