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**Vocal communication of cetaceans (Cetacea) with
emphasis on development and learning**

**Vokální komunikace kytovců (Cetacea) se zaměřením na ontogenezi a
učení**

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Statement of authorship

I hereby declare that I am the sole author of this bachelor thesis and that all sources used are listed in the bibliography and identified as references. I further declare that I have not submitted this thesis, or its significant part, to obtain another academic degree.

In Prague, 6. 5. 2021

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Abstract

Vocal communication is the main mean of communication for cetaceans. Just like the species themselves, their repertoires are diverse, consisting of tonal, pulsed, and combined calls, with frequency and amplitude modulation. The two groups of cetaceans, Mysticeti (baleen whales) and Odontoceti (toothed whales), produce sounds of different parameters, mainly frequency, bandwidth, and duration.

Both production and contextual learning can be found in cetaceans. It is used to acquire two types of sounds: signature calls and songs. Signature calls are present only in species living in stable groups or fission-fusion society. They are used as an identification tool to maintain cohesion and contact with conspecifics. Songs are present in most baleen whales, but only humpback and bowhead whales' change within and between seasons. They use vocal learning to conform to one type used by all individuals.

It is also employed during vocal development in ontogenesis, together with maturation. Calves and juveniles' calls are chaotic, lacking in structure. With age, they gain stereotypy and resemble adults' repertoire.

Key words: cetaceans, vocal communication, signature calls, vocal learning, cultural transmission

Abstrakt

Vokalizace je hlavním komunikačním prostředkem kytovců. Paleta zvuků, které kytovci vydávají je stejně rozmanitá jako jednotlivé druhy. Zahrnuje tonální i pulzní zvuky, a také jejich kombinace, často s různě modulovanou frekvencí a amplitudou. Zvuky vydávané kosticovci (Mysticeti) a ozubenými (Odontoceti) se liší v mnoha parametrech, především ve frekvenci, šířce frekvenčního spektra a doby trvání.

U kytovců jsou známy dvě formy učení zvuků, a to jak učení vydávání zvuků, tak i kontextu. Slouží k osvojení dvou typů zvuků: tzv. signature calls a písni. Signature calls najdeme pouze u druhů žijících v stálých skupinách nebo societách typu fission-fusion. Jsou používány jako identifikační nástroj k udržení soudržnosti a kontaktu s ostatními jedinci. Písni se nachází v repertoáru většiny kosticovců, ale pouze u velryby grónské a keporkaka se mění, a to jak v rámci sezóny, tak i mezi nimi. Díky učení zpívají jeden typ písni, která je v daném okamžiku stejná pro všechny jedince.

Vokální učení se uplatňuje také v ontogenezi, společně s tělesným vývojem. Zvuky vydávané nedospělými jedinci jsou chaotické a postrádají strukturu. Během dospívání se stávají více stereotypními a postupně více připomínají zvuky dospělců.

Klíčová slova: kytovci, vokální komunikace, signature calls, vokální učení, kulturní přenos

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1 Introduction

Communication can be found all throughout the animal kingdom. It is defined as a transfer of information from a sender to a receiver, whose decision-making is influenced by the transferred information (see Ruxton & Schaefer (2011) for discussion). Both sender and receiver can be one individual or a group (Seyfarth & Cheney 2003). The main mean of transmission is a signal, of many forms: visual, acoustic, chemical, electric, motion, postural (Krebs & Dawkins 1984). Each species uses these forms and their combinations in distinct proportions (Wilson 1972). The signals convey a variety of information, from displaying aggressive, territorial, breeding, or parental intentions, to maintaining cohesion and contact, social relationship, or coordinating movements. Mammals and birds are also able to distinguish relatives and offspring, and in some cases the dominance rank, through signals (Wilson 1972).

Learning and memory play a big part in communication: animals need to learn and memorise the meaning behind each signal, and in some cases the individual behind the signal (Guilford & Dawkins 1991).

In vocal communication, apart from learning when to produce a signal, some species also learn how to produce it. These two main types of vocal learning are labelled contextual and production, consecutively. Production learning is the modification of sounds based on experience with conspecifics, resulting in (dis)similar sounds to the model. Contextual learning means using sounds in new contexts based on experience (Janik & Slater 1997). In short, during production learning, the sound itself is modified, whereas in contextual it is not.

Cetaceans are an aquatic group occupying the world's oceans, except for few species found in big rivers and estuaries. For long, it was considered its own order, however, modern molecular studies discovered it is an inner group of Artiodactyla, even toed ungulates, together forming the order Cetartiodactyla (Price et al. 2005). Since this discovery is relatively recent, and the traditional systematic names are ingrained, they will be used in this thesis to maintain clarity and intelligibility.

Cetaceans are divided into two groups, baleen whales (Mysticeti) and toothed whales (Odontoceti), together consisting of over 80 species (McGowen et al. 2009).

Acoustic communication is the most important for cetaceans, as sounds, out of all the signal forms, propagate the best in the water environment.

It is important to note that research focusing on vocal signals of cetaceans is usually not methodologically easy, depending on the species characteristics. Therefore, there is a serious disparity in the number of studies on each of them. The most studied is the bottlenose dolphin (*Tursiops truncatus*), often kept in captivity, offering a great opportunity for research. On the other hand, the least studied are species rarely spotted and difficult to localise, for example, beaked whales (*Ziphiidae*). The knowledge about vocal repertoires and the associated behaviour is important, as it can provide information about population structure and migration routes, which can be applied in conservation efforts.

The goals of this thesis are: review cetacean vocal repertoires in terms of communication, compare them and pinpoint the species that are known to be capable of vocal learning; determine if vocal repertoires and vocal learning are related to phylogeny and if phylogenetic branches differ in the produced sounds; delineate species with vocal traditions and culture; describe the distinct characteristics of species using vocal learning, and conclude the role of

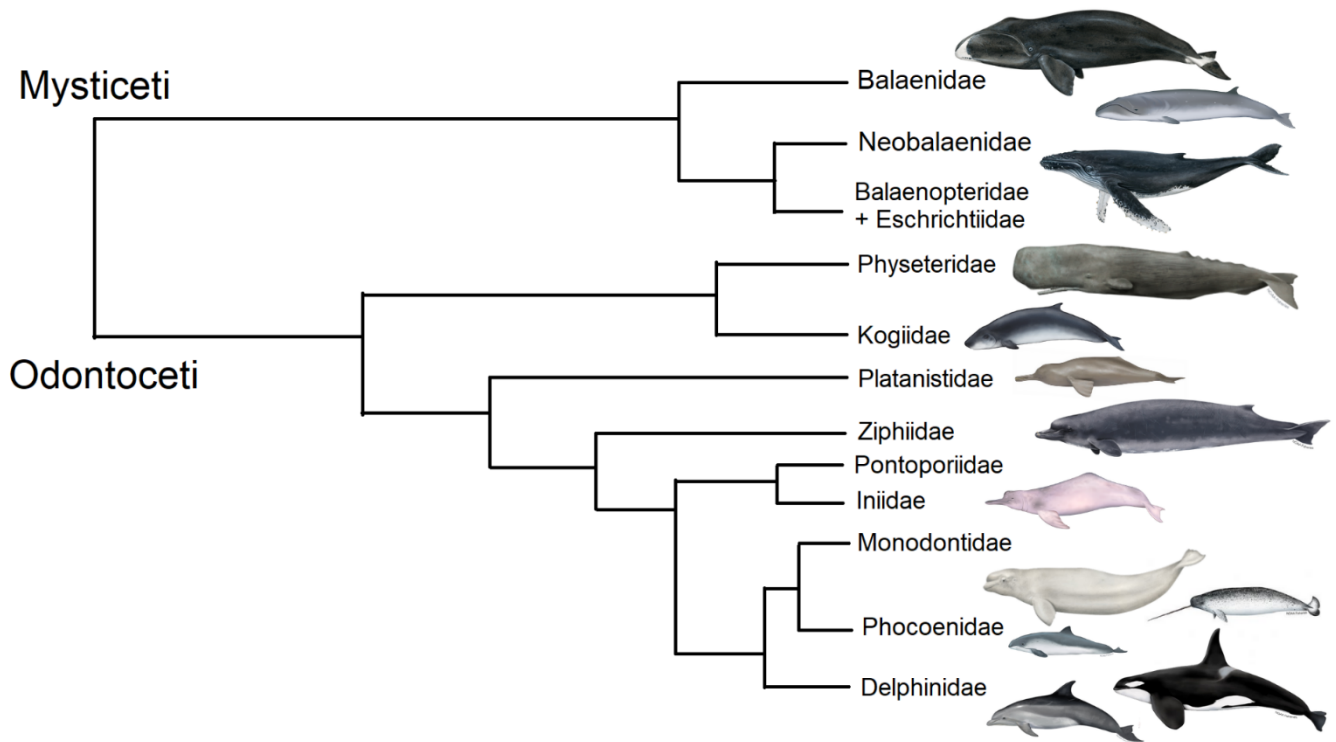


Fig.1: Cladogram based on McGowen et al. (2009) showing main families of Cetaceans. Pictures are illustrative only, not showing real-life size scale

vocal learning during ontogenesis, that is to what extent the repertoires are learned or inherited.

