Vocal repertoires of two matrilineal social whale species

Long-finned Pilot whales (*Globicephala melas*)

& Killer whales (*Orcinus orca*) in northern Norway

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ABSTRACT

The aim of this study was to describe and investigate the vocal repertoire and possible factors influencing the size and composition of two matrilineal social whale species: long-finned pilot whales and killer whales in Norway. I was not able to describe the entire vocal repertoire due to the large number of animals in this population and the limitations of fieldwork and time. In this thesis I describe a vocal repertoire subset from seven groups of pilot whales and 11 groups of killer whales recorded in the Vestfjord in northern Norway during the time period 2004 until 2011.

Using observer-based acoustic analysis I could discern 129 call types and 25 subtypes for long-finned pilot whales, and 60 call types and 25 subtypes for killer whales. Per group, pilot whales used an average of 36 call types and killer whales just 25. The general structure of call types was similar, with most call types consisting of one segment and two elements with different structures. The main element structure in pilot whale and killer whale calls was an ascending frequency band. The amount of two-voiced calls was 29% for pilot whales and 47% for killer whales. In addition, I further found different call type combinations and repetitions and investigated ultrasonic whistles, already known in killer whales, but newly described for pilot whales in this study.

The main difference between vocal repertoires of the two species appeared when I looked at call type sharing between the recorded groups. Here I found that pilot whales only shared 28% of their call types and 37% of their total calls with at least one other group, whereas killer whales shared 59% of their call types and 90% of their total calls. Average group size differed: pilot whales were found in larger groups (23 animals) than killer whales (9 animals). Overall number of calls increases with group size, however, I could not find that group size influenced the number of call types. I found rather that vocal repertoire size depends on the length of recording time and of a group's vocal activity. This must be over one hour at minimum before it can be compared with another. During carousel feeding in killer whales, vocal activity increased. This indicates that behaviour does play a role in vocal repertoire size and composition, at least in killer whales where behaviour is easier to detect and measure than in pilot whales.

In 2011 I discovered a new foraging method for salmon by killer whales in Norway. The publication is presented in Chapter 6. For the first time I was able to observe the same two groups of killer whales for over three months and describe a full repertoire with 59 call types and 25 subtypes. It was not possible to separate the calling of the two groups, but nevertheless it shows that the vocal repertoire is larger than for my earlier, shorter observations. In addition, I found context-specific vocalisations during salmon feeding and non-feeding, and compared it to herring feeding and a food association call from the Icelandic killer whale

population. Specifically, certain call type combinations contained the same beginning part (call type NKW-15) in all feeding contexts, but the combinations differed for salmon and herring feeding and between groups. I discuss the possibility of referential and arousal calling in association with food in killer whales.

This thesis is summarised in Chapter 8 with a discussion of all presented results, the limitations of the research, and potential areas for further study to increase our understanding of the two species and study vocal communication more generally in cetaceans.

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CHAPTER 1 GENERAL INTRODUCTION

Vocal repertoires

For many social animals, vocal communication essentially underlies group affiliation, maintaining contact between individuals and coordinating behaviour. Vocal repertoires vary for different species and consist of all the sounds they produce, ranging from signals to address or manipulate another animal, to announce themselves and their intentions or emotional state, to sounds used for auto-communication (echolocation in bats, birds and dolphins) (Bradbury & Vehrencamp, 2011). Most animals use vocal communication, with large variations in size and complexity of the vocal repertoires. Some animals utilise only a small set of sounds to communicate. For instance, the nocturnal arboreal-dwelling lorids, such as the Calabar potto (*Arctocebus calabarensis*), use four contact calls between mother and offspring (Petter & Charles-Dominique, 1979). Most other animals exploiting vocal communication use a moderately-sized repertoire of sounds, for example bonobos (*Pan paniscus*) with around 15 vocal units and 19 sequences (Bermejo & Omedes, 1999), or ravens (*Corvus corax*) with around 12 calls/individual (Enggist-Dueblin & Pfister, 2002). There are however some species, in particular songbirds, that have increased their vocal repertoire dramatically: male nightingales (*Luscinia megarhynchos*) have over 190 discrete song types—the most diverse singing species on this planet (Kipper, Mundry, Hultsch, & Todt, 2004).

Influencing factors

The evolution of vocal repertoires is shaped and influenced by various factors. Most animals are born with a set of calls which are a result of sexual selection; in fact most mammal vocalisations are innate and species specific, and vocal learning seems rare. Signals can contain information about the species with geographical differences, gender and reproduction state of individuals—which can range from mating displays, territory claims, dominance and aggressive calls, parental care, mother–offspring communication, and contact and distress calls.

Different habitats can shape vocal behaviour, for example calling in an open space is different than in a dense forest where vegetation absorbs much of the calls and there is a high fraction of reverberation. Animals living in forests adjust their call frequencies to the scattering effect and reduce frequency modulations, producing more narrow-frequency bandwidth tonal vocalisations. One of the most complex, elongated and loud songs of terrestrial mammals are made by tree dwelling gibbons (family *Hylobatidae*) in the morning (Marshall & Marshall, 1976). In an open space habitat, daytime with high temperatures will reduce and change sound propagation of the calls, therefore animals such as songbirds call mostly at dawn and early mornings. Geographical separation between isolated populations over time will change vocal repertoires of a species and geographic dialects will develop. For example, male chimpanzees (*Pan troglodytes*) from two different populations that are geographically isolated (from the Mahale Mountains National Park, Tanzania, and the Kibale National Park, Uganda) show differences within their pant hoot vocalisations, where factors like different environment and body size might have shaped the different call structures (Mitani et al., 1999).

Many animals live in the sea and their habitat is quite different from terrestrial habitats. For instance the physical properties of sound transmission in the ocean are substantially different than in air; sound travels at a speed of around five times higher than in air and transmission loss is 60dB less. In the ocean, sound offers the primary source of information for animals living in it. Fully aquatic mammals have evolved to facilitate sounds in the sea in a way comparable to vision in humans. Toothed whales evolved a sophisticated echolocation system using a variety of different clicks and buzzes as well pulsed calls to scan their environment and build a soundscape to orient themselves in the dark, maintain contact with others, and forage. In many species echolocation sounds comprise the whole or main part of their vocal repertoires (Thomas et al., 2004). Baleen whales use the long transmission of low-frequency sounds in the sea to communicate with 20Hz songs over hundreds and even thousands of kilometres (e.g. fin whales (*Balaenoptera physalus*) (Croll et al., 2002). Social toothed whales and some baleen whales are highly vocal, which may include a variety of echolocation sounds as well as social sounds and songs.

In response to predators, prey species often change and adapt their vocal communication. Predator detection signals are relatively common in most vertebrates; for example predator deterrent signals are produced by potential prey species to avoid being attacked by predators. Predator detection signals are mainly directed towards predators, but can also function to warn other prey individuals of the presence of a predator; examples include deer calls or nonhuman primate alarm calls that function partly as warning calls to others (for review of the topic see (Bradbury & Vehrencamp, 2011)). Alarm calls are produced to warn other individuals of the presence of a predator. These signals are directed to other potential prey individuals in the surrounding, often group members. There are distinct alarm calls, or variable calls for differences in predator type or urgency of the alarm. Repetitions of calls often signal the urgency of the alarm, whereas differences in structure or calls emitted in sequence may refer to the type of predator and its environment (e.g. aerial or terrestrial); many alarm calls include additional individual identity information, perhaps to assess the reliability of the signal (e.g. false alarms from juveniles) (for review of the topic see (Bradbury & Vehrencamp, 2011). Male Campbell’s monkeys (*Cercopithecus campbelli*) use six different call types in sequences, for example; sequences of ‘krak-oo’ calls are produced in response of predator calls or other monkey alarm calls, however a ’boom’ call in the beginning of a sequence of ‘krak-oo’ calls is used to warn of environmental dangers such as falling tree branches (Zuberbühler, 2002).

On the other hand, prey can adapt their own vocal communication to their predator’s behaviour. In small cetaceans that are predated by killer whales we find an adaptation of their vocalisation to reduce predator detection: in Harbour porpoises (*Phocoena phocoena*) and Dall’s porpoises (*Phocoenoides dalli*), for example, the echolocation clicks are higher in frequency, more narrow in their bandwidth and less intense; and the centroid frequencies are above killer whales’ upper effective hearing range and have a shorter detection range, which reduces the likelihood of being detected by their main predators (Kyhn et al., 2013). Harbour seals (*Phoca vitulina*) react differently to two ecotypes of killer whales in British Columbia: when hearing calls from resident killer whales that only feed on fish, the seals do not change their behaviour in their presence; this is significantly different when confronted with calls from transient killer whales that feed on marine mammals including seals—who immediately moved away from the surface (Deecke et al., 2002). In return this predator–prey arms race resulted in adaptations of killer whales towards marine mammals: transient (marine mammal–eating) killer whales are more silent than resident killer whales in order to avoid being detected acoustically by their prey, and communication only increases after a marine mammal kill (Deecke et al., 2005).

Food association signals are produced to advertise food, its location, or quantity and quality of the food items. These signals are mainly directed and shared by conspecifics in a group of animals to attract and recruit others. Food association vocalisations are often seen in cooperative hunting operations when animals increase their hunting success with the help of others (for example, dolphins rely on others to catch schools of fish (Wursig, 1986)). In social groups food sharing can facilitate reciprocity and can help maintain contacts between specific members of the group (Slocombe et al., 2010), but also can be directed to juvenile members or to attract mates; however calling often depends whether conspecifics are nearby and on the hierarchical position of the caller (Bradbury & Vehrencamp, 2011). Some food association calls are directed at the prey to manipulate it, such as herding calls in killer whales and bray calls in bottlenose dolphins (Janik, 2000a; Simon et al., 2006). Food associated calls reported in birds and terrestrial mammals carry information about arousal but can also convey information about food: in many species the calling rate increased with the quantity and quality of food available, however specificity of calls may be insufficient for referential signalling. Most food association calls can also be used during non-feeding contexts, however these calls often show meaningful variations in structure; graded versions can convey food quality, or series or sequences of food association calls can change according to high, rare, or low quality foods (review of food association calls in (Clay et al., 2012).

Some species like bats and toothed whales developed auto-communication (an animal communicates with "itself" by sending out sounds and receiving their returning echoes) to echolocate the shape of their environment, as well as movement and composition of prey. Depending on the environment, bats use high-frequency constant or frequency-modulated pulses that are highly directional to detect obstacles in their environment. While bat echolocation ranges up to 5m in the air, due to lower high-frequency sound attenuation in the sea, dolphin echolocation ranges up to 300m. Toothed whales use short broadband or narrow-band clicks to detect their environment and moving prey. In echolocating animals vocal activity increases drastically during foraging, and clicks and pulses are the main sounds emitted (for more details on this topic see (Bradbury & Vehrencamp, 2011; Thomas et al., 2004).

Another aspect driving vocal diversity and complexity is group size and social complexity. The social complexity hypothesis of vocal communication postulates that "groups with complex social systems require more complex communicative systems to regulate interactions and relations among group members resulting from the need for increased social cognition" (Freeberg et al., 2012). A comparative study on three closely related tree-dwelling nonhuman primates species showed that the species with the most complex social structure, the red-capped mangabey (*Cercocebus torquatus*), exhibit the largest and most complex vocal repertoire of all three (Bouchet et al., 2013). In nonhuman primate species there is an indication that increasing group size and time spent grooming (social bonding) correlates with increasing size of vocal repertoires (McComb & Semple, 2005). However, due to many alternative and additional selective pressures (some of which are listed above), this is a challenging hypothesis to test.

In summary, vocal communication is complex and diverse and studying vocal communication in animals is far from simple; all aspects of environmental, social, and foraging influences have to be considered when describing and understanding vocal repertoires and behaviour of animals.

Social whales and dolphins, living in an aquatic environment where sound is the major sensory information, have evolved large and complex vocal repertoires.

Vocal communication in whales and dolphins

Terrestrial ancestors of cetaceans evolved to live in the sea, ca. 50 million years ago, and adapted to a fully aquatic lifestyle. Modern cetaceans are represented in two parv-orders: Mysticeti (baleen whales) with 15 living species and Odontoceti (toothed whales) with 70 species. Toothed whales include the super family of dolphins with 40 species, sperm whales, river dolphins, and beaked whales (e.g. Rice, 1998). Echolocation in toothed whales evolved soon after their origin, approximately around 34 mil years ago (Park & Fitzgerald, 2016). Toothed whales produce narrow beam clicks behind their melon with phonic lips and direct them forward to detect upcoming obstacles by assessing the returning echo (Au, 1997). Four groups of toothed whales have evolved special narrow-band high-frequency (NBHF) clicks, above 100 kHz, as adaptation to predator avoidance of killer whales (click frequency is above their best hearing range) (Kyhn et al., 2013; Morisaka & Connor, 2007).

Toothed whales are piscivores and often live and hunt in groups, with social organisation ranging from complex fission-fusion to multilevel matrilineal societies in which females build the core element with strong and lasting female bonds. In these matrilineal societies, group composition is stable over many years or generations and maternal care is often long, sometimes lasting a lifetime (Connor et al., 1998; Olesiuk et al., 1990). Complex, group-specific vocalisations are characteristic for matrilineal social whales, and are learned from members of the group and transmitted culturally (see e.g. (Deecke et al., 2000; Rendell & Whitehead, 2003; Yurk et al., 2002)). In contrast, fewer vocalisations with some geographical differences are used by more solitary baleen whales such as blue whales (see e.g. (Berchok et al., 2006)) or fin whales (Delarue et al., 2009).

One of the pioneers in studying vocal communication in whales was John Ford. When he started in 1978 to study the vocal behaviour of resident killer whales in British Columbia, he recorded sounds of 16 pods of resident killer whales. In his first publication he described the vocal repertoire of each of the pods (7–17 call types per pod) and investigated whether behavioural states of the pods would influence the repertoire (Ford, 1989). Further, he found that the dialects don’t change much over a period of 25 years and that such dialects evolved within a population (in different acoustic clans) due to vocal tradition through learning (Ford, 1991). The large repertoire compared to other species along with pod dialects opened up new questions, and numerous studies followed Ford’s pioneering work (e.g. (Barrett-Lennard, 2000; Beck et al., 2012; Croft et al., 2017; Deecke et al., 2000; Foster et al., 2012; Miller et al., 2004; Yurk, 2005)). Now the killer whales of the northeast Pacific are among the most studied and best understood whale population in the world.

Killer whales in the north Pacific acquired group specific dialects with each group sharing a certain amount of call types with other groups within a vocal clan, while retaining their own distinct vocal repertoire (Ford, 1991). These dialects reflect kinship and might aid their complex reproduction behaviour in avoiding in- and out-breeding (Barrett-Lennard, 2000; Deecke et al., 2010). Sperm whale matrilineal clans communicate in different patterns of coda clicks, and there are local dialects between the clans (Weilgart & Whitehead, 1997). In both species the vocal repertoire and group specific communication is learned vertically from mother to offspring but also horizontally through conspecifics or other group members (Filatova et al., 2010; Ford, 1991). Vocal learning, mimicry, and long-term vocal traditions play a major role in the development of their vocal repertoires (Foote et al., 2006; Whitehead & Rendell, 2015; Yurk et al., 2002).

Another example of vocal learning and vocal tradition is the song of the male humpback whale: the same complex songs are produced by males in one population, which differ from each population. These songs undergo yearly changes transmitted between all males in one population to sing the same song, but the same songs are never repeated (Payne & Payne, 1985). Males from one population may rapidly learn and adopt songs from a neighbouring population when confronted with it (Noad et al., 2000). The reason for the singing males is still unclear but lekking aggregations of males to attract females and other males was proposed (Herman et al., 2013).

Individual signatures have evolved in dolphins which live in complex fluid multilevel fission-fusion societies where members of groups interact with different groups frequently, and long-term associations only exist between male alliances or mother-offspring pairs (Connor et al., 2000). Through vocal learning and innovation each bottlenose dolphin creates its own signature whistle early in life. These signature whistles carry information in their time-frequency contour about the identify of a caller and are used individually, but also copied by others to address other individuals and even during the absence of the whistle owner, probably to search or refer to specific individuals (for a review of signature whistles see (Janik & Sayigh, 2013)). How widespread individual signatures are among dolphins is not yet clear, but individual signature calls and whistles were also proposed for belugas (*Delphinapterus leucas*) (Morisaka et al., 2013) and narwhals (*Monodon monoceros*) (Shapiro, 2006).

Though all social whale species seem to have evolved large and complex vocal repertoires partly or mainly through vocal learning, matrilineal social toothed whales are particularly interesting due to their closely associated groups, which can be studied for many years, and their cooperative behaviour.

Study populations (matrilineal social toothed whales)

Long-finned pilot whales (in the northeast Atlantic)

Long-finned pilot whales belong to the dolphin family and represent the second largest dolphin species after killer whales, with adult males reaching 6.5m and females 5.5m in length (Bloch & Lastein, 1993). They are widely distributed and live in circumpolar regions in both the northern and southern hemispheres and in the Mediterranean (see (Rice, 1998) and refs. therein). Long-finned pilot whales mainly occur in waters deeper than 100m, often at the edge of a geographical drop-off, with migrations between offshore and inshore waters, which correlates with the distribution of their main prey, squid. In the North Atlantic they mainly feed on squid (*Gonatus spp* and *Todarodes sagittatus*), and other deep-diving prey (Desportes & Mouritsen, 1993). Deep foraging dives up to 800 m are signalled by high activity of echolocation vocalisation and are often conducted in synchrony with other animals (Aguilar Soto et al., 2008; Visser et al., 2014).

The social structures of long-finned pilot whales seem to be similar to the resident type of killer whales of the northeastern Pacific, as they live and travel in groups with core social units consisting of 11–14 animals—which represents a matriline of mother and her direct offspring of both sexes (De Stephanis et al., 2008). These matrilines are often seen travelling together with other related matrilines in groups described as pods, with up to 100 animals gathered together a common sight. Large temporary aggregations of several pods can exceed 150 animals, called superpods, with social interactions described as both casual acquaintances and constant companions for at least 5 years (De Stephanis et al., 2008; Ottensmeyer & Whitehead, 2003).

The distribution of long-finned pilot whales in the northeast Atlantic ranges from the Norwegian coast in the east to the Faroe Islands, Iceland, and Greenland in the west. The northeast Atlantic population of pilot whales is not well studied, but they likely live in stable matrilineal groups throughout their lives, as do other pilot whales in Gibraltar (De Stephanis et al., 2008) and the northwest Atlantic (Ottensmeyer & Whitehead, 2003). Genetic investigations have shown that pilot whales killed in the Faroe hunts are all related and that males in the group do not father offspring (Amos, et al., 1993; Amos et al., 1991). It was therefore postulated that long-finned pilot whales in the northeast Atlantic live in close matrilines. Whether these matrilines all originate from the same population is not known. Given the fact that long-finned pilot whales often travel 70–111 km with a maximum of 200 km a day (Bloch et al., 2003), it is likely that the pods seen in Norway migrate to the Faroe Islands and therefore belong to the same population. The long-finned pilot whale population of my study migrated into the Vestfjord in northern Norway and stayed there for several days or weeks. Their migration behaviour or population sizes are unknown.

Long-finned pilot whales produce typical delphinid sounds, such as clicks, buzzes, and a variety of pulsed calls and whistles (Nemiroff & Whitehead, 2009; Taruski, 1979; Weilgart & Whitehead, 1990). Clicks and buzzes are mostly used in echolocation of prey and environment (Au et al., 2004); and whistles, which are tonal signals, may serve as contact calls between individuals or to maintain group contact during foraging and travelling (Taruski, 1979; Weilgart & Whitehead, 1990). Pulsed calls of long-finned pilot whales are similar in structure to killer whale calls. They are complex with different structural components, such as elements and segments (see methods); calls can be two-voiced with a lower (LFC) and an higher frequency component (HFC) (Nemiroff & Whitehead, 2009). However, in contrast to discrete killer whale call types, pilot whales seem to use a more graded call repertoire (Nemiroff & Whitehead, 2009). The vocal behaviour of long-finned pilot whales in the northeast Atlantic has not been studied before.

In summary, our knowledge about long-finned pilot whales is limited to a few studies in three different places (Strait of Gibraltar, Nova Scotia, and the Faroe Islands), thus the northeastern Atlantic population is especially poorly understood.

Killer whales (in the northeast Atlantic)

Killer whales (*Orcinus orca*) are the largest of the dolphins with males reaching up to 8–10m and weighing over 6 tons, females reaching 5–7m and weighing 3–4 tons. They are long-lived social whales with the longest living female in the wild just passing away at age 105 ((Ford et al., 2000) BBC news). Their life cycle is slow: adults reach maturity at 15–20 years, with females giving birth to 4–5 single calves during their reproductive time and entering menopause around 30–40 years of age (Foster et al., 2012; Olesiuk et al., 1990).

Of all matrilineal social odontocetes, the killer whales are the most studied, particularly regarding their vocal behaviour. There are several populations of killer whales worldwide with different foraging behaviours that separate the populations; some of them overlap in geographical areas, however they do not mix or interbreed (Ford, 2002). Most of the populations are not well studied, however it is a common agreed fact that all killer whales live in stable basic matrilineal units with different association patterns between the units and in some populations forming complex multilevel societies (Tavares et al., 2016). It seems that a difference in feeding ecology characterises the separation of three sympatric populations in the northeast Pacific: transient killer whales that feed mostly on marine mammals (Ford et al., 1998), resident killer whales that feed mainly on salmon (Ford et al., 1998), and offshore killer whales that feed mainly on sharks (Ford et al., 2011). The different feeding behaviour results in different social organisations and dynamics as well as different acoustic behaviour. Transient killer whales live in small matrilineal groups of 1–3 animals (average 2.4) which comprise a mother and 1 or 2 of her offspring. Females disperse from their mother when they are sexually mature; males either stay with their mother or disperse as well and continue to live solitary lives, adult males rarely associating with each other (Baird & Whitehead, 2000). Transient killer whales produce significantly less calls and clicks than resident killer whales, their vocalisation rate only increasing after feeding; this different vocal behaviour was correlated to their hearing sensitive prey, which increases the costs of vocalising (Deecke et al., 2005). In contrast, resident killer whales in the northeastern Pacific live in natal philopatric matrilineal societies with several matrilines where offspring from both genders stay a lifetime within or closely associated with their natal matrilineal group (Barrett-Lennard, 2000). They are highly vocal compared to transient killer whales, producing a wide range of echolocation and communication signals, such as clicks, whistles, and pulsed calls (Ford, 1989). Within resident killer whales off the coast of British Columbia group-specific dialects were first discovered in the early 1980s (Ford, 1982). Most calls were transmitted vertically from mother to offspring, and dialects evolved through accumulated copying errors, resulting in similar dialects in closely related pods (Deecke et al., 2010). However, killer whales are capable of vocal mimicry and learning (Foote et al., 2006), and therefore horizontal (intra-pod between adult animals) transmission of vocal traditions is also likely to create repertoire changes in dialects, adding more diversity to their vocal repertoire (Filatova et al., 2012).

At least three different populations of killer whales exist in the North Atlantic, one associated with the North Atlantic herring stock, one associated with Northeast mackerel stock and one farther south partly associated with the North Atlantic bluefin tuna stock (Foote et al., 2011). The killer whales in northern Norway belong to the population associated with herring, and during winter their diet is specialised on herring (Foote et al., 2012). A cooperative hunting technique has evolved, where killer whales move in an organised manner to herd herring into tight balls and chase them under the surface, where they hit the ball of herring with their tails ("tail slaps") and then feed on them individually. This technique was named "carousel feeding" (Similä & Ugarte, 1993). In the northeast Atlantic the organisation and association patterns of basic matrilineal groups is not so clear, most studies were done during large feeding aggregations when herring was abundant (Kuningas et al. 2008; Tavares et al., 2016). During this time many groups are gathered in a small area and individuals from different groups frequently associate with each other. The population in Norway is assumed to live in similar matrilineal groups as resident killer whales in the northeastern Pacific, however matrilineal groups have suffered severe damage during the long and heavy whaling era when probably as much as 2/3 of their total population was removed randomly (Oien, 1988). Many groups have been destroyed and the present killer whale population in Norway may not show a natural social lineage from descendant groups. Therefore I expect a mixture of social organisation including complete matrilineal groups as well as solitary animals and small group formations.

The vocal behaviour of this population was first described in 1995, when Hanne Strager revealed a set of call types, group dialects, and compound calls (combination of calls) of nine different matrilineal groups (Strager, 1995). Her work was followed up by Van Oopzeland et al., and Ari Shapiro and a catalogue of 103 discrete call types was developed based on the Strager classification (Shapiro, 2008; Van Opzeeland et al., 2005).

It has always been challenging to correlate behaviour to vocal communication in cetaceans due to their elusive underwater lifestyle. John Ford tried early to correlate behavioural categories to the vocalisation of resident killer whales. He could not find context-specific call types, however the vocal activity of whistles and variable calls increased during social activities (Ford, 1989). Whistles play an important role in close range communication and socialising in resident killer whales (Thomsen et al., 2002), and stereotyped whistles were produced in sequences (Riesch et al., 2008). Variable calls have been associated with arousal and close range social interactions (Ford, 1989; Rehn et al., 2007), one specific variable call type (V4) has been identified across ecotypes, thus indicating that "excitement calls" are universal (Rehn et al., 2011).

In Norway and Iceland, killer whales seem to be highly vocal during herring feeding and almost silent while travelling, with their vocalisation increasing during herring feeding (Simon et al., 2007). Vocalisations during carousel feeding include an increase of echolocation clicks, buzzes, and tail-slaps, and in Iceland a special call was identified which was suitable to manipulate herring into closer schooling during the last stages of carousel feeding (Simon et al., 2006; Simon et al., 2007). This herding call is characterised by its low frequency and long duration (ca 3 seconds) with few or no frequency modulations; thusfar this call type has only been recorded from killer whales in Iceland and Shetland, not in Norway (Deecke et al., 2011; Samarra, 2015). A study comparing vocalisation between different foraging situations of killer whales in Norway did not reveal context specific feeding vocalisation, neither during carousel feeding nor seine feeding, when killer whales feed on discarded herring from fishing boats (Van Opzeeland et al., 2005).

In summary, killer whales are well studied in many places in the world and there is substantial knowledge about their social and vocal behaviours. The northeastern Atlantic population has been studied continuously since the late 1980s: groups and individuals were photographically identified, for killer whales in Norway a vocal call type repertoire was described, and group dialects were suggested by one study on six identified groups. So far, no specific vocalisation patterns have been identified and correlated to behavioural context.

AIM OF THIS STUDY

This study aims to describe the composition and usage of vocal repertoires of groups of long-finned pilot whales and killer whales in northern Norway, thereby creating a database enabling researchers to investigate different factors influencing vocal repertoire, possible context-specific communication, as well as differences between the two species. With the results I aim to contribute to the overall knowledge of vocal behaviour in social matrilineal toothed whales, and help to understand more specific driving factors behind the evolution of complex vocal repertoires.

In particular, I will describe the vocal repertoire of both study populations in more detail in order to add important information on both structure and usage of vocalisations.

In killer whales I expect additional call types in a general larger group vocal repertoire than previously described, due to longer observations and recording times.

In long-finned pilot whales our knowledge is poor, however I would expect the vocal repertoire to include echolocation sounds such as clicks and buzzes; whistles might be more diverse including ultrasonic whistles, and there should be discrete call types in addition to graded calls similar to killer whales.

Next, I will look into factors influencing the vocal repertoire, which first might depend on the data collection (recording time) itself, e.g. a certain amount of time of vocalisation recordings must be collected for each group, in order to assess a decent vocal repertoire size. Next, I expect the size of the vocal repertoire increases with increasing group size (more animals mean more calls, and interactions between group members increases). Last, I will look into how different behavioural states will influence calling rate; we know that Norwegian killer whales are silent during travelling and highly vocal during feeding. I expect that feeding and socialising animals will vocalise more than resting and travelling animals, due to their increased social activity and cooperative feeding methods.

Further, by comparing the vocal repertoires of these two species, I aim to find out how differences in social and foraging behaviour shape vocal repertoires. Both species live in the same area and cover the same ecosystem, however they are specialised in different hunting methods and live in slightly different matrilineal group organisations. The repertoires of both killer whales and pilot whales are expected to be similar in size and complexity (number of discrete call types, variable and graded calls, sequences of calls, and the same overall structure segmentation and elements within call types) due to their similar social organisation. However, I expect structural differences (time-frequency contour) and different compositions of elements within the whales' call types due to species identification and different group dynamics.

Killer whales live in conservative, relatively closed groups and only rarely travel with other related groups or meet with distant groups for foraging and mating. The population in Norway is relatively large, with over 1000 animals, and overall relatedness between groups might be low; therefore I expect a relatively small set of discrete calls for each group and low call type sharing between groups, as found in previous studies.

Long-finned pilot whales live in a more fluid society, where matrilines often travel with related matrilines, and meetings of many matrilines are a common sight. Due to the larger pilot whale groups, I expect a larger repertoire than in killer whales and more call type sharing between groups.

Another question I aimed to answer was whether the whales show context specific vocal behaviour. In other words: Does the vocal repertoire change according to changes in behavioural contexts?

Killer whales in Norway have two distinct hunting methods on different prey; they hunt schooling herring with a method called carousel feeding and they hunt solitary salmon in a loose group formation. Although the only food-specific call found in killer whales is probably not referential but rather directed towards the prey, I expect differences in the overall call type production during feeding in contrast to non-feeding contexts. This will be shown in different calling rates and specific call types or combinations of call types. For that I look into the acoustic communication during our newly discovered salmon feeding and non-feeding communication to find feeding-specific vocalisations in Norway. In a second step I compare the structure of salmon feeding context-specific call types with call types produced during carousel herring feeding to look for similarities within the call types. I do expect differences in call type structure because the different prey and the foraging methods require different movement coordination of group members.

Hypothesis for pilot whales: as with killer whales I expect the clearest differences in vocal activity during feeding and resting and group contacts, as well as mother and offspring interactions. However, due to the low sample size of vocalisations recorded during specific behavioural contexts, my subset of data does not allow any conclusions on this topic, which remains to be answered in future investigations.

In the first two research chapters (chapter 3 and 4) I aim to answer the question of how diverse are the vocal repertories in highly social matrilineal aquatic mammals, in this case long-finned pilot whales and killer whales; and which factors could be attributed to this diversity. In the next chapter (chapter 5), I compare the vocal repertoires of the two species. Differences will be discussed according to the whales' social structure, group cohesion and size, recording lengths, and behaviour. In chapter 6, I present the published article on our discovery of salmon feeding in Norwegian killer whales; and in chapter 7, I compare specific vocalisations recorded during different feeding and non-feeding behaviours in killer whales in order to investigate food-associated calls. In the final chapter, 8, I summarise all the chapters and end this thesis with a general discussion and future outlooks.

CHAPTER 2 GENERAL MATERIAL & METHODS

Ethics statements

All observations and recordings reported in this contribution were made in the Vestfjord in northern Norway. In general no permission is needed for non-invasive research on marine mammals along the Norwegian coast. To ensure that my research was conducted according to Norwegian ethical laws, I asked the Animal Test Committee (Forsøksdyrutvalget) of Norway for permission, and they confirmed that these studies do not require any permission (approval paper ID 6516).

Study location

The Gulf Stream brings constant warm water to European Arctic waters, which keeps the area ice-free in high altitudes and enriches the flora and fauna of the marine ecosystem. As a result large fish stocks, such as herring (*Clupea harengus*), mackerel (*Scomber scombrus*), cod (*Gadus morhua*), and capelin (*Mallotus villosus*) are abundant in the northeast Atlantic (e.g. yearly ICES reports http://www.ices.dk/publications/our-publications/Pages/Annual-Report.aspx). In addition, deep fjords and the continental shelf drop-off favour deep-dwelling species such as squid. Whales and dolphins, as top predators, feed on these fish and squid species and can be found in the entire northeast Atlantic. But humans were also attracted by the vast amount of fish and settled all along the northern coast.

Norway has a very long coastline (83,281km) with many deep fjords exposed to the northeast Atlantic. Fishing has been the main source of food and income in the numerous fishing villages along the entire coast, however it was most dominant on the Lofoten Islands, where fishing of cod stocks has been conducted for more than 1,000 years. From whaling records and more recent surveys (e.g. http://www.nammco.no/) we know that more than five species of baleen whales and seven species of toothed whales have been abundant in Norway and Lofoten.

The majority of Norwegian spring-spawning herring overwinters from late October to late January in the proximity of the northern Norwegian coast, often inside protected deep fjords (Dragesund & Johannessen, 1997). With herring overwintering so close to the coastal villages, conflict between whales and fishermen occurred. Between 1938 and 1981, killer whales in Norway that follow and feed on herring were hunted down to one-third of their pre-whaling population size, to an estimated size of around 1,500 individuals (Christensen, 1988) and newer estimates ranging from a minimum of 600 individuals (Kuningas et al., 2008). The effects on whale survival and population structure are unknown, however killer whales in Norway are known to feed on multiple species of prey and follow migrations of herring and mackerel distributions offshore during summer and inshore in winter (Nøttestad et al., 2014; Vester & Hammerschmidt, 2013; Vongraven & Bisther, 2013). In addition to killer whales, many humpback whales and fin whales feed on herring in the same fjords during the winter months (own observation 2010–2016).

Both transient and resident male sperm whales are abundant in northern Norwegian waters along the continental shelf where they feed primarily on squid and different fish (Rødland & Bjørge, 2015). Other whales such as long-finned pilot whales and beaked whales may also feed in deep waters for squid. Due to the high abundance of different fish and squid populations in northern Norway, it is a suitable place to study top predators such as whales and dolphins feeding on these fish and squid.

My study was conducted in the Vestfjord in northern Norway, which separates the mainland and the Lofoten Islands.

Vestfjord

The Vestfjord lies in northern Norway above the Arctic Circle and connects the mainland and the Lofoten Islands archipelago, has many side fjords, and is more than 180km long. It runs deep in the middle at 300–700m, with the deepest side fjord (Tysfjord) being almost 900m deep. The fjord’s opening stretches over 80km from Rødøy municipality on the mainland (66°43'12 N, 12°46'39 E) to Røst municipality in Lofoten (67°31'02 N, 12°07'03 E).
The present study sites covered most of the Vestfjord, on the Lofoten side of the Vestfjord as far south as the Moskenes Straumen at the end of the Archipelago and northeast to Lødingen, and from Bodø to Tysfjord on the mainland side of the Vestfjord (see Fig. 2-1 with tracks). In 2004 and 2005 data was mainly collected inside the Tysfjord area.

