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

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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

A R T I C L E   I N F O

A B S T R A C T

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).

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), *Platanistoidea* (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.

Table 1
List of cetacean species used in this article and sources of information of sound records.

Family	Scientific name	Source of information
Balaenidae	*Balaena mysticetus*	Voices in the Sea
	Eubalaena australis	Voices in the Sea
	Eubalaena glacialis	Voices in the Sea
	Eubalaena japonica	Voices in the Sea
Balaenopteridae	*Balaenoptera acutorostrata*	Voices in the Sea
	Balaenoptera borealis	Voices in the Sea
	Balaenoptera edeni	Voices in the Sea
	Balaenoptera musculus	Voices in the Sea
	Balaenoptera physalus	Voices in the Sea
	Megaptera novaeangliae	Voices in the Sea
Delphinidae	*Cephalorhynchus commersonii*	Dawson (1988)
	Cephalorhynchus eutropia	Götz et al. (2010)
	Cephalorhynchus heavisidii	Morisaka et al. (2011)
	Cephalorhynchus hectori	Dawson (1988)
	Delphinus capensis	Private donation
	Delphinus delphis	Voices in the Sea
	Feresa attenuata	Macauly Library
	Globicephala macrorhynchus	Voices in the Sea
	Globicephala melas	Macauly Library
	Grampus griseus	Voices in the Sea
	Lagenodelphis hosei	Voices in the Sea
	Lagenorhynchus acutus	Macauly Library
	Lagenorhynchus albirostris	Macauly Library
	Lagenorhynchus obliquidens	Voices in the Sea
	Lagenorhynchus obscurus	Au and Würsig (2004)
	Lissodelphis borealis	Voices in the Sea
	Orcaella brevirostris	Macauly Library
	Orcaella heinsohni	Macauly Library
	Orcinus orca	Voices in the Sea
	Pepenocephala electra	Mobysound
	Pseudorca crassidens	Voices in the Sea
	Sotalia fluviatilis	Macauly Library
	Sousa chinensis	Macauly Library
	Stenella attenuata	Mobysound
	Stenella clymene	Private donation
	Stenella coeruleoalba	Mobysound
	Stenella frontalis	Voices in the Sea
	Stenella longirostris	Voices in the Sea
	Steno bredanensis	Mobysound
	Tursiops aduncus	Private donation
	Tursiops australis	Private donation
	Tursiops truncatus	Voices in the Sea
Eschrichtiidae	*Eschrichtius robustus*	Voices in the Sea
Kogiidae	*Kogia breviceps*	Voices in the Sea
	Kogia sima	Voices in the Sea
Lipotidae	*Lipotes vexillifer*	DOSITS
Monodontidae	*Delphinapterus leucas*	Voices in the Sea
	Monodon monoceros	Voices in the Sea
Neobalaenidae	*Caperea marginata*	NAVY USA (2007)
Phocoenidae	*Neophocaena phocaenoides*	DOSITS
Phocoenidae	*Phocoena phocoena*	Voices in the Sea
	Phocoena sinus	Voices in the Sea
	Phocoenoides dalli	Voices in the Sea
Physeteridae	*Physeter macrocephalus*	Voices in the Sea
Platanistidae	*Inia geoffrensis*	Voices in the Sea
	Platanista gangetica	Macauly Library
	Pontoporia blainvillei	Mariana Melcon (Scripps Whale Acoustic Lab)
Ziphiidae	*Berardius bairdii*	Voices in the Sea
	Berardius arnuxii	Mobysound
	Hyperoodon ampulatus	Voices in the Sea
	Indopacetus pacificus	Rankin et al. (2011)
	Mesoplodon bidens	Baumann-Pickering et al. (2013)
	Mesoplodon carlhubbsi	Baumann-Pickering et al. (2013)
	Mesoplodon densirostris	Mobysound
	Mesoplodon europaeus	Gillespie et al. (2009)
	Mesoplodon ginkgodens	Baumann-Pickering et al. (2013)
	Mesoplodon hectori	Baumann-Pickering et al. (2013)
	Mesoplodon stejnegeri	Baumann-Pickering et al. (2013)
	Ziphius cavirostris	Mobysound

org), Voices in the Sea (http://cetus.ucsd.edu/voicesinthesea.org) and private donations (Table 1) do not show statistical differences according to Hierarchical Partitioning test ($Z = -0.42$, p-value > 0.05). Thereafter, it is possible to find general patterns in the whole set of analyzed species without statistical noise related to conditions of recordings. As we have a single observation of each species, the taxonomic variation was better represented by the family. In that way, the possible influence of taxonomy (families) on the intensity of the Doppler effect, was not significant ($Z =$