This thesis is divided into three chapters. The first one briefly describes the vocal repertoire of the two cetacean groups, with more detailed review of best-studied species. Chapter two focuses on vocal learning and cultural transmission and chapter three reports on the vocal development during ontogenesis.

2 Vocal repertoires of cetacean groups and species

As the cetacean order includes great diversity of species in all spectra i.e., morphology, life histories, social structures, behaviour; so do its acoustic signals. There are a few basic characteristics used to describe them: **1) Frequency:** either low (LF) or high (HF)¹, describing the length of the soundwave and energy, pitch **2) Duration** **3) Frequency modulation (FM):** the change of frequency over time. **4) Amplitude modulation (AM):** the change of amplitude² over time. **5) Bandwidth:** range of the frequency spectrum, narrowband or broadband.

Tonal sounds are narrowband, concentrated around a certain frequency. Pulses are brief, broadband vocalisations, usually forming clicks or pulsed calls, which can also be characterised by the inter-click (ICIs) and inter-pulse intervals (IPIs).

The sounds of cetaceans range from 20 Hz to over 100 kHz and differ in duration and modulation, as well as structure (Herman & Tavolga 1980; Richardson et al. 1995). In other words, cetaceans produce both LF and HF sounds, distinct in complexity and duration. While some sounds are only a split of a second long, long series can last for hours (Sayigh 2014).

There is a great disparity in the number of studies throughout this order. While some species are being researched for decades (humpback whale (*Megaptera novaeangliae*), orca (*Orcinus orca*), some have barely been recorded and there is virtually no information about their acoustic presence (pygmy and dwarf sperm whales: Kogiidae, pygmy right whale: *Caperea marginata*).

2.1 Baleen whales (*Mysticeti*)

Though most baleen whales' repertoires have been described, only a few are sufficiently documented, and the functions are mostly unknown (Richardson et al. 1995). They produce both simple and complex sounds with differences in the types and amount of vocalisations, including pulses, tones, FM, AM and click sounds (Herman & Tavolga 1980). A lot of these sounds are named onomatopoeically by the authors, therefore the same name could depict two different sounds and vice versa. One common feature is LF, as the fundamental energy rarely exceeds 1 kHz (Herman & Tavolga 1980; Richardson et al. 1995), although HF sounds can also occur (Au et al. 2006).

2.1.1 Right whales (*Balaenidae*)

2.1.1.1 Bowhead whale (*Balaena mysticetus*)

Bowhead whale's vocalisations include both patterned sequences (= songs) and single calls, labelled moans. Ljungbald et al. (1982) differentiated simple and complex moans, a categorisation that has been used by most authors since. They defined simple moans as tonal FM sounds, often with harmonics. They are more narrowband and of LF than complex moans, which are AM with complicated structure. All are around 1 s long (up to 7), with a frequency range < 100 Hz to 1kHz, harmonic components reaching over 2 kHz (Clark & Johnson 1984; Cummings & Holliday 1987; Blackwell et al. 2007; Tervo et al. 2009). Complex moans are produced by socialising whales, while simple ones by distant conspecifics (Richardson et al. 1995a).

¹ Low frequency is any sound below 2kHz, above which it is classified as high frequency.

² Amplitude is the height of the soundwave, determining the loudness of a sound.

Songs are complex patterned sequences combined of different phrases, that span from 20 Hz to 5 kHz (Cummings & Holliday 1987; Tervo et al. 2009) and between 1 to 3,5 s (Tervo et al. 2009). The whole song is only seconds or minutes long (Stafford et al. 2008; Delarue et al. 2009) but forms long bouts that can last hours (Tervo et al. 2009). As was first suggested by Cummings & Holliday (1987) and later confirmed (Delarue et al. 2009; Tervo et al. 2011), the structure (i.e., the number of phrases and their structure, length of the song) changes every year. It might serve as a breeding advertisement display of females or males (Tervo et al. 2011), as it was recorded during the breeding season (Stafford et al. 2008; Delarue et al. 2009).

2.1.1.2 Right whales (*Eubalaena japonica*, *E. australis*, *E. glacialis*)

There are three forms (species or subspecies) of right whales: Southern, North Pacific and North Atlantic. Each of them has been studied in a different amount, therefore information of some is lacking. All have similar vocalisation repertoire including simple tonal, FM or pulsive sound and their various combinations (Payne & Payne 1971; Cummings et al. 1972; Clark 1982; Webster et al. 2016).

Two sounds that have been recorded from all three right whales are upcalls and gunshots. Gunshots are short (ms), loud, intense broadband sounds (Clark 1982; Crance et al. 2017; Matthews et al. 2001; Parks et al. 2005) ranging up to 24 kHz and possibly more (Webster et al. 2016). They are frequently produced by lone males (Parks et al. 2005; Parks et al. 2011) and in surface-active groups (Matthews et al. 2001; Parks & Tyack 2005), either singly or in a bout (Parks et al. 2005). Their function is speculated, but since the vocalising rate increases with the size of the group (Matthews et al. 2001) and no females approach this sound (Parks 2003; Parks et al. 2005), the role of male agonistic display used for competing for females and determining dominance has been suggested (Parks et al. 2005).

Upcalls are the most common sounds produced by right whales (McDonald & Moore 2002; Parks et al. 2011; Dombroski et al. 2016). They are tonal FM narrowband sweeps below 200 Hz about one second long (Clark 1982; Melling et al. 2004).

Upcalls are contact calls among whales (Parks & Tyack 2005; Dombroski et al. 2016; Root-Gutteridge et al. 2018) and even contain information about individual identity (McCordic et al. 2016).

Right whale vocalisation is typical for its episodic and clustering character: calls are often produced in bouts with long periods of silence in between (McDonald & Moore 2002; Parks et al. 2011; Webster et al. 2016) during few active days followed by days of silence (Mellinger et al. 2007; Munger et al. 2008).

2.1.2 Rorquals (*Balaenopteridae*)

The family Balaenopteridae includes two genera: *Balaenoptera* and *Megaptera*. *Megaptera* includes only one species, the humpback whale, distinct with its vocalisations from the other species, that all belong to the *Balaenoptera* genus.

2.1.2.1 *Balaenoptera* whales

Blue and finback whales (*Balaenoptera musculus*, *B. physalus*) have quite similar repertoires. Both produce short, down sweeping sounds, labelled D-calls and 40 Hz calls, consecutively.

D-calls sweep from 60 to 40 Hz (Mellinger & Clark 2003), 40 Hz calls from 70 to 40 Hz (Schevill & Watkins. 1962; Thompson et al. 1992; Širović et al. 2013), and both are used as counter-calls between whales, having been recorded in groups (Watkins 1981; McDonald et

al. 2001), usually during shallow diving of the whales (Oleson et al. 2007), most frequently during feeding in summer (Watkins 1981; Širović et al. 2013).

The other common vocalisation for these two species is a song. A song is a sequence of vocalisations, which have a form of pulses in fin whales, and M, constant or pulsed units in blue whales (Northrop et al. 1971; Rivers 1997; Mellinger & Clark 2003). Both are around 20 Hz (Edds 1982; Watkins et al. 1987; Thompson et al. 1992; Rivers 1997; Stafford et al. 2001; Berchok et al. 2006), last several hours (Watkins et al. 1987; McDonald et al. 2001) and are geographically varied (Northrop et al. 1968; Watkins et al. 1987; Thompson et al. 1992; Stafford et al. 2001; Clark et al. 2002; Mellinger & Clark 2003; McDonald et al. 2006). In fin whales, the song is an acoustic breeding display, as it is only produced by males in the breeding season (Croll et al. 2002). This has not been confirmed for the blue whale yet, though it is likely (McDonald et al. 2001; Oleson et al. 2007).

Song, though in different forms, has also been hinted at in minke (*B. acutorostrata*), Omura's (*B. omurai*), and sei whales (*B. borealis*). Minke whales from the southern hemisphere were recorded producing "Star Wars" song, a complex stereotyped patterned sequence. The components are pulsed, FM and AM sounds, ranging up to 9,4kHz (Gedamke et al. 2001). Omura's whales typical phrases (< 50 Hz, broadband AM and narrowband part) are formed into stereotyped rhythmic sequences with a regular repetition interval of 2 to 3 minutes, which can last up to 13 hours (Cerchio et al. 2018). Sei whales produce a patterned sequence of down sweep calls, including two phrases of 3 rapidly produced down sweeps (Tremblay et al. 2019). However, if they also function as a breeding display is not known.

Typical sounds of sei whales are short FM calls, found singly, in pairs or triplets, below 150 Hz (Rankin & Barlow 2007b; Baumgartner et al. 2008; Romagosa et al. 2015; Español-Jiménez et al. 2019). Most of them are down sweeping, though Calderan et al. (2014) recorded a call with both up and down sweeping parts.

Similarly, minke whales produce short down-sweeps below 250 Hz (Schevill & Watkins 1972; Edds-Walton 2000; Gedamke et al. 2001; Risch et al. 2014). In both species, these calls function as a counter-call to maintain contact (Edds-Walton 2000; McDonald et al. 2005; Baumgartner et al. 2008).