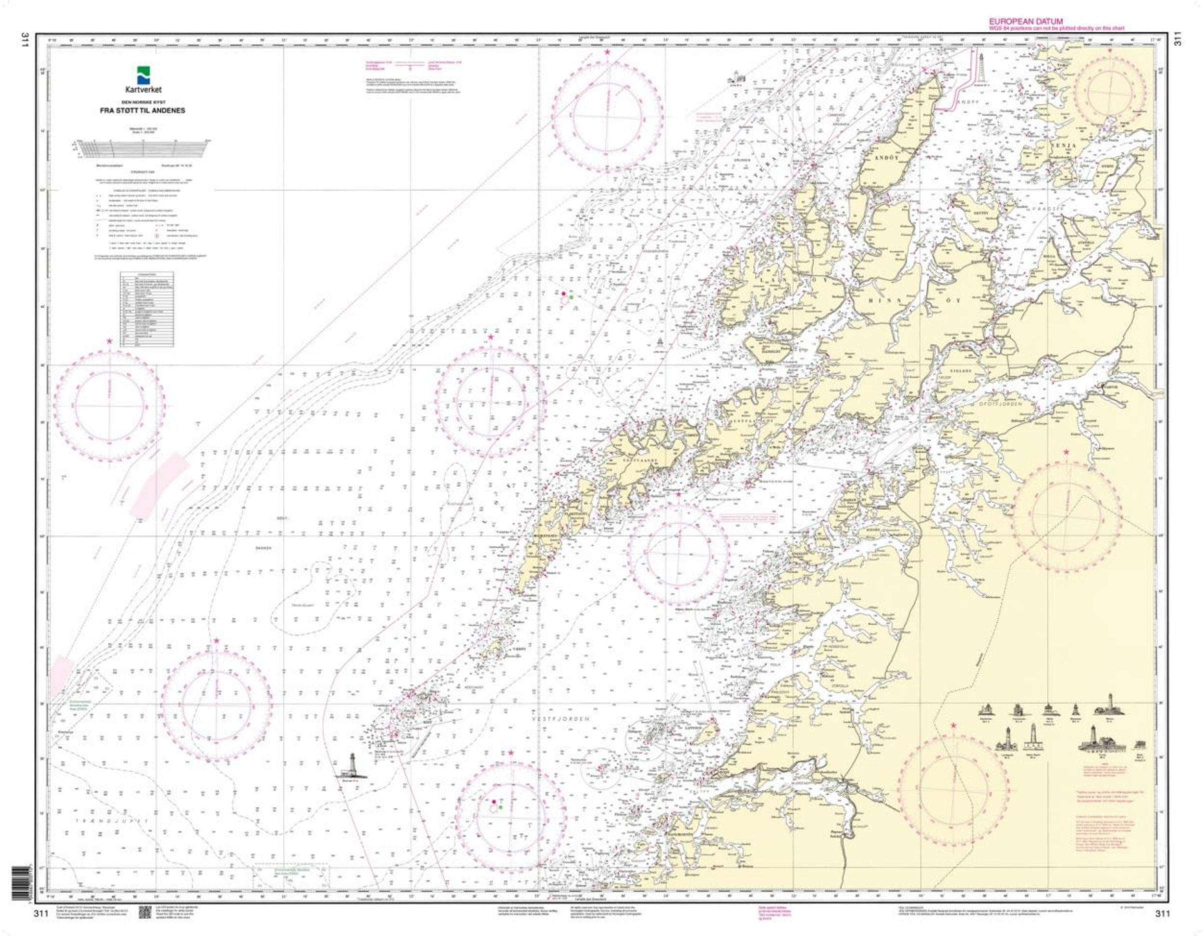


Figure 2-1. Archipelago of Lofoten (from Røst to Lødingen) and the adjacent Vestfjord towards the mainland, from Narvik in the east to Bodø in the south. The continental shelf runs along the outside of Lofoten north towards the islands of Vesteralen (Andøy, Langøy, and Hinnøy) and Senja, which can be seen in the north. (Source: Kartverket Norway.)

From 2006 the base harbour was Henningsvær, a small fishing village on an island in the middle of the Lofoten archipelago (Vagan municipality) facing the Vestfjord. From there daily boat trips were conducted in a 7.3-meter Zodiac RIB with a 250 HP outboard engine (see Fig. 2-2). From 2006 until 2010 we combined the research with whale-watching trips and had up to 10 guests on board, which financed the fieldwork. This restricted the length of tours to 4 hrs, but up two trips per day could be conducted. Additional research trips were done whenever possible. From 2011 only dedicated research trips were conducted, where time spent with whales was limited only by their behaviour, the amount of gasoline in the boat, or weather conditions. However, only in 2011 was sufficient research funding secured, resulting in more field trips.

Figure 2-2. Fieldwork in the Vestfjord, in northern Norway, using a 7.3-m Zodiac with outboard engine (Picture: Tobias Kostial).

Daily field protocol

The daily routes usually started from the Henningsvær harbour southeast towards the 100m depth line. At the 100m depth line a hydrophone was used to listen to possible cetacean vocalisations. Depending on whether or not whales were detected the trips continued either northeast to Øksfjord, south towards the middle of Vestfjorden, then either towards the southernmost tip of Lofoten or towards the mainland and Bodø; or east towards the inner part of Vestfjorden (Tranøy or Lødingen). Several listening stops were conducted to find the whales, done by ear to determine sound intensity, moving towards louder sounds until the whales became visible. Phone calls from a network of local people also directed us towards whales. Once whales were within a 50–100m range, GPS waypoints and notes were taken and then individual whales were photographed for identification. The photographs were later sorted and individual whales were classified by several human observers. Once enough photographs were taken and the whales stayed in one area, sound recordings were conducted by stopping the boat engine and lowering one or two hydrophones into the water. As long as whales were within good signal to noise ratio recording range (within 500 m, depending on sea state and background noise) sounds and behaviour as well as photos were taken continuously. When whales moved out of this range, recordings were stopped and we drove closer to the whales and repeated the recordings. This was done as long as whales were not disturbed and did not show avoidance behaviour. The end of an encounter was marked with a waypoint and notes were written down in a notebook. Back in the harbour an endnote and tracks were saved for each day.

Assessing group structure of whale encounters

During an encounter with a group of pilot whales or killer whales, first the group's structure was determined by group size and composition (how many males, females, and juveniles), and by group behaviour (coordinated behaviour, travelling, milling, resting together, synchronous feeding bouts, group splitting, etc.). Once the overall structure of an encounter was determined as one matriline or several matrilines, photos of individuals were taken within one matriline. In groups consisting of several matrilines, each matriline was studied until we had sufficient data and then we moved to the next matriline. On occasions when several matrilines were seen mixed together we positioned the boat close to the centre of the aggregations and recorded as long as possible (until the whales moved out of recording range), following them until they split again into their separate matrilines. Photos were later in the lab compared to earlier encounters in order to look for resightings of individuals, to understand the smallest matrilineal structure within an encounter.

Data Collection

In total I conducted field trips and collected data for over 13 years starting in 2004 until 2016. For this thesis I included only a sub-dataset of pilot whale and killer whale observations from the first 8 years, from 2004 until 2011, which includes 379 field trips. This subset of data was used to create baseline data for both photo-identification and vocal repertoires for pilot whales and killer whales in northern Norway.

I conducted early fieldwork mainly inside the Tysfjord area during winter months in 2004 and 2005 in cooperation with whale-watching companies and in 2006 with my own boat. The Norwegian spring-spawning herring population used this area as overwintering grounds. In 2007 a shift in migration and overwintering grounds towards more offshore areas and in more recent years farther north along the Norwegian coast moved my fieldwork towards the summer months around the Lofoten Islands and the Vestfjord. Fieldwork from 2007 until 2011 was conducted with my own boat and from the harbour of Henningsvaer on Lofoten.

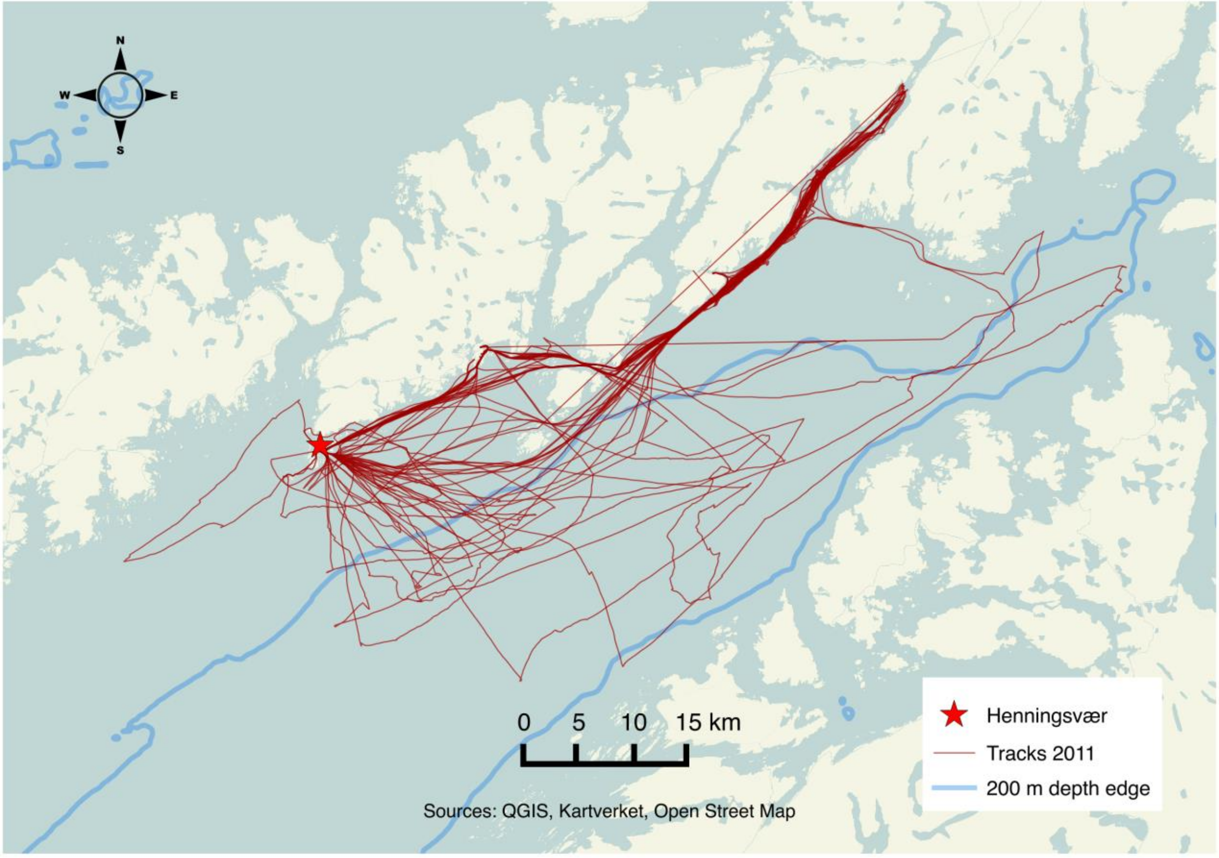


Figure 2-3. Example of the range of daily boat research trips conducted in one year (2011, N=43). This map shows the overall study area with the GPS tracks of daily research trips recorded with a handheld Garmin Etrex20 (map by Felipe Matos 2015 based on my logs).

Behavioural notes

The entire track of the boat trips and waypoints at the beginning and end of an encounter with whales was recorded using a Raymarine E80 chart plotter mounted on the boat, and a handheld Garmin GPSmap 78S or a Garmin Etrex 20 (see example of tracks in Fig. 2-3).

During the course of the day, recording track numbers and data on the whales' behaviour were written down in a notebook, and all field notes were later copied into an Excel table. Behavioural categories were of daily research trips and sorted in overall group behaviour; and pooled in broad behavioural categories of surface behaviour such as travelling (different speed), resting, milling, socializing, and feeding were collected using continuous or ad libitum sampling (Mann, 1999). In addition individual behaviour was collected as event sampling in which short-term behaviour such as jumps, spy hops, mother and offspring meetings, and other behaviours were noted (see Table 2-1).

Table 2-1. Behavioural categories and explanations of group behaviour (continuous sampling or ad lib) and examples of individual behaviour (as event sampling).

Continuous sampling group	**Event sampling individuals**
Travelling: slow (≤3 knots) medium (4–5 knots) fast (6-10 knots)	Breaching Animals swim in a row or close to each other, body contacts Animals are spread out
Resting: Animals calm at surface very slow travelling	Body contacts Mother-calf contact Nursing
Milling/logging: Animals calm at surface, body emerged look like logs floating in the sea	Body contacts and vocalisation in air
Socialising: Active surface behaviour of most of the animals in the group, often after feeding. Group meetings, events increase, Vocalisation increases	Approaching our boat Vocalising in air Play: Turn on back, roll-over, jumps Peeing in air, body contacts Spy hops: head out of water
Feeding: Killer whales carousel feeding: buzzes and tail slaps, high surface activity, group chase, birds. Killer whales salmon feeding: scan fjord, jumps, loud vocalisations, individual chase Pilot whale deep dive feeding: Echolocation clicks increases, synchronous diving and whales are underwater for 10 min or more, synchronous surfacing.	Breaching Fish in mouth Body contacts Tails in air Spy hops Synchronous swimming

Photo-ID

Photo identification of individual whales has been used for over three decades (Bigg, 1982). In this study I tried to take as many pictures (see e.g. Fig.2-4) of individuals in a group as possible using different equipment. In 2006–2009 I used a Canon EOS-D30 and in 2010 a Canon EOS-D1 Mark IV camera, with either a Canon EF 70–200 mm or a Canon EF 100–400 mm lens, depending on light conditions.

Figure 2-4. During fieldwork in northern Norway, Photo-ID picture-taking of killer whales using a Canon EOS-D1 Mark IV camera, with a Canon EF 100–400 mm lens.

During encounters I started by taking right-side pictures, also trying to photograph each side of single whales' dorsal fins (see Fig. 2-5, 2-6, 2-7), and when possible their entire bodies during jumps in order to identity scars, pigmentations, and nicks distinguishing individual whales, e.g. (Auger-Méthé & Whitehead, 2007). Whales sometimes have deformed bodies and can be identified through overall body shape (see Fig. 2-8) or by the shape of the white eye patch of killer whales (Berghan & Visser, 2000). For both species, pilot whales and killer whales, Photo-ID catalogues of individuals with associated animals in the group encounter were created. For each encounter the date, time, place, and source of data; as well as group composition and direct associations—e.g. mother calves—were written down. These catalogues provide a foundation for understanding group dynamics and for further studies on behaviour and acoustics.

In encounters with many whales and several matrilines that can move fast over a large area, it becomes difficult to take pictures of all individuals in such a large group. In this case I therefore focused on photographing whales within 150m of the boat, and whales closely associating with one another representing a matrilineal group. Once sufficient photographs of individuals in one matrilineal group for Photo-ID were taken, the boat was stopped, the engine turned off, and sound recordings were started.

Figure 2-5. Example of Photo-ID of a male pilot whale (NPW-D-10) with nicks and scars.

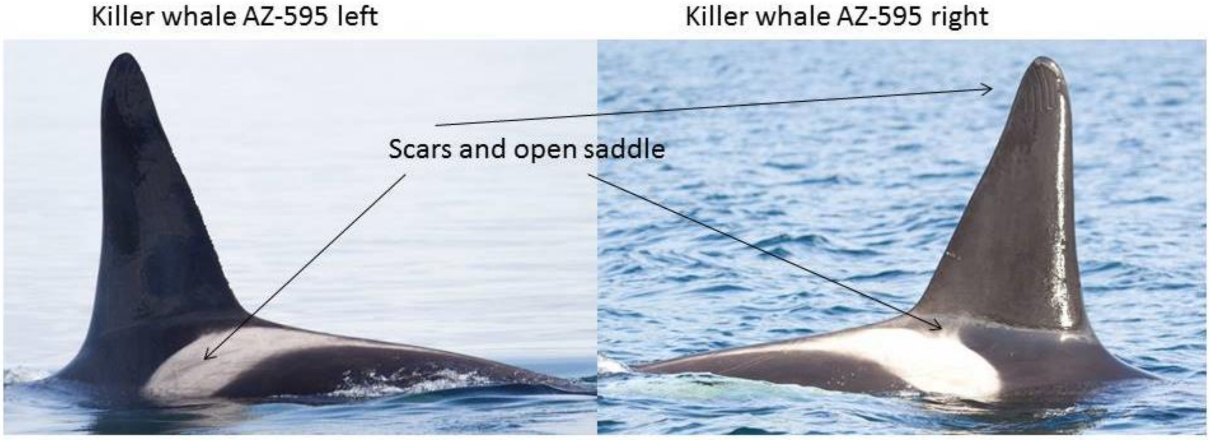


Figure 2-6. Example of Photo-ID of a male killer whale (NKW-AZ-595) with scars and open saddle.

Figure 2-7. Example of Photo-ID of a female killer whale (NKW-BR-03) with middle nick, scars and open saddle.

Figure 2-8. Killer whales can have unique shapes or cut dorsal tops. This is an example of NKW-X-163, an individual with a deformed spine.

Sound recording

During the course of my study I used different sound recording equipment (see Table 2-2). Initially in 2004, I borrowed a hydrophone system (B&Kjær 8103, Nexus 2692-A0S4, B&K, Sony Dat recorder), and in 2005 I bought my own hydrophone with a broadband recording range (Reson TC4032, see Fig. 2-9). From 2005 onwards one or two Reson TC4032 hydrophones (usable frequency range 5Hz–120kHz with a linear range of 10Hz to 80kHz, receiving sensitivity: ±2.5dB, -170dB re 1V/ µPa, omnidirectional ±2dB at 100kHz) were used, which I lowered directly ca. 18m into the water from the Zodiac boat, when in close proximity (50–100m) to the whales. Sound was amplified and recorded with different mobile recording devices, in 2004–2008 with a sampling frequency of 48kHz and in 2009–2015 with a sampling rate of 192kHz. The filters of the amplifiers were set as follows: low pass filter to 100kHz to avoid aliasing effects of the lower recorder sampling rate, and high pass filter turned off if no background noise was present or set to 100Hz to minimise flutter noise from water movement and waves or boat noise. The hydrophone has a pre-amplifier of 10dB, and additional amplification was set and adjusted to keep an optimal recording level. In good signal to noise ratio situations, e.g. sea state zero, no background noise and animals close to the hydrophone, no additional amplification was needed. But when whales moved away and the vocalisations became weaker the amplification was increased so the recording levels stayed the same. No more than an additional 20dB were used, and recordings were stopped when signals became weaker or background noise increased. When possible whales were approached and recorded again with higher signal to noise ratios. At the first sign of disturbance of the whales (disappearing at approach, sudden change of swimming direction or behaviour, repeated tail slapping), we ceased the recordings and waited 30 min before resuming our studies. If the whales were repeatedly disturbed we terminated the field encounter with that group.

GPS coordinates were taken at the beginning and end of an encounter, and notes of the whales' behaviour were continuously written down simultaneously with the sound recordings.

Figure 2-9. From 2005–2011 I used one or two Reson TC4032 hydrophones with a 20m cable and an ETEC A2002 amplifier in a watertight Pelicase for underwater sound recordings.

Table 2-2. Sound recording equipment used in different years:

Year	Hydrophone	Amplifier	Recorder	Sampling rate
2004	B&Kjær 8103	Nexus 2692-A0S4, B&K	Sony Dat recorder	48kHz
2005–2009	Reson TC4032	Etec A2002	Edirol-R09 (Roland)	48kHz
2009–2010	Reson TC4032	Etec A2002	Korg MR-1000	192kHz
2011–2016	Reson TC4032	Etec A2002	744T Sound Devices	192kHz

Sound analysis for visual categorization

The sound recordings (PCM-24 format) were analysed using Avisoft-SASLab Pro 5.2 (R. Specht, Berlin, Germany) (see Fig. 2-10). All recordings were scanned by audiovisual inspection of the sounds, based on FFT spectrograms. Different vocalisations of the whales were annotated and classified by "hand".

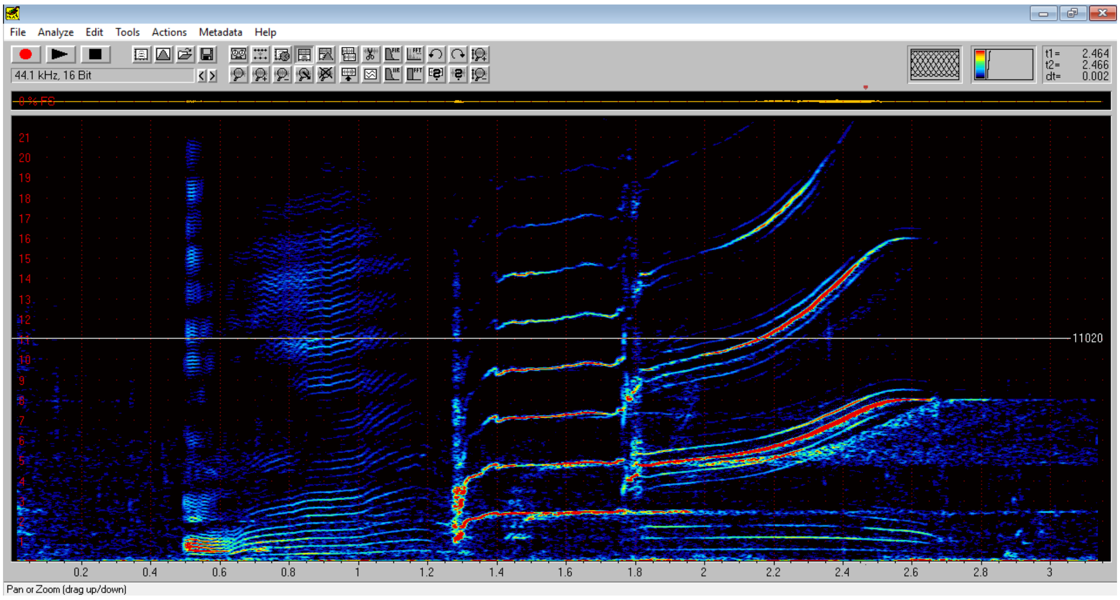


Figure 2-10. Spectrogram of killer whale sounds using sound analysing program Avisoft-SASLab Pro 5.2 (R. Specht, Berlin, Germany).

I described the entire vocal repertoires, including clicks, buzzes, tonal and noisy sounds, by analysing spectrograms from recordings at two frequency ranges: 0–24kHz and 0–96kHz (only for 2009–2010 recordings). The lower frequency range recordings with a sampling rate of 48kHz were computed using an FFT spectrogram window length of 1024 time steps, frame size 100% and a Hamming window with a temporal resolution of 87.5% overlap unless otherwise noted. The higher frequency range recordings with sampling rates of 192Hz were first computed using an FFT spectrogram length of 1024 time steps; and high frequency (24–96kHz) clicks, buzzes, and whistles were detected. Then in a second step I down-sampled the recordings to a sample rate of 48kHz in 512 time steps with an anti-aliasing filter in order to compare them to other recordings with lower sampling rates.

The recordings where systematically scanned for whale calls that could be distinguished and described according to their spectral features. Whale calls are pulsed calls consisting of rapidly produced broadband sound pulses; the calls' tonal properties are caused by high pulse-repetition rates (PRR) which are reflected in the frequency intervals between the frequency bands as harmonics (Schevill & Watkins, 1966). These calls can vary from simple, single element and single time-frequency contour to more complex structures with two components of time-frequency contours (biphonic or "two-voiced" calls, according to a study which found that dolphins produce their clicks on the "right" sides and whistles on the "left" sides of their heads (Madsen et al., 2013)). To define the two different components in time-frequency contours within a call I followed the definition by Miller 2002, who described two-voiced-calls as those with a lower frequency component (LFC) and a higher frequency component (HFC) with sidebands of HFC's representing the PRR of LFC (Miller, 2002; Miller et al., 2007). The HFC has a weaker attenuation than the LFC and encodes cues of the signallers' orientation (Miller et al., 2007).

I sorted calls from Norwegian pilot whales (NPW) and Norwegian killer whales (NKW) that were visually and audibly possible to identify according to recording quality, signal to noise ratio, and overlaps with other vocalisations. I then classified the calls that had similar distinct frequency contours (same frequency and temporal structures such as segments and elements) into different call types and numbered them, added the group, the quality and date as well as the time digit of the position in the recordings, e.g. NPW-001-A-B-2016-02-16_00-01. Distinctive features that identify call types are different structures in LFC's, HFC's, segments, and elements (see Fig. 2-11). Segments are separated by a silent part, whereas elements are subunits of a call that are separated by abrupt frequency shifts (see (Yurk, 2005)). Shapiro et al., found that using subunit based methods for categorizing Norwegian killer whales seemed more promising in understanding how killer whales generate their vocal repertoire (Shapiro et al., 2011). I used the composition of segments and elements as well as the overall contour of an element structure to classify discrete call types. Further, I described elements according to their overall shape in frequency and time into ascending-, descending-frequency band, U-shape (descending—one inflection point—ascending frequency band), ∩-shape (inverted U), buzzes (clicks in rapid repetition), noise parts (no harmonic structure visible), whistles (frequency band with many inflection points), constant sidebands and hook shape (with 2 inflection points), frequency bands (see Figs. 11 and 12). I classified the calls into different call types based on their similar acoustic features, such as fundamental and main frequency contours, two-voiced components, segments and, most of all, the same elements within a call type, and duration.

A call was categorized as a subtype of the same call type if the call varied in duration, did or did not have an HFC, or had an additional structure in the beginning or in the end which was not detected by itself as an element (due to short duration or variable structure). Thus call types with the same core element but small additional structures have been categorized as call sub-types. In this respect I don't follow the same method as described in earlier studies (Shapiro, 2008; Strager, 1995; Van Opzeeland et al., 2005; Van Parijs et al., 2004), they classified calls into subtypes if their defined core elements had additional elements, whether or not they were seen separately. For example in (Strager, 1995) Figure 2, following these classified subtypes of call type N9 (call type NKW-28 in my study), would have resulted in my classification into different call type combinations (e.g. NKW28+11+42) and only 3 subtypes would have been included (NKW28i, NKW28ii, NKW28iii). This is the reason I did not use the earlier call type repertoire description of Norwegian killer whales, which included 103 different call types (Shapiro, 2008; Strager, 1995; Van Opzeeland et al., 2005), instead starting my own vocal repertoire catalogue.

Calls were further described according to their quality (signal to noise ratio and completion of the signal): category A calls have a very good signal to noise ratio, and the whole contour with LFC and HFC is visible on the spectrogram without background noise; category B describes calls with complete contours but some background noise or overlap with other calls; category C calls have some disruption in their contour due to less signal to noise ratio and greater distance from the receiver; and category D calls had the worst signal to noise ratio where calls are disrupted and can hardly be detected. All other calls were excluded from the analysis and saved in a folder of weak calls. Calls from all 4 categories were used for the description of the vocal repertoire of the two species. For the statistical analysis, only calls from quality categories A and B were used.

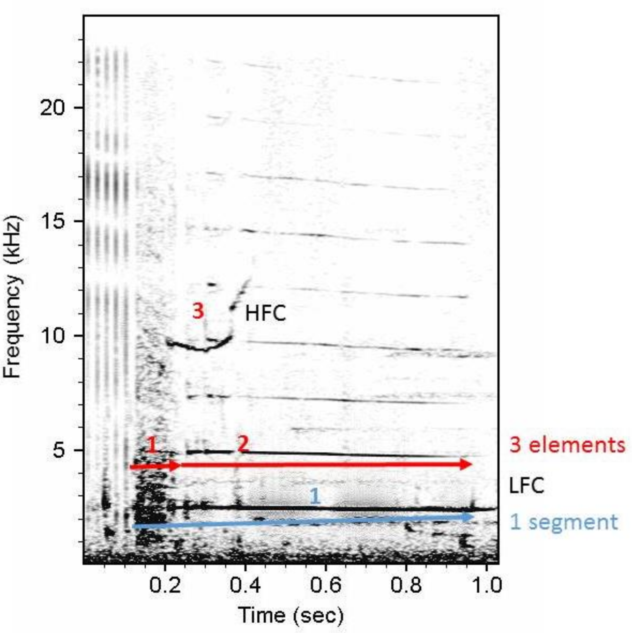


Figure 2-11. Example of a call type (NPW-49) from long-finned pilot whales with one segment and three different structured elements (buzz + descending sideband + HFC ascending) and a lower (LFC) and higher frequency component (HFC).

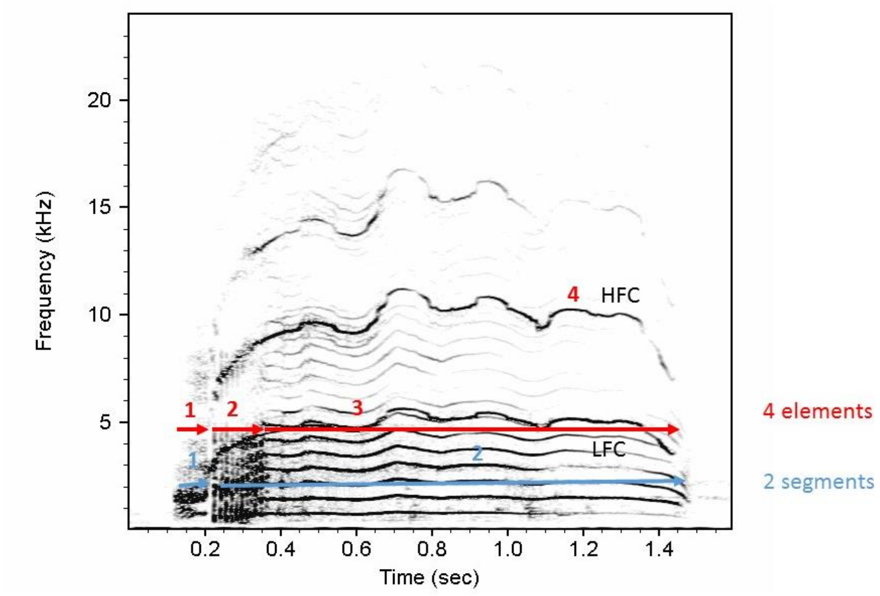


Figure 2-12. Example of NKW call type (NKW-061) with two segments and 4 elements (LFC buzz + buzz + constant sideband; HFC whistle).

Call type combinations: Whenever call types were detected in series with no or only a short time gap in between and no overlap of the calls, they were classified as call type combinations, e.g. NKW-28+11.

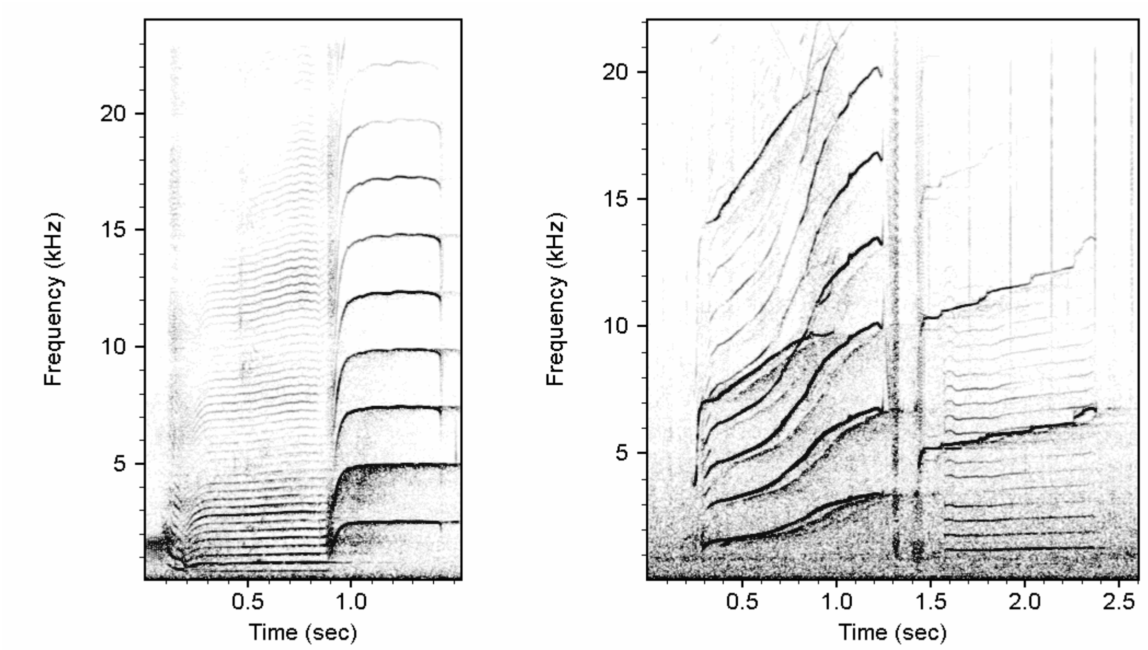


Figure 2-13. Killer whales combine call types; here are two examples of call type combinations: NKW-28+11 without time gap in between the calls and NKW-46+41 with a short time gap, but no overlaps of the calls.

Whistles of dolphins are described as pure tonal sounds that vary in frequency, infliction points and duration (e.g. (Ralston & Herman, 1995; Taruski, 1979)). In two-voiced calls of pilot whales and killer whales the higher frequency component represents a tonal call that if produced alone would resemble this previous description of dolphin whistles. However, the significance of whistles of pilot whales and killer whales in contrast to pulsed calls is not well studied, yet it has been suggested that whistles are used for close range communication (Riesch et al., 2008; Taruski, 1979; Thomsen et al., 2002; Weilgart & Whitehead, 1990). It is therefore important to include whistles in the vocal repertoire together with call types. Since many of the call types were purely tonal in structure or mixed with buzzes, pulsed/noisy elements (see Fig. 2-14), making a clear distinction between a whistle and call type was difficult. False killer whales and short-finned pilot whales also showed transitional stages between pulsed calls and whistles, and calls were visually classified into different categories without differentiating between them (Murray, et al., 1998; Sayigh et al., 2013). In addition most of the two-voiced call types had higher frequency components resembling such a distinct structured whistle and were part of a call type. For this reason I classified tonal whistles, or mixed calls with distinct frequencies, as new call types. In my classification I categorized vocal signals as whistles when the sounds were tonal in structure but with a variable frequency contour that made it impossible to classify into a distinct call type. Further, these whistles were classified in audible (0–20kHz) and ultrasonic (20–90kHz) frequency categories.

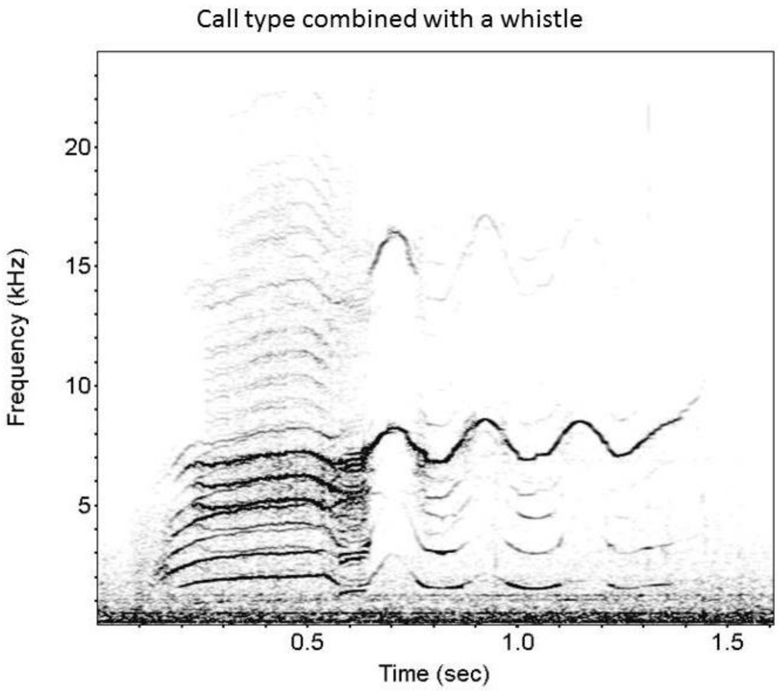


Figure 2-14. Mixed pulsed call of a long-finned pilot whale with whistle element. Whistles are often combined with pulsed calls; it is therefore difficult to make a clear distinction between a whistle and a pulsed call. This is the reason I classified discrete whistles into call types.

Classification and observer agreement:

To verify the observer-based classification of the calls into different call types, two additional trained reviewers independently rated all calls categorized into this classification. Calls were either agreed or not agreed upon call type classification, or were rated as uncertain.

Description of the vocal repertoire—catalogues

After all recordings were systematically scanned, and calls classified into call types and subtypes and verified by the two reviewers, I created a vocal repertoire catalogue of all call types and call type combinations. All copied calls produced by the different groups were sorted into different folders and I arranged sample spectrograms in a Word document and described all call types and subtypes along with information about date, place, group, equipment, and basic acoustic features (frequencies, duration, segments, structure, and arrangement of elements). Behavioural notes with date and location were correlated with the different recordings on different tapes. This way vocalisations could be isolated for different group encounters and behaviour.

Call type sharing—investigation of group-specific calls

After all call types were sorted and double checked I assessed the vocal repertoire for each group, compared call type sharing between the different groups, and identified the degree of group-specific calls and call type sharing. Due to the high variability of data collected between group encounters, weighted arithmetic means were calculated for call types produced by groups and call type sharing between groups.

The results from the pilot whale recordings were validated with an another analysis not based on my classification, rather on the distributions of cepstral coefficients in randomly selected ensembles of calls from each group; for a more detailed description of the method please refer to (Vester et al., 2016). This analysis could not be performed on the killer whale data due to the low number of high quality samples from the groups.

CHAPTER 3 VOCAL REPERTOIRE OF LONG-FINNED PILOT WHALES

Summary: The vocal repertoire of long-finned pilot whales in Norway was previously unknown. Here I describe 129 different call types and 25 call subtypes, as well as a variety of other calls and ultrasonic whistles from recordings of 7 different long-finned pilot whales. Pilot whale groups used 36 call types per group (weighted mean) which ranged from 7 to 47 call types per group. This makes it the largest and most complex vocal repertoire reported in mammalian species. Further, the pilot whales I recorded belong to the same acoustic clan and exhibit group-specific vocal communication.

