Journal of Experimental Marine Biology and Ecology 455 (2014) 50–55

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Maintaining of low Doppler shifts in cetaceans as strategy to avoid predation

Daniel Patón *, Roberto Reinosa, Maria del Carmén Galán, Gloria Lozano, Margarita Manzano

Ecology Unit, Faculty of Sciences, Extremadura University, Avda. Elvas s/n, 06071 Badajoz, Spain

ARTICLE INFO

Article history:
Received 5 September 2013
Received in revised form 10 February 2014
Accepted 12 February 2014
Available online xxxx

Keywords:
Doppler shifts
Cetaceans
Depredation

ABSTRACT

Cetaceans are widely diversified in their sonometric characteristics but no comparative research has determined the general patterns that condition their bio-acoustic evolution across a large number of species. Echolocation calls of 69 cetaceans species has been obtained from different data sources. Through analysis by a Hierarchical Partitioning test, a non-parametric substitute of variance analysis, the absence of statistical differences between bioacoustic data sources has been demonstrated. Sounds were normalized and the fundamental frequency of each species was determined by autocorrelation. Also, the average swimming speed of each species was obtained from published papers. Finally, the intensity of the Doppler effect was calculated for each species using the mathematical equation of underwater sound physics. Doppler shifts lower than 160 Hz were found for the majority of species. This can be explained as a behavioral strategy to avoid depredation by Killer Whales. Only certain species of *Ziphidae* (genus *Mesoplodon*, *Indopacetus pacificus* and *Ziphius cavirostris*) and six species of *Delphinidae* (from *Lagenorhynchus* and *Cephalorhynchus* genus) present higher Doppler shifts. These species had found other strategies to avoid depredation such as the use of echolocation only in deep waters, very high average swimming speeds, large flocks or the use of very high frequencies. From these results it is possible to conclude that depredation conditions all the evolution of echolocation signals of cetaceans except in a reduced number of species that had developed different behavioral strategies to escape from Killer Whales.

1. Introduction

Many groups of animals such as birds, insects and amphibians emit their calls from a static position. However, cetaceans produce sound while swimming. Consequently, the Doppler effect could be relevant for explaining sound transmission in this group. The Doppler effect is the change in frequency of a sound wave when the emitting source is moving (Rosen and Gothard, 2009). This change is not the same in front of the sound source and behind this. In front of the sound source, the acoustic waves decrease by compression and this produces an increase in frequency. Behind the animal, the process is the opposite with an elongation of sound waves and a decrease in frequency. A conclusion that cetaceans must modify their relative swimming speed and sound frequency to minimize the Doppler effect can be hypothesized. This allows them to avoid predators except if another adaptation is possible. The Cetacean order is very complex and includes over 90 species of marine mammals, commonly known as whales, dolphins and porpoises (Wilson and Reeder, 2005). This group is formed by the mammals with the most diverse and evolved adaptations to aquatic environments such as freshwater and marine ecosystems, deep and shallow waters and tropical to polar. These animals are characterized by their high intelligence that is likely related to the generation of a high acoustic complexity for social communication (Marino et al., 2004; McGowen et al., 2011; Morisaka, 2012). This variability in sound repertory is firstly caused by the different anatomical structures of Toothed and Baleen Whales (Reidenberg and Laitman, 2007) and secondly by the different ecological, taxonomic and behavioral factors of each cetacean species. This complexity in acoustic communication produces the difficulty of separating the social aspects of acoustic behavior from other uses such as prey detection, echolocation, group and individual recognition, reproduction, prey–predator interactions and parental care. The majority of cetaceans live in oceans, where the sound is transmitted at 1524 ms^{-1}. In this media, the low-frequencies can travel very long distances whereas high-frequency calls are sent under 100 m. By this reason, it has been traditionally supposed that the high-frequencies are mainly used for echolocation over short distances and low-frequencies for social communication over long distances (Payne and McVay, 1971). Nevertheless, recent studies indicate that the general bioacoustical patterns are much more complex in cetaceans. In fact, the Blue Whale can transmit their low and narrow frequency calls to many kilometers in just a few minutes (Samaran et al., 2010). In this animal, the fundamental frequency is related to population densities and acoustic pollution caused by humans (McDonald et al., 2009). Contrarily, the Humpback Whale shows a very complex acoustic repertoire with higher and wider frequencies. It has been