Another common thing for these two species is that other vocalisations depend on the area of research. For instance, minke whales produce pulse trains in the North Atlantic (Edds-Walton 2000; Mellinger et al. 2000; Risch et al. 2013), boing sound in the North Pacific (Rankin & Barlow 2005; Oswald et al. 2011), and Antarctic minke whales (*B. bonearensis*) produce bio-duck sounds (Matthews et al. 2004; Risch et al. 2014). Sei whales produce short HF pulsed calls in Nova Scotia (Thompson et al. 1979; Knowlton et al. 1991) and around 500 Hz FM and constant calls in Antarctica (McDonald et al. 2005; Gedamke & Robinson 2010).

Bryde's whales make a variety of sounds, which include constant and FM tones, pulsed moans and multi-component calls. All are generally LF with a fundamental frequency below 100 Hz and harmonies under 1 kHz (Edds et al. 1993; Oleson et al. 2003; Heimlich et al. 2005; Figueiredo & Simão 2014).

2.1.2.2 Humpback whale (*Megaptera novaeangliae*)

Probably the best-known sound of any cetacean, and the best-studied too, is the humpback whale's song. It is a highly rhythmic, complex, fixed sequence of various sounds of both LF and HF (Winn & Winn 1978). It is hierarchically structured; from subunits to units that make

up phrases that are part of themes. The length is up to 30 mins depending on the number of repetitions of phrases and units in a theme, which is not set; and varies even among songs produced by one individual (Payne & McVay 1971; Winn & Winn 1978). Songs are performed in sessions that last for hours with less than 1min pauses between them (Payne & McVay 1971; Payne & Payne 1985). The frequency spans from 30 Hz to 4 kHz (Payne & Payne 1985), fundamental energy lies below 1 kHz (Mercado et al. 2005) but harmonics can reach 24 kHz (Au et al. 2006).

The song is produced only by males (Winn & Winn 1978; Medrano et al. 1994), most often lone individuals (Tyack 1981; Darling et al. 2006) or escorts, that is a male accompanying a female, sometimes with a calf (Darling & Bérubé 2001; Darling et al. 2006). It is abundant in the tropics during the breeding season (Payne & McVay 1971; Winn & Winn 1978; Payne & Payne 1985) but also heard during migration and feeding season (Mattila et al. 1987; Clark & Clapham 2004; Stimpert et al. 2012; Garland et al. 2013; Owen et al. 2019). Song serves a role in reproduction, but how exactly is not known. Presented hypothesis include attracting females (Winn & Winn 1978), spacing among males (Tyack 1981) and male-male communication display (Darling & Bérubé 2001) used for reciprocal altruism (Darling et al. 2006). Since females (apart from few exceptions: Medrano et al. 1994) do not join singers, on the contrary, males do (Darling & Bérubé 2001; Darling et al. 2006; Smith et al. 2008), resulting mostly in non-agonistic interactions (Darling et al. 2006); it seems explaining the function is not simple and is yet to be specified.

Humpback whales also produce a variety of non-song or social sounds: LF and HF, pulsed, AM and FM (Thompson et al. 1986; Dunlop et al. 2007; Zoidis et al. 2008; Fournet et al. 2015; Recalde-Salas et al. 2020). They are mostly produced by whales in groups with high activity (Silber 1986) with long periods of silence between clusters (Silber 1986; Thompson et al. 1986; Rekdahl et al. 2015). The production rate increases with the size of the group, especially during the joining of new whales (Silber 1986; Rekdahl et al. 2015).

Some of these sounds can be categorised into types or resemble song units (Dunlop et al. 2007; Fournet et al. 2015; Rekdahl et al. 2015; Dunlop 2017; Recalde-Salas et al. 2020), others are variable. They range from 50 Hz to 3,5 kHz (Silber 1986; Fournet et al. 2015) and are usually up to 5s long (Silber 1986; Fournet et al. 2015; Recalde-Salas et al. 2020).

Silber (1986) labelled them as vocal threats, as he found them to be correlated to aggressive behaviour. However, playback experiments (Tyack 1983; Mobley et al. 1988) showed they are an attractant for males. Dunlop (2017) noted they are found on both ends of motivational clusters (fear and aggression), depending on their composition.

2.1.3 Gray whale (*Eschrichtius robustus*)

The most recorded and the best-described sounds of gray whales are moans and knocks. Moans are most abundant during migration (Crane & Lashkari 1996; Guazzo et al. 2017; Burnham et al. 2018), on breeding grounds they make up only 7% (Dahlheim 1987). They are LF calls, often AM or FM with harmonics (Crane & Lashkari 1996). The central frequency is below 200Hz, while harmonics can reach up to 1,5kHz. Moans last about 1 s, ranging up to 4 (Cummings et al. 1968; Fish et al. 1974; Dahlheim 1987). They are most likely used for long-distance communication (Crane & Lashkari 1996), as a cohesion call during migration (Burnham et al. 2018). This is supported by the fact moans show less variety than other calls, and the vocalisation rate is higher at night, during lower visibility and bigger pressure to remain cohesion (Guazzo et al. 2017; Burnham et al. 2018).

Knocks are intense, short, metallic-sounding pulsed sounds. The number of pulses, each only a few ms long, varies, as well as the frequency among them (Cummings et al. 1968; Fish et al. 1974; Dahlheim 1987; Crane & Lashkari 1996). This call is the most variable: frequency recorded ranged from < 100 Hz up to 10 kHz (Fish et al. 1974; Stafford et al. 2007; Guazzo et al. 2017). It is the most prevalent sound on both feeding and breeding grounds (Dahlheim 1987), but only when social activity (sometimes with sexual components) takes place (Youngson & Darling 2016).

2.2 *Toothed whales (Odontoceti)*

Generally, there are two types of sounds produced by toothed whales: tonal, FM narrowband signals, called whistles, and pulsed signals; further divided into burst-pulse calls of many sorts and click trains. Click trains are used for echolocation in foraging activities, can reach frequencies above 100 kHz and are found in every species of toothed whales (Herman & Tavolga 1980). They will not be discussed further in this thesis since they do not play a role in communication, as whistles and burst-pulse calls do (Herman & Tavolga 1980; Richardson et al. 1995b). While some species have a wide repertoire of both types, some produce only pulsed calls. They are categorised into types based on their duration, frequency, repetition rate and often labelled as the sounds they resemble for humans. Whistles are categorised based on their contour i.e., frequency pattern over time (Richardson et al. 1995b).

Whistling species seem to be communal foragers forming large groups, in which whistles help them to maintain contact and spacing. On the other hand, non-whistlers are often found alone or in small groups. This seems to be the general rule, although there are exceptions. (Herman & Tavolga 1980).

2.2.1 *Sperm whales (Physeteridae)*

2.2.1.1 *Sperm whale (Physeter macrocephalus)*

The repertoire of sperm whale consists of different variants of clicks: regular and so-called creaks used for echolocation; codas and slow clicks for communication (Watkins & Schevill 1977; Whitehead & Weilgart 1991; Madsen et al. 2002).

Slow clicks are male-specific. Their inter-click interval is 6 s and they are 72 ms long. Include two peaks at 1,8 and 2,8 kHz (Weilgart & Whitehead 1988), central frequency is at 3 kHz but ranges from 1 to 5 kHz (Madsen et al. 2002). They are produced either singly or in trains of 15 clicks and more, lasting around a minute (Madsen et al. 2002). They could be a show of maturity in males and serving as repelling males or attracting females (Weilgart & Whitehead 1988), or an acoustic display in competition for food in long-range communication (Madsen et al. 2002).

Codas are produced mainly by females and young whales in social units (Marcoux et al. 2006) during resting and socialising periods (Whitehead & Weilgart 1991; Rendell & Whitehead 2003) and when meeting other groups (Watkins & Schevill 1977; Watkins 1980). They are short sequences of clicks, usually about 1 s long (Watkins & Schevill 1977; Watkins 1980) and appear in clusters, often in the form of exchange between more whales (Watkins & Schevill 1977; Moore et al. 1993; Weilgart & Whitehead 1993). There are many different stereotyped types of codas, differing in their pattern, i.e., the number of clicks and intervals between them (Watkins & Schevill 1977; Watkins 1980; Moore et al. 1993; Weilgart & Whitehead 1993). Coda repertoire determines vocal clans, groupings of many units and

individuals that share a similar dialect i.e., coda-use pattern, which is stable over many years. Some vocal clans are sympatric, but they usually do not associate with each other (Rendell & Whitehead 2003). Codas are therefore used for group (unit and clan) identification (Rendell & Whitehead 2003; Gero et al. 2016b), as well as individuality (Gero et al. 2016b; Oliveira et al. 2016), and play a role in the creation and maintenance of social bonds and associations (Moore et al. 1993; Weilgart & Whitehead 1993; Marcoux et al. 2006).