Introduction: Long-finned pilot whales (*Globicephala melas*)

Figure 3-1. Long-finned pilot whales often spy hop (raise their heads out of the water) during socialising and observing activities above water; here are two pilot whales in the Vestfjord in northern Norway spy hopping together (Photo: H. Vester).

Long-finned pilot whales are common in Norwegian waters and can be seen year-round with peak occurrences during summer months. They are often sighted by whale watching boats in northern Norway, sometimes in large numbers exceeding 200 animals (own observation and personal communication with Arctic Whale Tours, Seasafari and Andenes Whale Watching). However, no study has been conducted on the species and I commenced my research on the occurrence, abundance, and vocal and social behaviour of long-finned pilot whales in the Vestfjord in June 2007. In this thesis I present the results from my early study through 2012.

Methods (see chapter 2 for data collection and analysis)

Results

Data collected and Photo-ID

I studied long-finned pilot whales in the Vestfjord in northern Norway from 2006–2016 (see Fig. 3-2). For the present Photo-ID studies I used a subsample of photos from 2006–2012 during 26 encounters and a total observation time of 64:24 hrs (see Table 3-1). Through Photo-ID I could identify a total of 271 individual pilot whales in 11 groups (group A with 22 members, B with 36 members, C with 7 members, D with 32 members, E with 18 members, F with 9 members, G with 4 members, H with 47 members, I with 8 members, J with 26 members, and K with 62 members).

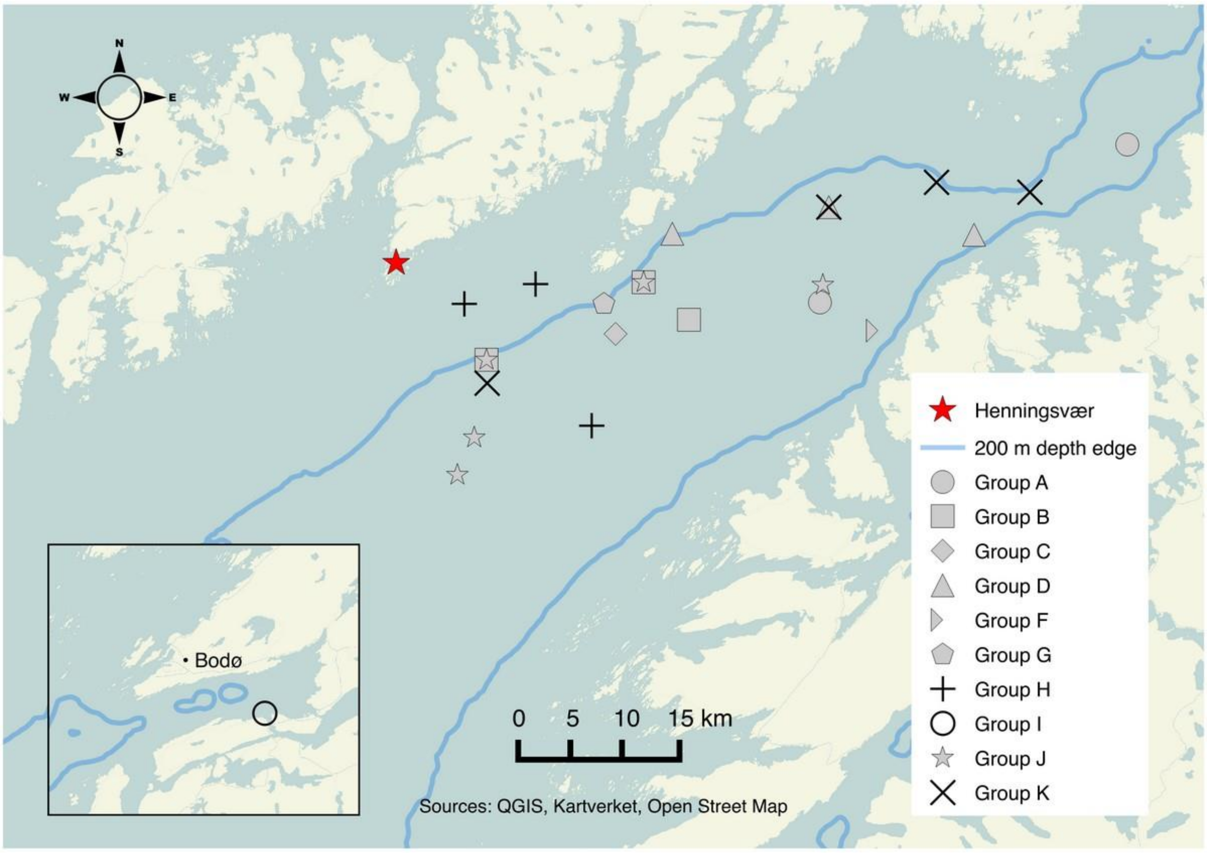


Figure 3-2. During my fieldwork from 2006–2012 I encountered long-finned pilot whales in deep areas of the Vestfjord. In total I encountered 10 different groups on one or more days. One encounter (group E) was excluded from the map since the photographs were collected outside the study area (Vesterålen, Stø) (map by Felipe Matos, based on my logs).

Over 271 whales were identified through Photo-ID using distinguishing markings on individual pilot whales. When identified individuals did not appear in another encounter they were considered a new group, however due to the low number of encounters and resightings this may not represent their natal pods. Some animals and their groups appear to return from year to year, and spend time in the same locations inside the Vestfjord (e.g. group J in Table 3-1). During the encounters pilot whale group size varied from 4 to 62 animals, with an average group size of 25, one matrilineal group typically consisting of 7–20 animals and several matrilines travelling together creating pods of up to ca. 60 animals. Sometimes several pods combined to create superpods, which can contain more than 200 animals. A group of animals was considered a pod when specific matrilines were photographed together in the same encounter and at least some members within the matrilines were resighted in another year. However at this stage I am unable to conclude that members of a pod are related matrilines. For simplicity matters the pod encounters were given a capital letter and called group A, group B, and so on.

From my observations, it seems that at least one group of pilot whales enters the Vestfjord every month with peak occurrences (several groups and matrilines at the same time) from April to September when food (squid but also fish, such as mackerel) availability is highest.

Table 3-1. Pilot whale encounters in northern Norway from 2006 until 2012, with group affiliation and total number of identified members in the group; identified individuals during this specific encounter and resightings of identified individuals; and the location, observation time and recording, and behavioural stages and comments on the encounters.* Three encounters were conducted by photographers outside this study. Recordings from highlighted encounters were used for the acoustic analysis of this thesis.

Date	**Groups**	**Location (N/E)**	**group ID**	**ID's**	**Re-sighting**	**start**	**end**	**Observation time**	**Sound recording**	**Behaviour**
2011-05-15	Group A	68 07.68/15 08.95	22	6	0	15:38:00	0:51:00	9:03	02:44:00	Travelling, resting, milling, feeding
2011-06-19	Group A	68 15.39/15 49.34	22	16	1	17:41:00	20:11:00	2:30	01:00:00	Travelling slowly, resting, meeting AWSD
2010-07-03	Group B	68 04.87/14 25.13	36	28	0	11:45:00	18:40:00	6:55	03:00:00	Slow travelling, socialising
2012-07-07	Group B	68 06.83/14 51.74	36	14	8	21:05:00	21:57:00	0:52	00:47:30	Slow travelling, foraging
2012-07-08	Group B	68 08.67/14 45.78	36	1	1	04:30:00	5:30:00	1:00	00:00:00	Slow to medium travelling, meeting, foraging, J-1 was with them
2006-11-10	Group C	68 06.14/14 42.09	7	7	0	10:00:00	10:43:00	0:43	00:13:00	Milling, slow travelling, boat approach
2007-06-15	Group D	69 07.49/15 19.53	32	8	0	15:16:00	15:58:00	0:42	00:00:00	Slow travelling, boat approach
2009-08-10	Group D	68 11.04/14 49.55	32	4	3	19:26:00	23:58:00	4:32	01:07:00	Milling, slow travelling, socialising
2009-08-11	Group D	68 10.99/15 29.20	32	32	8	10:44:00	14:55:00	4:11	02:25:00	Milling, socialising, foraging, resting
2012-06-13	Group D	68 12.34/15 10.12	32	2	2	13:23:16	14:08:42	0:45	00:00:00	2 males of D with group K
2007-09-16	Group E	Andenes*	18	18	0	14:52:00	15:19:00	0:27	00:00:00	boat approach, socialising
2007-06-28	Group F	68 06.30/14 76.56	9	9	0	11:02:00	11:52:00	0:50	00:31:00	Milling, boat approach
2008-07-14	Group G	68 07.61/14 40.56	4	4	0	17:06:00	19:16:00	2:10	00:50:00	Milling, socialising, boat friendly
2009-06-09	Group I	Vestfjord Saltstraumen by Bodø*	8	8	0	08:54:00	9:31:00	0:37	00:00:00	approached boat
2009-05-22	Group H	68 08.58/14 31.58	47	3	0	11:37:00	14:36:00	2:59	00:00:00	Milling, socialising, resting
2009-05-22	Group H	68 07.61/14 22.22	47	29	0	18:47:00	20:24:00	1:37	02:45:17	milling, resting, boat approach
2009-05-24	Group H	68 01.63/14 38.96	47	15	7	10:02:00	12:53:56	2:51	01:20:39	Milling, resting, spread out
2009-07-13	Group J	68 01.05/14 23.52	26	13	0	19:35:00	21:20:00	1:45	00:41:00	Travelling slowly, boat approach
2009-07-13	Group J	67 59.21/14 21.31	26	7	3	23:17:00	2:22:00	3:05	02:30:00	same group, milling, socialising: spyhopping, tail-splashing, boat approach
2010-06-08	Group J	68 08.54/15 09.33	26	17	8	20:18:00	21:58:00	1:40	01:06:23	First fast travelling - avoided boat, later calmed down, slow travelling
2010-07-03	Group J	68 04.87/14 25.13	26	4	4	16:44:00	18:40:00	1:56	00:18:00	Travelling and milling with group B
2012-07-08	Group J	68 08.67/14 45.78	26	1	1	04:30:00	5:30:00	1:00	00:00:00	J 1 seen travelling with group B (26), more animals in the distance
2012-06-10	Group K	68 03.72/14 25.22	62	16	0	21:30:00	01:15	3:45	01:56:00	Travelling slowly, meeting, foraging, AWSD
2012-06-13	Group K	68 12.34/15 10.12	62	46	1	13:52:00	19:36:00	5:44	01:18:00	2 males from D were seen (D6, D15)
2012-06-16	(Group K)	68 13.55/15 24.27	62	n/a	n/a	23:46:00	2:30:00	2:44	00:43:00	foraging, AWSD with them, impossible to get close, only blurry pictures
2012-07-05	Group K	Vestfjord, Tranøy*	62	2	2	n/a	n/a			boat approach
Total					49			64:24:22	25:15:49	

Sound recordings and analysis

For the present sound analysis I used a sub-dataset from 2006–2010. Recordings and observations were made between November 2006 and August 2010 in the Vestfjord in northern Norway, over 13 encounters with multiple recording sessions from each of the different groups of long-finned pilot whales we encountered.

During the 13 encounters with pilot whales I collected 35:15 hours of observation and a total of 16:47 hours of usable sound recordings. I found the pilot whales in an area more than 150km in range, mainly in waters deeper than 200m, over a period of 2–6 weeks. The study sites covered most of the Vestfjord, on the Lofoten side of the Vestfjord as far south as Reine and northeast to Lødingen, and from Stegen to Tysfjord on the mainland side of the Vestfjord (see Fig. 3-2 map of encounters in Vestfjord).

From the recording and observation sessions I could identify 161 individual pilot whales from seven different groups/encounters (group B with 36 members, C with 7 members, D with 32 members, F with 9 members, G with 4 members, H with 47 members, and J with 26 members). The average group size was 23 with the smallest group consisting of 4 identified members and the largest 47 members. Two groups were encountered during two different years; only groups B and J were seen together during one encounter in 2010 (see Table 3-2).

Table 3-2. Data collected from long-finned pilot whales and killer whales in the Vestfjord in northern Norway from 2004–2011. The pilot whales were observed and recorded from 2007 to 2010 during 13 different encounters with seven groups; 4572 calls were used and classified into 154 different call types.

DATA COLLECTION	LONG-FINNED PILOT WHALES	KILLER WHALES
Date	2007–2010	2004–2011
Recording time (hh:mm)	**16:47**	**23:02**
Groups with ID’s	7	11
Individual ID’s	161	159
Group size ID’s	23 (min 4 max 47)	9 (min 4 max 20)
Average call types / group	36 (min 7 max 47)	25 (min 2 max 37)
Total calls (N)	**4572**	**3731**
Call types	**129**	**60**
Call subtypes	**25**	**25**

Vocal repertoire—description

The following description of long-finned pilot whales' vocal repertoires is based on 1007 minutes of recording time and 4572 selected calls. As previously described (Nemiroff & Whitehead, 2009; Taruski, 1979; Weilgart & Whitehead, 1990), I found a variety of broadband clicks and buzzes, which are clicks produced in repetition with small intervals in different frequency ranges, with the main energy at frequencies 20–30kHz and 40–60kHz (see Fig. 3-3). These clicks and buzzes are typical for dolphin echolocation (Au, 2004).

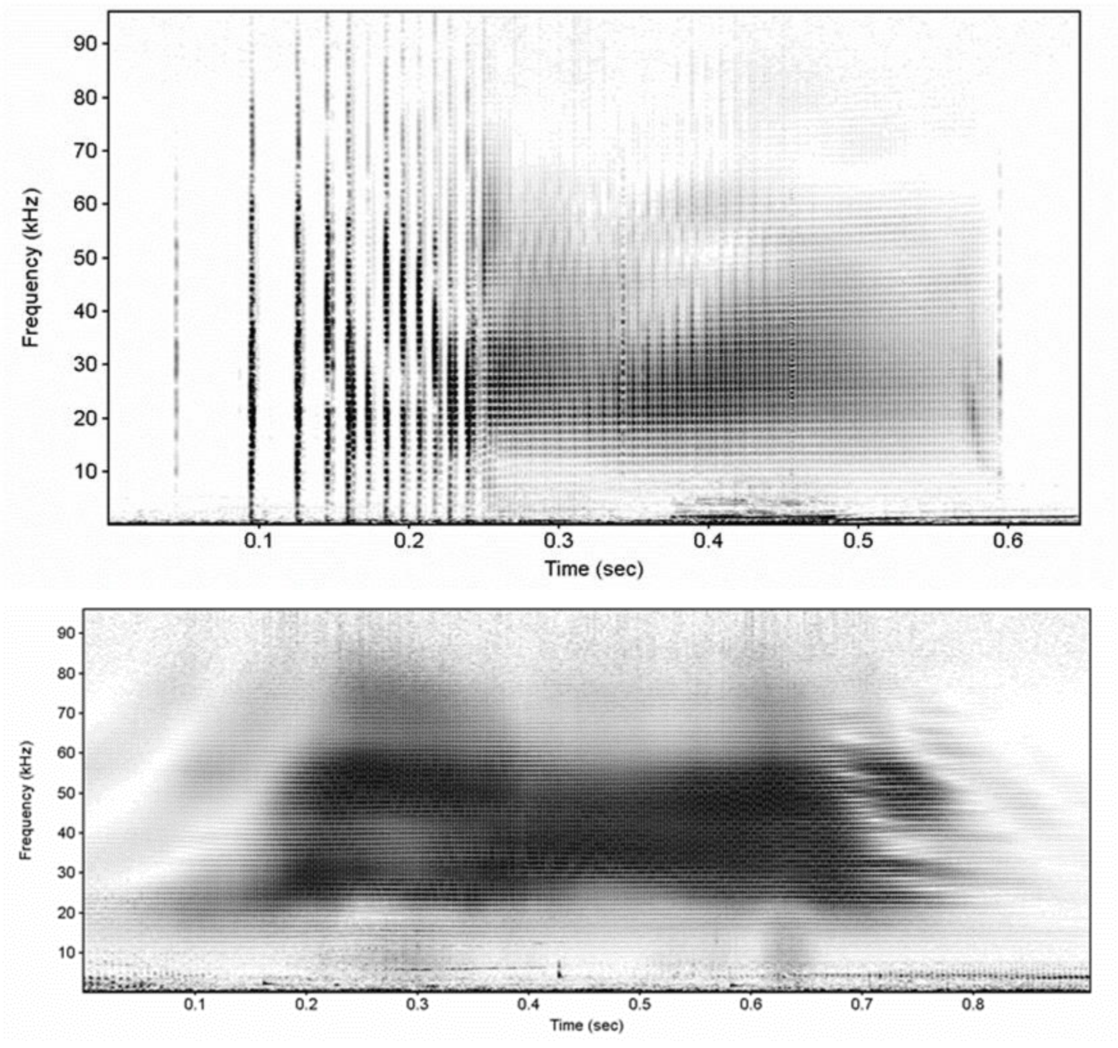


Figure 3-3. Long-finned pilot whales produce clicks (upper spectrogram) and buzzes (rapid repetition of clicks with short interval) with the main energy in the frequency area of 20–30kHz (upper spectrogram) and between 30–60kHz (lower spectrogram).

Whistles

Norwegian long-finned pilot whales produce whistles similar in frequency and structure to those of other dolphin species and killer whales (see e.g. (Herzing, 2000; Thomsen et al., 2001) Fig. 3-4). In addition, I found whistles in the ultrasonic range similar to those described in killer whales (Andriolo et al., 2015; Filatova et al., 2012; Samarra et al., 2010). I classified the whistles in three categories: whistles with main energy below 20kHz (see Fig. 3-4 A); whistles in the lower ultrasonic range of 25–40kHz (see Fig. 3-4 B); and ultrasonic whistles above 60kHz (see Fig. 3-4 C). In a total of 794 low-frequency whistles, 65 whistles were recorded in the lower ultrasonic range and two whistles in the higher ultrasonic range.

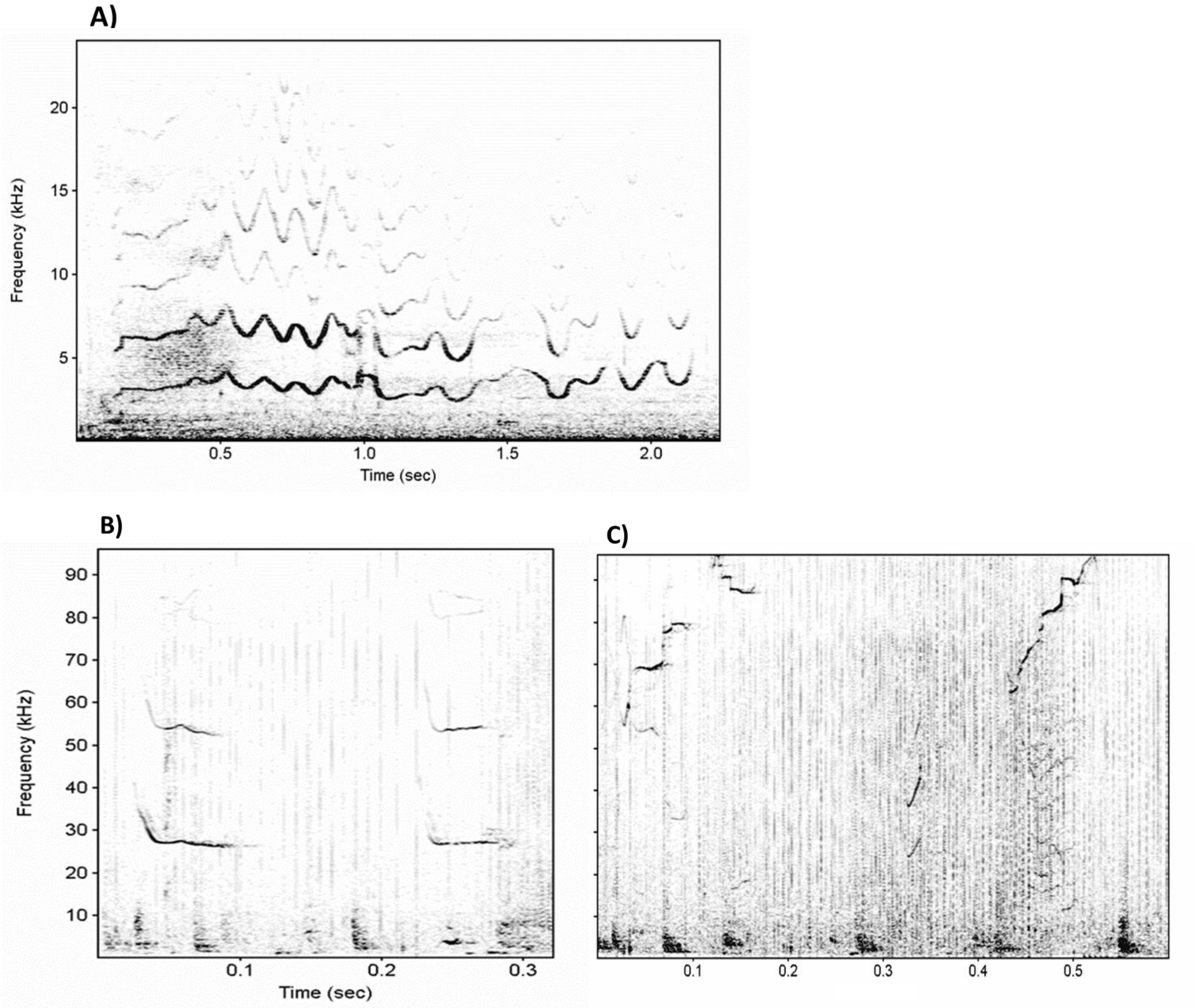


Figure 3-4. Long-finned pilot whales produce whistles with lower (below 20kHz) (A) and higher frequency content with either main energy around 30kHz (B) or (C) above 60kHz. Whistles in this study are described as tonal variable vocalisations; discrete whistle types detected more than once are sorted into call types.

Pulsed calls

Pulsed-type calls contained a large variation in sound structure ranging from a single simple segment, one element, and one frequency component to highly complex structures with several segments and elements, and two-frequency components. I classified 4572 calls into 129 different call types and 25 subtypes according to their similar vocal structure. This was tested by two independent trained reviewers and the rating difference was less than 1%; only 7 calls were classified as uncertain, and were removed from the present description of the vocal repertoire. The vocal repertoire catalogue of long-finned pilot whales in northern Norway (NPW) which I created contains 154 different call types from 7 different groups and encounters. The call types were not produced equally often: some call types were produced more than 300 times, whereas the majority of call types were only produced 1–50 times (see Fig. 3-5). Call type 021 (see Fig. 3-6) was the most common call type and was identified 429 times from Group J only.

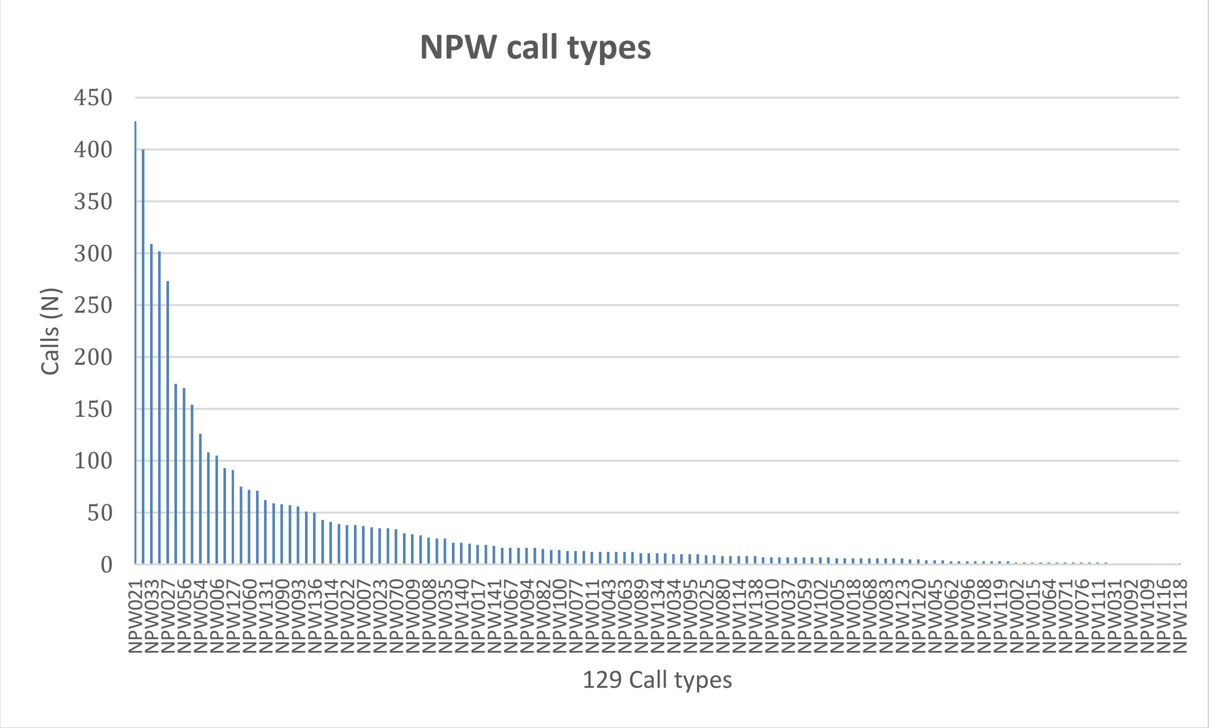


Figure 3-5. Norwegian long-finned pilot whales (NPW) in northern Norway produce discrete call types. In this study 129 different types and 25 call subtypes were classified; in this figure the 25 subtypes were pooled into their main call types. The call types were not produced equally often, call type 021 was produced more than 400 times and is the most commonly used call, whereas at the other end nine call types occurred only once.

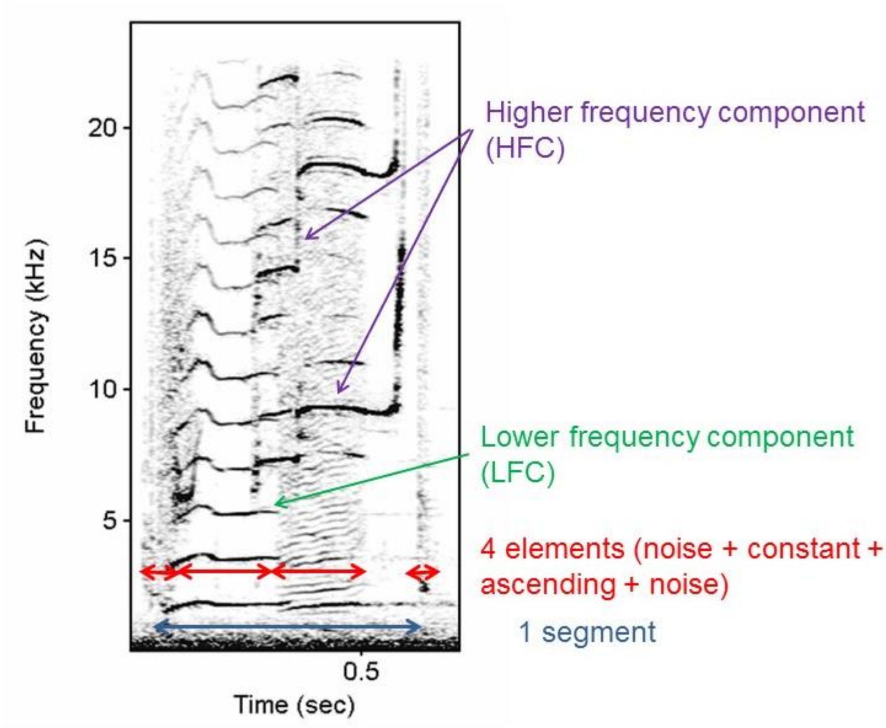


Figure 3-6. Long-finned pilot whales produce two-voiced call types. This figure shows call type NPW-21, the most commonly used call in pilot whales from northern Norway (N:429 by group J).

Call type distribution among groups

Call production during the 7 different encounters was not equal: during some encounters only 31 or 155 calls were produced, but in other encounters as many as 1635 calls were produced (see Fig. 3-7). This large variation might be due to variation in recording length: Fig. 3-9 shows that short recording lengths (less than 1 hr) result in less call types and number of calls. Only recordings ≥ 3 hrs were comparable with each, call types ranging between 21 and 47 and the number of calls ≥ 500 calls. However, the call types did not correlate to longer recording times and call numbers: group D with 3:32 hrs of recording time produced the most call types (47) with the least amount of calls (501). Nor did the amount of calls recorded influence the number of call types: group D produced 501 calls but had the most call types (47), whereas group J which produced more than three times the amount of calls (1635) only showed 41 call types (see Fig. 3-7).

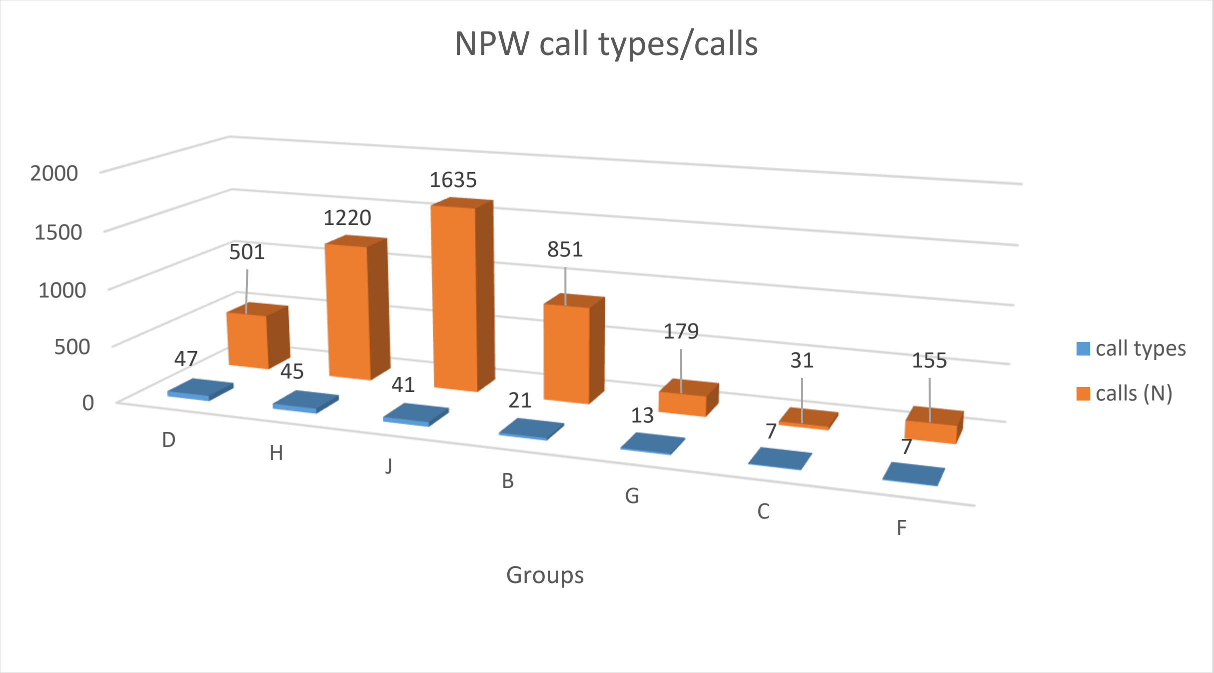


Figure 3-7. Different groups of NPW produced different amount of call types (blue) and calls (orange). There was no correlation between amount of calls recorded for each group and amount of call types classified. The weighted mean is 36 call types/group with a variation of 7 to 47 call types/group.

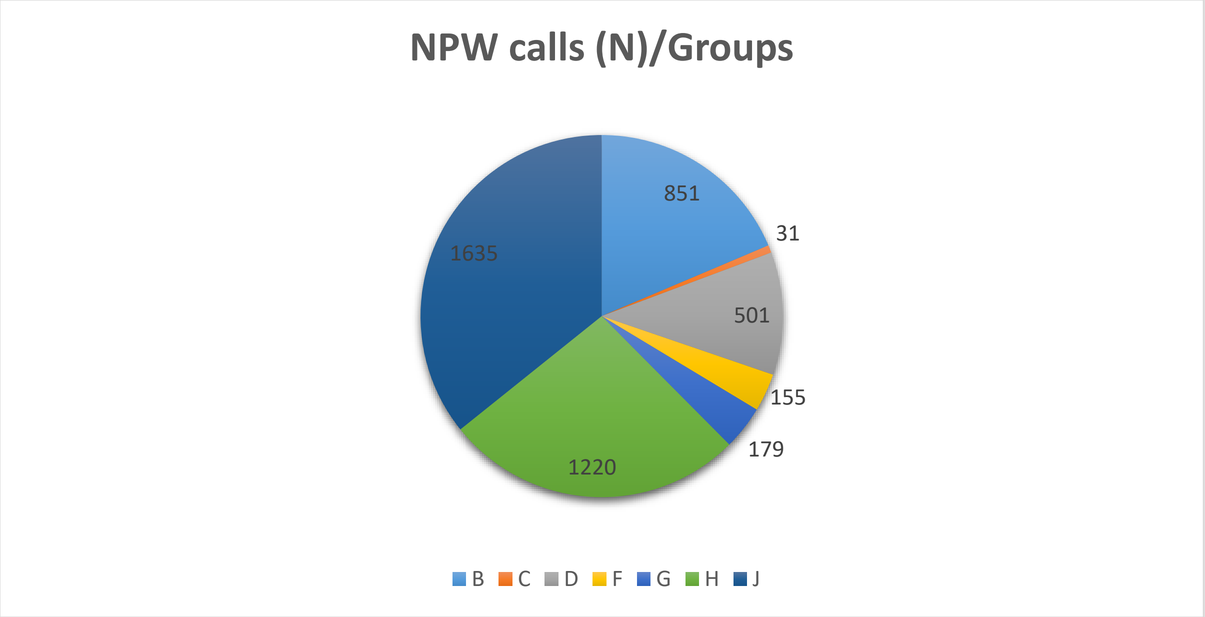


Figure 3-8. Number of calls produced during the 7 different long-finned pilot whale group encounters (colour codes); some groups were only briefly observed and recording times were short—these groups also show the lowest number of calls produced (groups C, F, and G, see Fig. 3-9).

Influence of recording length

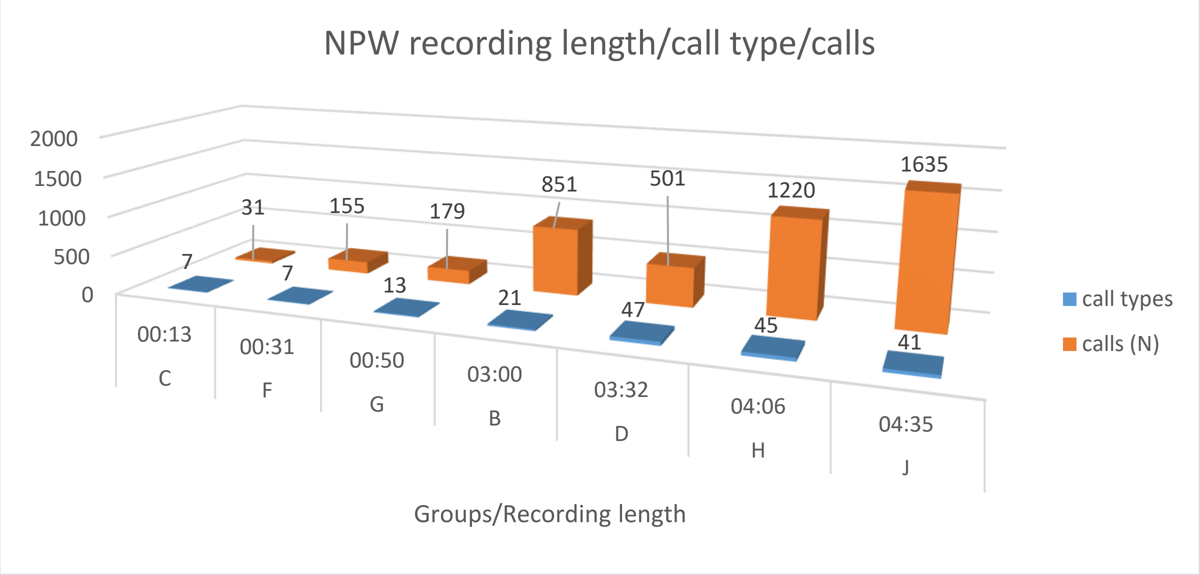


Figure 3-9. Length of recording time per NPW group encounter (from group C with 00:13 hrs:min to group J with 4:35 hrs:min) with the number of call types (blue) and total amount of calls produced (orange).