1.55, p-value > 0.05). This result indicates that the functional characteristics that produce a very constant Doppler shift in cetaceans, under 160 Hz (Fig. 1), are basically the same. The only exceptions to this general pattern are present in three groups (Fig. 1). The first group is formed of two species of *Lagenorhynchus*, *Lagenorhynchus obliquidens* and *Lagenorhynchus obscurus* with characteristic bimodal ultrasound spectra (Au and Würsig, 2004). Mitochondrial DNA analyses suggest that these species together *L. australis* (not included in this study) form the *Lissodelphinae* clade. According to LeDuc et al. (1999) these species must be included in a new genus, *Leucoplurus*, that would be closely related to the *Cephalorhynchus* genus. Consequently, this second group with the high Doppler shift is very related taxonomically to the first because it is formed by the species of genus *Cephalorhynchus* that are considered the most evolved dolphins (Morisaka, 2012). *Cephalorhynchus heavisidii* show the highest average swimming speed with 44.24 km h^{-1} and a very high fundamental frequency of 125 kHz (Leeney et al., 2011). This produces the highest Doppler shift observed in the 69 studied cetaceans with 7.6 kHz (Fig. 1). Other species of *Cephalorhynchus* present very similar high frequency signals but their swimming speeds are lower producing less intense Doppler shifts (Götz et al., 2010; Leeney et al., 2011). Certain studies show that the high frequency calls of *Cephalorhynchus* genus are also very narrow, producing high fundamental frequencies (Dawson, 1988). On the contrary, the calls of many species of porpoises are bimodal due to social communication being produced at lower frequencies than echolocation (DeRuiter et al., 2009). This creates lower fundamental frequencies when sound is analyzed. Consequently, the porpoises are attacked by Killer Whales during their social communications (Szymanski et al., 1999). However, if the depredator uses low frequency echolocation for detecting fishes, the porpoises can detect Killer Whales (Au et al., 2004). Finally, the third group with the high Doppler effect is formed by certain species of the *Ziphidae* family, particularly the genus *Mesoplodon*, *Indopacetus pacificus* and *Ziphius cavirostris*. Our results for *Mesoplodon* genus are characteristics of deepest immersions when these animals increase the frequencies for more precise echolocation (Johnson et al., 2006; Tyack et al., 2006). Other Beaked whales such as *Berardius* genus show low levels of Doppler effect due to both their low fundamental frequencies and swimming speeds. Inside the *Mesoplodon* genus, the highest Doppler effects are present in *Mesoplodon europaeus*, *Mesoplodon hectori* and *Mesoplodon ginkgodens*. Therefore, only 15 species of cetaceans generate Doppler shifts over 160 Hz representing 16.7% of the species studied herein.

4. Discussion

This study shows the results of a comparative analysis of Doppler shift in sound transmission of a wide representation of cetacean species. Acquisition of sounds of these animals was very time consuming due to the high dispersion of this information in web resources, such as data bases, web pages of institutions, scientific publications, web pages of specialists in bio-acoustic and private donations. The Hierarchical Partitioning test did not show statistical differences in Doppler effects associated to the use of data obtained from different sources. A possible explanation is that the bioacoustic analysis of cetacean sounds requires very expensive resources (hydrophones, ships, diving equipment among others) and highly qualified personnel, and this produces a high quality of records. The high quality sound records of oceanographic institutions normally contain the reduced number of species that are frequent in each area. Therefore, combining the data sources summarized in Table 1, acoustic information has been obtained for a high number of species that are a representative sample of the whole cetacean
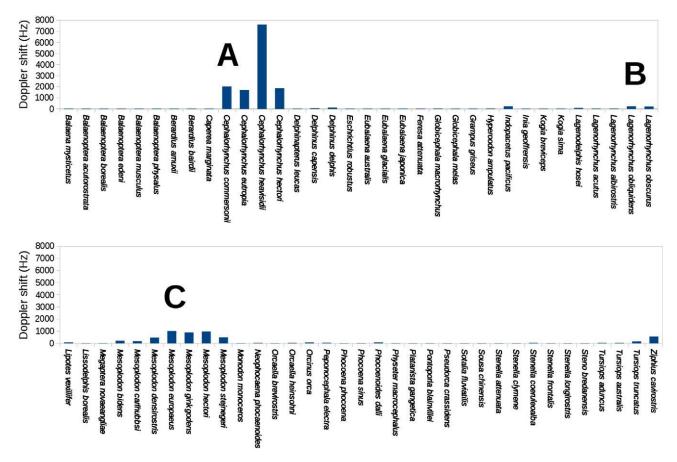