2.2.2 Dolphins (Delphinidae)

Delphinids' repertoire is varied and complex (Moore & Ridgway 1995; Bazúa-Durán & Au 2002), consisting of burst-pulsed calls, whistles, and combined calls, containing both tonal and pulsed part (Herzing 1996; Van Parijs & Corkeron 2001). Some species use predominantly pulsed calls (orca) or whistles (most dolphins) with the other type representing a significant part, while in some species whistles are found rarely or not at all (see further).

Due to the variability and complications with categorisation, the sounds of melon-headed (*Peponocephala electra*) and pilot whales (*Globicephala melas*, *G. macrorhynchus*) have been referred to as graded signals on a continuum (Kaplan et al. 2014; Vester et al. 2017), rather than distinct types. Complex sounds are used during high surface activity for maintenance of coordination and contact, while simpler ones occur during resting (Weilgart & Whitehead 1990).

Whistles are the main communication signal found in delphinids, either distinguished into types (Van Parijs & Corkeron 2001; May-Collado & Wartzok 2009; Petrella et al. 2012) or variable, unable of classification (Caldwell et al. 1990; dos Santos et al. 2005). The whistling rate is higher during foraging and socialising than other activities (Cook et al. 2004; dos Santos et al. 2005) and behavioural context determines types used (Díaz López 2011; Petrella et al. 2012). They are mainly used for localisation and recognition (Monteiro-Filho & Monteiro 2001) and can be modified based on motivation and emotion (Caldwell & Caldwell 1965; Janik et al. 1994). They can function in long-distance signalling, as their active space is several kms wide (Janik 2000a).

Frequency reaches 25 kHz in most species (Moore & Ridgway 1995; Herzing 1996; Corkeron & Van Parijs 2001; Bazúa-Durán & Au 2002; Díaz López 2011). Guiana's dolphin (*Sotalia guianensis*), however, produces 65 kHz whistles (May-Collado & Wartzok 2009; Andrade et al. 2015).

A special type of whistles are signature whistles, reported from Atlantic spotted (*Stenella frontalis*) (Herzing 1996) and common dolphin (*Delphinus delphis*) (Caldwell & Caldwell 1968) but studied extensively and confirmed only in the bottlenose dolphin (*Tursiops truncatus*) (see further).

Burst-pulse calls show great diversity (Herzing 1996; Monteiro-Filho & Monteiro 2001). They are correlated with behavioural contexts and group structure (Overstrom 1983; Henderson et al. 2012; Deconto & Monteiro-Filho 2019).

Dolphins of the *Cephalorhynchus* genus (Hector's, Commerson's) produce only HF (130 kHz) pulsed sounds (Dawson & Thorpe 1990; Yoshida et al. 2014), which are characterised based on ICIs (Yoshida et al. 2014). Repetition rate and complexity increase with group size (Dawson 1991; Yoshida et al. 2014), resulting in sounds named as squeals and cries. Since there are no whistles, it is likely these sounds are used for communication, or dolphins are capable of eavesdropping and drawing information from each other's biosonar

Name	Frequency	Duration	Behaviour	Reference	Note
Squawk	0,2 - 12kHz	1 s	aggressive	Herzing 1996	
Bark	6 - 9 kHz 2 – 20 kHz 1 – 20 kHz	2,5 – 4 s 12 s up to 7 s	aggressive socializing and foraging	Herzing 1996 Corkeron & Van Parijs 2001 Van Parijs & Corkeron 2001	
Scream	up to 2 kHz	1 s	aggressive	Herzing 1996	
Thunks	0,3 - 3,7kHz		disciplinary by mother towards calf	McCowan & Reiss 1995a	Ceased with independence of calf
Excitement calls		2 – 30 s	excitement/ distress	Herzing 1996	Signature whistles with clicks
Grunts	0,3 - 0,8kHz up to 1,5kHz	4 s	socialising	Corkeron & Van Parijs 2001; Van Parijs & Corkeron 2001	Narrowband Very short
Chirps	2 - 4kHz	1 s		Corkeron & Van Parijs 2001 Caldwell & Caldwell 1968	Similar with grunts Brief, pure-tone up-sweep
Quacks	Up to 4kHz		socialising	Van Parijs & Corkeron 2001	Similar to bark, but shorter

Fig. 2: Examples of labelled pulsed calls of Delphinidae and their characteristics

(Dawson & Thorpe 1990; Dawson 1991).

No whistles were reported in the Northern right whale dolphin (*Lissodelphis borealis*), instead, they use stereotyped series of burst-pulse sounds, about 16kHz, each unique to a different group (Rankin et al. 2007). A parallel situation is found in the Pacific white-sided dolphin (*Sagmatias obliquidens*), which produces whistles only rarely and instead exchanges pulsed call sequences as contact calls (Mishima et al. 2019). They reach 27 kHz (Soldevilla et al. 2008) and some carry individual or group identity information (Soldevilla et al. 2008; Mishima et al. 2019).

2.2.2.1 Killer whale (*Orcinus orca*)

Both whistles and pulsed calls are found in orcas' repertoire as communication signals (Steiner et al. 1979; Ford 1989), but the latter is the dominant type (Ford & Fisher 1983; Ford 1989).

Whistles reach frequencies of 18 kHz but usually are under 10 kHz (Ford & Fisher 1983). Samarra et al. (2010) even recorded whistles in the ultrasonic spectrum, extending up to 75kHz. Duration is very variable, from 50ms to 18 s (Steiner et al. 1979; Riesch et al. 2006). Even though most whistles are variable (Thomsen et al. 2001), there are stereotyped types that are community-specific and stable across years (Riesch et al. 2006). These were also recorded in complex patterned sequences, which presumably play a role in male-only social behaviours (Riesch et al. 2008). Generally, whistles are produced in close, social interactions (Thomsen et al. 2001, 2002), functioning as short-range signals (Riesch et al. 2006; Simon et al. 2007).

The frequency of pulsed calls can reach 30 kHz (Ford 1989), but the fundamental energy lies below 6 kHz (Steiner et al. 1979; Ford 1989). There are three categories of pulsed sounds: variable, aberrant and discrete. Aberrant are modified, distorted call types; variable offer a huge variety of nonrecurrent forms and discrete are distinguished into types (Ford & Fisher 1983; Ford 1989), which most studies concentrate on.

Call types form a unique repertoire in each pod (Ford & Fisher 1983; Ford 1989) and matriline (Miller & Bain 2000). The repertoire of one pod includes 7 to 17 call types (Ford 1989), most of them are shared across pods but usually specifically modulated in each one (Ford & Fisher 1983; Ford 1991; Yurk et al. 2002). Pods share a different number of types

with each other, but if they share at least one call type, they belong to one vocal clan (Ford 1991). Some vocal clans are sympatric and associate with each other, however, the unique repertoire is maintained, as calls are not transmitted across vocal clans (Ford 1991; Yurk et al. 2002) Dialects are therefore found on two levels in killer whales, both within and between vocal clans (Ford & Fisher 1983; Ford 1991; Yurk et al. 2002)

Discrete calls function is intra-pod affiliation contact-call (Ford 1989; Foote et al. 2008), maintaining cohesion and coordinating space and movement organisation of dispersed whales (Ford & Fisher 1983; Ford 1989; Miller 2002). They are often produced in signal exchanges, where one vocalising animal triggers the others to answer (Ford 1989; Miller et al. 2004), usually during foraging (Ford 1989; Simon et al. 2007). Variable and aberrant calls, on the other hand, are common during close-range interactions (Ford & Fisher 1983; Ford 1989; Thomsen et al. 2002).

During multi-pod aggregations, the proportions of calls in the pod's repertoire, which is normally stable, changes (Weiß et al. 2007; Foote et al. 2008). The production of the dominant types decreases in those situations (Foote et al. 2008) and aberrant calls increase. (Weiß et al. 2007). The vocalisation rate is much higher in these engagements, with many overlapping and excitement calls (Ford 1989).

*2.2.2.2 Bottlenose dolphin (*Tursiops truncatus*) signature whistles*

The signature whistle hypothesis was first introduced by Caldwell & Caldwell (1965) who recorded individual-specific, stereotyped whistles, distinct with their contour. Signature whistles remain stable over years (Caldwell et al. 1990; dos Santos et al. 2005), even though some parameters, such as intensity, duration, and repetition, change slightly depending on stress or excitement levels (Caldwell et al. 1990; Esch et al. 2009).

The hypothesis has been questioned by McCowan & Reiss (1995b; 2001) who found only a shared repertoire of whistles in their studies. However, their methodology was criticised as flawed in the categorisation of whistles by Sayigh et al. (2007) and the hypothesis was later confirmed by Janik et al. (2006), who presented bulletproof evidence that whistle contour carries identity information and dolphins use it to recognise others. They found that dolphins react to electronic versions of related conspecifics' individual contours more than non-related ones, demonstrating individual discrimination. It was not kin discrimination because whistles of related animals were no more similar to each other than unrelated ones, and also the animals did not react more to whistles similar to theirs.