Influence of group size

To investigate if the difference in call types and number of calls depends on group size, e.g. amount of identified members, I plotted the numbers in the graph in Fig. 3-10. In the graph is a visible trend of number of calls increasing as group size increases. However, the amount of call types does not seem to have such a clear correlation (see group D with the most (47) call types and 32 members, versus group J with the most members (47) but only 40 call types).

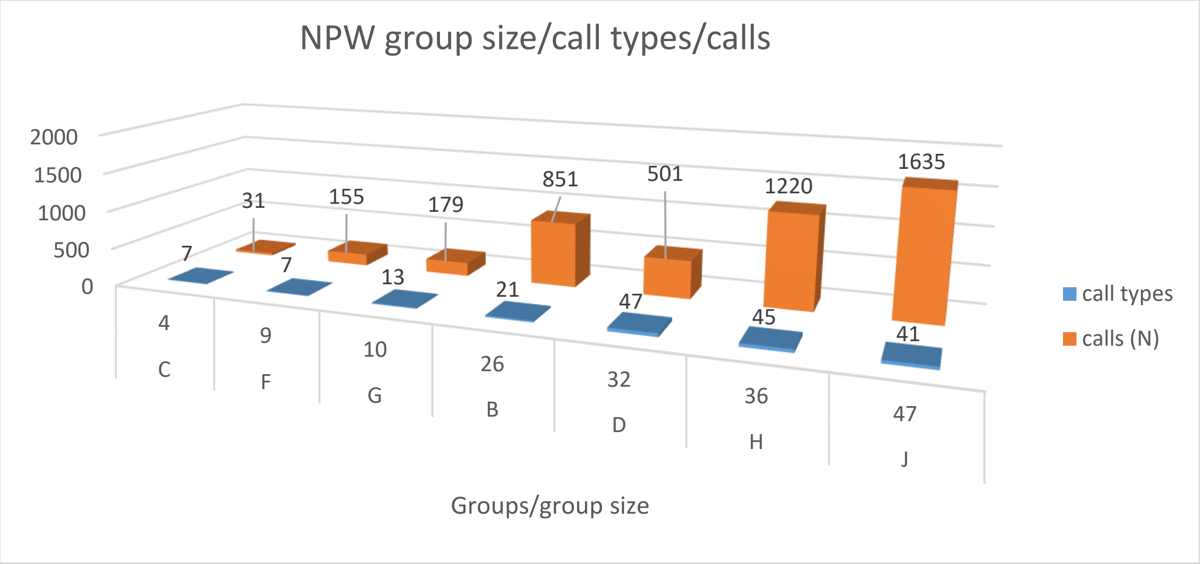


Figure 3-11. When increasing group sizes (from group C with 4 members to group J with 47 members) are plotted with call types (blue) and number of calls (orange) for each group encounter, the trend is that with increasing numbers of group members the number of calls increases; however the call types don't seem to depend on group size (see group D, with the most call types).

Influence of behaviour

In order to investigate if different behaviour influences the call type and call number production, I have plotted observation against call types and number of calls produced for each group encounter (see Fig. 3-12). However, it is difficult to apply specific behaviours to a group of pilot whales; often members of the group are engaged in different behaviours at the same time, e.g. while the group seems to rest, some youngsters may be active and playing (socialising). In this plot I only look at the overall group behaviour, which is by no means fine scaled. Group behaviour includes resting (R) when all animals were almost motionless at the surface, slow and short dives (no tails when diving); milling (M) when all animals were calm on the surface, close together, swimming back and forth in same area, often logging or slowly moving between each other, young animals may be playing/socialising; socialising (S) was indicated by increased surface activity, with animals swimming towards each other, body contact, and events such as breaching and spy hopping increased; travelling (T) when all animals were swimming at more or less the same speed (slowly—less than 3 knots, medium—3–5 knots, and fast—more than 5 knots) in the same direction; feeding (F) was indicated by synchronous diving bouts and increased clicking activity. Figure 3-12 illustrates that in groups with long recordings and high numbers of group size (B, D, H, J), the behavioural categories don’t seem to influence call type and number of call production. It seems that feeding alone does not result in an increase in call production and even during milling, socialising, and travelling the pilot whales communicated frequently.

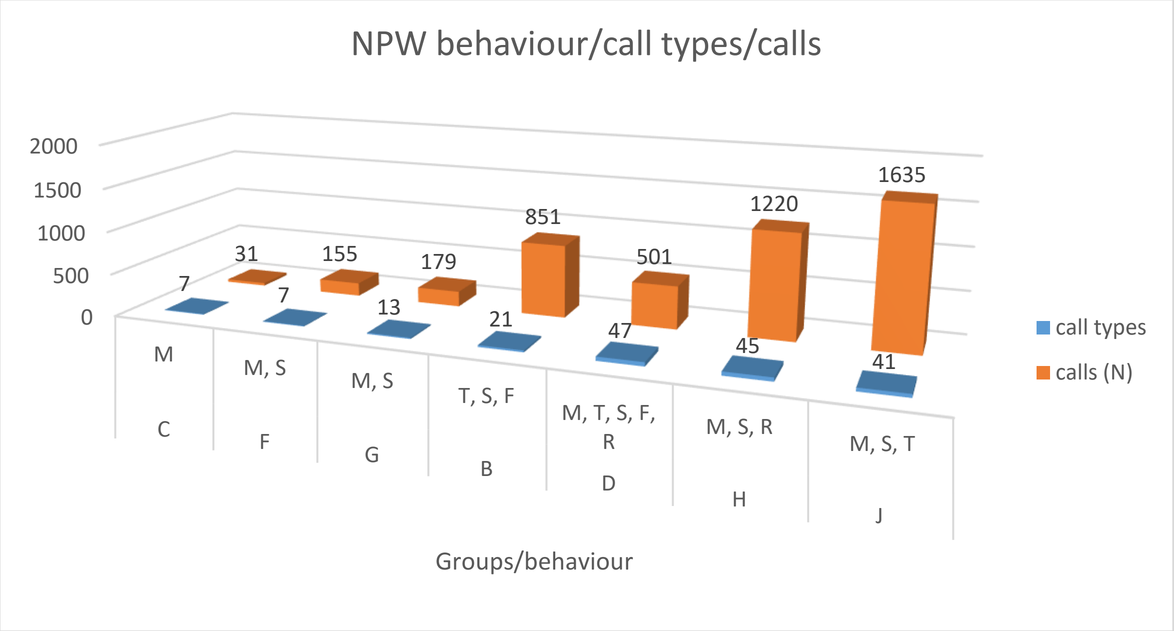


Figure 3-12. NPW group encounters (C to J) and overall group behaviour does not seem to influence call production. Group behavioural categories were M=milling, S=socialising, T=travelling, F=feeding, R=resting.

Call type structures

Most call types (127 call types, N=3264) only consist of LFCs, whereas 27 call types (N=1308) contained both LFCs and HFCs (see Fig. 3-13). Further, most calls (N=3648) consist of only one segment: 87% of LFC-only calls (N=2832) and 62% of LFC+HFC calls (N=816); however 13% (N=584) of calls have more than one (between two and six) segment (see Fig. 3-14). 33% of the LFC call types are simple in structure (N=1075), containing just one element (see Fig. 3-14 a); the other call types contained two to eight elements. Most of the LFC+HFC calls contain three elements (52%; N=675; see Fig. 3-14 b), the rest one or up to seven elements. Most of the HFCs consist of just one element (N=15), the others contain two (N=10) or three (N=2). A detailed breakdown of the calls is displayed in supplement 1.

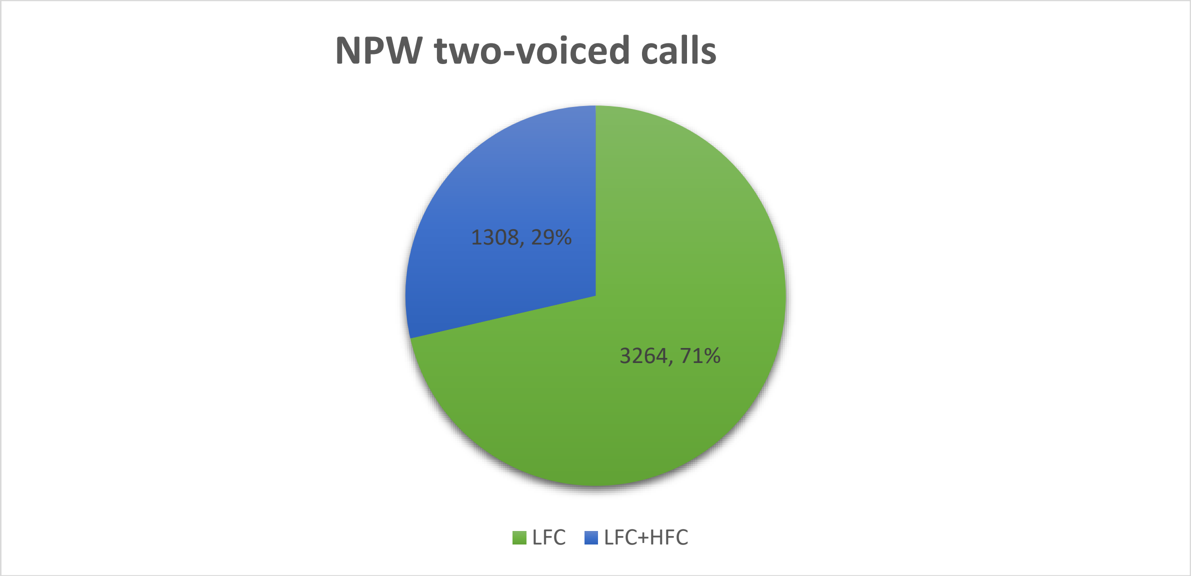


Figure 3-13. NPW's produce two-voiced and simple one-voiced calls. The majority of calls produced were simple without HFC (71% versus 29%).

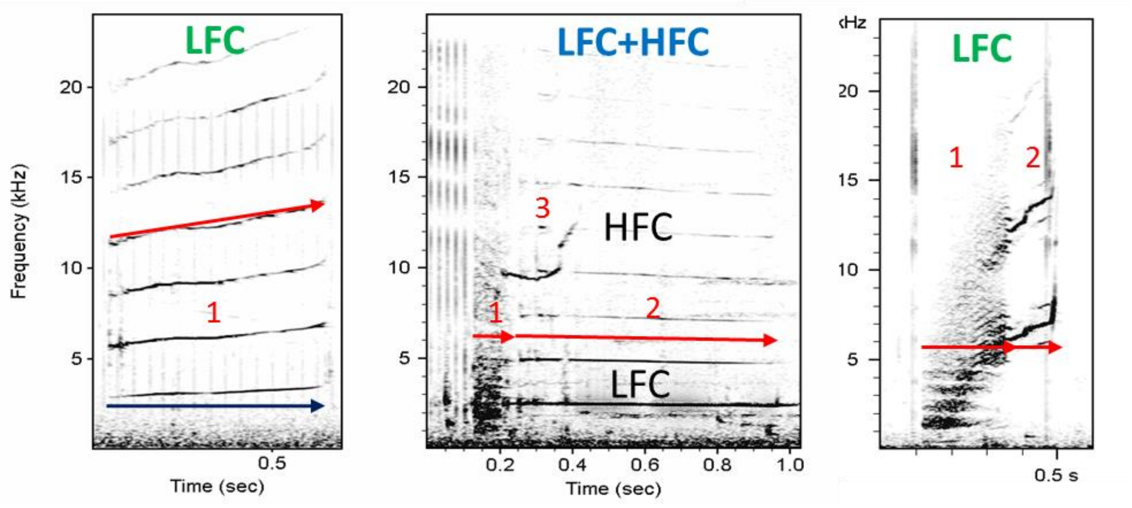


Figure 3-14. Three examples of main call types: a) LFC call with one segment and one element (ascending time frequency contour); b) two-voiced call type with one segment and 3 elements (LFC buzz + descending; HFC ascending contours); and c) simple LFC call type with one segment and 2 elements

(noise + ascending contour).

Within the calls I described 8 different element structures according to their time frequency contour as ascending, descending, U-shape, ∩-shape, noise, buzz, whistle, and constant (see Fig. 3-15). Within the 154 different call types I found over 444 elements. Most of the elements appear to be similar in structure; 36% of the elements consist of ascending contours (N=156), followed by a constant frequency (20%, N=87) and 18% are descending elements (N=81); the remaining 26% are either U-shaped, ∩-shaped, noise, buzzes, or whistles (see Table 3-3 and supplement 1).

Table 3-3. NPW's call types are made of different elements. There are eight different structures of elements and this table lists a summary of elements within the call types, the amount of different shapes and the amount of elements within call types. The most commonly used element structure is an ascending frequency time contour for both one- and two-voiced call types and most one-voiced call types (LFC) consist of 2 elements, whereas two-voiced call types (LFC+HFC) consist mostly of 1–3 elements.

elements (N)			*SUM*
	LFC	*LFC+HFC*	
ascending	**91**	**67**	**158**
descending	60	21	81
U-shape	32	16	48
∩-shape	13	8	21
noise	18	10	28
buzz	4	2	6
whistle	10	0	10
constant	45	0	45
total	273	124	397
call types			
1 element	46	**5**	51
2 element	**48**	**5**	**53**
3 element	18	**5**	23
4 element	10	2	12
5 element	1	4	5
6 element	2	3	5
7 element	0	3	3
8 element	2	0	2
total	127	27	154

Pulsed calls—elements example:

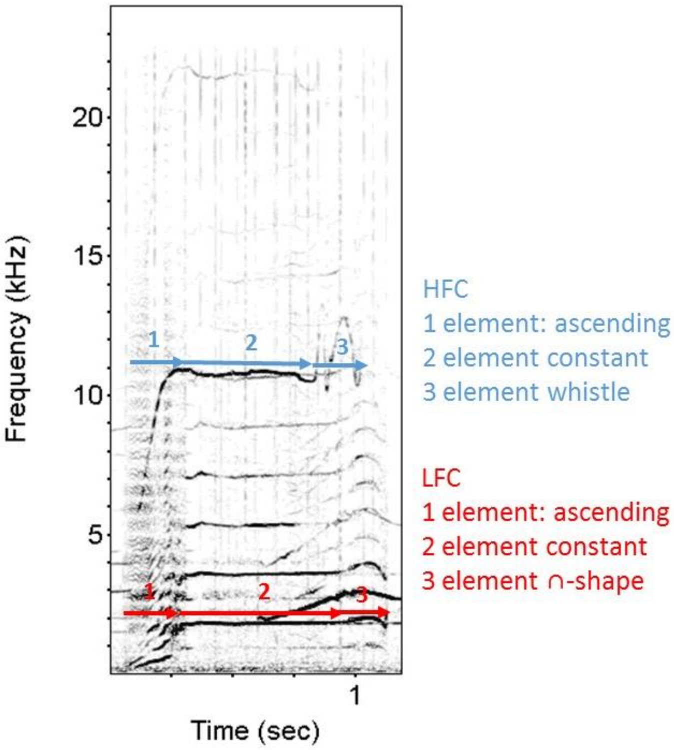


Figure 3-15. Spectrogram of a two-voiced long-finned pilot whale call type (NPW-119) with one segment and many elements: the lower frequency component (LFC) and higher frequency component (HFC) both contain 3 elements with different time frequency contours. Note that a second call overlaps the last part of the call.

Call type combinations

As part of the vocal repertoire I recognised several combinations of calls and call types that were repeated more than once (see Figs. 3-16 to 3-19). Distinct call types can be combined in different patterns, and broadband nonharmonic calls that did not have a distinct structure were often repeated with variable time gaps, giving them a rhythmical nature (see Figs. 3-16 and 3-18). Call types were often graded or mixed with noisy low frequency broadband calls (see Fig. 3-17). This made it impossible to quantify call type combinations based on distinct call types from the vocal repertoire. I therefore left the analysis of call type/graded calls/mixed call combinations for further studies in which algorithms such as Fuzzy Clustering can be applied (Fischer et al., 2016).

In addition to the call combination patterns, I recognised that some call types appeared to be repeated more often than others and in some cases certain call types were repeated over a long period of time ranging up to over two minutes (see Fig. 3-19). Examining the meaning of the combination patterns and repetitions lies beyond the scope of this thesis and remains an interesting task for further studies on the topic.

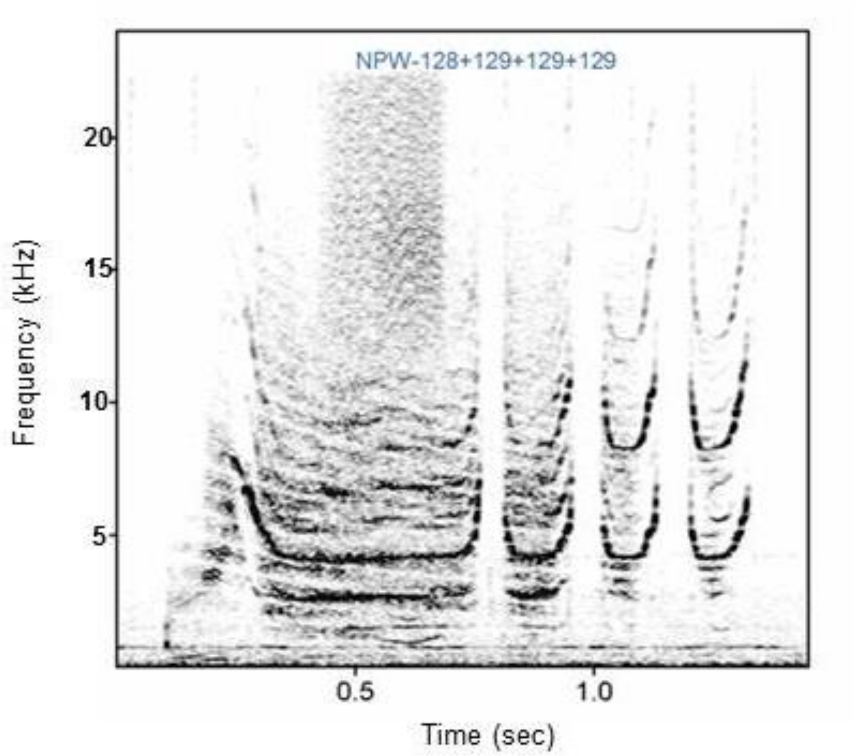


Figure 3-16. NPW's produce call type combinations of distinct call types. Here is an example of a combination of 128 and 129, where call type 128 always initiates a call type combination with call type 129 or call type 130 following.

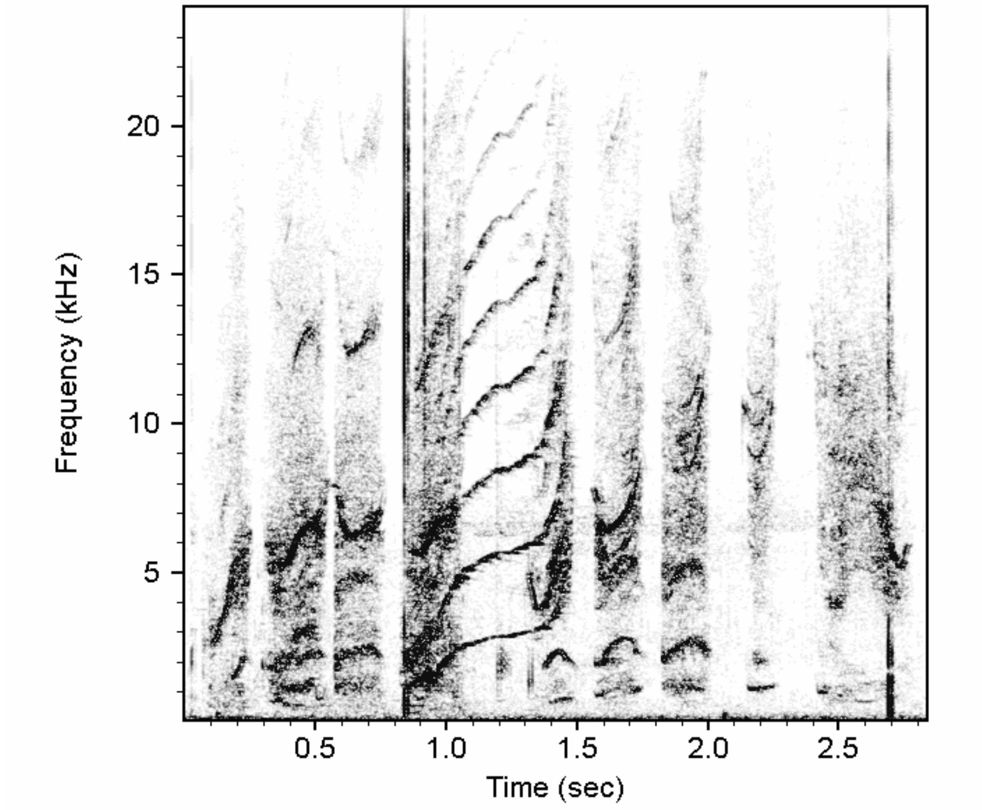


Figure 3-17. Often call type combinations of long-finned pilot whales are mixed, like in this example where discrete call types are combined with nonharmonic calls and graded call types. Spectrogram parameters: FFT size 1024, overlap 50%.

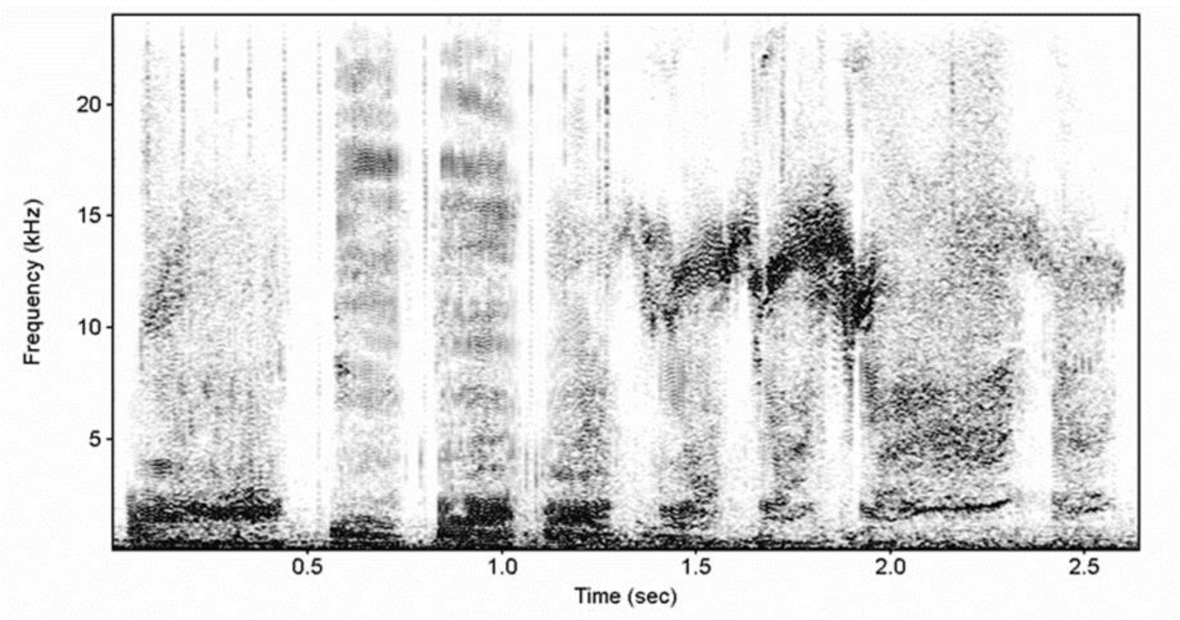


Figure 3-18. Lower frequency nonharmonic broadband calls produced in series are common in NPW's, they are often graded and rhythmical in nature. Spectrogram parameters: FFT size 1024, overlap 75%.

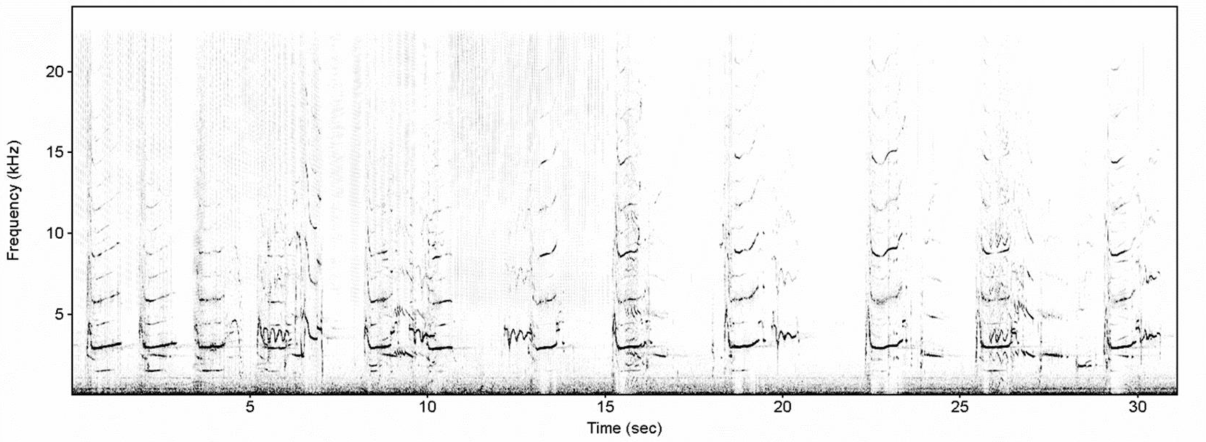


Figure 3-19. Certain call types are more often used and repeated than others in NPW's; here is an example of a sequence of call type NPW-56 repetitions. Spectrogram parameters: FFT size 1024, no overlap.

Call type sharing between groups/recordings

My data allowed me to look into differences of vocal repertoires between the different group encounters—even though I was limited by having no information on individual whale vocalising, nor was it possible to separate calls according to individual callers. However, the overall repertoire and usage of call types per group (in one or several encounters) could be investigated and call type sharing between the groups evaluated. Long-finned pilot whales in my study produced 37 call types per group (weighted arithmetic mean) which ranged from 7 to 47 call types per group. However, due to low sample sizes I have excluded groups C and F from the following comparison. I looked at the degree of call types and number of calls' usage by five different group encounters (group B, D, G, H, and J).

In summary, I found that 35 out of 124 call types (28%) and 1621 out of 4386 calls (37%) are shared between at least two groups (see Fig. 3-20). Most calls (63%), however, were only produced during one group encounter, which indicates that there is group-specific vocal communication in pilot whales.

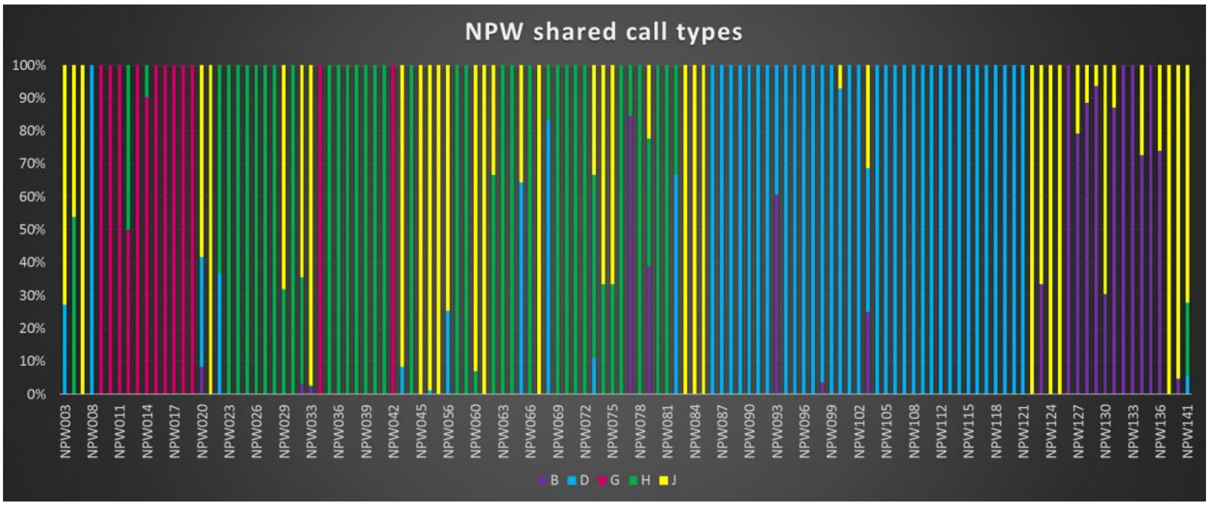


Figure 3-20. Norwegian long-finned pilot whale (NPW) groups produced discrete call types. Call types were shared to a certain extent between five group encounters. This figure shows the degree of call type sharing between groups B (purple), D (light blue), G (red), H (green), and J (yellow). Call types were pooled with subtypes, thus 129 different call types (x-axis from NPW003 to NPW141) were produced by five different groups. The colour code shows the degree (in %) of call type production and sharing with other groups, hence the more colourful a column, the more the call type was shared between groups, e.g. call type NPW-141 was produced by 3 different groups (D, H, and J).

Table 3-4. All calls and call types produced by the five different NPW groups, shared calls and call types, and the number of group specific calls and call types. Note that the same call types can be produced by more than one group, therefore the total call type numbers are not the overall number of different call types (129) of the vocal repertoire.

groups	*B*	*D*	*G*	*H*	*J*	*Total*
calls (N)	851	501	179	1220	1635	4386
call types	21	47	13	45	41	167
shared calls (N)	487	148	38	124	824	1621
shared call types	17	14	2	17	27	77
group spec calls (N)	364	353	141	1096	811	2765
group spec call types	4	33	11	28	14	90

On average, groups produced 37 call types per group (weighted arithmetic mean range 13–45), 21 call types were shared with other groups (weighted arithmetic mean range 2–27, N=1621), and 20 call types were not shared with other groups (weighted arithmetic mean range 4–33 CT, N=2765). In general, groups shared 56% of their call types with at least one other group, with groups B and J at the highest sharing rate of call types (81% and 68%), and group G the lowest sharing rate at 15%.

Table 3-5. Call types and number of calls (N) shared with other groups (bold numbers are call types recorded only during their own group encounters). Group H shared call types with all other groups, whereas the other groups shared call types with 3 other groups. Group G only shared calls with group H (note this is also the group with the shortest recording length (00:50 hrs:min) and lowest vocal repertoire (13 call types and 170 calls, which could have resulted in the low sharing rate). Group B shared the most call types with group J (14). During the recordings of group B, members of group J were travelling together with them. The high sharing rate and the fact that they were closely associated could indicate that they belong to the same matrilineal group, are closely related or spend a lot of time together, or that they were communicating together. More recordings from group B alone would help to understand this high sharing rate.

	Group B	*Group D*	*Group G*	*Group H*	*Group J*
Group B	**4 (364)**	4 (40)	0	4 (61)	14 (441)
Group D	4 (60)	**33 (353)**	0	5 (31)	9 (70)
Group G	0	0	**11 (141)**	2 (38)	0
Group H	4 (55)	5 (39)	2 (5)	**28 (1096)**	11 (87)
Group J	14 (468)	9 (271)	0	11 (446)	**14 (811)**

In summary, groups shared 2 to 14 call types with other groups, although overall call type sharing rates were only about half (56%) of all call types recorded. One group (G) only shared calls with one other group (H), but the others shared calls with all other groups. On average 20 CT per group (range 4–32, N=2765)) were only recorded during one group encounter, which means that 54% of the call types/group were used by one group only. The sharing of call types indicates that pilot whales do belong to the same acoustic clans (see (Ford, 1991)); for explanations of killer whale acoustic clans, however, they show a high degree of within group vocalisations that were not shared with other groups.

In order to validate the result of my observer-based analysis of call type sharing and possible group specific vocal communication in pilot whales, I cooperated with Dr. Sarah Hallerberg and Prof. Marc Timme at the nonlinear dynamics group at the Max Planck Institute in Gottingen. As a result we published our findings in the journal *Physics Review* in 2016 (Vester et al., 2016).

Hallerberg and Timme proposed and tested a new automated method, the BOCCA, to study group-dependent differences in vocalisation in my dataset. The main idea of this approach was that they omit separating and sorting vocalisations into call types and instead compare ensembles of vocalisations produced by each group. Investigating ensembles of calls rather than identifying individual call types is conceptually similar to the bag-of-words model (Harris, 2015) used in text analysis. In the original bag-of-words model, a text is represented as the bag (multiset) of words—disregarding grammar and even word order but keeping multiplicity. Here group specific vocalisations were investigated by comparing ensembles, i.e., bags of calls, which contain the calls of a specific group of whales. Comparing the statistical properties of all features computed for each ensemble circumvents the necessity to establish subjective vocal categories or select specific acoustic features. Note that the way the ensembles of calls were constructed (choosing only high-quality sounds, and additionally applying a random sampling to data from several recording sessions per group) implies that calls within an ensemble most likely originate from different behavioural contexts and that the temporal correlation of calls is destroyed due to the random sampling. Hallerberg and Timme then quantified differences in vocalisation among six groups of pilot whales by computing differences in distribution. To reason whether the calculated differences in distribution were relevant, they introduced two types of coefficients which summarise the relation between inter- and intragroup differences. Intergroup differences were significantly larger than intragroup differences for all but 1 of 15 intergroup comparisons. Interestingly, groups B and J, the two groups with no significant difference in vocalisations, have also been observed travelling and milling together. One possible explanation for their similarity in vocalisation is that they are related or that they are subgroups of a bigger group. The common encounter of groups B and J allowed us also to estimate the effect that a similar acoustic environment could have on the similarity of two groups: Even if calls recorded from group J during the common encounter are excluded from the analysis, we still find the same results when comparing ensembles of calls from groups B and J. Since the calls of group J used for this later comparison were recorded on a different day at a different location, we can conclude that the effect of the different acoustic environments on the computed similarity of vocalisations is rather negligible.

In summary both observer-based classification of calls and the bag-of calls model yield similar results concerning vocal group communication in pilot whales.

Discussion

Vocal repertoire

Similar to the description of the vocal repertoire of long-finned pilot whales in the northwest Atlantic by Nemiroff and Whitehead (Nemiroff & Whitehead, 2009), the repertoire of long-finned pilot whales in the northeast Atlantic comprises a variety of clicks and buzzes, broadband nonharmonic calls, and different types of whistles, as well as different types of pulsed calls that range from simple, single-segment calls to calls of highly complex structures composed of up to six segments and eight elements. However, there are slight differences in the description of the calls; Nemiroff and Whitehead described most pulsed calls as simple, consisting of only one segment (93% versus 87% in our study). In addition to the higher number of pulsed calls with several segments and elements, there are more two-voiced calls than in the former study (29% versus 20%). No discrete patterns in the structures of pulsed calls were described before, instead the calls were described as graded. In my study, based on observer analysis discrete calls could be identified and I classified them into 129 different call types, and 25 subtypes. These differences might not readily be explained by structural differences in the repertoire of northwest and northeast Atlantic long-finned pilot whales, but more because of different methodological approaches. The smaller number of analysed calls (419 calls in the 2009 study of Nemiroff and colleagues, and 4572 calls in my study) and the different analysing approach—an automatic classification compared to an observer-based classification—might account for such different results. Sayigh et al. investigated discrete call types in short-finned pilot whales using observer-based classifications and they could classify 42% of their pulsed calls into 173 call types (Sayigh et al., 2013). Consequently, these different findings emphasize the importance of developing a common methodological approach.

