

Whale Voices from the Deep: Temporal Patterns and Signal Structures as Adaptations for Living in an Acoustic Medium.

Christopher W. Clark

Section of Neurobiology and Behavior, Bioacoustics Research Program, Cornell University, Ithaca, New York 14850, cwc2@cornell.edu

Abstract: Whales produce long, rhythmic patterns of sounds and their low-frequency sounds (< 100 Hz) can travel many hundreds of miles underwater. Each species' signals are distinguishable acoustically by temporal features but there has been a history of infatuation with melodic qualities as the primary features of measurement. Temporal rates and time-bandwidth products are generally related to bathymetry and transmission properties, suggesting that signal features are adapted for communication and navigation. Pelagic species such as blue and fin whales rely on signals in the 10-30 Hz band, presumably to take advantage of the excellent low-frequency propagation properties of the deep ocean, with 10-200 s patterns of sound delivery. The cadence of signal delivery for blue and fin whales is such that an individual retains the rhythm of the delivery after minutes of silence. Shallow water species produce mid-frequency signals (50-1000 Hz) with temporal patterns on the order of seconds. These species with faster rhythms have greater signal variability covering a greater range of frequencies.

Animal acoustic production and perception systems are determined and constrained in ways that are quite different than those in an engineered system. Although certain components of the engineering - biological communication analogy have value (e.g. the basic complement of sender, channel, and receiver) the evolutionary constraints imposed by natural and sexual selection and the central role of variability in the selection process result in biological communication systems that are poorly modeled using traditional engineering perspectives. Likewise, it is tempting to interpret features of a biological system (e.g., signal complexity) as though they were optimizing an engineering parameter when in fact they are most probably evolved under the highly non-linear forces of selection. In some cases, can one expect to find bioacoustic features well mapped by the constraints of physical acoustics. Thus, for example, alarm calls in birds are selected to have features that render them difficult to locate but easy to detect (i.e., loud and audible, but with very little bandwidth; Marler 1955), or long range calls in blue whales have features that make them detectable over extremely long ranges (i.e. very loud, infrasonic, narrowband and redundant).

One acoustic dimension often overlooked in quantitative analysis of animal acoustic signaling behavior is rhythmicity, especially when frequency or amplitude modulations are dominant salient features of the signal. For the two species of whales that are known to produce very loud, long patterns of infrasonic signals, this is not the case since variability in signal structure is low and rhythm is the most salient acoustic feature. These blue and fin whale sounds are well matched to the acoustic environment, especially the deep sound channel, leading to speculation that communication could occur over extremely loud distances on the order of hundreds of miles (Payne and Webb, 1971). Recent advances in acoustic propagation modeling and empirical measurements raise the possibility that these animals could use their infrasonic signals to detect gross bathymetric features such as seamounts, continental shelves and mid-ocean ridges in a form of low-frequency navigation. In this case temporal stability could be more important than FM variability. Figure 1. (upper two panels) shows typical blue and fin whale signal patterns as recorded in the North Atlantic. This illustrates species specific separation of temporal and spectral features as well as the conservation of signal repetition rate. Throughout the entire Northern Hemisphere the inter-sound intervals for blue whales are ca. 70 or 130 s depending on the subpopulation, while inter sound intervals for fin whales are between 12-34 s. The primary frequency band for patterned blue whale sounds is 16-19 Hz, and they typically combine simple CW, AM and FM signals into signal complexes to achieve increased time-bandwidth product. In contrast, the primary frequency band for patterned fin whale sounds is 19-26 Hz, and they introduce variability by changing the rhythm or shifting the center frequency of the FM signals. Blue and fin whale signals are recognizable even after traveling more than 1000 nmi through the ocean because of their unique, relatively stable features.

These fairly simple levels of acoustic variability for pelagic species are in dramatic contrast to species, such as bowhead, humpback or right whales that inhabit coastal areas during breeding, calving or migration. For these species, temporal stability is diminished while frequency bandwidth and variability are increased (see Figure 1 lower two panels). Thus, although some portion of humpback song occurs in the low-frequency range and can sometimes be detected out to ranges of a few hundred miles, the acoustic audience for these coastal species is restricted by the shallow water environment. Acoustic propagation considerations alone predict that signal structures in the deep water

species are adapted for long range transmission whether for communication or navigation, while coastal species signals are instead a trade off between detection range and increased variability. The upper limit of communication rate is therefore limited by the propagation channel. However, the actual rate may not be the limiting factor for long lived pelagic species that are constrained to find patchily distributed food the occurrence of which is tied to oceanographic features. Unlike humpback male singing, all present evidence shows no restriction on when and where blue and fin whales vocalize.