Lilly (1963) recorded "distress calls": whistles produced during real or potential physical damage with differences between individuals. Kuczaj et al. (2015) later noted that they were signature whistles, distorted due to stressful conditions. Producing them resulted in help from conspecifics, in the way of pushing the distressed animal to the surface to breathe (Lilly 1963; Kuczaj et al. 2015)

Dolphins can mimic and copy each other's signature whistles (Tyack 1986), using the copies in vocal exchanges for labelling and addressing conspecifics (Tyack 1986; Janik 2000b). This was confirmed with the fact that individuals reply with the same type when hearing their signature whistle as if someone called them by a name (King & Janik 2013). These exchanges also happen in the open sea when two groups meet each other, as a form of identification upon meeting (Quick & Janik 2012).

Signature whistles form half of wild dolphins' repertoire in non-disturbed conditions (Cook et al. 2004). This contradicts to findings of Janik & Slater (1998) that they are only

common during group separation or disturbance. Esch et al. (2009) reported a higher signature whistle rate during stressful conditions of a capture-release experiment. This is likely due to the fact that signature whistles serve to maintain group cohesion (Janik & Slater 1998; Cook et al. 2004) and in small captive pools (Janik & Slater's study) dolphins see each other and therefore rather use visual contact than energy-consuming vocalisation.

Mother-calf pairs use signature whistles to maintain proximity and contact. The calf whistle rate increases during separation and is significantly lower after reunion (Smolker et al. 1993; Mello & Amundin 2005). Mothers whistle more when reunited, unable to return to a calf, or during its retrieval when out of visual range (Smolker et al. 1993; Mello & Amundin 2005; King et al. 2016).

Calves probably whistle more to inform the mother about their location and motivation to rejoin (Smolker et al. 1993) and to make her vocalise, so they can locate her (Mello & Amundin 2005). On the other hand, cows may not whistle unless their calf is distressed (Smolker et al. 1993), or they do not see it (King et al. 2016).

All these studies point to signature whistles being used as an identification tool for individual recognition and as group cohesion call by bottlenose dolphins, therefore the production rate increases in situations that disrupt group cohesion, such as separation (Caldwell et al. 1990).

2.2.3 White whales (Monodontidae)

Monodontidae includes only two species: narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*). Both possess a repertoire of a variety of calls: tonal, pulsed, and combined ones (tonal, FM part overlapping a click sequence). However, they differ in the proportion of these calls: whistles are belugas' predominant signal (Sjare & Smith 1986a; Belikov & Bel'Kovich 2007; Chmelnitsky & Ferguson 2012), while they form the lesser part of narwhals' repertoire, occurring quite rarely and sporadically (Ford & Fisher 1978; Miller et al. 1995).

2.2.3.1 Narwhal (*Monodon monoceros*)

Whistles of narwhals are usually FM, around 1 s long (Ford & Fisher 1978; Miller et al. 1995). The frequency ranges from 400 Hz to 10 kHz (Ford & Fisher 1978; Shapiro 2006), sometimes up to 15 kHz (Marcoux et al. 2012) and harmonics can reach 48 kHz (Shapiro 2006). Whistles can be categorised into different types (Shapiro 2006) which are behaviour specific (Marcoux et al. 2012).

Pulsed calls are more variable than whistles, defined by repetition rates, frequency, and duration. They can be distinguished into few categories: 1) Pulsed tones, narrowband signals under 5 kHz with regular intervals between pulses (Ford & Fisher 1978) 2) Burst-pulsed calls reaching 69 kHz (Blackwell et al. 2018) 3) Repetitive sequences of burst-pulsed calls, common during high vocal activity 4) Strictly ordered paired pattern sequences formed of two interchanging subunits, common during otherwise silent periods (Walmsley et al. 2020) 5) Combined calls, composed of FM tonal component overlapped by pulses (Shapiro 2006).

All of them are used for communication (Ford & Fisher 1978; Blackwell et al. 2018), paired pattern sequences likely for long-distance (Walmsley et al. 2020).

Some studies suggested that narwhals may produce signature sounds: Shapiro (2006) found significant differences in duration and frequency of whistles and combined calls of two captive individuals that each showed distinct repertoire, and therefore speculated they may be

signature signals of individuals or groups, used as contact calls. Marcoux et al. (2012) noted that herds' intra-variability of whistles and calls is much lower than inter-variability, suggesting this difference is due to group or individual-specific, signature sounds.

2.2.3.2 *Beluga (Delphinapterus leucas)*

Beluga is known for its wide repertoire of sounds (Bel'kovitch & She'kotov 1993), which earned it the nickname "canary of the sea". Since it is challenging to classify them, more researchers noted that they form a graded continuum rather than distinct types (Karlsen et al. 2002; Belikov & Bel'Kovich 2007; Garland et al. 2015).

Despite this, whistles are often categorised based on their contours (Sjare & Smith 1986a; Chmelnitsky & Ferguson 2012; Panova et al. 2019). They are usually variable both in frequency and duration (Sjare & Smith 1986a; Alekseeva et al. 2013), but some whistles are stereotyped and distinct (Karlsen et al. 2002; Belikov & Bel'kovich 2006; Panova et al. 2019). Frequencies reach up to 14 kHz (Sjare & Smith 1986a; Karlsen et al. 2002; Belikov & Bel'kovich 2006; 2007) and 20 kHz in HF whistles, LF are produced under 5kHz. (Chmelnitsky & Ferguson 2012; Panova et al. 2019). Duration spans from 0,2 s to 4 s (Sjare & Smith 1986a; Karlsen et al. 2002; Chmelnitsky & Ferguson 2012; Panova et al. 2019).

Pulsed calls, even though not prevalent, represent a significant proportion of belugas' repertoire (Sjare & Smith 1986a; Garland et al. 2015). On top of duration and frequency, they are also variable in repetition rate, which determines their categories (Sjare & Smith 1986a; Karlsen et al. 2002; Belikov & Bel'kovich 2008). Pulsed calls are both broadband and narrowband, usually around 10 kHz (Sjare & Smith 1986a; Garland et al. 2015), but can reach over 20 kHz (Karlsen et al. 2002; Belikov & Bel'kovich 2008). Some are so broadband they seem to lack structure; these are referred to as noisy vocalisations (Sjare & Smith 1986a) and are generally uncommon (Garland et al. 2015).

Combined calls reach frequencies of 12 kHz in tonal and 20 kHz in pulsed part (Karlsen et al. 2002) and compose only 10% of all sounds (Chmelnitsky & Ferguson 2012).

Each behaviour context can be characterised with proportions of call types (Sjare & Smith 1986b; Panova et al. 2012; Alekseeva et al. 2013). Pulsed sounds are used for short-range communication and are indicative of emotional states (Belikov & Bel'kovich 2008; Alekseeva et al. 2013), just like combined calls and variable whistles (Belikov & Bel'kovich 2006; 2007; Panova et al. 2012). Stereotyped whistles on the other hand function as long-distance signals to maintain coordination of groups (Belikov & Bel'kovich 2006; Panova et al. 2012; Alekseeva et al. 2013). The overall vocalisation rate is the highest during socialising and joining of groups (Sjare & Smith 1986b; Panova et al. 2012).

Few studies presented a possibility of signature calls in belugas' repertoire. Panova et al. (2016) found "vowels", a pulsed call type functioning as a contact call (Panova et al. 2012), is unique to population aggregations, within which it remains stable for at least 12 years. Distant populations show bigger differences than neighbouring ones, so the purpose may be a group signature call. They presented cultural drift as a probable explanation of the differences. Another study (Panova et al. 2017) found individuality in combined calls and squeaks, on top of vowels. Each female had a distinct type, while males used a joint one, which could be explained by different life histories of sexes and suggests that belugas have contact call showing both individual and group identity. Morisaka et al. (2013) and Mishima et al. (2015) found individuality in IPIs and the number of pulses in a burst-pulse call which they labelled

PS1. It was found in vocal exchanges of animals, being repeated until a conspecific answered, as a mother-calf contact call and dominant sound during isolation.

Lastly, Vergara et al. (2010) recorded a combination call characteristic to mother-calf interactions. The call had more variants, probably reflecting urgency and distress. It was dominant during the birth and death of a calf, isolation, separation, and re-introduction. In other situations, it formed only 4% of the repertoire. Though it was not individual-specific, it was specific to a mother and later her calves, which started producing it with age.

2.2.4 Porpoises (Phocoenidae)

Porpoises are one of the toothed whales that communicate only with pulsed sounds. The pulses consist of narrowband LF (2kHz) (Schevill et al. 1969) and HF (110-145kHz) component (Verboom & Kastelein 1995). Even though Verboom & Kastelein (2003) observed social sounds, labelled grunts, whoops, bleats, up to 2kHz, Hansen et al. (2008) noted the LF component is only a by-product and not intentionally made, therefore serving no role in communication.

Pulses occur both singly and in bursts or series, which are of different, mostly high, repetition rates and lengths (Schevill et al. 1969; Verboom & Kastelein 1995). The repetition rate differs depending on the behaviour situation: aggressive encounters are accompanied by click bursts with up to 1000 pulses/s, while approach never exceeds 650 pulses/s and grooming behaviour by mothers 100 pulses/s. The rate can also change during a burst, showing up or down sweeping tendencies (Clausen et al. 2010). Together with the fact high repetition click trains of different porpoises are often found together, in clusters (Sørensen et al. 2018), this clearly shows that clicks are used for communication and their function in different behaviours is distinguished by the repetition rate (Clausen et al. 2010).