* Corresponding author. Tel./fax: +34 924 289300x86930.
E-mail address: d.paton.d@gmail.com (D. Patón).

http://dx.doi.org/10.1016/j.jembe.2014.02.016
0022-0981/

proposed that this complexity is due to a mix of factors that act simultaneously such as its complex social structure, its necessity of individual recognition during breeding and the use of echolocation for detecting preys of different sizes (May-Collado, 2007). The Humpback Whales can even adapt their calls according to distances, depths and individual densities and transmit to long distances making the sea floor vibrate similarly to earthquakes (Tyack, 1997). In addition to this general complexity, in the cetacean calls it is possible to observe very different strategies in the use of ultrasound between the Bottlenose dolphin that can adapt its ultrasonic clicks to prey size and distance and some porpoises that can use rhythmic patterns of clicks, usually used for echolocation, with communicative purposes (Tyack, 1997). Thus many cetaceans that inhabit deep waters use sonar for prey detection such as the Beaked Whales that can transmit to 120 kHz immersing until 2000 m. However, many factors that could affect sound transmission, such as the swimming speed, have been traditionally overlooked and deserve to be studied with more detail. In the present paper, the influence of swimming speed and fundamental frequency in sound transmission and Doppler effect has been determined for more than 76% of cetacean species. A very reduced Doppler effect has been observed in the majority of these species. Consequently the existence of a strict functional requirement has been proposed. A priori, the most plausible explanation is that the majority of species reduce the Doppler effect to avoid detection by predators, specially Killer whales (*Orcinus orca*) and certain species of sharks. Consequently predation seems to be the main ecological factor that conditions the evolution of the majority of the cetacean group. To understand these general rules and the exceptions, a comparative analysis of Doppler shifts between 69 cetacean species using different statistical approaches has been developed.

2. Materials and methods

2.1. Sources of acoustic information

All the sound records on cetacean species were obtained in different web pages from research organisms except some files that were submitted by different specialists in bio-acoustics. Some uncommon species were included using sound-parameters previously published. In our data set, 69 species from 12 families (Table 1) that represent the 76% of about 90 species of Cetacean order were included. This data set covers the main biological characteristics of this group where only very rare species are absent. Almost 10 min of sound information including both social as echolocation calls when it was possible were selected. All the sound files were obtained in non-compressed formats, wav and quicktime. Both sound types conserve the full acoustic frequency information of animals, including both ultrasound and infrasound (Rumsey and McCormick, 2009). This is especially relevant in cetaceans whose calls are characterized by a wide range of frequencies (Rendell et al., 1999; Tyack, 1997). Although, the recording conditions can differ between species and sources of information, only sound records of a high quality and low levels of background noise produced by ships, water or other factors were selected. Moreover, the organisms and specialists that give records are recognized experts in bio-acoustics of cetaceans. Finally, all the sound recordings were normalized to permit accurate comparisons between species according to criteria of Mellinger et al. (2011). In the normalization process we use the software Audacity (Schroder, 2011).