The relationship between signal intensity, temporal pattern stability, spectral bandwidth and habitat could be indicative of adaptation to optimize signal features for communication and navigation. For pelagic species, temporal pattern coupled into the sound channel could be a retained, conservative feature that serves to reliably communicate a simple message over great distance. For coastal species, where range is not the critical factor, temporal and spectral variability are more of an embellishment by individuals to adjust to local conditions.

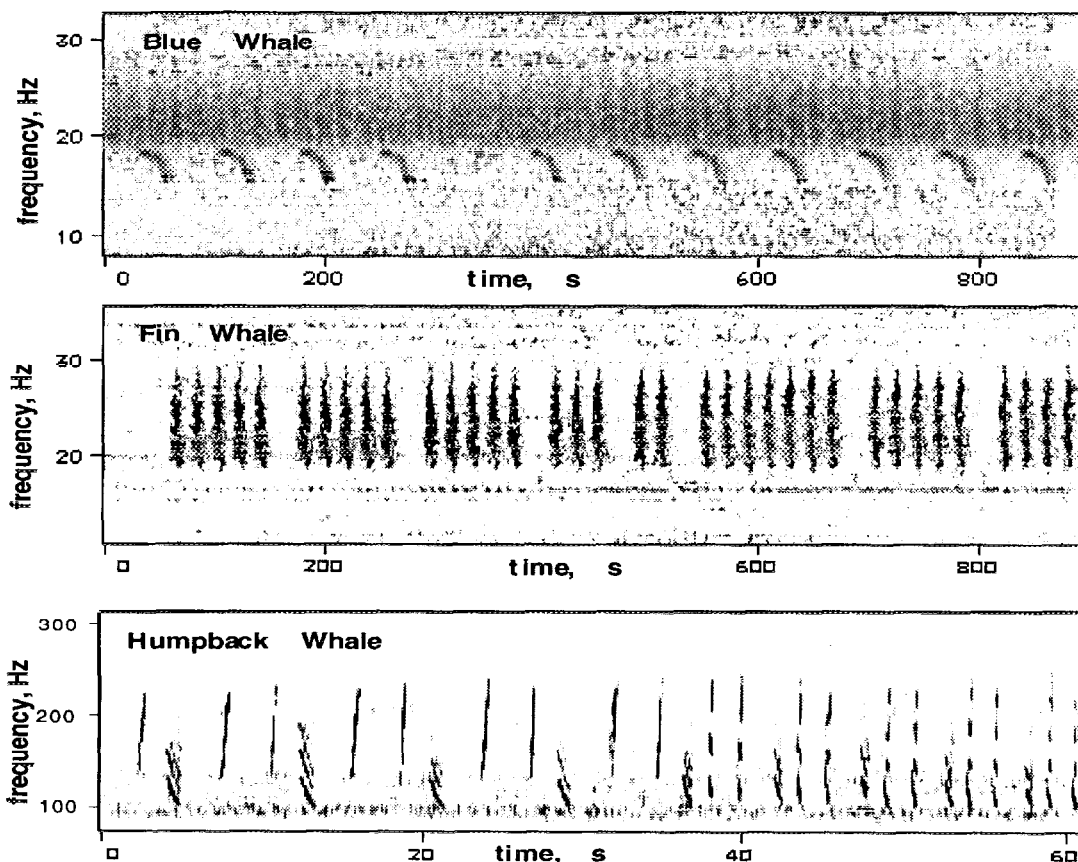


FIGURE 1. audio spectrograms of three species of whales illustrating their different temporal and spectral features. Note that time and frequency scales for blue and fin whales are different from those for the humpback whale.

ACKNOWLEDGEMENTS

Many of the ideas in this paper came from lengthy conversations with William T. Ellison. Funding for the research was provided by Cornell University, Naval Research Lab, and the Office of Naval Research.

REFERENCES

- Marler, P., Characteristics of some animal calls. *Nature* 176, 6-8 (1955).
- Payne, R and Webb, D., Orientation by means of long range acoustic signaling in baleen whales. *Annals of the New York Academy of Sciences* 188, 110-142 (1971).