2.2.5 Beaked whales (Ziiphiidae)

Beaked whales are cetaceans with one of the least known vocal repertoires. Even though there are more than 20 species in this group, only a few have been recorded. They produce both whistles and pulsed sounds, but the most recorded are echolocation trains. The precise characteristics differ between species, but generally are very similar, of the same structure.

Whistles are under 1 s long and their fundamental frequency lies between 4 and 13 kHz (Dawson et al. 1998; Rankin & Barlow 2007a; Aguilar de Soto et al. 2012). They include harmonics that can reach over 80 kHz (Aguilar de Soto et al. 2012). Burst pulse sounds consist of broadband clicks higher in frequency than whistles (9 to 20kHz), but lower than echolocation clicks (Rankin & Barlow 2007a; Rankin et al. 2011; Leunissen et al. 2018). Aguilar de Soto et al. (2012) named one type of burst-pulse sound rasp, which they found more often than whistles. Because they were produced deeper than 170 m, it was suggested they are a communication element to keep coordination when dispersing in the deep to forage. Other than that, behavioural associations with beaked whales' sounds are yet unknown.

2.2.6 River dolphins (Inidae, Platanistidae, Pontoporiidae)

As is apparent from the name, river dolphins are freshwater inhabitants, occupying big rivers in South America and south-east Asia. Very often, they are compared to delphinids with their vocalisations, mostly in pursue of explanation of the evolutionary origin of whistles, as river dolphins are the basic groups of toothed whales.

The overall vocal activity is low and infrequent (Caldwell et al. 1966; Podos et al. 2002; Cremer et al. 2017). Still, vocalisations of river dolphins are diverse in temporal, harmonic and frequency features (Podos et al. 2002; Melo-Santos et al. 2019). They communicate with both whistles and pulsed calls. However, whistles represent only a small fraction of their repertoire (Caldwell et al. 1970; Mizue et al. 1971).

Burst-pulsed calls vary in repetition rate and frequency, based on which names such as squawk, squeal, screech, bark, whimper, and twitter were created. (Caldwell et al. 1966; 1970; Mizue et al. 1971). Even though the first studies reported frequencies little over 10 kHz (Caldwell et al. 1966; 1970), Cremer et al. (2017) recorded much higher sounds, between 70 and 84 kHz. This difference could be explained by higher recognition range equipment and stressful conditions, caused by tagging of the animals, in the recent study, or by different frequency ranges of certain species, given that it focuses on La Plata dolphin (*Pontopora blainvillei*), while the others on the Amazon (*Inia geoffrensis*) (Caldwell et al. 1966, 1970; Podos et al. 2002) and Ganges river dolphins (*Platanista gangetica*) (Mizue et al. 1971). Even though the first two explanations seem more likely, the latter cannot be ruled out, considering that whistle frequencies follow a similar pattern, being lower in Amazon river dolphin: 3,5 to 48 kHz (May-Collado & Wartzok 2007; Melo-Santos et al. 2020) than La Plata: up to 95 kHz (Cremer et al. 2017).

Whistles with descending contour are most common, produced either singly or in bouts with variable intervals (May-Collado & Wartzok 2007; Melo-Santos et al. 2020). Both solitary animals and groups whistle (May-Collado & Wartzok 2007), most often during resting and social activities as a group recognition and to maintain spacing (May-Collado & Wartzok 2007; Melo-Santos et al. 2020).

2.3 Comparison and conclusion

As can be seen from this chapter, the sounds of baleen and toothed whales differ, mainly in the frequency. On top of being lower, baleen whales' calls are usually also longer and have narrower bandwidths. These features enable the signals to be used for long-distance communication, as baleen whales are generally less social than toothed whales. However, the sounds cannot be labelled as simpler, as both groups include species with simple and complex signals. However, toothed whales produce sounds that can be categorised either as pulsed or tonal, while baleen whales' calls are not easily categorised (Herman & Tavolga 1980). Baleen whale sounds are often influenced by geographical variation, which was not studied enough in toothed whales.

Individual and group-specific calls, though suggested in some species of Mysticeti, were only proved in toothed whales. Group-specific signals are found in sperm whales and orcas, both living in maternal units. Individual signature calls were proved in bottlenose and other dolphins. Both types were suggested to be present in Monodontidae. It seems that the presence of these calls depends on the social structure. As orcas and sperm whales both live in stable maternal units, they need to have a signal identifying the group, to help maintain cohesion and contact. On the other hand, dolphins live in a fission-fusion society, meaning the groups they form are not stable and change. In such a situation, it is advantageous to have an individual-recognition system, as individual identity is more important than a group one.

A lot of the times, studies, especially older ones, were limited by their research equipment. We can see that recent studies are discovering higher frequencies, wider ranges and more details about the sounds cetaceans produce, thanks to the development of equipment and

methodology. That suggests that more information about the repertoire of cetaceans is yet to be discovered.

In some species, there are only a few pieces of research describing its repertoire, while others have a numerous list. However, an overall lack of studies on the association of sound with a behavioural context in this field is apparent from the review. These types of studies are difficult to conduct due to the nature of life strategies of cetaceans and their environment, therefore were mostly done in captive species.

3 Vocal learning and cultural transmission of sounds in cetaceans

The definition of culture slightly varies between publications and authors. Here, the definition used is from Rendell & Whitehead (2001a), who modified a version from Boyd & Richerson (1996, in Rendell & Whitehead 2001b), defining culture as “information or behaviour - shared by a population or subpopulation – which is acquired from conspecifics through some form of social learning.”

Culture in the animal kingdom is not scarce, but accumulative culture, meaning cultural traditions, behaviours that one individual could not invent by itself, is (Boyd & Richerson 1996).

Cultural transmission between animals can be put into categories, based on the individuals included: vertical, from parent to offspring; horizontal, among conspecifics of the same generation (=age peers) and oblique, between an individual and member of the older generation that is not a parent (Cavalli Sforza & Feldman 1981). In cetaceans, these transmissions are known from various behavioural aspects (such as feeding strategies), including vocalisations (Rendell & Whitehead 2001b).

Vocal learning is a form of social learning and therefore can lead to establishing cultures. Cetaceans use both main types: production learning and contextual learning (Janik & Slater 1997), to acquire their repertoire.

3.1 *Horizontal transmission*

Humpback whale’s song is a classic example of horizontal cultural transmission in cetaceans. The song is characteristic of its ever-changing nature that is maintained through vocal learning (Payne & Payne 1985; Eriksen et al. 2005). Segmentation is used to bring new parts into the repertoire, i.e., replacing one theme with a new, similar-sounding one, creating temporary hybrid songs before establishing a new one (Garland et al. 2017).

The changes can be labelled as cultural evolution and revolution (Noad et al. 2000). Cultural evolution is the constant change within and between years in a population’s song (Payne & Payne 1985). At the start of a new season, it resembles the old song, before alteration or replacement of some parts takes place (Payne 1985, Eriksen 2005). In the end, the song is different from those of previous seasons, though some units may prevail in upcoming years (Payne & Payne 1985). The longer the seasons are apart from each other, the more different the songs are (Eriksen 2005). No old song type or themes are ever brought back (Payne 1985, Eriksen 2005).

Despite the constant changes, little variety (except the song’s duration and precise configuration of units) is seen among individuals in one year. All males in one population culturally conform to singing the same song at any given time (Payne & McVay 1971; Winn & Winn 1978; Payne & Payne 1985). It is also important to note that although it changes frequently, it does so only within a fixed framework of the sequence of themes and temporal characteristics (Payne & McVay 1971; Payne & Payne 1985).

Songs in one year in different populations vary (Garland 2011), the further the distance the bigger the dissimilarity (Garland 2015).

Revolution describes a situation when a certain song type is completely replaced by another one in a short time. The new type is from a different population and can be present with the old and intermediate type, before completely taking over (Noad et al. 2000).

Transmission of song types across populations can be explained by movement of a couple of individuals to different areas (Noad et al. 2000), singing on shared feeding grounds (Garland et al. 2013) or migration route (Owen et al. 2019). One example of a vast horizontal cultural transmission is the South Pacific, where one song type transferred from the Eastern Australia population to others in the eastern direction. The song appeared in the consecutive areas 1-2 years apart (Garland et al. 2011). The question of why it is changing remains to be answered, though some speculated avoiding habituation (Winn 1978).

Bowhead whales' song is much akin to humpback's: the structure (i.e., the number of phrases and their structure, length of the song) changes every year (suggested by Cummings & Holliday (1987), confirmed by Delarue et al. (2009), components are either completely new or similar to previous years' ones, and all whales sing an identical version of the song, showing no variation in any characteristics (Delarue et al. 2009; Tervo et al. 2011). The song also changes within a season, evolving from a primitive version to a complex one (Delarue et al. 2009), therefore more than one type of song can be present in one season (Stafford et al. 2008; Tervo et al. 2009, 2011). The complexity is much lower at the end of the season, and spring songs are only a remnant of the winter breeding season (Tervo et al. 2009).