The new finding in my study of ultrasonic whistles with frequencies above 20kHz and even above 60kHz in the northern Norwegian long-finned pilot whale population, which were previously not described for this species, is probably due to technical differences in the recording system (I used a higher sampling rate to record frequencies up to 96kHz). The same sampling frequency applied in studies in other populations will probably yield ultrasonic production in pilot whales in all populations. In killer whales, ultrasonic whistles are known from the northeast Atlantic (Samarra et al., 2010), the western south Atlantic (Andriolo et al., 2015), and the north Pacific (Filatova et al., 2012). It seems that ultrasonic whistles are more commonly used by different dolphin species than earlier reported (Hiley et al., 2017). The reason for ultrasonic signals in top predators is unknown, but it may be used in short-range communication as has been suggested for killer whales (Samarra et al., 2010).

In general, the use of whistles in long-finned pilot whales seems to be highly context dependent (Weilgart & Whitehead, 1990); during my observations I have noticed that simple structured whistles or call types (here discrete structured whistles) without loops seemed more apparent during resting behaviour such as milling and during times when the matrilines were spread out in the fjord over an area of many kilometres. More complicated structured whistles (variable with several loops) and pulsed calls occurred more frequently during active surface behaviour, such as body contacts, breaching, spy hopping, boat approaches, and feeding behaviour which can be detected on the surface by group diving and during diving by an increase in echolocation clicks. I have also noticed that whistle activity seemed to increase during multipod meetings, and when Atlantic white-sided dolphins joined the group. My observations could not be quantified and need closer investigation, however they do support the hypothesis that whistles act as contact vocalisation as well as coordination of movements of the whole group (Weilgart & Whitehead, 1990).

In summary, the vocal repertoire of long-finned pilot whales in northern Norway is highly variable and among the most complex repertoires described in mammalian species. Similarly complex vocal repertoires are known in killer whales, with discrete call types, variable and low frequency calls, stereotyped and aberrant whistles, clicks and buzzes as well as two-voiced calls with lower- and upper-frequency components (Ford, 1989, 1991). In the next chapter I will investigate the vocal repertoire of killer whales in Norway and compare them to pilot whales in chapter 5. Both killer whales and long-finned pilot whales are long-lived marine mammals living in small matrilineal groups with some populations showing natal group philopatry (Amos et al., 1993; Amos et al., 1991; Amos et al., 1993; Barrett-Lennard, 2000), and vocal complexity may reflect their similarity in social intra- and inter-group interactions (Deecke et al., 2010; Ford, 1991). However, in contrast to killer whales, long-finned pilot whales produce a larger variety of whistles, more similar in structure to the whistles of bottlenose dolphins. It was first suggested by Taruski (Taruski, 1979), then by Weilgart and Whitehead (Weilgart & Whitehead, 1990), and more recently by Sayigh and colleagues (Sayigh et al., 2013), that pilot whales may use stereotyped individual whistles, similar to the bottlenose signature whistles. In a more fluid fission-fusion gathering of pilot whales—which travel in large groups containing many related pods, signature whistles may be of importance to maintain contact to their natal pod. Killer whales, however, largely travel only with their natal pods and therefore individuals may be easily recognized. In contrast to this, we observed large groups of long-finned pilot whales often containing 8–12 matrilines meeting in summer in the Vestfjord. During these meetings social contacts between groups and breeding behaviour (mating, calving, and nursing) were commonly observed. Similar bottlenose dolphins' use of signals, individual signalling in such superpod meetings could help to maintain close contact to members of the natal pod, to announce each individual and to recognize/find each other again after separation (Janik & Sayigh, 2013; Quick & Janik, 2012).

Call type combinations and sequences

Dolphin species have evolved advanced communication and sound production flexibility, ranging from signature whistles and group-specific calls to different combinations of calls (Caldwell & Caldwell, 1965) (Ford, 1989) (Strager, 1995). Vocal exchange of matching call types has been demonstrated in whales and dolphins. Southern right whales (*Eubalaena australis*) exchange one call as they approach one another and react to playback with calling and approaching (Clark & Clark, 1980); bottlenose dolphins match whistles within 3 seconds in the wild, which seems to be a response to the initial caller (Janik, 2000b); and resident killer whales exchange stereotyped calls with call type matching (Miller et al., 2004). Compound calls, which are call combinations, were first described by (Strager, 1995) in Norwegian killer whales; in addition, unpublished data from recordings of killer whales in Norway shows that combinations of certain call types are a large part of these whales' vocal repertoire (Vester this thesis, chapter 4). It is also known that killer whales repeat call types and exhibit call type matching, however the function remains unknown (Miller et al., 2004).

Call type sequences in which different types are more likely to occur in sequence with other specific types were also described by Sayigh and colleagues for short-finned pilot whales (Sayigh et al., 2013). The structural descriptions of the call types are similar to our present findings; in addition they considered call types produced more than 10 times and found that these predominant call types are often repeated. I also found call types that are repeated and naturally they are the most abundant call types of our vocal repertoire catalogue. However, due to the nature of my recordings I have no information about the sender and whether these calls are produced by the same animal or matches between different individuals. A recent study on Canadian pilot whales describes repetition of the same call types and suggests that they could serve to maintain contact and cohesion (Zwamborn & Whitehead, 2017). The amount and variety of call combinations found in my study lead to the suggestion that call repetition in pilot whales is similarly common in killer whales. A closer investigation of their function promises further insight into their complex communication abilities.

Factors influencing the vocal repertoire

When looking at factors influencing the vocal repertoire size, it becomes clear that a certain amount of recording length is needed: in my study, recordings with less than one hour resulted in a much smaller vocal repertoire size (31–179 calls per group) than recordings over 3 hours (501–1635 calls per group). The longer recordings were collected in multiple recording sessions, sometimes on different days, and such multiple recording sessions will encompass more individuals communicating as well as more behavioural contexts, thus will result in a more complete vocal repertoire. The fact that increasing group size combined with increased recording time also resulted in an increased vocal repertoire shows that more recording time is needed to gather the whole repertoire of larger groups. However, a more detailed investigation into whether group size or other social factors could have shaped such a large repertoire was beyond the scope of this thesis and is an open question for future studies.

Call type sharing

Both observer-based classification of calls and the analysis of cepstrum coefficients showed clear differences in call types used between groups of pilot whales recorded in Norway. Although all groups shared some call types, other call types were exclusively used by only one group. Although the concordance between relatedness and vocal similarity cannot be finally answered without genetic studies, group specific vocalisations may be advantageous in several ways: in an open aquatic environment it becomes important to clearly recognise group members for offspring care, protection against predators, and cooperative social and feeding behaviour. In social toothed whales most dolphins live in a fission-fusion society in which bonding between male alliances, as well as female offspring is common and demands highly cognitive skills (Connor, 2007). In these fluid societies it is important to recognise individuals, and in the case of bottlenose dolphins signature whistles have evolved through vocal production learning (Janik & Sayigh, 2013).

Some other social toothed whale species live in matrilineal societies in which group signature is important, and many species developed group dialects. Roving males in such societies may recognise group members, even related animals, through group specific vocal repertoires and this may help distinguish between relatives and nonrelatives to avoid inbreeding and increase fitness (Barrett-Lennard, 2000; Weilgart & Whitehead, 1997). In the case of female choice, they will be able to distinguish between related and nonrelated mates by their vocal dialects (Barrett-Lennard, 2000). The degree of shared vocalisations does reflect kinship in killer whale call types and sperm whale codas (Deecke et al., 2010; Weilgart & Whitehead, 1997). The possibility of sharing more or less vocal types seems to evolve via vocal learning, as social systems have become more complex and the complexity of signals increased to recognize individuals, kin, or other social partners (Deecke et al., 2010; Foote et al., 2006). Killer whale group dialects were found in different parts of the world, first discovered in Canada in a resident population where groups use 7–17 distinct call types (Ford, 1991). These repertoires remain stable over time, but subtle changes do occur in call type structure, supporting the finding that killer whales have a high vocal flexibility (Deecke et al., 2000). The question is whether the group specific differences of vocal types found in the long-finned pilot whale population of northern Norway is also the result of similar social organisations and vocal learning. In a recent study Alves and colleagues (Alves et al., 2014) found that long-finned pilot whales from the northern Norwegian population match artificial sounds (sonar signals), supporting the view that the flexibility in vocal production of pilot whales is similar to the flexibility of killer whales.

We were able to show that calls within the groups of pilot whales were significantly more similar than between the different group encounters (Vester et al., 2016). In the same study we also demonstrated high concordance between this bag-of-calls and coefficients approach and the observer-based audiovisual inspection. All observed groups of pilot whales use vocalisations with generally the same structural complexity (Vester et al; submitted). Within this complex vocal repertoire it seems that smaller units, perhaps even matrilines, use specific variants of these general structural patterns. Due to the low number of encounters and re-sightings of individuals we cannot be sure if pilot whale aggregations we encountered belonged to the same natal groups. But it appears that some pilot whales return from year to year, and spend time in the same locations inside the Vestfjord. This finding suggests that long-finned pilot whales may exhibit migration patterns and site fidelity to potentially resource-rich feeding and breeding grounds. To which degree pilot whales possess group-specific vocal repertoires cannot be said at this stage because more studies are needed to justify the structure and stability of the observed group aggregations.

CHAPTER 4 VOCAL REPERTOIRE OF KILLER WHALES

Summary: The vocal repertoire of killer whales in Norway in my study included 60 different call types and 25 subtypes, as well as a variety of other calls and ultrasonic whistles. I found a higher degree of call type combinations (33) than previously described (21).

Further, the killer whales I recorded belong to the same acoustic clan, groups used 25 call types per group (weighted arithmetic mean, range 2–37), and call type sharing between groups is high, but they do exhibit group specific vocal communication. Behaviour seem to influence the amount of calls and call types produced in killer whales.

Introduction: Killer whales (*Orcinus orca*)

Figure 4-1. Killer whales spy hopping during carousel feeding in Lofoten in northern Norway (Photo: H. Vester).

Killer whales are common in Norwegian waters and can be seen year round, with peak occurrences from November to February when herring is overwintering in certain fjords in northern Norway. We know a great deal about their abundance, population size, and structure; as well as their vocal behaviour. However, considering the large size of the population, their wide distribution and complexity and fluidity of behaviour, more research is needed to fully understand the biology of this species.

I started with my research on the occurrence, abundance, and vocal and social behaviour of killer whales in the Vestfjord in winter 2004. In this thesis I present the results of my early study through 2011 on photo-identification and a description of the whales' vocal repertoire.

Methods (see chapter 2 for data collection and analysis)

Results

Data collected and Photo-ID

I studied killer whales in the Vestfjord in northern Norway from 2004–2016. For the present Photo-ID studies I used a subsample of photos from 2004–2011 during 37 encounters and a total observation time of 210 hrs (Table 4-1, without 2011 encounters/data). Individuals were grouped when they were seen together during an entire encounter, assuming that killer whales in Norway live in their natal pods similar to resident killer whales in British Columbia (Similä et al., 1996). Resightings of the groups with the same composition confirmed this social organisation. However, group size varied during the encounters with killer whales, ranging from 4 to 36 animals, with an average group size of 12, one matrilineal group typically consisting of 6 to 12 animals.

Through Photo-ID I could identify a total of 175 individual killer whales in 15 groups (group AA with 15 members, AB with 6 members, AD with 16 members, AE with 12 members, AF with 6 members, AM with 12 members, AN with 6 members, AP with 6 members, AV with 36 members, BI with 21 members, E with 11 members, K with 4 members, P with 10 members, T with 4 members, and Z with 10 members).

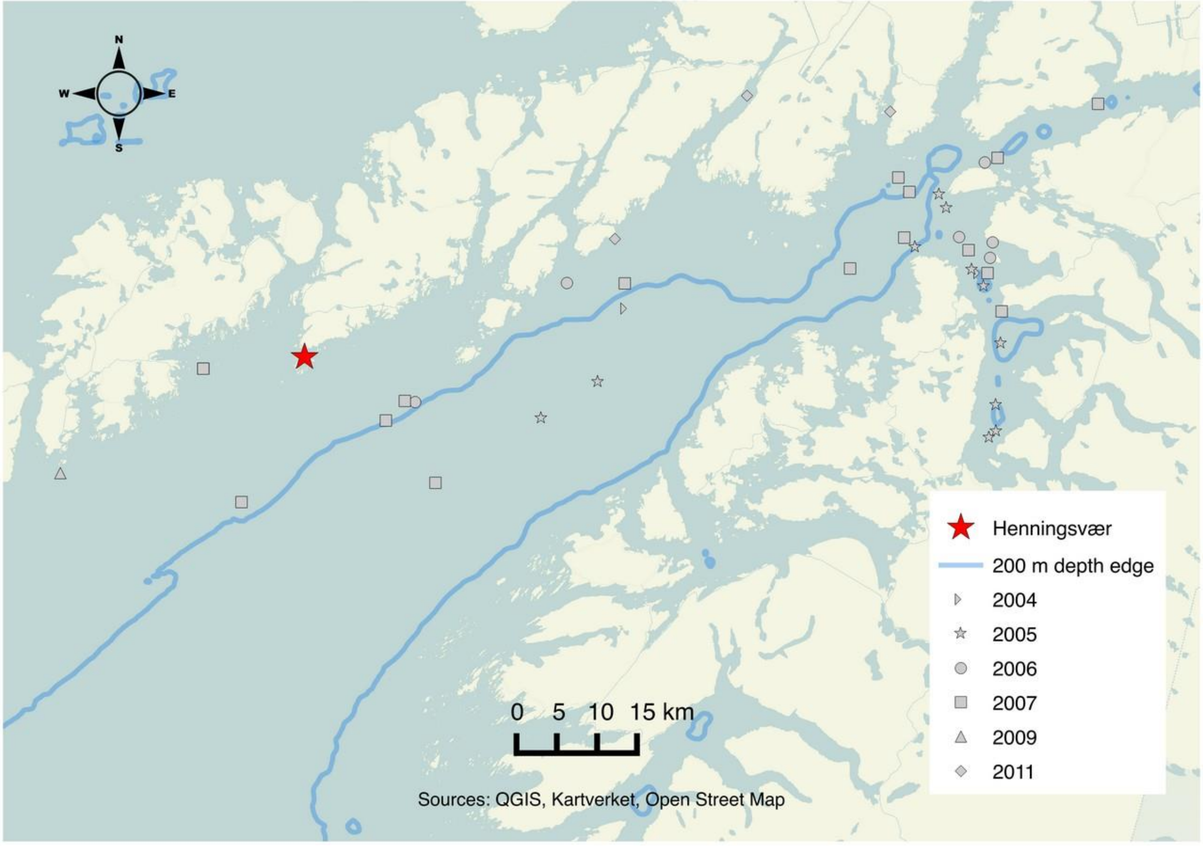


Figure 4-2. Killer whales encountered in the Vestfjord between 2004–2011; different symbols represent the different encounters of 11 different groups in different years (see box inside the figure). In the years 2004–2007 most groups were detected during the winter months inside the Tysfjord, following the herring migration. After 2007, herring changed their migration route to areas farther north (Tromsø) and no killer whales were encountered inside the Vestford during the winter months. In 2009 and 2011, groups of killer whales were seen during the summer months close to the Lofoten Islands (map by Felipe Matos).

During 2004 and 2007 killer whales followed the overwintering herring into the Vestfjord and deep into the adjacent Tysfjord. However, since 2007 I started to study the killer whale groups during the summer months as well. There were fewer groups than during the winter, but it seems that certain groups of killer whales enter the Vestfjord and come close to shore in Lofoten from April to September.

Table 4-1. Killer whale encounters in northern Norway, with group affiliation and total number of identified members in the group; identified individuals during this specific encounter and re-sightings of already identified individuals; the location, observation time, and recording and behavioural stages and comments on the encounters.

Date	Groups	Location (N/E)	approx. group size	group ID's	sighting	start	end	Observation time	Sound recording	Sounds	Behaviour
2004-11-20	n/a	68126771/1507820 (Vestfjord)	7-8	n/a	n/a	10:40:00	13:20:00	2:40:00	0:59:35	vocal	travelling, "stumpy" was with them, 3 groups meet and travel together
2004-12-17	n/a	Tysfjord	12-20	n/a	n/a	10:53:06	13:33:32	2:40:26	2:08:04	vocal	feeding in herring net / enclosure, no photos for ID, 2 groups
2005-01-04	n/a	6819861/16 00 724 (Tysfjord)	n/a	n/a	n/a	13:10:00	13:40:00	0:30:00	0:09:27	silent	travelling
2005-01-05	n/a	Between Korsnes and the other side	25	n/a	n/a	10:40:00	11:30:00	0:50:00	0:27:22	vocal	carousel feeding on herring
2005-01-06	n/a	Vestfjord, outside tysnes	n/a	n/a	n/a	11:05:00	12:15:00	1:10:00	0:12:48	silent	travelling
2005-11-05	n/a	Vestfjord, middle	n/a	n/a	n/a	14:00:00	15:00:00	1:00:00	0:07:27	vocal	travelling
2005-11-08	BI, A, AY, J, X, stumpy	Ofotfjord, outside Baroy	> 60	n/a	1	11:45:00	14:00:00	2:15:00	1:21:22	highly vocal	feeding from seiner, 4 groups, more than 60 animals, stumpy came close to our boat
2005-11-16	X92,X93,X94	Vestfjord	only 3 individuals	3	3	13:00:00	14:45:00	1:45:00	0:23:39	silent	travelling
2005-11-17	K	Tysfjord, outside Drag	10-12	4	4	13:00:00	14:30:00	1:30:00	1:01:58	vocal	carousel feeding on herring
2005-11-19	P	Tysfjord	10-12	10	10	10:50:00	14:00:00	3:10:00	1:31:22	vocal	carousel feeding on herring
2005-11-25	T	Tysfjord, outside Drag	10-12	4	4	11:10:00	13:30:00	2:20:00	1:30:19	vocal	carousel feeding on herring
2005-11-27	n/a	Tysfjord, outside Drag	n/a	0	0	10:10:00	13:53:00	3:43:00	0:44:46	vocal	socialising, carousel feeding, biopsy field trip, no photos from collaborators!
2005-11-29	n/a	Tysfjord, close to Bognes	n/a	0	0	09:00:00	10:17:00	1:17:00	0:01:25	silent	too many boats, noise, travelling
2006-11-09	Z	680177/143059 (Moholmen)	8	10	10	10:37:00	13:40:00	3:03:00	0:16:50	vocal	travelling, resting, many whale watching boats around
2006-11-21	AB	Vestfjord, outside store molla	15-20	6	6	13:10:00	14:41:00	1:31:00	0:20:00	vocal	carousel feeding on herring
2006-12-29	BI	Tysfjord, behind bekenesholmen	n/a	7	7	11:00:00	13:00:00	2:00:00	0:35:00	silent	travelling, resting
2006-12-30	AV	6813627/1609111 Tysfjord, behind Bekenesholmen	n/a	36	7	08:45:00	12:02:00	3:17:00	0:29:08	silent	travelling
2006-12-31	BI	6817168/1604168 Ofotfjord - Tysfjord	n/a	15	4	11:10:00	13:07:00	1:57:00	0:10:51	silent	travelling
2006-12-31	AV	6821841/1608524 Tysfjord	n/a	36	2	10:43:00	11:10:00	0:27:00	0:04:38	silent	travelling
2007-01-01	AV	Tysfjord, Korsnes	n/a	36	10	10:22:00	12:43:00	2:21:00	0:21:11	silent	travelling, many boats, noise

2007-01-01	BI	Ofotfjord - Baroya	n/a	15	7	10:22:00	12:43:00	2:21:00	0:06:40	silent	travelling, boats around
2007-01-02	AA+BI	6816476/1610421 Tysfjord,	n/a	15 and 21	7 and 7	09:18:00	12:27:00	3:09:00	1:45:21	vocal	seine feeding, many boats around
2007-01-03	AV	6814868/1606001 Ofotfjord - Tysfjord,	n/a	36	20	11:09:00	15:27:00	4:18:00	0:38:33	vocal	slow travelling, many boats, in the end matriarch came to boat vocalising
2007-01-04	BI	Vestfjord - Tranoy	n/a	21	5	n/a	n/a	0:00:00	0:20:00	silent	travelling, many boats around, noise
2007-01-05	AA	6817133/1554866 Vestfjord - Offersoy	n/a	15	5	10:55:00	13:22:00	2:27:00	0:35:52	silent	travelling, many boats around, noise, harassment from boats
2007-01-06	BI	Ofotfjord - Baroya	n/a	21	12	11:16:00	12:54:00	1:38:00	0:07:59	silent	travelling, many boats (harassment)
2007-01-08	AV	Tysfjord	n/a	15	12	15:02:00	15:35:00	0:33:00	0:17:45	vocal	carousel feeding on herring
2007-01-09	AV	6816348/1605769 Vestfjord, offersoy - baroya	n/a	36	11	13:09:00	14:51:00	1:42:00	0:28:46	silent	travelling, many boats
2007-01-10	AV	Vestfjord - flatoya	n/a	36	2	n/a	n/a	0:00:00	0:05:00	vocal	socialising around seiner, lots of noise
2007-11-02	AD	680871/135673 outside Stammsund	n/a	16	7	14:20:00	15:00:00	0:40:00	1:55:42	vocal	carousel feeding on herring
2007-11-07	S	6808884/1356107 outside Henningsvaer	n/a	28	15	10:40:00	14:58:00	4:18:00	0:20:02	silent	milling/ slow travelling
2007-11-10	AE	6806845/1430254 outside Henningsvaer	n/a	12	10	10:26:00	12:16:00	1:50:00	0:25:29	silent	milling
2007-11-16	E	6802/1408 outside Ballstad	n/a	11	10	11:04:00	13:07:00	2:03:00	0:14:34	vocal	travelling
2007-11-19	H	6801657/1435434 outside Henningsvaer	n/a	28	7	13:18:00	15:27:00	2:09:00	0:29:59	vocal	travelling, boat noise, milling
2007-12-08	AF	outside Henningsvaer	n/a	6	6	12:03:00	13:25:00	1:22:00	0:13:01	silent	travelling, socialising
2009-08-04	Q	Vestfjord: Henningsvaer - Nappstraumen	n/a	8	8	18:26:00	19:41:00	1:15:00	1:37:38	vocal	travelling, socialising, carousel feeding herring
2011-05-08	AM	6825019/1552494	12	6	6	20:26:00	22:05:00	1:39:00	0:22:06	vocal	travelling, milling
11.05 - 05.11.2011	AN	Oksfjord	6	6	0	11.05.2011	05.11.2011	0:00:00	0:00:00	vocal	salmon foraging, travelling, socialising, resting
11.05 - 18.07.2011	AP	Oksfjord	8 – 10	6	0	11.05.2011	18.07.2011	0:00:00	0:00:00	vocal	salmon foraging, travelling, socialising, resting
11.05 - 18.07.2011	AN-AP	Oksfjord	16	12	0	11.05.2011	18.07.2011	139:17:00	39:00:00	vocal	salmon foraging, travelling, socialising, resting
Total								210:07:26	62:01:39		

Sound recordings and analysis

For the present sound analysis I used a sub-dataset from 2004–2011. Recordings and observations were made between November 2006 and August 2010 in the Vestfjord in northern Norway over 36 encounters (including multiple recording sessions from each of the different killer whale groups we encountered).

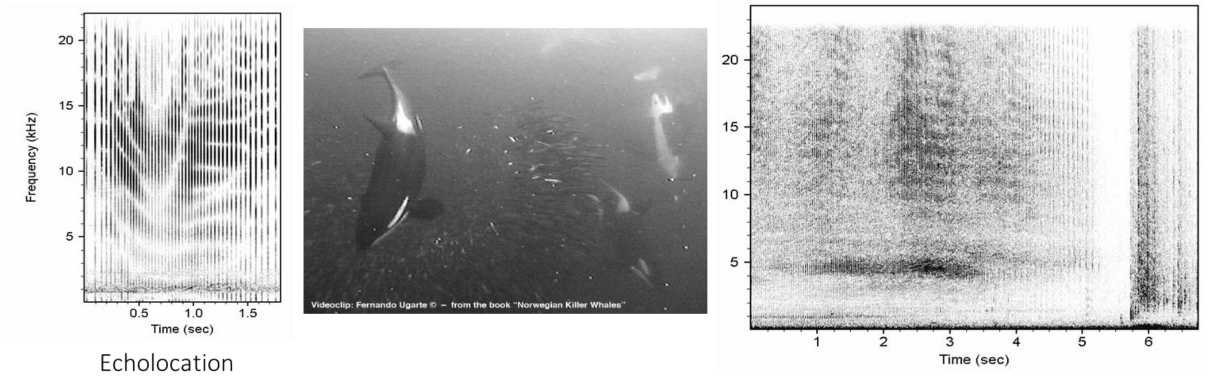
During the 36 encounters with killer whales I collected 194 hours of observation and a total of 62 hours of sound recordings. However only 23 hours were usable recordings when the whales were vocalising and the quality was good enough for sound analysis. From that subset of data I could identify 159 individual killer whales in eleven different groups. The average group size was 9, with the smallest group consisting of 4 identified members and the largest 20 members. Two groups (AN and AP) were encountered during the summer of 2011 for 3 and 6 months continuously inside the same fjord, and are described separately in chapter 7.

Table 4-2. Data collected from long-finned pilot whales and killer whales in the Vestfjord in northern Norway from 2004–2011. Eleven groups of killer whales were observed and recorded from 2004–2011, and 3731 calls were identified and classified into 85 different call types.

DATA COLLECTION	LONG-FINNED PILOT WHALES	KILLER WHALES
Date	2007–2010	2004–2011
Recording time (hh:mm)	**16:47**	**23:02**
Groups with ID's	7	11
Individual ID's	161	159
Group sizes ID's	23 (min 4 max 47)	9 (min 4 max 20)
Average call types / group	36 (min 4 max 47)	25 (min 2 max 37)
Total calls (N)	**4572**	**3803**
Call types	**129**	**60**
Call subtypes	**25**	**25**

Vocal repertoire—description

The following description of killer whales' vocal repertoires is based on 23 hours of recording time and 3731 selected calls. As previously described (Strager, 1995), I found a variety of broadband clicks and buzzes, which are clicks produced in repetition with small intervals in different frequency ranges, with the main energy at frequencies 20–30 and 40–60kHz (see Fig. 4-3). These clicks and buzzes are typical for dolphin echolocation (Au, 2004).



Echolocation

Carousel feeding – clicks, buzzes and tail slaps

Figure 4-3. Killer whales produce clicks and buzzes (rapid repetition of clicks with short intervals), with main energy in the frequency area of 10–20kHz. Buzzes are typically produced during carousel feeding just before a tail slap, possibly to herd the herring into tight balls and to detect the herring, maybe even to coordinate the movement of all killer whales during the hunt.

Whistles

Norwegian killer whales produce whistles similar in frequency and structure to those of other dolphin species and pilot whales (e.g.(Herzing, 2000; Taruski, 1979) (see Fig. 4-4)). I found whistles in a wide bandwidth with ultrasonic range similar to those described for killer whales in other places (Andriolo et al., 2015; Filatova et al., 2012; Samarra et al., 2010) (see Fig. 4-15). Ultrasonic whistles were only recorded with the newer equipment in 2011, which had a sampling rate of 192kHz. Group AM produced ultrasonic whistles while travelling in the Vestfjord (N=259) and groups AN and AP during their 5 and 3 month-long abundance inside a fjord on Lofoten (N=64).

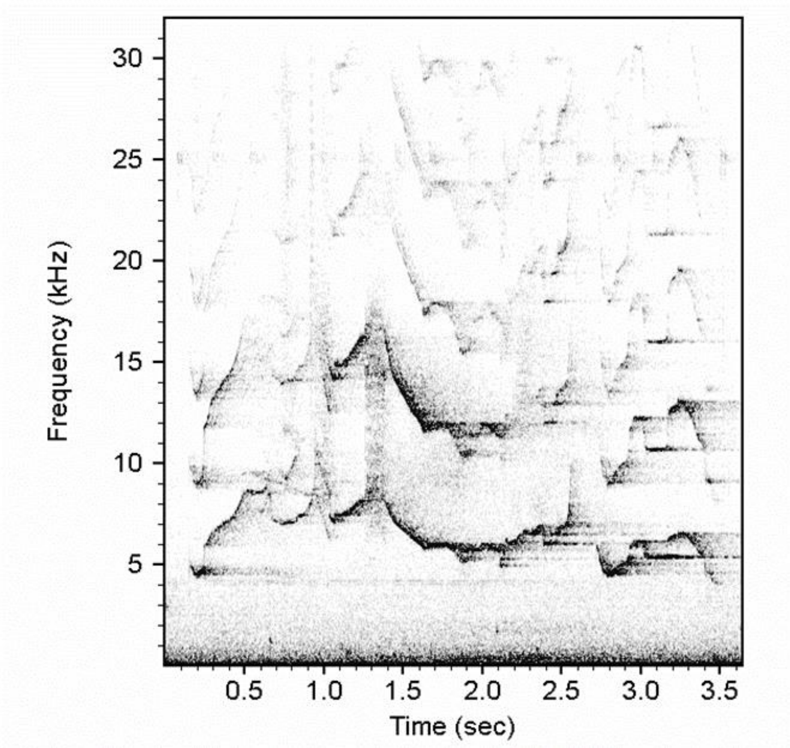


Figure 4-4. Killer whale whistles have typically lower frequency components (below 20kHz) with variable inflection points and loops. Spectrogram parameters: FFT size 1024, overlap 75%.

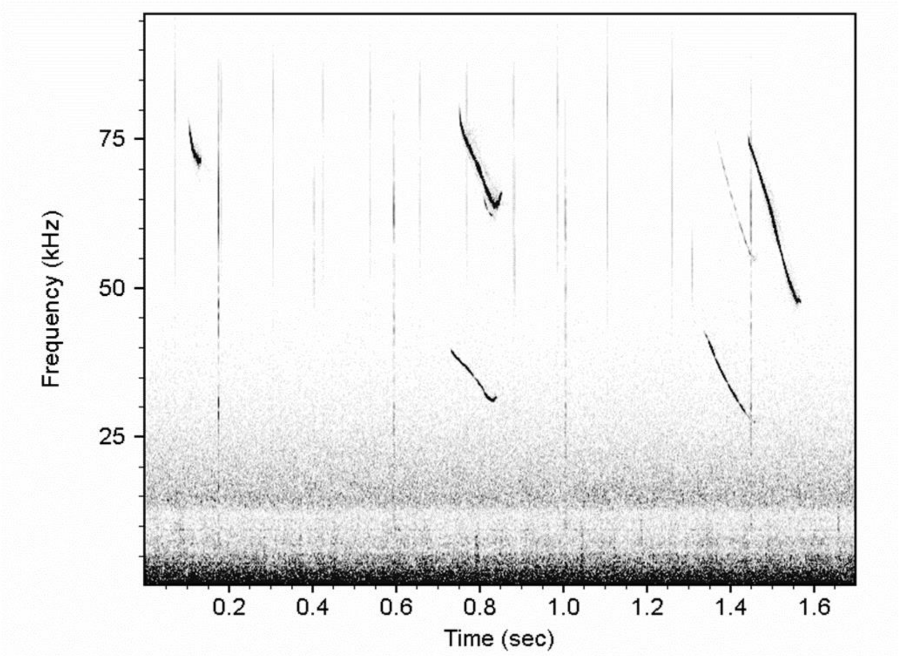


Figure 4-5. Ultrasonic killer whale whistles are short, with frequencies above 20kHz and as high as 70kHz with time frequency contour either down-sweeping, up-sweeping, or u-shaped. Ultrasonic whistles were recorded in 2011 with equipment that allowed sound recording of 96kHz, from three groups: AM (N=259), and AN+AP (N=64).

Pulsed Calls

Pulsed-type calls contained a large variation in sound structure ranging from a single simple segment, one element and one frequency component to highly complex structures with several segments, and elements and two frequency components. I classified 3731 calls into 60 different call types and 25 subtypes according to their similar vocal structure, and 33 call type combinations from 11 different groups and several encounters without identified groups. This was tested by two independent trained reviewers and the call type classification agreements were 97% and 96%; with no misclassifications, only 220 out of 3731 calls were labelled as uncertain. Since the reviewers did not agree on all the uncertain calls, these calls remained as part of the described vocal repertoire.

The call types were not produced equally often: some call types were produced more than 300 times, whereas the majority of call types were produced less than 50 times (see Fig. 4-6). Call types produced per group ranged from 2 to 37, with an average of 25 call types per group (weighted arithmetic mean) per call (see Fig. 4-8).

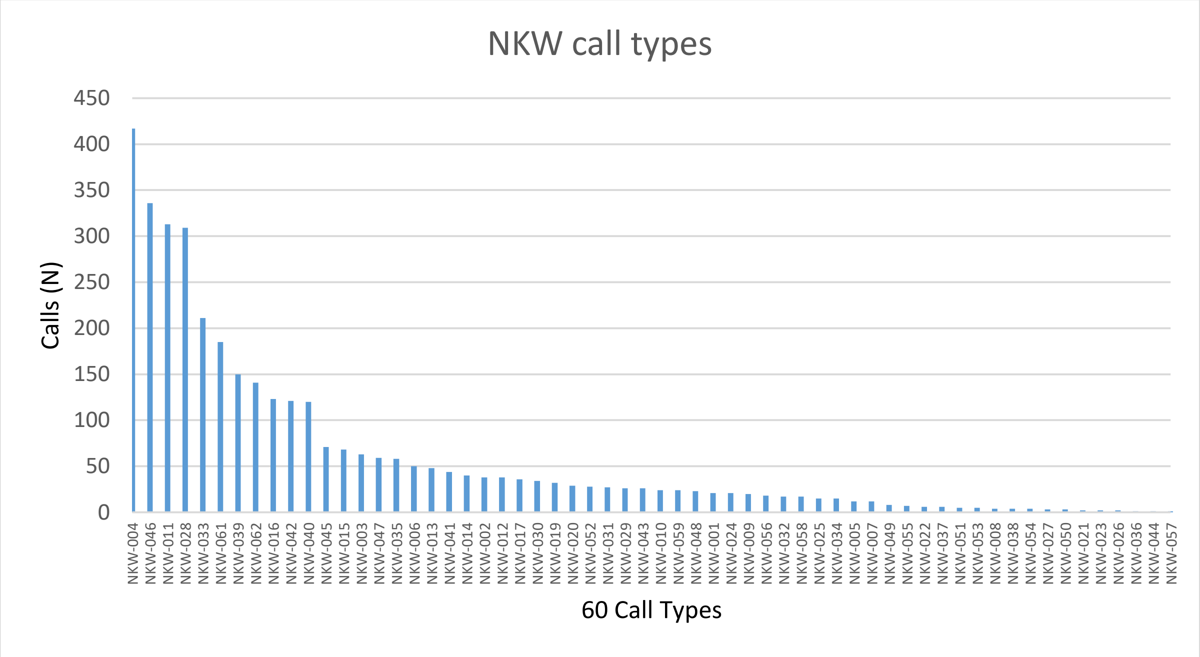


Figure 4-6. The amount of call types produced by killer whales in northern Norway were not equally recorded. 3731 calls were classified into 60 different types, and 25 subtypes and 33 call combinations were pooled into their main call types. Call type 004 was produced 417 times and is the most frequently-produced call; most call types were produced less than 50 times, and three call types occurred only once.

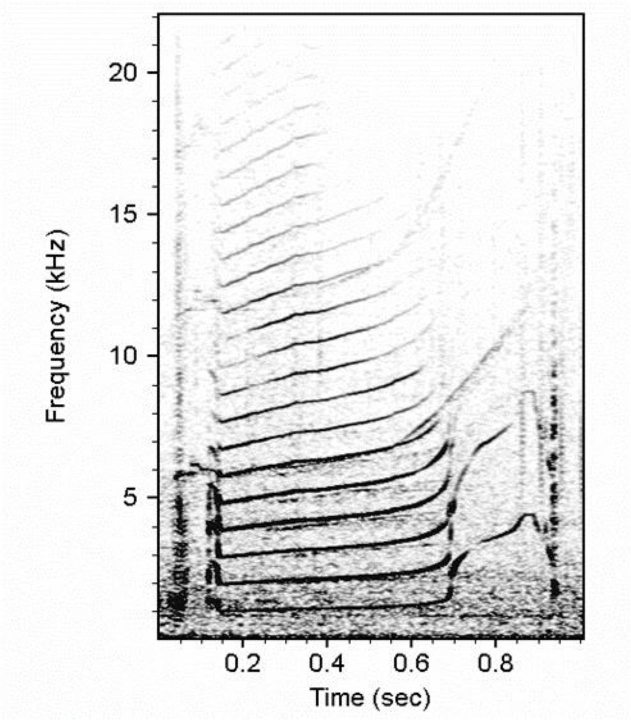


Figure 4-7. Killer whales frequently produce calls with two frequency components, two-voiced call type NKW-004 (in the figure) is the most commonly used call in killer whales from northern Norway (N=417 recorded from 6 different groups).