2.2. Determination of Doppler shift

The fundamental frequency is defined as the lowest frequency of a periodic waveform. Therefore, the sound spectrum contains energy mostly at integer multiples of this fundamental frequency. Fundamental frequency is a characteristic attribute of animal sounds and diverse methods have been implemented for its determination (Boersma, 1993; Mathews et al., 1999). However, diverse studies indicate that fundamental frequency of sounds with certain time constancy in intensity and frequency, as produced by cetaceans, are best analyzed using the autocorrelation of the Fast Fourier Transformation (FFT) of the sound signal (Khanna et al., 1997; Rabiner, 1977). The fundamental frequency of each cetacean species was determined using the software Praat (Boersma and Weenink, 2013). Also, these fundamental frequencies were used to determine the intensity of the Doppler effect of each species, according to the equation of Rosen and Gothard (2009). Consequently, when the animal is moving and emitting sounds simultaneously, at its front the total frequency is the sum of the first harmonic and the intensity of Doppler effect. Contrarily, behind the animal, the total frequency is the transmitted frequency minus the Doppler shift. In short, in front of cetaceans the sound increases its frequency and behind decreases. The intensity of this joined effect in absolute value is called Doppler shift (Nicholas, 2013). Using this approach, the Doppler shift was determined for all the species of Table 1. Finally, the degree to which the Doppler effect is affected by taxonomy (families) and data sources was calculated by Hierarchical Partitioning test (Patón et al., 2012). This test uses different regression models and detects the most appropriate equation by its total explained percentage of variance between species (Chevan and Sutherland, 1991). In the selected model, the test compares the whole explained variance against the variance associated with each individual factor. This method is a substitute of parametric variance analysis and it is recommended when data is not normally distributed or inter-group variances are not homogeneous as in this study (Mac Nally, 2000). A randomization test was employed to measure the significance of each factor (families and data source) in the analysis. If any factor has influence on the Doppler effect, there can be considered to be a general rule that explains the functional acoustic behavior in cetaceans.

3. Results

The data set covered 69 cetaceans representing 76% of the total number of species. This sample is a good representation of the main taxonomic groups and biological characteristics of cetaceans. Although not all the species were analyzed, this study allows for the extraction of the general rules that explain the sound transmission of this animal order. Inside, the suborder Mysticeti (Baleen whales) the families *Balaenidae* (four species), *Balaenopteridae* ($n = 6$), *Eschrichtiidae* ($n = 1$) and *Cetotheriidae* ($n = 1$) were studied. The Baleen whales that are not present in this study belong to *Balaenopteridae* family and were the Antarctic minke whale (*Balaenoptera bonaerensis*) and the Omura's whale (*Balaenoptera omurai*). In Odontocetii (Toothed whales) sound information of *Delphinidae* ($n = 31$), *Kogiidae* ($n = 2$), *Lipotidae* ($n = 1$), *Monodontidae* ($n = 2$), *Phocoenidae* ($n = 4$), *Physeteridae* ($n = 1$), *Platanistoidae* ($n = 3$) and *Ziphiidae* ($n = 12$) was obtained. Inside this group, some rare species of *Delphinidae*, are absent such as *Delphinus tropicalis*, *Lagenorhynchus australis*, *Lagenorhynchus crucifer*, *Lissodelphis peronii*, *Sotalia guianensis* and *Sousa teuszii*. *Phocoena dioptrica* and *Phocoena spinipinnis* are absent in *Phocoenidae*. In *Platanistoidea* acoustic information on *Inia boliviensis* was not available. In the extensive group of *Ziphiidae*, it was impossible to find appropriate sound information of *Mesoplodon bowdoini*, *Mesoplodon grayi*, *Mesoplodon layardii*, *Mesoplodon mirus*, *Mesoplodon perrini*, *Mesoplodon peruvianus*, *Mesoplodon traversii* and *Tasmacetus shepherdi*. However, the studied beaked whales represent the major taxonomic variations, including all the families of this cetacean group. Only a genus, *Tasmacetus* with a single species, *T. shepherdi*, is absent in this study but this species is considered to be one of the least known cetaceans (Pitman et al., 2006).

In the comparative study done in this work, the possible influence of other sources of variation different to those related to species has been controlled. The sound quality between the different data sources: DOSITS (http://www.dosits.org/audio/marinemammals), Macauly Library (http://macaulaylibrary.org/), Mobysound (http://www.mobysound.