All this indicates horizontal cultural transmission occurring in bowhead whales (Delarue et al. 2009)

3.2 *Vertical and oblique transmission*

3.2.1 **Vocal clans of sperm whale**

All types of transmission are found in sperm whale societies, however vertical is the major one. As was stated in chapter two, sperm whales live in social units that form a vocal clan based on their similar coda repertoire. It is maintained on a clan level, forming dialects within a population (Rendell & Whitehead 2003). No clans share a repertoire, even though one type of coda, the 5R coda, has been found in more clans (Weilgart & Whitehead 1993; Gero et al. 2016b; Oliveira et al. 2016). However, it seems to contain individual identity, as it shows high individual variety (Gero et al. 2016b), especially in the ICIs and IPIs (Oliveira et al. 2016). Also, it often initiates an exchange (Weilgart & Whitehead 1993) and belongs to the most common coda types (Gero et al. 2016a; Oliveira et al. 2016).

Units within a clan can differ in their repertoires. However, there is only little distinction between them, and they have at least 2 shared types covering more than 10% (Gero et al. 2016b). For example, 1+1+3 coda was found in all units of only one vocal clan near Dominica Island, as one of the most common types (Gero et al. 2016a). It is stereotyped across all units, even in calves' repertoires, therefore likely used as clan identification coda (Gero et al. 2016b). Individuals in a unit also differ in the usage proportions of coda types and may produce some distinctively (Gero et al. 2016b) but all types are shared and the most common compose over 75% of the unit's repertoire (Rendell & Whitehead 2004).

Overall, there is a tendency for convergence both at unit and clan level, being one of the biggest reasons for homogenised repertoire (Konrad et al. 2018).

Repertoire dialects are stable for years (Weilgart & Whitehead 1997; Gero et al. 2016b), conserved in matrilineal units, even after splitting (Weilgart & Whitehead 1997; Whitehead et al. 1998). They are culturally transmitted through social learning, resulting in variations and dialects (Rendell & Whitehead 2003, 2004; Amorim et al. 2020). The repertoire is learned by

young whales from their mother and other members of the unit, by vertical and oblique transmission (Weilgart & Whitehead 1997; Rendell et al. 2012; Konrad et al. 2018). Calves and juveniles' codas are generally less stereotyped and stable than adults' ones (Watkins et al. 1988). They also produce more coda types and some shared types more frequently (Gero et al. 2016b). The younger the calf, the more variable click sequences, which increase in stability, stereotypy, and complexity with age (Watkins et al. 1988), gradually crystallising into their natal unit's repertoire (Gero et al. 2016b).

Horizontal transmission has been suggested to occur between units within a clan (Konrad et al. 2018), but also between clans, when females switch, although it happens very rarely (Rendell et al. 2012).

The presence of dialects can be explained neither by environmental conditions nor genetics. Firstly, some vocal clans are sympatric, inhabiting the same area and they all have a distinct repertoire (Rendell & Whitehead 2003; Amorim et al. 2020). Secondly, intra-clan mtDNA haplotype sharing does not occur more often than inter-clan, and haplotypes are shared among clans (Rendell & Whitehead 2003; Rendell et al. 2012). It is true, however, that maternally related units, meaning with common dominant mtDNA haplotypes, have more similar coda repertoires. This is easily explained by the parallelism of learning and inheriting genetics from the mother (Whitehead et al. 1998).

3.2.2 Killer whale pulsed calls dialects

Pod-specific pulsed calls of killer whales are also culturally transmitted. It is known that orcas are vocal production learners, capable of imitation and copying various sounds (Foote et al. 2006), even out of their usual repertoire (Abramson et al. 2018). In one cross-fostering experiment with bottlenose dolphin and orca, the orca produced significantly more whistles and clicks (typical of bottlenose dolphin) than wild orcas normally do (Musser et al. 2014). In another experiment, juvenile males produced calls of an adult male after he was introduced into the pool (Crance et al. 2014).

Therefore, it is not surprising that orcas learn their pod-specific pulsed calls repertoire (Ford 1989; Miller & Bain 2000; Foote et al. 2006; Filatova & Miller 2015).

They are learned by calves mainly from their mothers (Ford & Fisher 1983; Ford 1991; Deecke et al. 2010) but also from other maternal relatives, members of a matriline (Yurk et al. 2002). After birth, the production of family-specific calls increases significantly for about 14 days, enhancing the calf's recognition of those calls and thus maintaining spatial proximity with matriline members (Weiß et al. 2006).

The social system of orcas starts with a maternal unit (MU) – a family of mother and her offspring up to 4 generations. Related MUs form a pod, and pods belong to a vocal clan (Bigg et al. 1990), distinct in its repertoire. Vocal clans are likely to have a common maternal ancestor (Ford 1991; Yurk et al. 2002); and form dialects within a community.

Dialects within a clan develop due to differences in repertoire between MUs accumulated over time (Miller & Bain 2000): when a pod/MU splits, their repertoire starts to diverge, evolving independently. The mechanisms that lead to the unique repertoires include innovation, cultural drift (Ford 1991; Yurk et al. 2002), and vertical and selection learning (Yurk et al. 2002).

In contrast to the sperm whale, in orca, MUs/pods with the most similar repertoire are the most recently split (Ford 1991), or closely related, as repertoire similarity correlates with relatedness (Yurk et al. 2002; Deecke et al. 2010). The more closely related MUs are, the

more similar their repertoire is, even if they do not preferentially associate with each other. That means orcas use selection learning, choosing who to learn call types from (Deecke et al. 2010).

Even though rarely, imitation of calls from other clans occurs (Ford 1991; Weiß et al. 2011), but they are never transferred into the repertoire (Ford 1991), further proving selection learning, as even though orcas copy sounds from more whales, they only learn and sustain the ones from family.

Horizontal transmission seems to also be present in orcas' societies. Firstly, parallel changes in one vocal type were found between two matriline, in a form of vocal matching, which implies learning between matriline within a pod (Deecke et al. 2000). Secondly, community-specific stereotyped whistle types are learned throughout the life of adult whales when an association between clans occurs, possibly functioning as a community-level recognition signal (Riesch et al. 2006).

The complex repertoires of killer whales likely exist due to their social structure (Ford 1991), increasing the efficiency of intra-pod communication and maintaining its cohesion (Ford 1989).

3.2.3 Bottlenose dolphin signature whistles

Bottlenose dolphins use production and both subtypes of contextual learning, comprehension and usage (Janik & Slater 2000), to acquire their individually specific signature whistles (Janik 2013). The development of a signature whistle takes 1 to 2 years. Once it is learned, it remains stable for long years (Sayigh et al. 1990).

Calves mimic and incorporate into their repertoire sounds from their natal environment and surroundings (Fripp et al. 2005), as they learn from both related and unrelated conspecifics within their community (McCowan & Reiss 1995b; Fripp et al. 2005). On average, there are 6 adult models with similar whistles, although it is unknown if calves learn from all or only some of them (Fripp et al. 2005). Association and whistle copying were not found to be correlated (McCowan & Reiss 1995), though Fripp et al. (2005) noted that the 6 models were dolphins who spend the least amount of time with them.

Males seem to have similar whistles to their mothers more often than females do, which can be explained by the different life histories of the sexes. Males disperse, while females stay close to their matriline, which puts forward a need for a distinct type (Sayigh et al. 1990, 1995).

Calves are also able to learn sounds from other species, such as humans: captive dolphin calves' whistles are much flatter and of lower frequency than their wild counterparts, reminiscent of trainers' whistle sounds (Miksis et al. 2002).

Learning continues throughout dolphin's life in adulthood, as they mimic others' signature whistles (Tyack 1986; King et al. 2013) to address the individual (King & Janik 2013), developing an association between a specific whistle and a dolphin (Caldwell et al. 1990; King & Janik 2013). Copies of such whistles are similar in contour to the original, however differ in frequency parameters. It was suggested the sound is altered at will, as a form of identification of the copying dolphin (King et al. 2013). Signature whistle matching occurs mainly between closely associated animals (King et al. 2013).

Another example is the convergence of whistles in a male alliance reported by Smolker & Pepper (1999). They noted that the three males gradually altered their repertoire, losing individual whistles and replacing them with a shared contour. Over time, they were

indistinguishable from each other. However, King et al. (2018) found distinctive signature whistles in male alliances, noting they play a central role in such a group formation.

Vocal production learning was also found in Risso's dolphin (*Grampus griseus*). In a cross-fostering experiment, it produced whistles very alike bottlenose dolphins', which were rarely found in wild conspecifics. It shows that just like bottlenose, Risso's dolphins use models during whistle development (Favaro et al. 2016)

3.2.4 Beluga signature calls

Just like dolphins, belugas are capable of imitating and copying sounds they hear. They do so spontaneously, and can even mimic unnatural, computer-made sounds they have never encountered before (Murayama et al. 2014).