Call type distribution among groups

From the 3731 calls, 2399 could be attributed to 11 identified groups via Photo-ID.

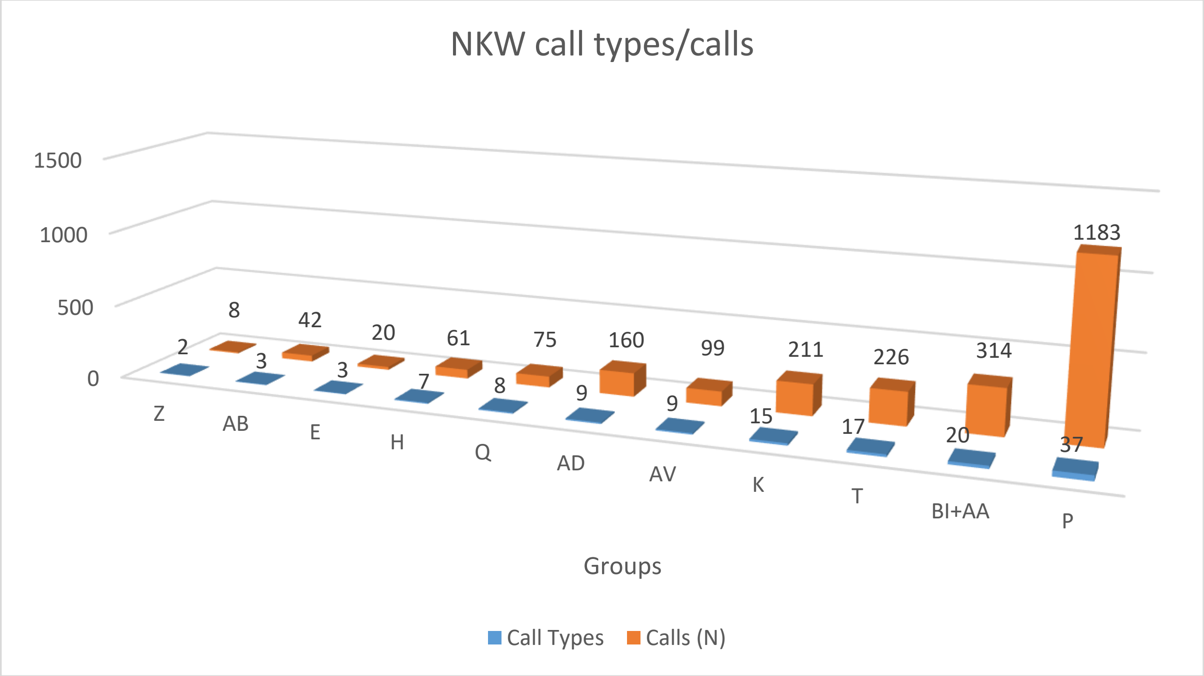


Figure 4-8. Amount of call types per group of killer whales. In total 2399 calls from 11 different killer whale groups were analysed. Amount of calls increases with call type number: group P produced both the most calls (N=1183) and the most call types (N37), whereas group Z only produced 8 calls in 2 call types. The weighted mean shows 25 call types/group (range from 2 to 37 call types/group).

Call production during the eleven different encounters was not equal, during some encounters only 8 or 20 calls were produced, yet in other encounters there were as many as 1183 calls (see Fig. 4-9). This large variation might be due to different recording lengths; Fig. 4-10 shows that short recording lengths (less than 1 hr) result in fewer call types and smaller number of calls. Only recordings ≥ 1 hr were comparable with each other, with call types ranging between 8 and 37 and the number of calls varying between 75 and 1183 per group. However, the call types did not correlate with longer recording times and call numbers, group P with 1:31 hrs of recording time produced the most call types (37) and the greatest numbers of calls (1183), whereas group AV was recorded for 02:25 hrs and produced only 9 call types and 99 calls.

There seems to be a relationship between the amount of calls and the amount of call types produced—the more calls were recorded, the more call types could be identified (see Fig. 4-8). Group P produced 1183 calls in a recording of 1:31 hrs and had the most call types (37) of all groups.

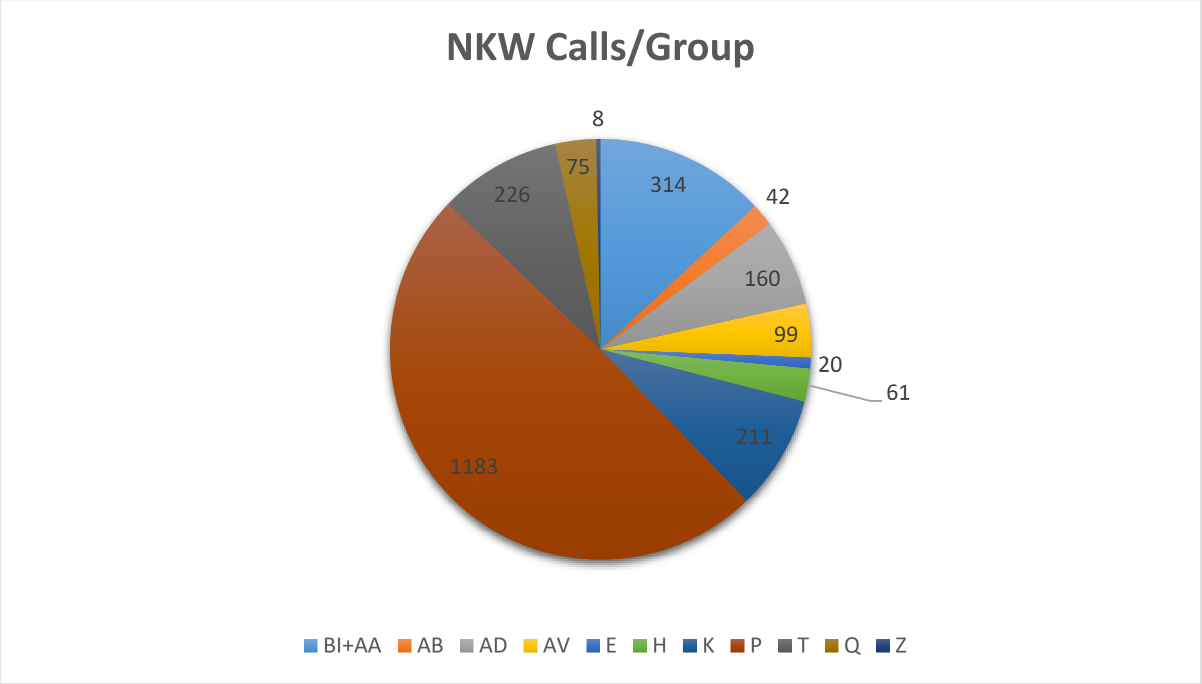


Figure 4-9. Number of calls produced during the 11 different NKW group encounters (different colour codes); some groups were only shortly observed and recording times were low. These groups also show the lowest number of calls produced (groups Z, E, AB, and H, see next figure).

Influence of recording length

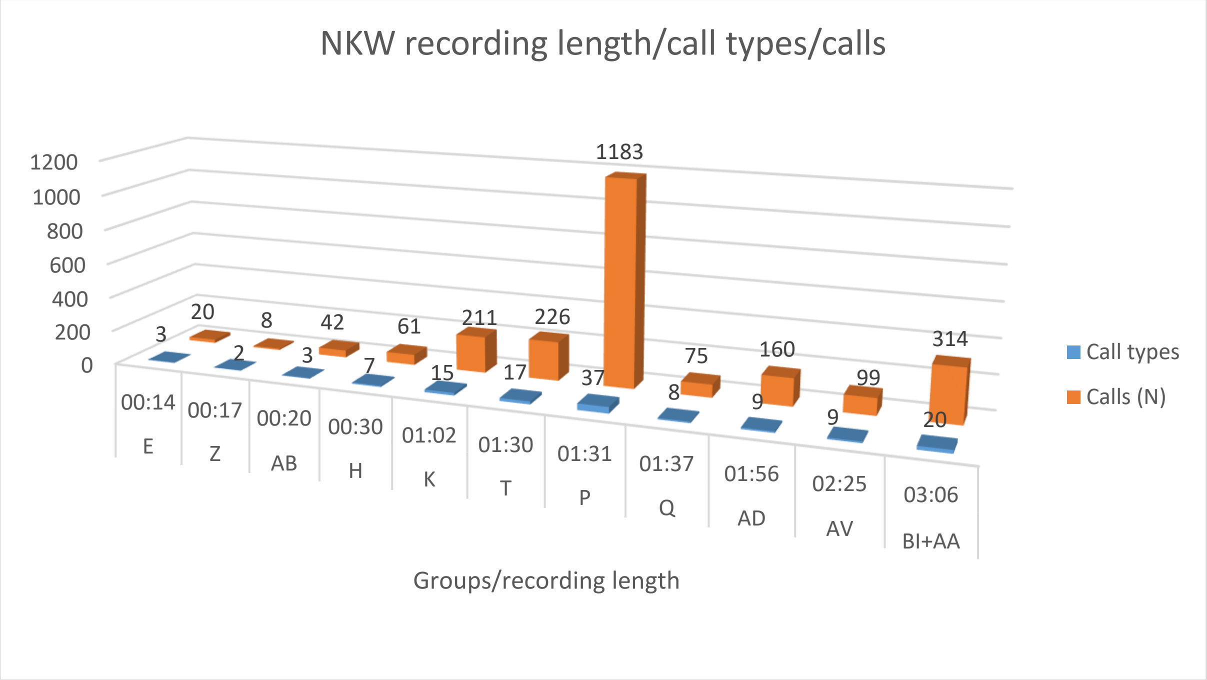


Figure 4-10. Length of recording time per group encounter (from group E with 00:14 hrs:min to group BI=AA with 3:06 hrs:min), with the number of call types (blue) and total amount of calls produced (orange). Both call types and amount of calls recorded were low with recording times less than one hour. But no clear correlation between recording time and amount of call types or amount of calls can be detected in longer recordings (more than one hour).

Influence of group size

To investigate if the difference in call types and number of calls depends on group size, i.e. amount of identified members, I plotted the numbers in the graph of Fig. 4-11. The group size of identified individuals does not seem to influence the number of call types or calls. For example, groups Z and P both have 10 members but very different numbers of call types. However, note that the number of members are identified individuals in a group and during data collection of groups K and T the light conditions did not favour good quality photographs and only 4 individuals of groups of around 10 could be identified. But even with the correction of the group size, no trend of increased call types/calls with increased group size can be detected. Other influences such as recording length (e.g. short recording length for group E but not BI+AA or AV) or different behaviour could explain the differences.

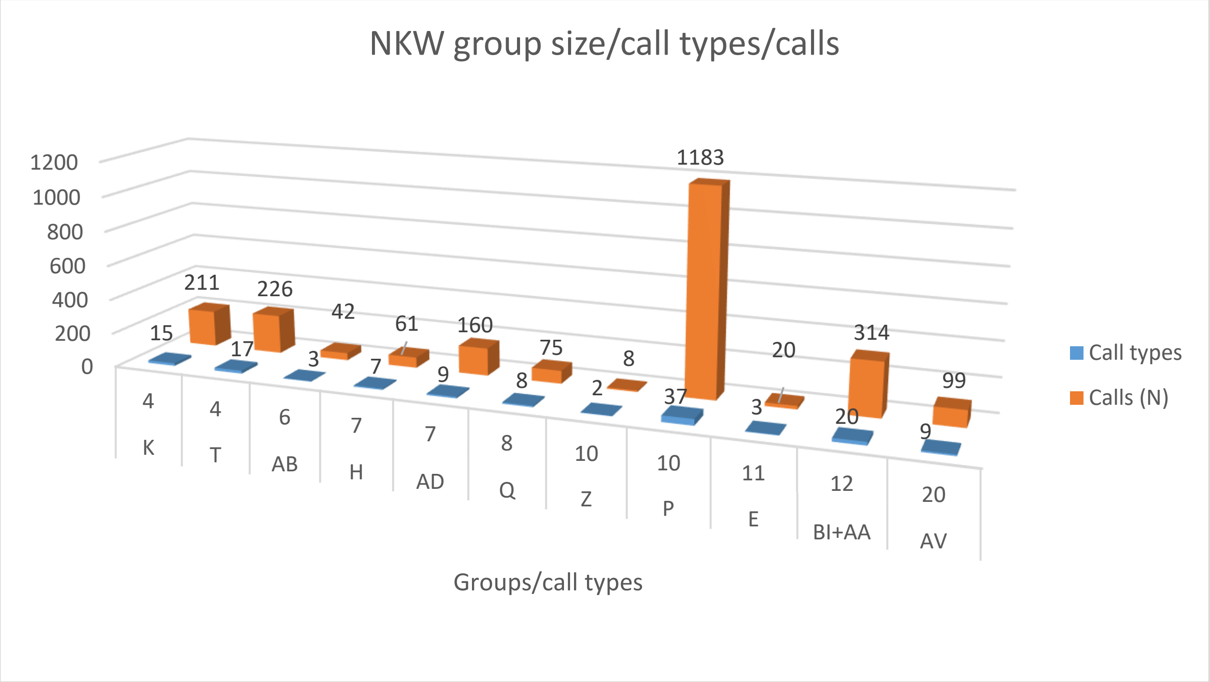


Figure 4-11. Increasing group sizes (from groups K and T with 4 members to group AV with 20 identified members) are plotted with call types (blue) and number of calls (orange) for each group encounter. No trend of increasing call types with increasing number of group members can be seen.

Influence of behaviour

In order to investigate if different behaviour influences call type and call number production, I have plotted observations against call types and number of calls produced for each group encounter (see Fig. 4-12). In this plotting I only look at overall group behaviour, which is by no means fine scaled. The main group behavioural categories during sound recordings were:

Resting (R) when all animals were almost motionless at surface, slow and short dives (no flukes showing when diving);
Travelling (T) when all animals were swimming at more or less the same speed (slowly less than 3 knots, medium 3–5 knots, and fast more than 5 knots) in the same direction;
Socialising (S) when groups were meeting or animals were involved in body contact, play, and high surface activity such as jumps, breaching, and spy hops;
Carousel feeding (CF) was indicated by high diving activity, fast swimming back and forth in the same area, increased underwater clicking activity, and tail slaps.

Figure 4-12 shows that the behavioural categories do seem to influence both call type and number of call production. Vocal activity was lowest when travelling (groups H, E, and Z), increased with socialising (group BI+AA), and was highest during carousel feeding in most groups except group AB. These results have to be handled with care, since low vocal activity is also correlated with short recording length in groups AB, E, H, and Z (less than 31 minutes, see Fig. 4-10).

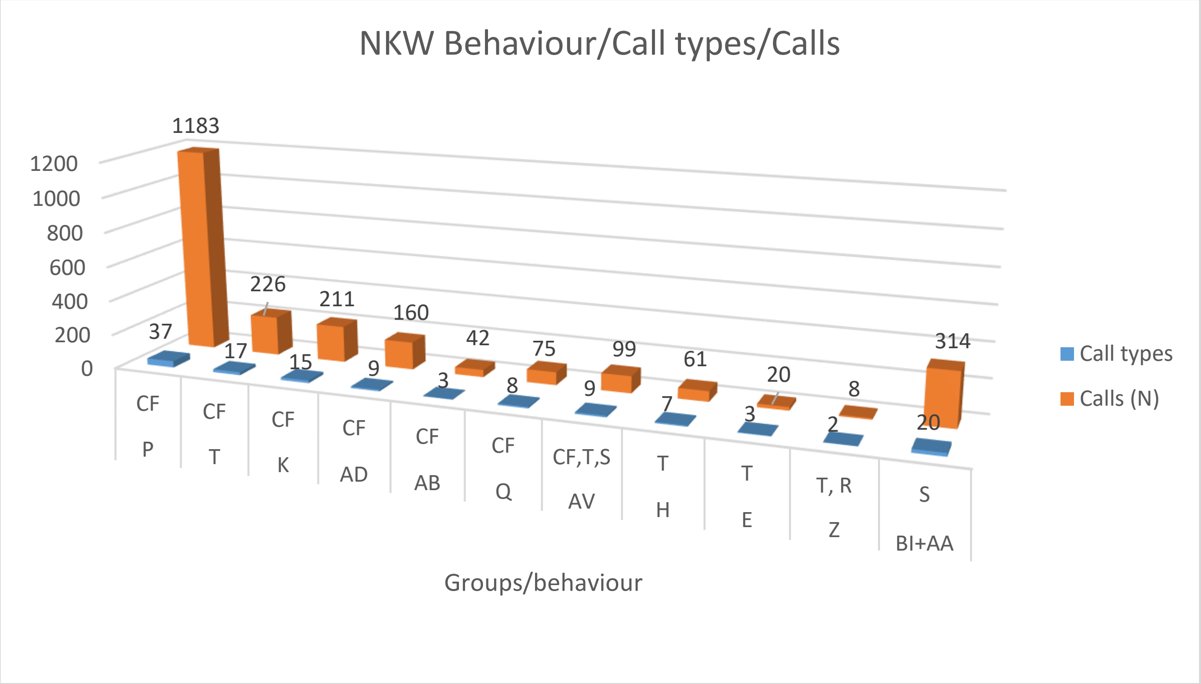


Figure 4-12. Killer whales' overall group behaviour does seem to influence call production; during carousel feeding (CF) numbers of both call types and calls is highest in all groups except AB, which has a short recording length (20min, see Fig. 4-10). During group BI+AA encounters, two groups were meeting while travelling and surface activity increased, thus it was considered socialising. Group behavioural categories were T=travelling, S=socialising, CF=carousel feeding, R=resting.

Call type structures

Most call types (46 call types (N=1857)) only consist of LFCs, whereas 37 call types (N=1763) contained both LFC and HFC, and 2 call types (N=111) consist of only HFC (see Fig. 4-13).

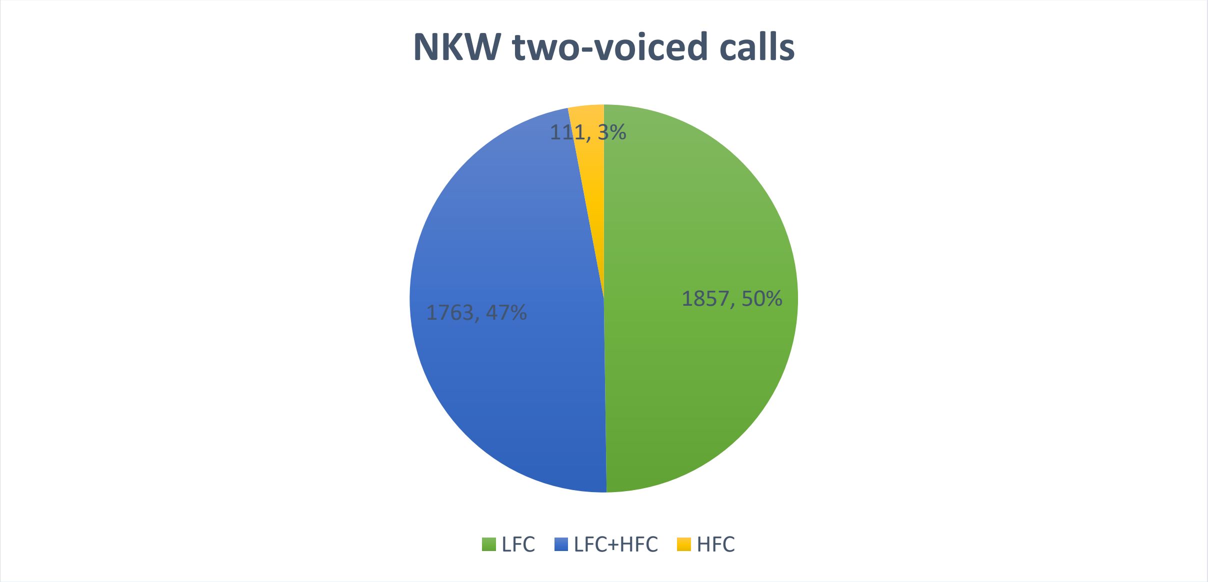


Figure 4-13. Degree of two-voiced calls in killer whales was 47% (LFC+HFC), 50% were simple calls with only low frequency components (LFC), and 3% consisted of only high frequency components (HFC).

Further, most calls (70 CT; N=2902) consist of only one segment: 83% of only LFC calls (39 CT; N=1546), and 73% of LFC+HFC calls (30 CT; N=1284), however 22% (N=829) of the calls have more than one (between two and five) segment (see Fig. 4-14). The most LFC calls consisted of two elements (43% N=805) and 26% of LFC call types (N=485) contained only one element (see Fig. 4-14 a); the other call types contain two to ten elements. Most of the LFC+HFC calls contain four elements (45% N=803); see Fig. 4-14 b), the rest contain from one to ten elements (see Fig. 4-15). The HFC call types consist of one or two elements. A detailed breakdown of the calls is displayed in supplement 2. More complex call types contained up to 10 elements in different variations (see Table 4-2 and Fig. 4-15). Complex call types were less common than more simple call types with up to four elements.

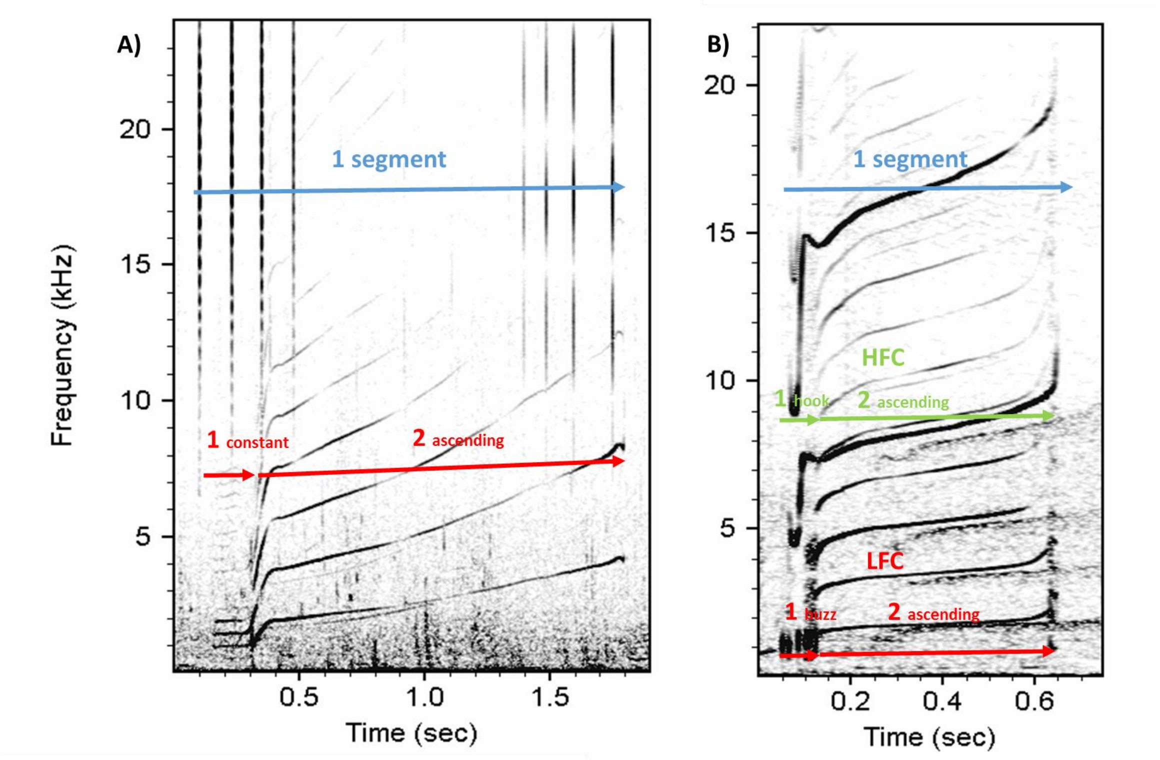


Figure 4-14. Killer whales produce discrete call types. These two spectrogram examples show the main call types: A) most commonly structured LFC call (NKW-45i) with one segment and two elements (constant + ascending time-frequency contour; B) most commonly structured two-voiced call type (NKW-11iii) with one segment and four elements (LFC buzz + ascending frequency time contour; HFC hook + ascending time-frequency contour).

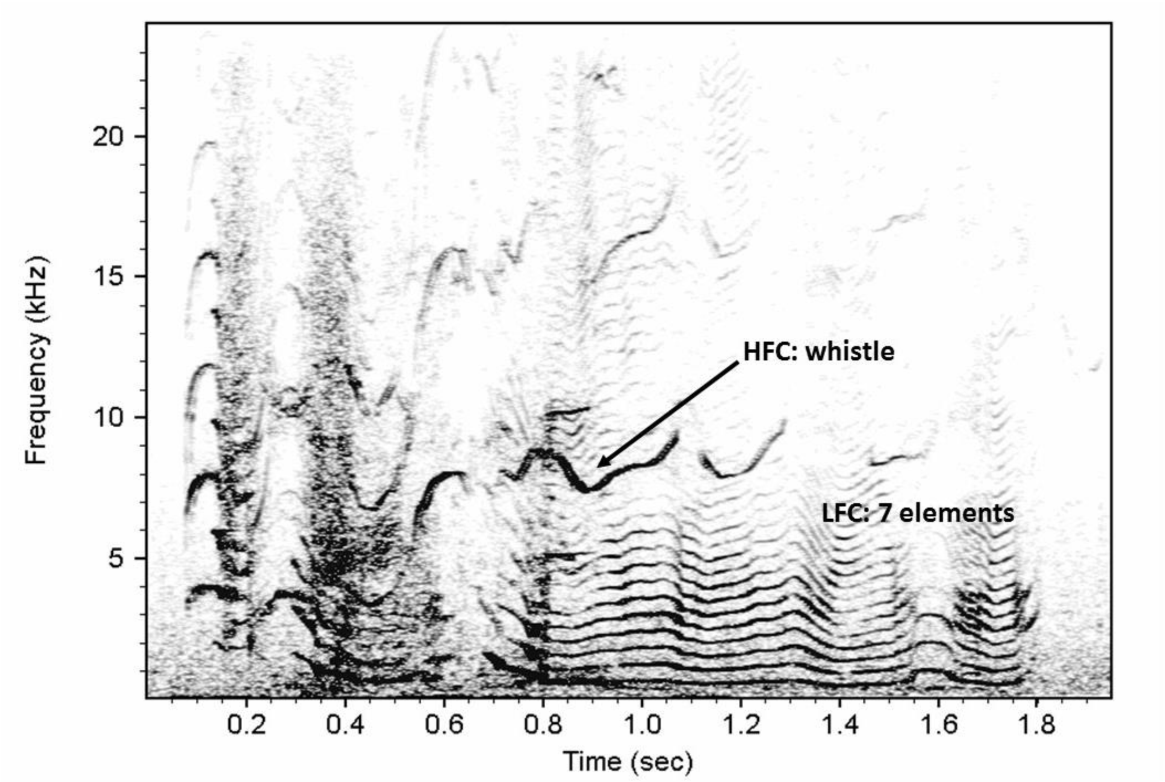


Figure 4-15. Killer whales produce complex call types. This example shows a spectrogram of a complex two-voiced killer whale call type (NPW-54) with one segment and seven elements: LFC buzz + long u-shape + descending + constant + ∩-shape + u-shape; UFC whistle, (N=4). Spectrogram parameters: FFT size 1024, overlap 75%.

Within the calls I described 9 different element structures according to their harmonic time frequency contour as: ascending, descending, U-shape, ∩-shape, noise, buzz, whistle, hook, and constant. Within the 85 different call types I found over 281 elements. Most of the elements appear to be similar in structure: 36% of the elements consist of ascending contours (N=101), followed by a constant frequency contour (22%, N=62), and 9% are descending elements (N=26); the remaining 33% are either U-shaped, ∩-shaped, noise, buzzes, hooks, or whistles (see Table 4-2 and supplement 2).

Table 4-2. Summary of elements within the NKW call types; amount of differently shaped and amount of elements within call types.

elements (N)	*LFC*	*LFC+HFC*	*HFC*	*SUM*
ascending	**38**	**61**	**2**	**101**
descending	13	13	0	26
U-shape	11	17	1	29
∩-shape	4	9	0	13
noise	1	3	0	4
buzz	7	8	0	15
whistle	0	7	0	7
constant	**30**	**31**	1	**62**
hook	1	22	1	24
total	105	171	5	281
call types				
1 element	13	0	0	13
2 elements	**16**	2	1	19
3 elements	13	7	1	**21**
4 elements	2	**10**	0	12
5 elements	1	6	0	7
6 elements	0	4	0	4
7 elements	0	3	0	3
8 elements	1	0	0	1
9 elements	0	1	0	1
10 elements	0	1	0	1
total	46	34	2	82

Call type combinations

Many call types were combined with other call types and these sequences occurred more than once. The criteria I used to classify call combinations was a) no silent gap and no overlap between the calls; b) with a time gap between calls but gap length had to be the same for the same call combinations; c) calls that were combined were also recorded alone or in combination with other calls. I found 33 call combinations (N=464) out of a call type repertoire of 60 call types and 25 call subtypes (N=3731) (see Fig. 4-16). Call combinations were recorded from 8 different groups and from unidentified groups.

Such call combinations were first described by Strager in 1995 as compound calls; she found 21 such combinations of calls in a vocal repertoire of 34 call types and 20 call subtypes from killer whale groups in northern Norway, however classification was done in a different way and results from both studies cannot be compared directly.

The call types that I described in combination were also recorded alone without combinations or in combination with other calls. In the spectrograms the call combinations are named as Norwegian killer whales (NKW), call type numbers of the combined calls (e.g. 28i-11iv), and the capital letter of the group (e.g. Q). The combination NKW-46-4 was the most commonly recorded (N=231) and shared by 4 different groups (AV, (AA+BI), P, T) (see Fig. 4-17); whereas call type NKW-28, the most diverse call type, was found in 4 different versions (subtypes) and combined in 9 different combinations with other call types. Figure 4-16 shows an example of call types produced alone and in combination with each other: NKW-28i with NKW-11iv, and NKW-28i with NKW-11iv and NKW-42i. These calls were more often produced alone (N=121) than combined (N=45), but the combinations appear independently in 4 different groups/encounters; group Q was recorded outside the winter herring feeding season 2004–2007, in August 2009.

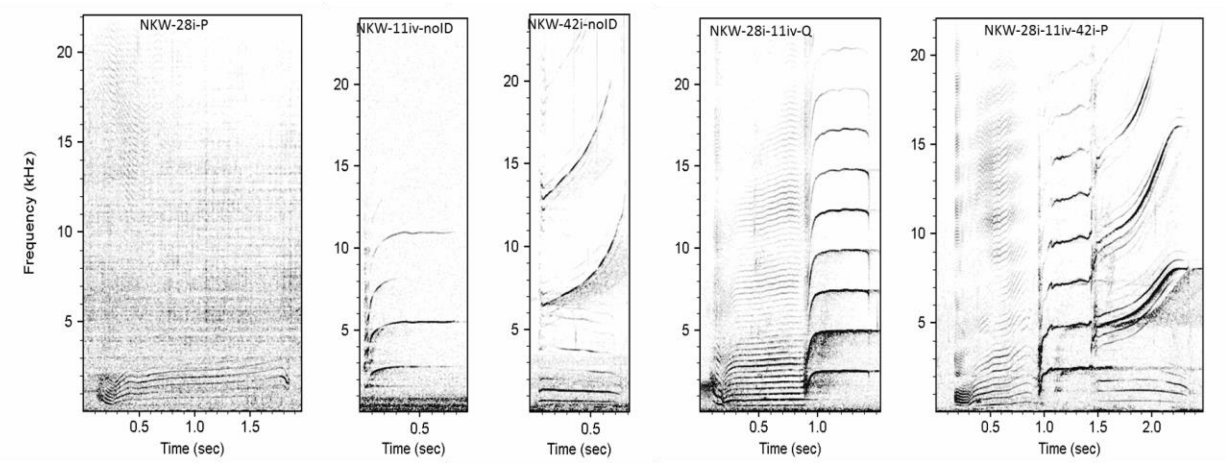


Figure 4-16. One example of call type combinations in killer whales: Call type NKW-28, produced by groups P and AD (N=56); call type NKW-11iv, produced by groups AA+BI, AD, K, P, Z, and 3 unidentified encounters (noID) (N=51); and call type NKW-42i produced by group P, group BI+AA, and one unidentified encounter (N=14) were found un-combined. Call type NKW-28i was combined with NKW-11iv by groups P and Q and two unidentified encounters (N=35). Call type NKW-28i was combined with NKW-11iv and NKW-42i by group P and one unidentified encounter (N=10). Note that call type NKW-28i was shortened by almost 50% when combined with other call types.

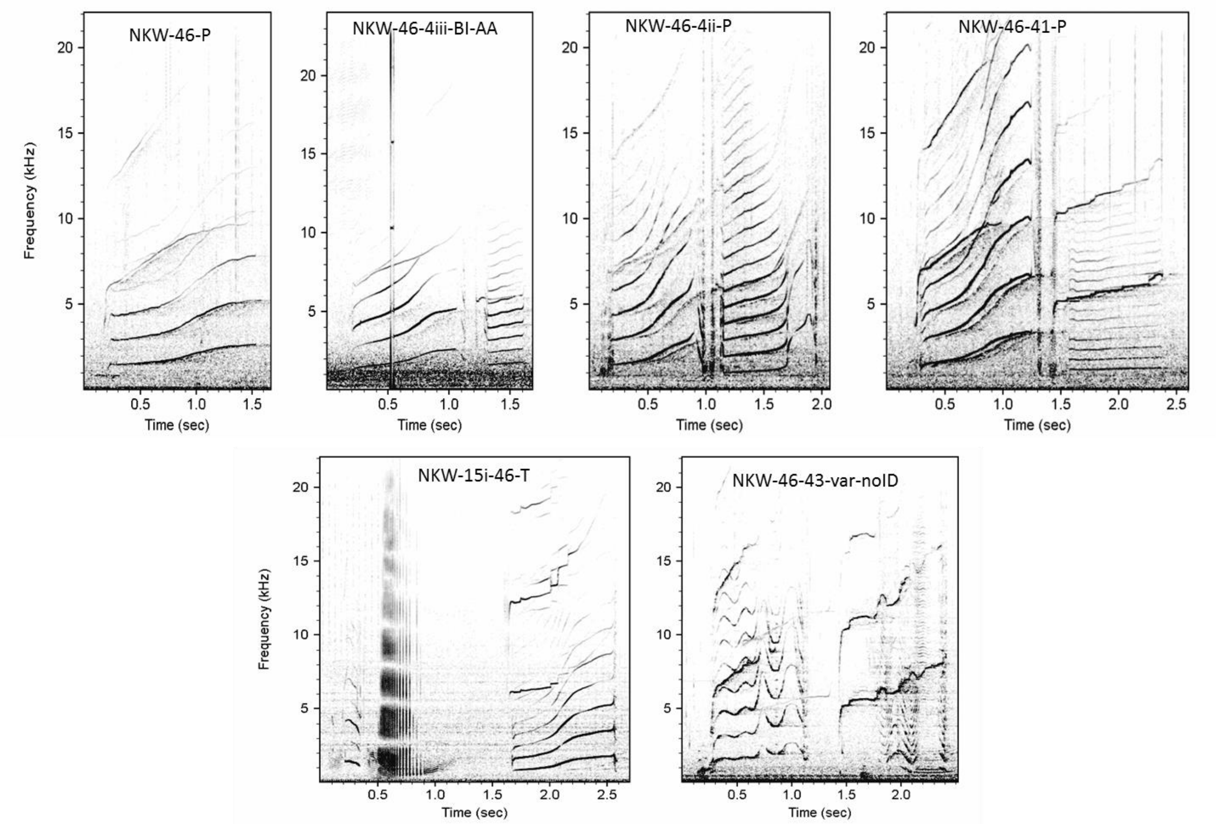


Figure 4-17. Another example of the most numerous call type combination in killer whales: NKW-46 alone was produced by groups BI+AA, P, T, and one unidentified encounter (N=70); NKW=46 combined with NKW-4ii by groups Bi+AA, AV, P, and T (N=161); combined with NKW-4iii by groups Bi+AA, P, and T (N=70); and combined with NKW-41 by groups P and T (N=24). Aberrant versions of NKW-46 were combined with NKW-43 in one unidentified encounter (N=7), and call type NKW-46 was preceded by call type NKW-15i in a recording from group T (N=4).