Fig. 1. Intensity of Doppler effect in the 69 cetacean species alphabetically ordered. Three groups of high Doppler shifts (over 160 Hz) are observed. A: *Cephalorhynchus* genus, B: *Lagenorhynchus obliquidens* and *Lagenorhynchus obscurus*. C: Some species of Beaked Whales (*Indopacetus pacificus*, *Mesoplodon* spp. and *Ziphius cavirostris*).

order. Only 21 species were not included and these are very uncommon and of very reduced geographic distribution. Despite this wide representation of species, the theoretical possibility that some of the cetaceans not included here can show very different bio-acoustic characteristics cannot be excluded. However, of the 69 species analyzed, only 15 showed high Doppler shifts (over 160 Hz) and this does not invalidate the observed general pattern characterized by low intensities of the Doppler effects. The absence of high Doppler effects, observed in the majority of species, can be due to three different factors: a low average swimming speed, a low frequency in the calls or the use of bimodal calls that decrease the fundamental frequency. The low average speed is a characteristic of species that show high frequency calls such as *Berardius* genus. Low frequencies are observed in many Baleen Whales. The bimodality in frequencies, observed in many beaked whales (Madsen et al., 2005), porpoises (Hansen et al., 2008) and dolphins (Madsen et al., 2004; Vaughn-Hirshorn et al., 2012), causes a compromise between detectability by predators and social communication and the animal can adapt its behavior according circumstances.

The main hypothesis of this paper is that the tendency of maintaining a low Doppler shift, is a general adaptation of the Cetacean order to avoid depredation, specially by Killer Whales. The change in frequency during movement, that is produced by the Doppler effect, can permit an easy detection of trajectory and distance by Killer Whales, specially when the vision is restricted or the prey abundance is low. In this sense, the study of Szymanski et al. (1999), shows that Killer Whales use echolocation clicks between 18 and 42 kHz while their best hearing area is between 20 Hz and 100 kHz (Szymanski et al., 1999). Consequently, the Killer Whales can detect sound emissions of the majority of species except if these are out of hearing range of this marine predator (Hemila et al., 2001). In this sense, sound calls under 20 Hz do not exist (Mathews et al., 1999). This is due to the fact that *Balaenoptera edeni*, the species with the lowest fundamental frequency, emits at 31 Hz and is perfectly audible by Killer Whales. However in the ultrasound frequency range, certain species can emit echolocation clicks over 100 kHz, particularly the *Cephalorhynchus* genus with an average of 123 kHz and *M. hectori* with 120 kHz. These species show also very high Doppler shifts and this is consistent with sound evolution in the cetaceans as a strategy to avoid depredation. These species do not need to adapt their frequencies because they emit outside of the Killer Whales hearing band. *Cephalorhynchus* genus is considered as one of the most evolved species of dolphins (Morisaka et al., 2011). Moreover, the use of very high frequencies by these dolphins could mark a new adaptation, not observed in other species of cetaceans. This is unlikely to result in a change in the auditive range of Killer Whales because *Cephalorhynchus* are not the most abundant prey (Jefferson et al., 1991). However, the Killer Whales can show a high capacity to adapt their audition area when the resources are abundant (Deecke et al., 2005). The species with the highest Doppler shift, *Cephalorhynchus heavisidii*, show two new adaptations; a very high average swimming speed and large flocks in battery during echolocation (Morisaka et al., 2011). Both strategies can be successful to avoid depredation by Killer Whales as is observed in other cetaceans (Ford and Reeves, 2008). Finally, certain species of *Ziphidae* family show high Doppler effects but with fundamental frequencies in the hearing range of Killer Whales. Therefore, how do these species avoid depredation? A single explanation is provided by the fact that Beaked whales only use echolocation during their deep immersions and are silent from zero to 200 m from the sea surface, that is the maximum depth that Killer Whales use (Baumann-Pickering et al., 2013; O'Malley et al., 2010). Notably, the two species of *Berardius* genus studied herein and *Z. cavirostris* present low Doppler shifts because they are very slow swimmers and their fundamental frequencies are lower than in *Mesoplodon* (Baumann-Pickering et al., 2013; Frantzis et al., 2002). Another fact that confirms our hypothesis is that Beaked Whales are archaic cetaceans that adopted whistles as an echolocation system previously to the evolutive origin of Killer Whales (Morisaka, 2012). These results allow the assumption that the maintaining of low Doppler shifts is so constant in cetaceans that it could be considered the main evolutive strength to avoid depredation above other possible ethological or biological strategies (Ford and Reeves, 2008).

Acknowledgments

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