One of the possible signature calls, the PS1 call, that differs between adults based on the unique stereotyped IPIs, was not stereotyped in a calf's repertoire (Mishima et al. 2015). This indicates that young belugas learn to produce these pulsed calls stereotypically, acquiring individual IPI with age. Similarly, Vergara & Barrett-Lennard (2008) observed the progression toward stereotypy in their study, especially with one mixed call type, frequently produced by the calf's mother after birth, as a response to its calls and a contact call. The calf's call gradually began to resemble it, becoming stereotyped in frequency and FM and at 3 years old, it was very similar to its mother's. The same call type was produced by its mother's other calf (Vergara et al. 2010). On top of that, the calf began producing calls characteristic of its father, 6 months after being exposed to him. This study also indicates that belugas learn stereotyped calls with age, in this case from their parents. However, Vergara & Barrett-Lennard (2008) suggested that there are more mechanisms in the ontogeny of calls, learning being only one of them.

3.3 Conclusion

In this chapter, species using vocal learning to acquire at least a part of their repertoire were presented. The two types of learned signals are individual/group-specific calls and song, a form of breeding display. Vocal learning in cetaceans with individual or group-specific sounds is present and used during (but not exclusively) the development of these signals. On the other hand, humpback and bowhead whales use it to conform to one specific song type, used by all individuals in a population during a season, and learn new ones in following years.

The presence of signature calls, although evidenced in only a few species, was suggested to be present in others, including some baleen whales. Since these signals are learned, if they proved to be existent in those species, it would mean they use vocal learning to acquire them.

As for the song of the baleen whales, it is found in more species besides humpbacks and bowheads. And since it is learned, that would mean vocal learning should be present in more baleen species. However, bowhead and humpback have the most complex songs, on top of the fact they change every year. The reason behind these changes has not been found yet. Also, they form big aggregations during the breeding season (when the song is mostly heard), which is not the case in the rest. If any of these factors influence the need for vocal learning is speculative.

Working with the available data, a possible conclusion would be that vocal learning is present only in species with signature calls or complex songs. However, the fact that in all four *most studied* species of cetaceans, that is sperm, killer, humpback whales and bottlenose dolphin, vocal learning functions in acquiring a repertoire, arises a question if more species

use it. Even though there is currently no empirical evidence to support this statement, it is important to note there is a serious lack of research focusing on vocal learning (and behavioural context of vocalisation in general), in cetaceans. Evidence was mostly found only in bottlenose dolphin, as it is commonly held captive, where experiments are easily conducted. The other studies were predominantly observational. Therefore, the possibility of a higher incidence of vocal learning in cetaceans cannot be ruled out with certainty.

4 Development of calls during ontogenesis

There is a severe lack of studies concerning the development of sounds in cetaceans. The main reason being the complications linked with experimental research on them, as it is quite challenging to find a cow-calf pair, especially in species that do not form aggregations. Moreover, assigning sounds from a recording to an individual producing it is generally difficult, let alone when a calf is almost always close to its mother, making it nearly impossible to identify the caller. Therefore, those who recorded calves were either lucky to encounter them or worked with captive individuals.

Edds et al. (1993) and Figueiredo & Simão (2014) both recorded young Bryde's whales, finding that calves' discrete pulses and juveniles' pulsed moans were of higher frequency and longer duration than the following age group (calves-juveniles-adults).

Humpback whales' calves produce calls that are more variable than adults', showing more FM and AM, as well as wider bandwidth (Zoidis et al. 2008; Indeck et al. 2020). Zoidis et al. (2008) found them to be longer, while Indeck et al. (2020) shorter, which only shows the variability and undefined structure in young whales.

Similarly, upcalls of right whales' calves and juveniles are shorter than adults' ones (Parks et al. 2011; Dombroski et al. 2016; Root-Gutteridge et al. 2018). Apart from duration, the presence of deterministic chaos, biphonation, and subharmonics also change with age. Calves' calls are chaotic, resembling a blabber, continuously crystalising into adults' ones (Root-Gutteridge et al. 2018).

Belugas' calves are vocal shortly after birth, but produce mostly pulse trains in the first month. The repertoire broadens with age, since whistles and mixed calls production increase in the second and fourth month, consecutively. The frequency and frequency range of sounds, as well as the repetition rate in pulsed calls, is lower in young belugas than in adults. Pulsed calls become more variable, opposed to whistles, which are quivery and have no regular FM in the first year, gaining stereotypy with age. Only at 10months old do they start to resemble adults' regular whistles sequences (Vergara & Barrett-Lennard 2008).

Bottlenose dolphins' vocal development traces a similar path as belugas. First whistles appear the second day after birth (Cockcroft & Ross 1990) and stereotyped ones after 45days (Caldwell et al. 1990). Variable, nonrepetitive whistles are predominant in young calves (Caldwell et al. 1990; McCowan & Reiss 1995b), as more stereotyped types are acquired with age, especially the ones shared with adults. Whistle repertoire changes drastically during the first year, increasing in complexity, duration and FM (Caldwell et al. 1990; McCowan & Reiss 1995b).

The changes of the calves' vocalisations are driven by a maturation mechanism (Edds et al. 1993; Figueiredo & Simão 2014), as they correlate with age. They are caused by physiological advancements as well as different behavioural needs and motivations (Root-Gutteridge et al. 2018; Indeck et al. 2020).

Another mechanism is vocal learning. It is certainly used in species with individual or group-specific calls (see the previous chapter), but there is no evidence for it in the rest. However, since the research is insufficient, no conclusion can be drawn whether or not it is present in other species of cetaceans during vocal development. Both mechanisms can work together to develop the final repertoire (McCowan & Reiss 1995b; Vergara & Barrett-Lennard 2008).

4.1 Conclusion

Despite the small number of research papers, all agree on few characteristics of calves' repertoire. Firstly, it is quite varied and mostly lacking structure. Secondly, the frequency and duration differ from adults' calls. And finally, with age, its calls resemble adults' repertoire, meaning juveniles produce sounds more alike adults' than calves do. Some authors compared the sounds of calves to the babbling stage of humans (McCowan & Reiss 1995b; Vergara & Barrett-Lennard 2008), because of the variety of variable sounds that later become stereotyped.

It is clear that maturation is one of the mechanisms behind vocal development, as physiological restraints relate to vocal production. As far as vocal learning is concerned, species that are capable of it use it (above others) to acquire their typical sound repertoire. However, since there are so few studies about vocal development, and learning in cetaceans in general, the incidence may be much higher. Therefore, right now, it is impossible to say how big of a portion of the cetacean repertoire is learned and determined genetically.

5 Summary

Cetaceans produce a variety of vocal signals: tonal, pulsed and their combinations. Between the two groups, Mysticeti and Odontoceti, the biggest differences are in frequency, duration, and bandwidth. Odontoceti's signals are usually easily categorised into pulsed, tonal, or combined ones, which does not apply to Mysticeti, but both groups contain species with simple and complex calls. The behavioural contexts are mostly unknown, apart from their utilisation in short or long-range communication.

Signature calls, used for individual or group recognition, are present only in toothed whales. They depend on the social system: group-specific calls were found in killer and sperm whales, both living in stable maternal units. On the other hand, individual-specific signature whistles were found in bottlenose and other dolphins which are characteristic with fission-fusion society. The presence of these calls in other species has been suggested.

Species that use vocal learning have one of two signal types, signature calls or songs. Signature calls are learned through vertical and oblique transmission. Learning is important during the early vocal development and to learn and recognise the calls of other individuals in a community. Since signature calls were suggested to be present in more species, and vocal learning is essential for their acquisition, it is quite likely the incidence is higher.

Horizontal transmission is used to conform to one type of song of humpback and bowhead whales. Other baleen whales also use songs in their repertoire, which raises the question of vocal learning being present in other singing species. However, only humpback and bowhead whales' songs are complex and constantly changing, which may be the factors determining the need for vocal learning. The reason behind the changes is unknown.

Young cetaceans produce chaotic and variable sounds, gaining more stereotypy and complexity in their calls with age. Most studies suggest there is more than one mechanism, maturation, behind the development of sounds during ontogenesis, and in species with signature calls vocal learning was found to be one of them. It is possible that in other species this is also the case, however, due to the lack of studies concerning this issue, any conclusion should be taken in with caution.

Even though vocalisations are not described sufficiently throughout the cetacean group, it is apparent that the sounds, traditions, and learning do not correlate (or only to some extent) with phylogenetic relatedness, but rather with social structure. The more complicated the social behaviour of a species or a family, the more complex are their sounds. It is clear this is not a case of phylogenetic conservatism but rather of the function of the sounds i.e., communication, which is closely tied to social structure. Traditions and culture have been found in sperm, killer, humpback whales, and bottlenose dolphin, the best-studied cetacean species, which means it is therefore probable that the incidence is higher.

Further research is needed to broaden our knowledge about cetacean vocal behaviour. Future studies should focus on the behavioural context of vocalisations, seeing as there is a big gap in information about this topic. The same thing applies to vocal learning. It is challenging to prove its presence in a species, but the research could be focused on broadening our knowledge on how exactly species we know use it, utilise it. For example, do species with group-specific calls only recognise theirs, or do they also distinguish between calls of other groups, just like bottlenose dolphin does with individuals. Understanding the transmissions of sounds in one species thoroughly could make it easier to find and describe them in less-studied species.

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