Call type sharing between groups/recordings

My data had limitations since I had no information on individual whales vocalising, nor was it possible to separate calls according to individual callers, but it allowed me to look into differences of vocal repertoires between the different group encounters. I studied the overall repertoire and usage of call types per group (in one or several encounters) and call type sharing between the groups.

Due to low sample sizes I have excluded groups AB, E, and Z from the following comparison. I examined the degree of call types and number of calls used by eight different groups (groups AD, (Bi+AA), AV, H, K, T, P, and Q): in total they produced 2329 calls in 51 different call types. Average CT/group was 25 with a range of 8–37 (weighted arithmetic mean).

In summary, I found that 30 out of 51 call types (59%) and 2101 out of 2329 calls (90%) are shared between at least two groups (see Fig. 4-18). 10% of the calls (228) were only produced during one group encounter, which indicates that there is only a low degree of group specific vocal communication in killer whales and most calls were shared with the other groups. However, the groups do have their own set of call types and the sharing rate varies from 54% to 97% between groups.

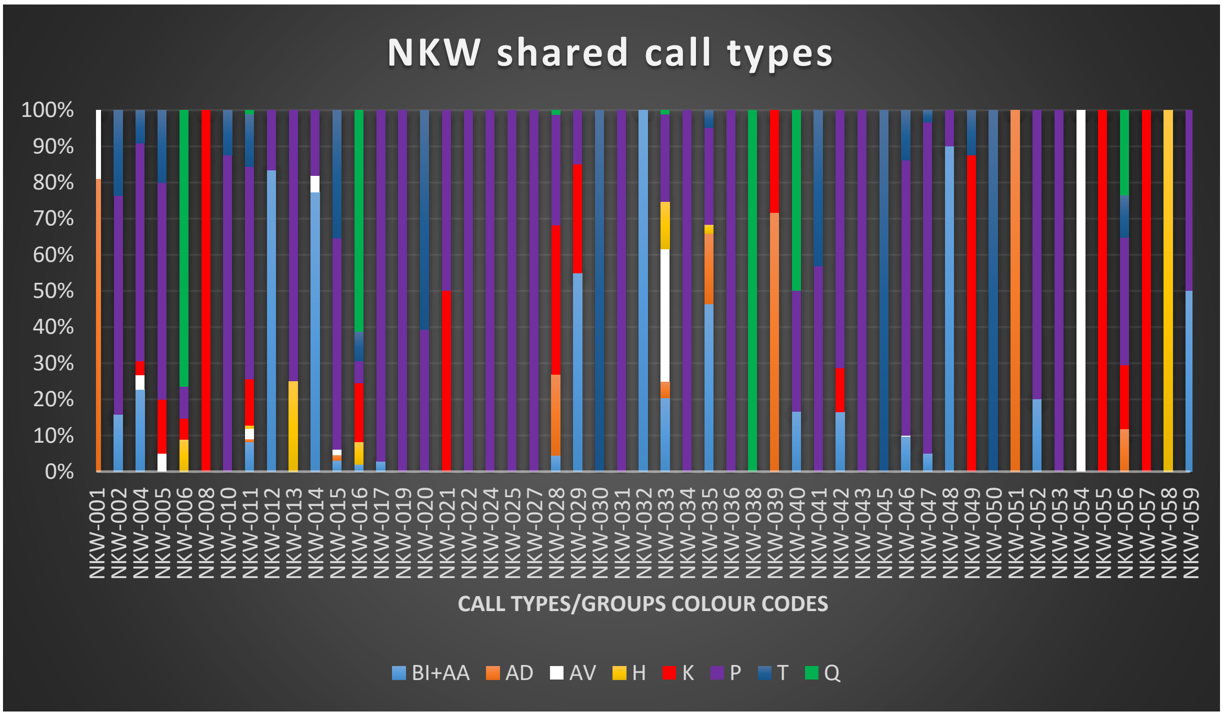


Figure 4-18. Call type sharing between 8 group encounters of killer whales. Call types were pooled with subtypes, thus 51 different call types (N=2329) were produced by 8 different groups. Out of the 51 call types, 30 were shared with other groups. The colour code shows the degree of call type production and sharing with other groups, hence the more colourful a column is, the more the call type was shared between groups, e.g. call type NPW-16 was produced by 6 different groups ((BI+AA), H, K, P, T, and Q). Group (BI+AA) were encounters with members of two groups present, but it cannot be ruled out that all animals are pooled together because they belong to the same group.

The eight different killer whale groups shared call types with at least two other groups, in total 81% of call types and 90% of calls were shared (Tables 4-3 and 4-4). Group K had the highest (97%) call type sharing with other groups, and group AD the lowest (54%). On average 20 CT/group were shared with a range 6–26 CT/groups (weighted arithmetic mean).

Table 4-3. All calls and call types produced by the eight different killer whale groups, showing shared calls, call types, and number of group specific calls and call types. Note that the same call types can be produced by more than one group, therefore the total call type numbers are not the overall number of different call types (60) of the vocal repertoire.

groups	*AA+BI*	*AD*	*AV*	*H*	*K*	*P*	*T*	*Q*
calls (N)	314	160	99	61	211	1183	226	75
call types	20	9	9	7	15	37	17	8
shared calls (N)	298	87	95	44	205	1101	200	71
shared call types	19	8	8	6	12	26	13	7
group spec calls (N)	15	4	4	17	6	82	26	4
group spec call types	1	1	1	1	3	10	3	1

Table 4-4. Call types and number of calls (N) shared with other groups. Bold numbers are call types recorded only during their own group encounters. All groups shared at least two call types with each other and the sharing rate is higher than the non-sharing rate. Group P shared the most call types with other groups, however it was also the most vocal group and produced the most call types (N=37) and calls (N=1183).

Groups	*(AA+BI)*	*AD*	*AV*	*H*	*K*	*P*	*T*	*Q*
(AA+BI)	**1 (15)**	4 (68)	6 (194)	4 (76)	6 (76)	19 (299)	8 (170)	5 (68)
AD	5 (68)	**1 (4)**	4 (28)	3 (18)	4 (121)	6 (70)	4 (13)	4 (61)
AV	6 (90)	4 (77)	**1 (4)**	2 (72)	3 (23)	7 (91)	5 (25)	2 (72)
H	4 (29)	3 (26)	2 (25)	**1 (17)**	3 (8)	6 (45)	3 (6)	3 (31)
K	6 (162)	4 (152)	3 (49)	3 (41)	**3 (6)**	10 (171)	6 (67)	5 (135)
P	19 (986)	6 (308)	7 (713)	5 (196)	10 (560)	**10 (82)**	12 (802)	7 (267)
T	8 (154)	5 (66)	4 (137)	3 (41)	6 (81)	12 (196)	**3 (26)**	3 (41)
Q	5 (41)	4 (12)	2 (5)	4 (61)	5 (66)	7 (71)	3 (37)	**1 (4)**

In summary, all groups shared at least 2 call types with the other groups, and more calls were shared with other groups than produced alone. The overall sharing of call types and calls was high (81% and 90%) and indicates that killer whales in this study belong to the same acoustic clans (see (Ford, 1991) for explanations of killer whale acoustic clans), and the matrilineal groups may even be closely related (Deecke et al., 2010).

Testing whether these results were significant and could be replicated with statistical analysis similar to the pilot whale repertoires (Vester et al., 2016) was not possible for the killer whale data, due to the low number of high quality recordings of call types.

Discussion

Vocal repertoire

Similar to the earlier description of the vocal repertoire of killer whales in northern Norway (Shapiro, 2008; Strager, 1995), I found a variety of clicks and buzzes, variable nonharmonic calls, and different types of whistles; as well as different types of pulsed calls ranging from simple, single-segment calls to calls of highly complex structures composed of up to five segments and ten elements. Strager assigned 3–16 call types to each group (average around 10 call types/group), whereas I found in my study that the groups produced 2–37 different call types per group with an average of 25 call types per group (weighted arithmetic mean). However, Strager's classification was slightly different than my classification. Many call subtypes from Strager would have resulted in new call types in my study. The reason I used a more detailed breakdown and sorted call types into new call types was that I considered elements within a call as independent parts similar to syllables or phonemes in words. A new arrangement of elements was therefore considered a new type of call with a possibly different meaning, similar to phonemes creating words. However, similar to Yurk, Shapiro et al. looked into subunits in killer whale calls for automatic classification of Norwegian killer whale calls (Shapiro et al., 2011; Yurk, 2005). They supported the thought that killer whales use subunits of calls to rearrange and generate a larger and more flexible vocal repertoire. In my study these subunits were similarly sorted into elements, however I could only detect eight different structures. My method may be biased towards observer liability and perception, and can only serve as a description of the vocal repertoire, and the functions behind the calls are still unknown. However, it has proven that the classical observer-based categorization of whale calls is reliable and even comparable to automatic classifications involving neural networks used for cetacean acoustics (Deecke & Janik, 2006).

Thus the difference in call type classifications resulted in different amounts of call types in my study, compared to earlier studies. Unfortunately there is no unique method and description of call types in cetacean acoustics, which makes comparative studies difficult.

However, a more detailed call type analysis did not alter the result of calls with two frequency components and revealed similar results; Strager reported 40% of two-voiced calls and in my study I found 47% of the calls to have two frequency components (Strager, 1995). This small difference might result from the much lower sample size of Strager's study. In a study of killer whales in Kamchatka the percentage of two-voiced call usage increased when more than one pod was present and ranged from 47% to 89% (Filatova et al., 2009). It seemed that killer whales globally use two-voiced calls in about half of their call type repertoire. Miller et al., found that the higher frequency component encodes information about the direction of the caller due to its different acoustic attenuation properties, more than lower frequency components of a call (Miller, 2002; Miller et al., 2007). Due to the directionality of the HFC many calls might not be detected or were classified as subtypes of two-voiced calls. Nevertheless the reported high percentage of usage along with the directional acoustic properties of higher frequency components underlines the importance of two-voiced call types in giving directional cues among constantly moving social animals in a three-dimensional space. This might be particularly important in the presence of several pods in order to maintain contact and synchronise swimming movements with their own pod members.

The ultrasonic whistles I found are concordant with the description of ultrasonic whistles known from the northeast Atlantic (Samarra et al., 2010), the western south Atlantic (Andriolo et al., 2015), and the north Pacific (Filatova et al., 2012). The reason for ultrasonic signals in top predators is unknown, but it may be used in short-range communication as has been suggested for killer whales (Samarra et al., 2010). In my study ultrasonic whistles were mostly recorded while one group was travelling in the Vestfjord and did not produce pulsed calls. However, the short down-sweep structures in the killer whale recordings look like reminiscent of ultrasonic sweeps used by bats during echolocation. Bats use ultrasonic calls for echolocation which often include frequency-modulated sweeps possibly determining target range and obstacles in the environment e.g. (Jones & Rayner, 1989). Such echolocation possibilities might be suitable in the open water environment and while in motion. However, typical echolocation signals in dolphins are described as clicks (Au, 1997), thus the function of ultrasonic whistles in killer whales needs more investigation.

Call type combinations

Distinct sequences of call types, or compound calls, have been reported from different killer whale populations (Filatova et al., 2015; Ford, 1989; Saulitis, Matkin, & Fay, 2005; Strager, 1995) and seemed a common feature of the killer whale vocal repertoire. Filatova et al., discussed that killer whales may combine syllables into compound calls, creating call types with multiple syllables and then reducing them again into more simple call types, which then could be combined again into compound calls, and so on. This would be analogous to the ‘linguistic cycle’ of human languages and would explain the diversity of vocal repertoires in killer whale populations (Filatova et al., 2015). However, the function and mechanisms behind the evolution of such call combinations is still unknown, and this task is beyond the scope of this thesis. It remains an interesting and promising question to be investigated in future studies.

Factors influencing the vocal repertoire

When examining factors influencing vocal repertoire size, it becomes clear that a certain amount of recording length is needed; in my study recordings with less than one hour resulted in a much smaller vocal repertoire size (31–179 calls per group) than recordings over 1 hour (501–1635 calls per group). The longer recordings were collected in multiple recording sessions, sometimes on different days, and such multiple recording sessions cover more individuals communicating as well as more behavioural contexts, thus result in a more complete vocal repertoire. When examining results from recording length over 1 hour, the correlation is less clear and behaviour such as carousel feeding seems to have a stronger effect on both call production and call type classification. Group size does not seem to influence amount of calls or call types produced, however group sizes in killer whales do not differ greatly with core matrilineal groups consisting of 6–12 animals and larger pods in my study with 36 animals. In killer whales a group's vocal repertoire is shaped by the fact that it reflects kinship (Deecke et al., 2010), and a fixed amount of vocal signals may be needed to encode this, rather than being influenced by the amount of members through social interactions.

In summary, the average vocal call type repertoire of killer whales in northern Norway in my study was composed of 25 call types per group. This small amount of call types was expanded by call type combinations. This and the fact that call types are built up by subunits, or elements combined in different ways, may give killer whales a higher flexibility in vocal production, and the vocal repertoire becomes more complex than in most other mammalian species.

Call type sharing

In my study I found a high degree of call type sharing (81%) and most calls (90%) were shared among different matrilineal groups. Most groups only used one call type within a group, indicating that among the eight groups I have recorded only a few calls and call types are group specific. The one group with more group specific call types was also the most vocal group, indicating that sharing rates depend to some degree on repertoire size; however the call type sharing rate with other groups was still high, at 73%.

A low number of group specific call types might be found in recordings of closely related matrilineal groups (Ford, 1991; Miller & Bain, 2000). According to Barrett-Lennard and Ford, my findings suggest that due to the high call type sharing rate between killer whale groups, they might all belong to closely related matrilineal groups (Barrett-Lennard, 2000; Ford, 1991). I have recorded most groups during herring aggregation in winter and they may all be to some degree related, but two groups were recorded in summer and the call type sharing was still high. The large population size of 600–1500 animals (Christensen, 1988; Kuningas et al., 2008), the wide distribution of killer whales along the entire Norwegian coast and offshore (Stenersen & Similä, 2004), and the fact that the whole population was drastically reduced during whaling (Oien, 1988) probably indicates that individuals from the whole population are not closely enough related for it to show in similar dialects. Genetic studies are needed which are correlated with Photo-ID and acoustic behaviour to reveal relatedness in matrilineal groups in the Norwegian killer whale population, and whether any relatedness is reflected in their dialects.

Another possible reason the differences between group repertoires was so small could be due to herring overwintering behaviour when a huge amount of herring is available for the whole population of killer whales during 3–4 months (Similä et al., 1996). Vocal repertoires in killer whale groups are being transmitted vertically from mother to calf by vocal learning and dialects evolve through gradual accumulation of copying errors (Ford, 1991). In addition horizontal transmission of calls between adult killer whales seem to change vocal repertoires and add to the development of dialects (Filatova et al., 2010).

In Norway during the herring overwintering aggregation most matrilineal groups of the killer whale population will have regular and frequent contact, thus vocal exchange among most groups may reduce isolation-induced diversion and changes of call types over time from original group dialects. Through this frequent horizontal transmission of calls and call types between individuals from different groups, group specific call types might be reduced. This may result in low vocal repertoire differences between the groups, which we see in my results. Group identification and cohesion might be achieved through vocal identification by the sound of group members' "voice cues" or by other sensory modalities such as vision. So far no other sympatric populations or ecotypes have been isolated in Norway, and as a result there might not be the same need for group separation to avoid inbreeding as in the special situation of the northeast Pacific populations (Barrett-Lennard, 2000).

My results show a trend towards high call type sharing and low degree of group specific vocalisation in killer whale groups in Norway. More recordings from different groups as well as resightings are necessary to confirm and to conclude the degree of call type sharing and group specific communication observed in my study.

CHAPTER 5 COMPARISON OF VOCAL REPERTOIRES

Introduction

Long-finned pilot whales and killer whales are highly social, capable of vocal learning and mimicry, and live in similar matrilineal social groups. They share many similar traits, they live in matrilineal groups consisting of siblings of both genders, and they are long-lived and highly vocal (explained in detail with references in chapter 1). However, there are subtle and profound differences in their group sizes, and social and feeding behaviours. To investigate differences between the two species, particularly how this is reflected in their vocal behaviour, was the question of this chapter. Results on the vocal repertoires of long-finned pilot whales are described in chapter 3 and of killer whales in chapter 4. Here I summarise and describe the differences of these results between the two species.

Methods (see chapter 2 for data collection and analysis)

General methods of fieldwork and analysis are described in chapter 2. All findings from the group composition and social structure through Photo-ID and the vocal repertoire, as well as call type sharing between groups, were compared and illustrated for pilot whale and killer groups with sufficient data (sound recordings with high vocal activity combined with Photo-ID and behavioural notes).

Results

Pilot whale social groups are larger than those of killer whales, consisting of 23 members in contrast to killer whale groups of 9 members. Their feeding behaviour differs too: pilot whales are deep divers specialising in hunting squid, and killer whales are surface feeders specialising in cooperative carousel herring feeding. Their vocal repertoire is large and complex, however. Pilot whales seem to use a larger repertoire of calls (129 versus 60) than killer whales, or 36 call types/group whereas killer whales have only 25 call types/group. Killer whales, on the other hand, show a high variability of call type usage and combine discrete call types; pilot whales use sequences of calls as well, but the combination of calls is often mixed and graded. The use of two-voiced call types is less in pilot whales than in killer whales (CT 18% versus 44%, and total number of calls 29% versus 47%). The structure of call types seems similar—no large differences could be found in either segmentation of calls or structure of main elements. No call types are shared between the species; they each exhibit their own distinct species' vocal repertoire. However, the degree of call type sharing is different among pilot whales and killer whales. Pilot whale groups share less call types with other groups than killer whales (56%

versus 81%) and exhibit a larger vocal repertoire usage only within their groups (54% versus 7%). (Fig. 5-1 and overview Table 5-1.)

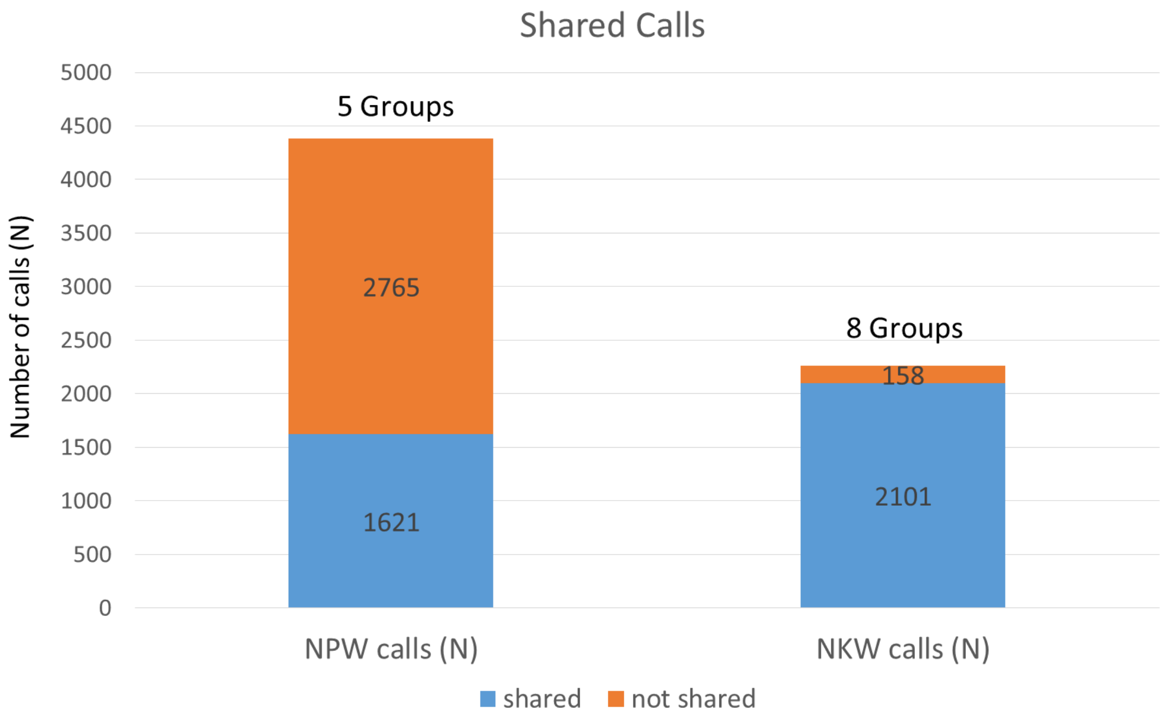


Figure 5-1. Amount of calls and call types (CT) shared between groups (blue) and only produced by one group (blue), for 5 groups of pilot whales (NPW) shown in the left column and for 8 groups of killer whales (NKW) in the right column.

The length of recording time seems to influence size of vocal repertoire in both species. To record a decent set of call types, recordings of whales vocalising should be more than 3 hours in large groups like pilot whales and more than 1 hour in smaller killer whale groups. Group size does influence vocal repertoire size in pilot whales: where groups can become very large, when several small matrilineal units come together, the repertoire increases. This seems an indication of vocal activity between the individuals.

In the case of the killer whales, feeding behaviour such as carousel feeding seems to increase vocal activity. This may be an indication of vocal exchange during cooperative hunting.
Both species use ultrasonic whistles. Killer whales in Norway are known to produce whistles with ultrasonic frequencies (ranging up to 75kHz) (Samarra et al., 2010; Andriolo et al., 2015). The whistles I have found for long-finned pilot whales were similar in frequency range but different in structure and length.

Table 5-1. Overview table: Comparison of the vocal repertoire of long-finned pilot whales and killer whales in northern Norway. This comparison is based on data collection from 2005 until 2010 in the Vestfjord of northern Norway. Through Photo-ID individuals could be attributed to different group encounters; this table shows both group composition and social organisation from groups of which I had sufficient sound recordings to analyse vocal repertoire. The main features of the vocal repertoire of call types were listed, as well as degree of call type sharing between the groups.

	Long-finned pilot whales	***Killer whales***	*comments*
Photo-ID data	7 (161)	11 (159)	groups (individuals)
average group sizes	23 (4-47)	9 (4-20)	average (range)
group social structure	matrilineal	matrifocal	
social dynamics	many matrilines, long group association	one matrifocal group, rare short group associations	group associations change in both species
Feeding behaviour	deep synchronous dives (≥10min)	carousel feeding close to surface	
Prey	squid, (mackerel)	herring, mackerel, marine mammals	
Vocal repertoire			
Calls	4572	3731	
Call types (CT)	129	60	
Call subtypes	25	25	
CT per group	36 (7-47)	25 (2-37)	weighted arithmetic mean with range
Call combinations	exist*	33	*mixed and graded calls made a quantitative analysis impossible
Two-voiced CT	29 % (1308)	47 % (1763)	
Simple CT	23 % (1075)	13% (485)	one segment, one element, no HFC
most common CT structure LFC	1 segment 2 elements	1 segment 2 elements	
most common CT structure HFC	1 segment 3 elements	1 segments 4 elements	
most complex CT structure	6 segments 8 elements	5 segments 10 elements	
most common element structure LFC	ascending	ascending	
most common element structure HFC	ascending	ascending	
whistles ultrasonic	67	323	
CT influenced by a) number of calls	No	Yes, more calls more CT	
b) by recording length	< 3 hrs low vocal activity, longer rec. higher vocal activity	< 1 hour low vocal activity, longer recordings mixed vocal activity	

c) by group size	larger groups - higher vocal activity (not CT)	no influence	
d) by behaviour	not clear, distribution same as group size	carousel feeding - higher vocal activity	behaviour for larger groups of pilot whales not specific
Repertoire sharing			
Data	5 groups (4386)	8 groups (2329)	
CT/group	37 (13-45)	25 CT (8-37)	weighted arithmetic mean
shared CT/group	21 CT (N=1621, range 2-27)	20 CT (N=2101, range 6-26)	weighted arithmetic mean
group specific CT/group	20 CT (range 4-33)	6 CT (range 1-10)	weighted arithmetic mean
total shared calls	37% (N=1621)	90% (N=2101)	All calls of CT shared
CT sharing between groups	56% (range 15-81%)	81% (range 54-97%)	group sharing of CT, weighted mean
group specific CT	54% (19-85%) (N=2765, range 141-1096)	7% (1-27%) (N=158, range 4-82)	group specific CT, weighted mean

Discussion

Both killer whales and long-finned pilot whales are long-lived marine mammals living in small matrilineal groups with some populations showing natal group philopatry (Amos et al., 1993; Amos et al., 1991; Amos et al., 1993; Barrett-Lennard, 2000), and vocal complexity may reflect their similarity in social intra- and inter-group interactions (Deecke et al., 2010; Ford, 1991). However, there is a small difference in social organisation between pilot whales and killer whales. Pilot whales live in larger matrilineal groups (average 23 members) with several of these travelling together, reaching group sizes of more than 60 animals; and these groups often meet and travel with other groups—more than 150 animals can meet in such super-aggregations. Even though the core matrilineal unit and the aggregation to a few other units remain stable, there seems to be a fluid interaction between the groups. Even other species such as Atlantic white-sided dolphins often travel with pilot whales (pers. observation). In such a fluid social organisation it is important to identify individuals and group members for group cohesion. Bottlenose dolphins live in fluid fission-fusion societies where members of groups interact with different groups frequently, and long-term associations only exist between male alliances in different levels or mother offspring pairs (Connor et al., 2000). Bottlenose dolphins use signature whistles which carry information in their time-frequency contour about the identity of a caller; these individual signatures are learned and used individually, but also copied by others to address other individuals and even during the absence of the whistler, probably to search or refer to specific individuals (for a review of signature whistles see (Janik & Sayigh, 2013)). Individual vocal signatures would help pilot whales maintain contact and find their group members during several group meetings or interspecies aggregations. Whistle structure and occurrences differ significantly according to main behavioural activities in long-finned pilot whales and are thought to facilitate group contact and coordinate movement (Weilgart & Whitehead, 1990). However with my dataset I cannot test whether some of the stereotypical whistles of pilot whales, which I classified as call types, may indeed be signature whistles. On the other hand, along with large group sizes, it would explain the large vocal repertoire of almost 130 different call types and an average usage of 37 call types/group. Thus the use of signature whistles in pilot whales should be further investigated.

In contrast, killer whales remain in a small core matrilineal unit, usually with around 9 members, only rarely travelling with other groups. Only in feeding grounds, e.g. in winter when herring is greatly abundant in a small area, can many matrilineal groups be seen together and interacting. Since resident killer whales live within or closely associated with their natal matrilineal group throughout their entire lives (Ford et al., 2000), individuals may be easily recognized visually and through their voice cues. So far, no individual signature could be found in killer whales, instead it has been shown that group recognition and group signature is reflected in their vocal repertoire through dialects (Ford, 1991). The vocal repertoire size of resident killer whales in British Columbia, which share 7–17 different call types among groups (Ford, 1989), is smaller than that of pilot whales. Instead of adding new individual signature calls, killer whales may use a combination of call types, which improve their vocal flexibility of communication and add to the group's vocal signature. The diversity of vocal repertoires in killer whale populations could be explained by multiple rearrangements of syllables into compound calls which are reduced again into more simple call types, analogous to the 'linguistic cycle' of human languages (Filatova et al., 2015).

Pilot whales also combine calls in specific sequences, some being repetitions of the same call (this study and (Sayigh et al., 2013; Zwamborn & Whitehead, 2017)) or call type sequences containing clearly defined call types with specific patterns; but many calls in combinations were nonharmonic and graded, so were impossible to quantify at this stage. However, pilot whales tend to use call type combinations in a fixed order, e.g. certain call types occur at the beginning of the combination and others at the end. Pilot whales also seem to regularly mix call type combinations with variable and graded call types as well as whistle components, separating them by a silent gap, thus adding more flexibility to their vocal communication. In summary, call type repetition and combinations might be more common in delphinid species than previously reported but this has to measured from individual callers in order to identify the order of combinations.

Ultrasonic whistles have been rarely described in dolphin species, this might be due to technical limitations of recording systems. However, my findings of ultrasonic whistles used by both long-finned pilot whales and killer whales, in addition to recent studies, suggest that ultrasonic whistles might be more common in some dolphin species than previously reported (Hiley et al., 2017). The function of ultrasonic whistles still remains unknown.

A trend in my study shows that call type sharing seems less profound in pilot whales than in killer whales, indicating that pilot whales may exhibit stronger group dialects than killer whales. The reason for this different vocal behaviour is unclear; it may be due to different group sizes and group association behaviour and the need to separate from different groups. However, my data is inconclusive on this matter. More acoustic and Photo-ID data needs to be analysed combined with social network studies to reveal group dynamics, and with genetic studies to reveal relatedness on individual and group levels.

The pilot whales showed a lower rate of two-voiced calls but commonly used graded calls which I did not find in killer whales. Two-voiced calls in killer whales are common and the high frequency component of calls is more directional than the lower frequency component, possibly carrying information about the signaller's orientation, independent from the caller's sex (Miller et al., 2007). These two-voiced calls are used over longer distances than monophonic calls to maintain contact and monitor the position of others when several pods are present and members of different pods are mixed (Deecke et al., 2005; Filatova et al., 2009; Foote et al., 2008; Ford, 1989). Almost half of the calls and 44% of the call types produced by killer whales I recorded from single groups in Norwegian waters were two-voiced. In comparison, the pilot whales in Norwegian waters used only 29% two-voiced calls and only 18% two-voiced call types. The recordings from my study came mainly from single group recordings and only one set of recordings came from two groups. These results contradict former studies in showing that two-voiced calls in killer whales are mainly used when several pods meet (Filatova et al., 2009). Pilot whales live in much larger groups and several matrilines were present during my recordings, whereas killer whales were mostly recorded from a single matriline, indicating that other reasons may also play an important role. Killer whales live in smaller groups, foraging on different prey in the upper water column with different specialised hunting behaviour than pilot whales, which are deep-diving predators. Group coordinated foraging behaviour may increase the need to keep track of swim movement direction of individuals, and killer whales may use two-voiced directed calls in addition to vision to organise and coordinate complex group foraging behaviour. Pilot whales forage in deep water and they use mainly echolocation clicks and buzzes to detect their prey. Studies on short-finned pilot whales showed that they forage non-synchronised in deep depths, mainly producing echolocation signals (Aguilar Soto et al., 2008). In addition they continued calling in great depths, although the calling rate was reduced and calls were mostly produced in the ascending phase of dives, probably to maintain or reestablish social bonds after individual dives (Jensen et al., 2011). No information was given if the calls recorded in the former study were two-voiced, but this difference in foraging behaviour may not require the same level of group coordination as in foraging killer whales and could explain the overall lower rate of two-voiced calls in pilot whales' vocal repertoire.

Graded call repertoires in which certain call types can be resolved and receivers may recode call types are commonly seen in non-human primate species (for review see (Fischer et al., 2016)). Similarly, pilot whales may increase their flexibly of vocal production and communication with the additional graded nature of some calls, in this way adding more possibilities to express emotional states in their communication. Some of the call types of killer whales, which were classified as variable and aberrant calls, may carry information about the emotional state of the caller (Ford, 1989). One of these variable "excitement" calls was found across different populations of the Pacific northeast which indicates an innate nature of the call (Rehn et al., 2011). Which call types in both pilot whales and killer whales were aberrant and graded, and which call types were variable and may be innate could not be determined in my study.

In killer whales there is an indication that vocalisation increases and becomes more complex during feeding than non-feeding. In particular, during the cooperative carousel feeding technique, calling rate as well as call type usage is high compared to other contexts. This might be explained by vocal coordination of complex moving patterns to herd and stun the herring (Similä & Ugarte, 1993).

In pilot whales, one study demonstrated vocal activity depending on behavioural context and found that vocal activity increases during active surface behaviour, possibly feeding, and socialising (Weilgart & Whitehead, 1990). Studying behaviour in cetaceans is challenging, especially in places where deep-diving species forage. However, pilot whales may remain at the surface for 60% of their time (Heide-Jorgensen et al., 2002), whereas large groups make clear correlations between individual behaviour and vocal behaviour difficult. Killer whales, on the other hand, live in smaller groups and forage closer to the surface, even though they spend most of their time underwater, so specific foraging techniques are easier to detect than in deep-diving pilot whales. This is why I focused instead on studying behavioural context and correlated vocal behaviour in killer whales. Results are presented in chapter 7.

CHAPTER 6 “FIRST RECORD OF KILLER WHALES (*ORCINUS ORCA*) FEEDING ON ATLANTIC SALMON (*SALMO SALAR*) IN NORTHERN NORWAY SUGGEST A MULTI-PREY FEEDING TYPE”

Summary: Here I describe specific call types and different vocal activity during three different behavioural contexts a) newly discovered salmon foraging, b) non-feeding and c) herring foraging in killer whales observed in northern Norway. The results suggest that killer whales use context specific call types and show different vocal activity depending on the context.

Figure 1. Photograph of a killer whale catching an Atlantic salmon (*Salmo salar*) in northern Norway during the summer months of 2011 (Photo: Geir Notnes). This was the first record of killer whales feeding on salmon in Norway: two groups were stationary for three and six months inside a fjord and they scanned the fjord up to three times per day in search of salmon (Vester & Hammerschmidt, 2013).

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“First record of killer whales (*Orcinus orca*) feeding on Atlantic salmon (*Salmo salar*) in northern Norway suggest a multi-prey feeding type”

HEIKE VESTER & KURT HAMMERSCHMIDT

Abstract

Occurrence of killer whales in Norway is linked to the migration of the herring population with most sightings during wintertime. Here we describe the first record of North Atlantic killer whales feeding on Atlantic salmon inside a fjord in northern Norway during summertime, thus adding an important factor in understanding the feeding ecology of North Atlantic killer whales.

Killer whales (*Orcinus orca*) are widely distributed throughout the world’s oceans, where they forage on a large variety of different prey species ranging from fish to marine mammals and birds (Forney & Wade, 2007). It has been shown that feeding ecology is of central importance to the killer whales’ social network. Food availability has a direct influence on group structure, and it is under debate to what extent the sociality of killer whales is flexible enough to adapt to local ecological conditions (Beck et al., 2012; Foster et al., 2012).

In the Northeast Pacific some highly specialised sympatric populations have evolved, with resident groups foraging on salmonids, transient groups feeding on marine mammals, and offshore groups feeding on fish such as sharks (Ford et al., 1998). Often these specialised populations show high site and time fidelity, such as the northern and southern resident lines in the Northeast Pacific which feed primarily on Chinook salmon (*Oncorhynchus tshawytscha*) (Ford & Ellis, 2006). The survival of these killer whales seems to depend on the Chinook salmon’s year-round abundance (Ford et al., 2010).

In the Northeast Atlantic at least two different populations have been recently identified, including a herring feeding population in Norway and Iceland (Foote et al., 2011). In addition, two ecotypes of North Atlantic killer whales with morphological differences were determined: Type 1, with severe apical tooth wear, a generalist type with a length of up to 6.6m, presumably feeding on fish and to some extent on seals; and Type 2, with no apical tooth wear, a highly specialised type with a length of up to 8.5m, presumably feeding on other whales (Foote et al., 2009). Further, marine mammal feeding killer whales were described from Scottish inshore waters (Bolt et al., 2009). In Irish waters, killer whales mostly feed on fish; stomach contents revealed a diet of siphonostomatoid copepods (*Cecrops latreilli*), ocean sunfish (*Mola mola*), mullet (*Chelon labrosus*) and salmon (*Salmo salar*) (McHugh et al., 2007;

Ryan & Holmes, 2012; Ryan et al., 2003), and in the 1970's a killer whale was observed hunting salmon in the Foyles Estuary (Wilson & Pitcher, 1979). In the waters around the British Isles, herring and salmon were identified as prey species (Evans, 1988). Thus, we are only starting to understand the variety of the North Atlantic killer whales' feeding ecology, especially the degree of prey specialisations.

Killer whales studied in Norway feed mostly on herring, with tagged animals showing high site and time fidelity to herring migrations, and are considered a herring-feeding population (Foote et al., 2011; Foote et al., 2012; Similä et al., 1996). The winter migration of herring in Norway brings a large number of killer whales close to shore in November. For many years the location of the wintering grounds was inside the Tysfjord and Vestfjord area in northern Norway (Røttingen, 1990). However, for the last two years herring spent the winter months close to Vesteralen, inside the Andfjord and the neighbouring island of Senja. In addition to killer whales, many humpback whales (*Megaptera novaeangliae*) and fin whales (*Balaenoptera physalus*) were seen feeding on herring next to killer whales (personal observations). When the sun returns to these arctic waters by the end of January, the herring starts its southward migration along the coast to spawn in southern Norway until the end of March, thereafter dispersing in the open Northeast Atlantic (Røttingen, 1990). During summer months, herring does occasionally occur close to the northern Norway coast, and killer whales have been seen feeding on it (Similä et al., 1996). These observations suggest that killer whales follow the year-round migration of the herring, because it represents their main food source (Similä et al., 1996).

However, occasional sightings of killer whales earlier identified feeding on herring making harbour seal, harbour porpoise, and minke whale hunts and kills, as well as unidentified killer whales attacking sperm whales have also been reported in Norwegian waters (Stenersen J. and Similä T., 2004) (Vester unpublished data). Therefore, it may be that the feeding ecology of killer whales in Norway is to some degree flexible and not as specialised as previously thought or found in other areas such as the Northeast Pacific.

Here we describe for the first time killer whales feeding on salmon during the summer months in northern Norway, and propose that at least some groups of the herring-feeding population have also specialised to feed on salmon when herring is offshore. We conducted daily field trips from Henningsvaer, northern Norway, to the adjacent Vestfjord from May until November 2011. During these trips the track and encounters of whales were recorded by their GPS locations, time and date. During encounters, we noted ad-libitum and event sampling of the whales' surface behaviour, and took Photo-ID pictures. Left-side pictures of saddle patches were taken according to the protocol of Bigg (1982). In addition, we made sound recordings whenever the weather conditions and behaviour of the whales allowed. From a total of 39 hours of underwater sound recordings, approximately 13 hours were taken during salmon feeding.

After the first sighting of killer whales on April 23rd 2011, our fieldwork started on May 5th 2011 and lasted until November 5th 2011. We were able to observe regular encounters of two groups of killer whales for six months, named in our Photo-ID catalogue as NKW (Norwegian Killer Whales) -AN (Group ID letter) with 5 individuals (one individual died during the course of the study), and NKW-AP with 16 individuals. Only group NKW-AN remained continuously in the same fjord throughout the entire course of our study (Table 1). Beginning in May 2011, we made a new discovery that these two groups of killer whales were feeding on salmon in a narrow northern Norwegian fjord (see Figure 1). Local residents reported that killer whales have regularly visited this fjord in summertime for at least 10 years, but were commonly thought to feed on local herring (*Clupea harengus*) and saithe (*Pollachius virens*) stocks.
We observed the killer whales inside Øksfjord (N68 19/E15 14), a side fjord off the main Vestfjord, that leads to the open Atlantic. The area used by the killer whales was approximately 30km long, up to 200m deep, and surrounded by islands without a deep water opening to the Vestfjord (see Figure 2). Inside the Øksfjord are several salmon rivers, where salmon runs start in April and last until the end of September. In addition, four operational and one non-operational salmon farms are located inside the fjord.

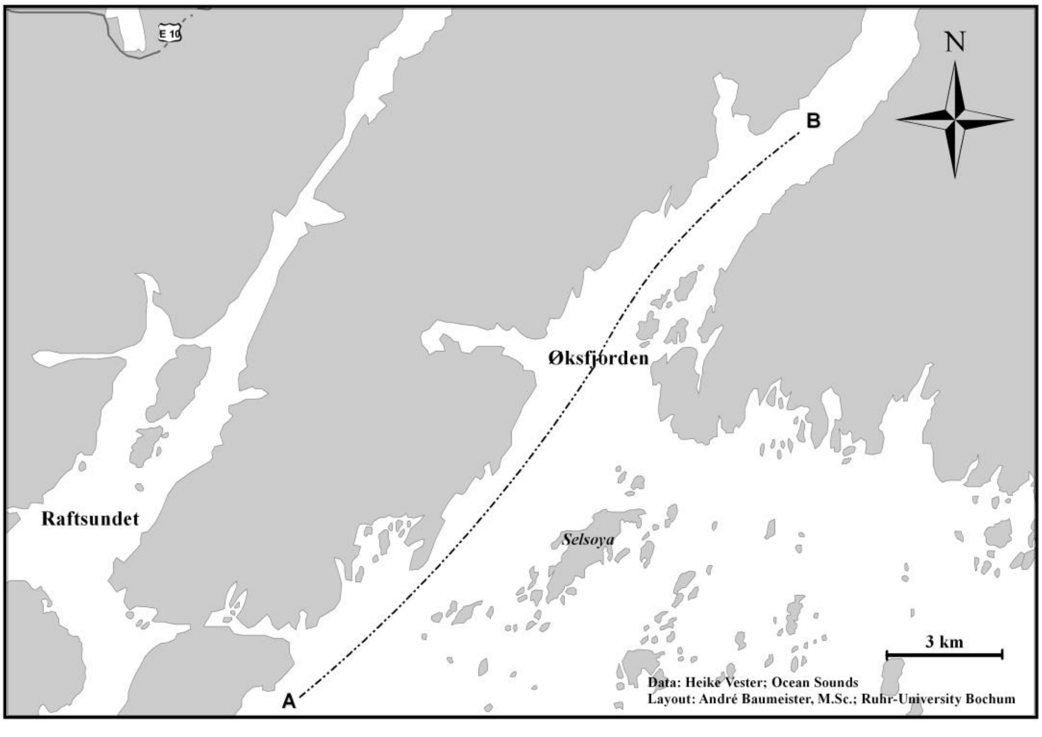


Figure 2. Map of a killer whale foraging area inside Øksfjord in northern Norway during summer months: (A) shows the resting area of group AN; (B) shows the resting area of group AP. The line indicates the main Foraging route of both groups.

Atlantic salmon (*Salmo salar*) in Scandinavia live 1–4 years at sea before migrating to their native rivers for spawning from the end of April until fall. Spawning happens from October-November, and eggs hatch in April–May. Juvenile salmon remain in the rivers for 2–5 years until migrating to the sea, when the cycle repeats (Pethon, 1998). Northern Norway's best salmon fishing season is between June 1st and August 31st. The period of salmon runs and catches fits within the period of killer whales' occurrence, from April to November.

Both groups often hunted together but separated when resting; the smaller group (NKW-AN) used the fjord entrance as a resting place (see Figure 2 pt. A), whereas the larger group (NKW-AP) used the other end of the fjord (see Figure 2 pt. B). After July 19th only group NKW-AN was seen in the fjord (without males) and they remained until the beginning of November.

One of the main behaviours observed was foraging, including scanning the fjord with loud echolocation clicks. During resting and milling, all group members were slowly swimming at the surface, either swimming back and forth in the same area or slowly travelling along the fjord in silence. Socializing was only observed when two groups met, or during resting or milling. The actual salmon hunt and catch usually lasted only a few minutes during which whales engaged in active surface behaviour, such as breaching, jumping and fast swimming manoeuvres. During this time, live salmon could be seen chased at the surface; also, red salmon body parts from killer whale predation or seagull scavenging could be detected. In the beginning of the season in April to mid-June, when salmon runs scarcely, feeding at river openings was observed by both groups, this behaviour included all animals waiting at the river opening and occasional catches of salmon swimming upriver were observed. When the two groups met for foraging, they often searched for fish together, with individuals spreading out across the fjord and swimming at the same speed (3–4 knots) in the same direction. Intense and continuously repeated echolocation clicks revealed that they were scanning the fjord for prey. The different observed behavioural states and predation activities for each encounter are listed in Table 1.

During the five months of observation, two calves were born, and we observed courtship behaviour between the groups several times. On five occasions, two males joined a female and they separated from the rest of the group. The two males chased the female slowly, triggering tail-slaps by the female, which was then approached by one male and belly-to-belly rolling of the male and female could be seen at the surface. During the courtship behaviour no sounds were audible, the animals were quiet.

In 2011 none of the individual killer whales feeding on salmon was known from earlier encounters, and they could not be matched to an existing Photo-ID catalogue of around 550 individuals collected in the Vestfjord (Vester unpublished data). However, given the fact that there may well be more than 1000 killer whales in the Norwegian herring-feeding population

(Kuningas et al., 2008), these animals simply may have been missed before. However, in 2012 we could identify one salmon-feeding individual which we registered before in 2003, 2004 and 2005 as individual X-163. This individual was first seen in 1996 as a one-year-old calf and, due to severe dorsal and spine injuries caused by boats, was called “Stumpy” (Stenersen & Similä, 2004). At these earlier observations X-163 was seen associated with different groups, engaged in herring feeding (pers observations).

This represents the first continuous six-month study of a killer whale group in northern Norway. Our study revealed a different foraging behaviour than previously described for killer whale groups in Norway. Salmon feeding is well known in resident groups in Canada (Northeast Pacific), but was until now unknown in Norway.

However, whether this form of salmon foraging behaviour is specialised and exclusive for these groups of killer whales, or whether it is additional to herring foraging, is not conclusive at this stage. We have already started a larger study in Norway comparing vocal repertoires of salmon-feeding killer whales and herring-feeding killer whales. First results indicated some overlap of both vocal repertoires (Vester et al. unpublished data). Such comparisons, in addition to future observations, may help us reveal whether killer whales in Norway are specialised in salmon feeding or have developed an opportunistic feeding behaviour.

Table 1. Data collection, predation, and behavioural stages of two groups of killer whales (*Orcinus orca*) observed in Øksfjord in northern Norway in 2011. Data was collected on 23 days with over 139 hrs of observations and 39 hrs of sound recordings of which 13 hrs were from salmon foraging. During confirmed observation of salmon kill, dead salmon in the whales' mouths or floating salmon body parts were observed. Probable salmon catch was indicated by typical fish-chasing movements by the whales at the surface and vocalisations. This table was modified from the publication due to additional Photo-ID work.

Date	*Observation (hrs:min)*	*ID*	*Amount*	*Predation*
11-05-11	7:20:00	NKW-AN, NKW-AP	12	probable salmon catch
13-05-11	5:38:00	NKW-AN, NKW-AP	12	probable salmon catch
14-05-11	5:27:00	NKW-AN, NKW-AP	6+6	probable salmon catch
06-06-11	8:00:00	NKW-AN, males from NKW-AP	6+2	confirmed observation of salmon kill
10-06-11	6:12:00	NKW-AN, males from NKW-AP	6+3	confirmed by feeding sounds
11-06-11	7:48:00	NKW-AN, NKW-AP	6+6	probable salmon catch
13-06-11	0:55:00	NKW-AN, males from NKW-AP	6+2	probable salmon catch
15-06-11	6:05:00	NKW-AN, males from NKW-AP	6+2	confirmed observation of salmon kill
24-06-11	3:31:00	NKW-AN, male from NKW-AP	6+1	probable salmon catch
29-06-11	3:51:00	NKW-AN, males from NKW-AP	6+3	
04-07-11	7:42:00	NKW-AN, NKW-AP	6+6	confirmed observation of salmon kill
05-07-11	9:18:00	NKW-AN, NKW-AP	6+6	
07-07-11	2:53:00	NKW-AN	6	probable salmon catch
08-07-11	8:53:00	NKW-AN, males from NKW-AP	6+3	confirmed observation of salmon kill
15-07-11	16:00:00	NKW-AN, KNW-AP	6+6	notes missing
17-07-11	9:46:00	NKW-AP	6	confirmed observation of salmon kill
18-07-11	6:18:00	NKW-AN, males from NKW-AP	6+2	confirmed observation of salmon kill
22-07-11	4:21:00	NKW-AN	6	
29-07-11	4:50:00	NKW-AN	6	confirmed observation of salmon kill
03-08-11	2:57:00	NKW-AN	6	probable salmon catch
22-08-11	2:34:00	NKW-AN	6	probable salmon catch
31-08-11	2:43:00	NKW-AN	6	probable salmon catch
25-09-11	6:15:00	NKW-AN	6	confirmed observation of salmon kill
05-11-12	n/a	NKW-AN	6	
	139:17:00			

CHAPTER 7 SALMON VERSUS HERRING FEEDING CALLS

In this part I study the different vocalisations of killer whales in northern Norway during salmon feeding and non-feeding and compare it to data from herring feeding contexts.

Introduction

Vocal communication has been studied extensively in cetaceans since the 1970s, and several vocal repertoires of species and differences between groups and populations were described (e.g. (Delarue et al., 2009; Ford, 1991; Payne & McVay, 1971; Stafford et al., 2008; Weilgart & Whitehead, 1997)). Another aspect that has been well documented is echolocation in dolphins (Au, 2004), however connecting vocal communication to behavioural contexts in cetaceans is difficult (Ford, 1989). One of the major challenges in studying cetacean context-dependent vocal activity is due to the vast marine environment they live in. Whales and dolphins spend most their time submerged and out of range for human observers and can be observed only when they come to the surface for breathing, resting, and socialising. Studying their behaviour is therefore often limited to a relatively short time when they surface. Surface activities were commonly categorized in a few roughly described categories for group behaviour, such as resting, travelling, and feeding, plus other surface activities connected to social behaviour (Mann, 1999). Evaluation of context specific calling has been notoriously challenging due to difficulties in associating calling, which mainly occurs underwater and out of view, with visual observations that occur at the surface. When studying groups of whales it is often impossible to determine which individual is calling, and to track it from one visual encounter to the other, adding to the difficulties in studying context specific vocalisation in cetaceans. Attempts have been made to study specific behavioural contexts and vocal communication in cetaceans and the results look promising. Cetaceans, unlike most other mammals, are capable of vocal production learning; dolphins at least are capable of vocal and gestural mimicry, and many whales and dolphins form cultural lives (review book (Whitehead & Rendell, 2015)). These skills are prerequisites for referential signalling and language.

Killer whales (*Orcinus orca*) in British Columbia increase their calling rate of aberrant versions of call types and variable calls during and after a calf is born in a group (Weiss et al., 2006). Group specific call types were produced significantly more often after a calf was born and decreased gradually to the pre-birth rate for two weeks after birth. It has been suggested that the adults in a group are teaching the calf their group affiliation calls for close group cohesion and identity (Weiss et al., 2006). Certain calls are associated with excitement, and are variable in structure but could be easily be distinguished by ear and are found across different populations, suggesting an innate nature of the calls (Ford, 1989; Rehn et al., 2011). One report showed that vocal behaviour changed, and certain call types and patterns were used, during agonistic interaction of two killer whale males in captivity (Graham & Noonan, 2010); however, one must be careful in comparing the behaviour of captive animals in artificial environments to their natural behaviour in the wild.

One example of contextual vocalising in mysticetes is the complex song of humpback whales (*Megaptera novaeangliae*), which has been studied since the 1970s (Payne & McVay, 1971). Only males sing long songs consisting of repeating units and themes that change from year to year by all males in a population (Payne & Payne, 1985). The reason for males singing has not completely been resolved, but one theory suggests that it could function as lekking aggregations to attract females to the breeding grounds and benefit mature males by gaining access to females and immature males to learn and practise social and vocal skills (Herman et al., 2013).

Referential signalling seems rare among mammals, in non-human primates alarm calls were described as such, however further studies revealed that similar calls elicit other responses, which rules out designation of certain calls to a predator or event. Further, nonhuman primates lack vocal production learning and their vocalisation is largely innate (review in (Fischer, 2016). In contrast, bottlenose dolphins (*Tursiops truncatus*) are capable of vocal production learning and use learned referential signals for individual recognition, such as signature whistles carrying the individual information in their distinct frequency structure (for summary of signature whistles see (Janik & Sayigh, 2013). Signature whistles are individually developed by changing an existing whistle from the animal's environment to create a novel signal that carries the individual's signature. These whistles can be copied by others to address a specific dolphin or used in absence of the individual, probably to search or to refer to it (e.g. (Janik & Sayigh, 2013).

Food associated calls reported in birds and terrestrial mammals carry information about arousal but can also convey information about food; in many species calling rate increased with quantity and quality of food available, however specificity of the calls may be insufficient for referential signalling. Food association calls are also used during non-feeding contexts, which indicates that these calls may rather be used for social recruitment and revealing the motivational state of the caller. These calls often show meaningful variations in structure; graded versions often convey quality of food items, or series or sequences of food association calls change accordingly to rare, high, or low quality foods (review of food association calls in (Clay et al., 2012).

In marine mammals, in particular cetaceans, food-associated vocalisations, excluding echolocation, have been proposed to be directed towards prey and show physical properties which can manipulate the prey, rather than being used for intra-specific communication. Bottlenose dolphin (*Tursiops truncatus*) in Scotland foraging for salmonids produce low-frequency bray calls which were attributed to prey manipulation rather than being directed towards conspecifics, although this could be a by-product effect (Janik, 2000a). Another example are humpback whale (*Megaptera novaeangliae*) loud cries, or stereotyped rhythmic feeding calls, which may be used for herding of prey—although because of variations these calls may also carry individual signature information (Cerchio & Dahlheim, 2001; D'Vincent et al., 1985). Herding calls used presumably to gather schools of herring into tight groups were first reported from killer whales in Iceland (Simon et al., 2006). These calls have the low frequency properties and intensity to affect the swim bladders of herring and are assumed to manipulate and affect the swimming behaviour of schooling fish (Doksaeter et al., 2009; Simon et al., 2006). However, these calls are not always heard during feeding activity (i.e., before a tail slap), and the herding calls vary in peak frequency and can show nonlinear phenomena, suggesting that they were a result of cultural drift by individuals in different groups (Samarra, 2015; Simon et al., 2006). Whether these calls are used to manipulate herring and/or carry individual signature or group signature information has yet to be tested (Samarra, 2015). These herding calls were only detected in killer whale recordings from Iceland and Shetland but not from Norway (Deecke et al., 2011; Samarra, 2015; Simon et al., 2006). Killer whales in Norway and Iceland change their vocal behaviour during different behavioural stages, for example vocal activity was lowest during travel and highest during feeding (Simon et al., 2007). In Norway, two different foraging methods were studied and compared to each other: cooperative carousel feeding and non-cooperative feeding from discards of seine fishing vessels; even though differences in vocal activity were observed, no specific call types or pattern could be detected (Van Opzeeland et al., 2005). Whether killer whales from the Norwegian population use food specific or any other context vocalisation is not known.

Social whales and dolphins live in groups that can exceed 100 animals, often use group dialects or individual signature whistles, which obscures clear correlations of vocal signals to a specific behaviour. To reduce this pitfall and clearly investigate context or group related correlations one must identify and study a population for a long time. It is necessary to be able to identify individuals and know their vocal repertoire while studying the same whales repeatedly during different behavioural contexts. During the summer months of 2011 a unique discovery made it possible to study two groups of killer whales in more detail over the course of six months in an isolated fjord in northern Norway.

Methods (see chapter 2 for data collection and analysis)

In addition to the vocal repertoire of killer whales derived from data from 2004–2009 described in chapter 4, I also analysed recordings from 2011. These recordings came from the two groups of killer whales (NKW-AN and NKW-AP) observed during the summer months from May to September when almost 39 hours of sound recordings were collected during multiple encounters per observation day (see Table 6-1).

Through the observer-based analysis described in the method section I classified 3246 pulsed calls into discrete categories (quality category A–D), resulting in 59 different call types, 25 call subtypes, and 35 call type combinations.

Results

Vocal activity—behavioural contexts

Salmon feeding and non-feeding contexts

Two killer whale groups (AP and AN, see Fig. 7-1) were studied from May until September 2011 and a total of 38:58 (hh:mm) of underwater sound recordings were collected; 13:20 (hh:mm) during salmon feeding (foraging, single, and cooperative feeding, as described above) and 25:38 (hh:mm) during non-feeding contexts such as resting (group closely associated, calm movements, slow breathing, long surface time, slow travelling (less than 3 knots)); travelling (group together or spread out, all swimming in same direction, slow (3–4 knots), medium 5–6, fast (> 7 knots) travel); courtship behaviour and socialising (active surface behaviour, events such as breaching, body contact, spy hopping, this was often observed after feeding or when groups meet).

Figure 7-1. Two groups of killer whales that were observed for over six months during summer 2011 inside the Oksfjord in northern Norway. Group NKW-AN (upper group), consisting of 6 individuals, 4 females, one juvenile, and one calf. and group NKW-AP (lower group) consisting of 6 identified animals (and 4 unidentified animals), 3 males, 2 females, juveniles, and a calf.

Table 7-1. Number of call types and number of calls of killer whales recorded during salmon feeding and during non-feeding contexts. Data was collected and pooled from two groups of killer whales on 23 days during multiple recording sessions between May and September 2011 with a total 13:20 (hh:mm) recording time during salmon feeding and 25:38 (hh:mm) during non-feeding contexts. 'Salmon feeding only' represents call types and total number of calls produced exclusively during a salmon feeding context while 'Salmon feeding all' represents all calls recorded during this context. The same terminology applies to other contexts and 'shared' represents all calls produced during both contexts.

	call types	**calls (N)**
salmon feeding only	**29**	**872**
salmon feeding all	44	1579
other context only	**13**	**341**
other context all	28	1069
shared	15	1425
SUM	**57**	**2638**

In general, more calls and specific call types were produced during salmon foraging than in other contexts. In total 57 call types could be categorized, and half (29 call types 50%) were exclusively produced when the killer whales were hunting and feeding on salmon. 33% (N=872) of the total number of calls recorded were produced during salmon feeding. Fewer call types (23%, 13 call types, 341 calls) were exclusively produced during other contexts, such as travelling, resting, and socialising (data was pooled into non-feeding context). 15 call types were produced in both salmon feeding and non-feeding/other contexts (see Table 7-1).

Calls could not be distinguished between the two groups, because they were often travelling and foraging together, thus all calls were pooled together in a joint repertoire. Killer whales use group dialects (Ford, 1991) and part of the differences found in call type usage could be attributed to this. However, during my study I found a large overlap in call type usage between 8 groups of killer whales in Norway (chapter 4, groups only used 1 to 10 group specific call types). If the two salmon feeding groups would have been recorded separately the call type dialect difference of AN and AP may be less than ≤10 call types. When we take call types used explicitly during one context, both numbers (exclusive feeding or non-feeding context N=42) of call types are higher than the maximum group specific call types/group recorded earlier, thus differences of vocalisation between contexts seen in this study are probably mainly dialect independent.

Herring feeding calls

Killer whales were recorded in 2004–2007 and 2009, from 13 different identified groups and five encounters without identification:
Total of 2784 calls were analysed, including call types, call subtypes and call combinations including all qualities from categories A–D. Most calls (N=1745) were produced during carousel feeding by seven different killer whale groups and one unidentified group, followed by seine feeding (feeding from discarded fish of fishing vessels or from fish inside fishing nets) by two different groups (N=528). Calls produced during non-feeding contexts such as socialising (N=305) were recorded from one identified and one unidentified group, while calls produced during resting and travelling (N=206) were recorded from seven identified and two unidentified groups (see Table 7-2).

Only group behaviour was used to correlate with call types produced by the different groups. For description of group behaviour, see Table 2-1 in material & methods (chapter 2).

Table 7-2. Number of call types and total number of calls produced by groups observed in winter during herring feeding. 2784 calls were analysed including call subtypes and call combinations, in total 107 types. Data was pooled from different groups and encounters from 2004–2009. Most call types were produced exclusively during feeding and the majority of call types were shared between feeding and non-feeding contexts.

	call types	**calls (N)**
herring feeding exclusively	**66**	**939**
other context exclusively	6	63
both contexts	35	1782
SUM	**107**	**2784**

Due to the fact that killer whales are mostly silent during travelling (Simon, McGregor, et al., 2007), we did not obtain similar sample sizes from feeding and non-feeding in recordings from winter months when killer whales were feeding on herring. There was also a large difference in data collection between wintertime, when single groups only stayed for a few days and recording sessions could be done only for a few minutes to hours/day due to daylight and often only one encounter/group; and summertime long-term data collection of salmon feeding groups (feeding and non-feeding contexts). This makes quantitative comparisons between the winter (herring feeding) and summer (salmon feeding) contexts impossible.

Call type structures

Certain call types and call type combinations were exclusively recorded during specific behaviours. By looking at the structure of the different call types recorded during feeding and non-feeding, I investigated certain occurring patterns. Single- and two-voiced calls were recorded during all contexts (see Figs. 7-2 and 7-3). A total of 1277 single-voiced calls were produced, 829 during salmon feeding and 448 during non-feeding contexts. 1359 two-voiced calls were produced, 748 during salmon feeding and 611 during non-feeding contexts.

More than seven different call type combinations or sequences with NKW-15 (N=189) were recorded exclusively during salmon foraging, especially in the final chasing part of the salmon catch (see Figs. 7-3 to 7-6). Most were discrete call types (see Figs. 7-3 and 7-4), others were mixed discrete and variable call types often repeated towards the final part of the combination (see Fig. 7-5).

Due to the recording method it was not possible to identify the caller, and several animals may have been calling at the same time. However the gaps between calls were short or non-existent and there was no overlap of calls (see Figs. 7-3 to 7-6), which is an indication for one animal calling.

A) Structures of call types during salmon non-feeding context:

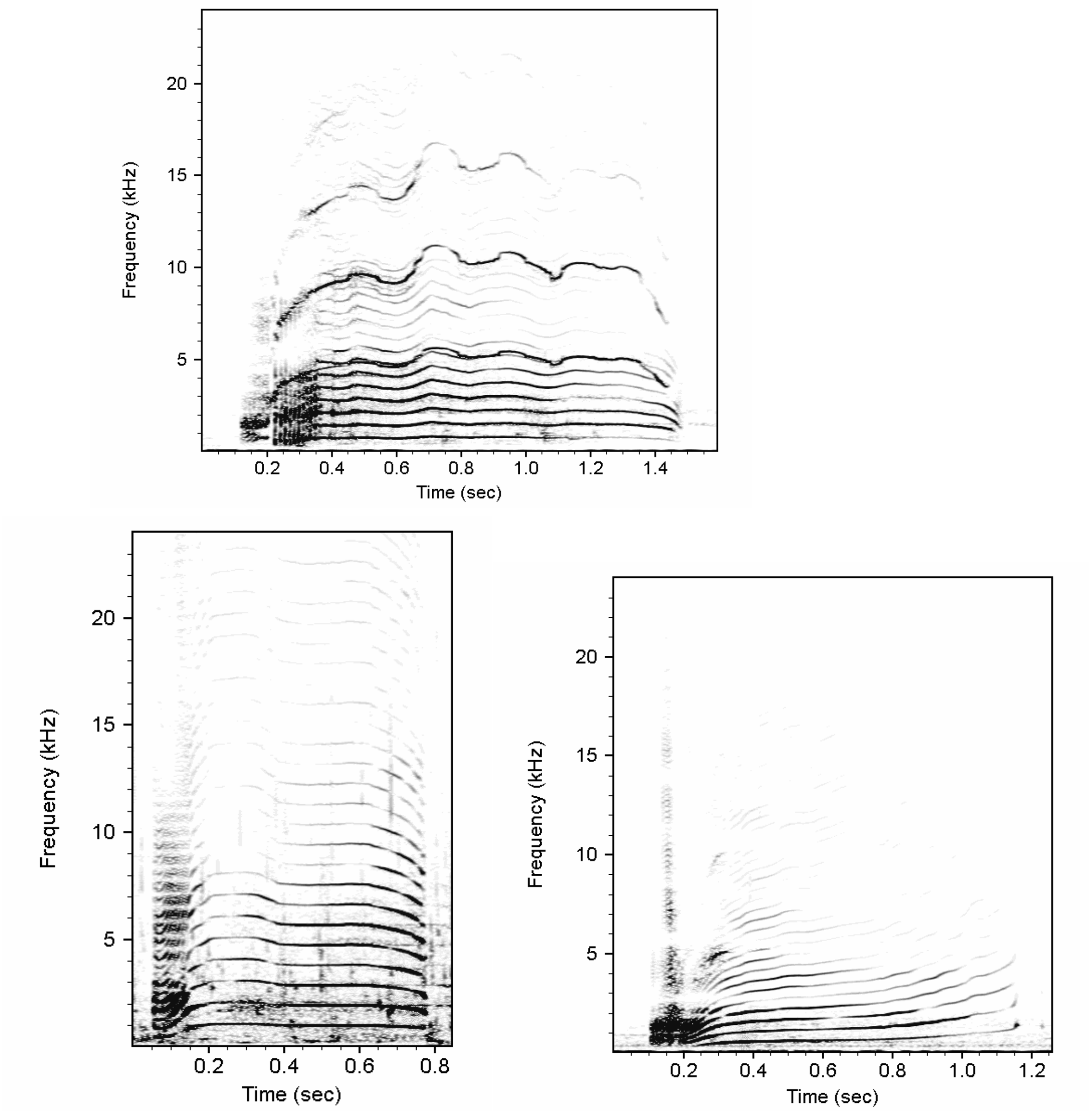


Figure 7-2. Spectrograms of examples of call types recorded during non-feeding contexts such as travelling, socialising, and resting. The first two-voiced call type with a buzz in the beginning and few frequency modulations and a frequency modulated high frequency component (HFC) was recorded most often. The last two calls are single-voiced and newly discovered (i.e. not in the previous vocal repertoire catalogue).

B) Spectrograms of exclusive salmon feeding vocalisation:

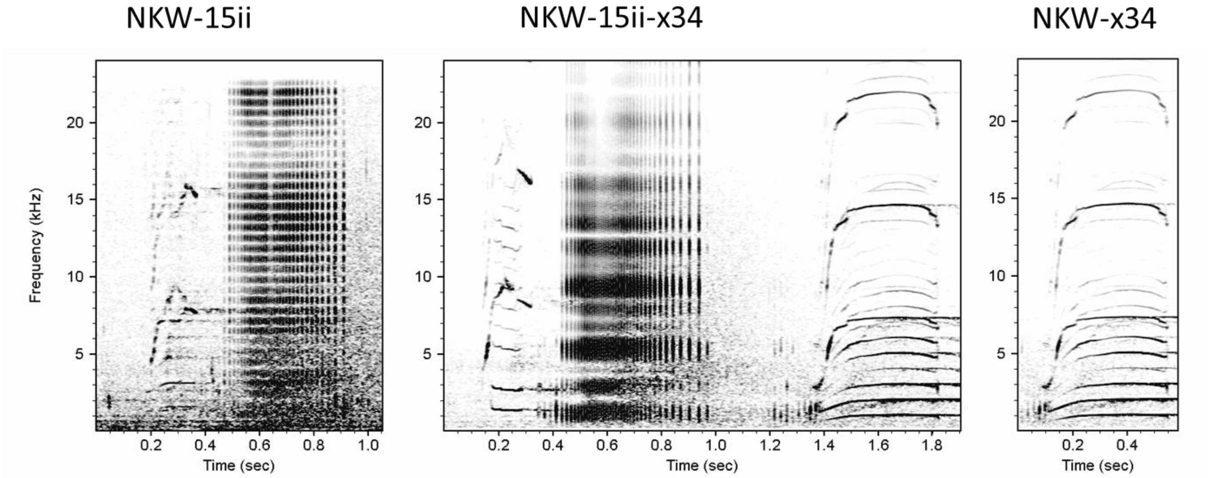


Figure 7-3. Spectrograms of discrete call type combinations recorded during salmon feeding in Norwegian killer whales in 2011. The leading two-voiced call and buzz represent a call subtype (NKW-15ii) already known from the existing vocal repertoire of killer whales feeding on herring, however the last call type (x34) and the combinations shown here are new (x stands for formerly unknown).

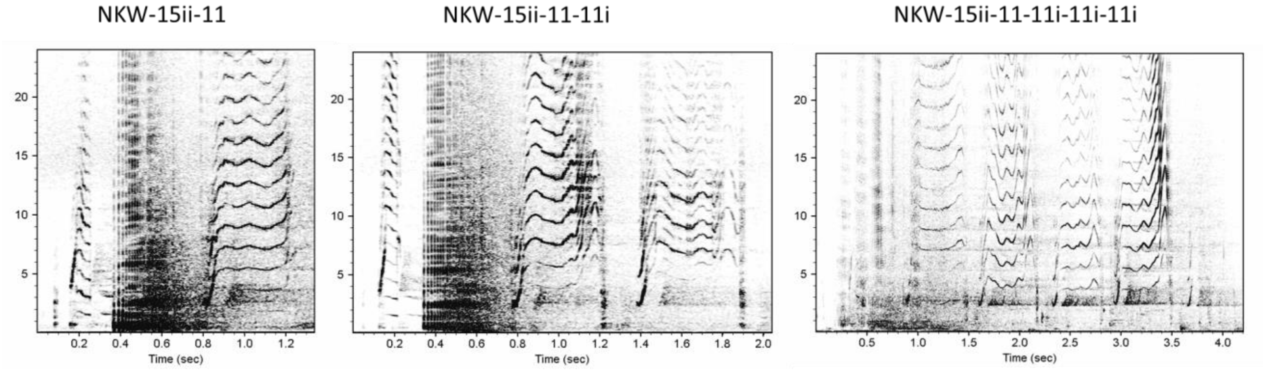


Figure 7-4. Spectrograms of call type combinations recorded during salmon feeding NKW-15ii-11 plus various numbers of a variable version of N11 (labelled as 11i). Both call types NKW-15ii and NKW-11 were previously known (but not the combination of the two); the variable forms of the last part of the combinations (11i) could be aberrant versions of NKW-11. Last spectrogram parameters: FFT size 1024, overlap 75%.

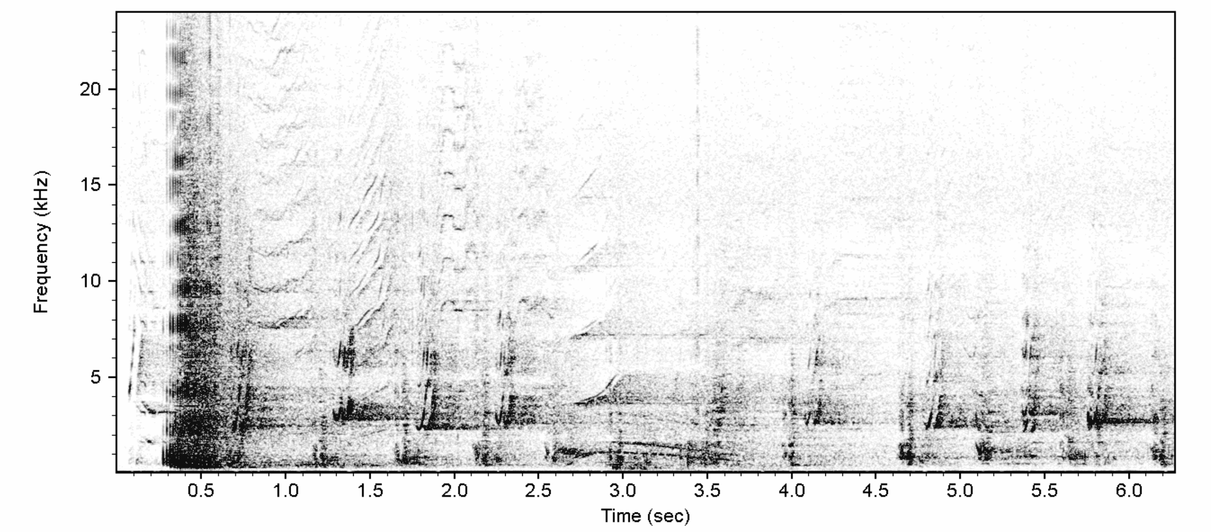


Figure 7-5. Spectrograms of a long call type combination recorded during salmon feeding; the first part is a combination of discrete calls which resembles NKW-15ii-11 (see Fig. 7-4 first spectrogram). This discrete call type combination is further combined with several aberrant and variable forms of N11 following, see Fig. 7-4 second and third spectrograms and this spectrogram with many variations of call type 11. The N15+11 combination with many repeated variable versions of N11 was heard during salmon chase and could be an indication of degree of arousal.

Spectrogram parameters: FFT size 1024, overlap 75%.

NKW-42v-15ii-x-42v-x

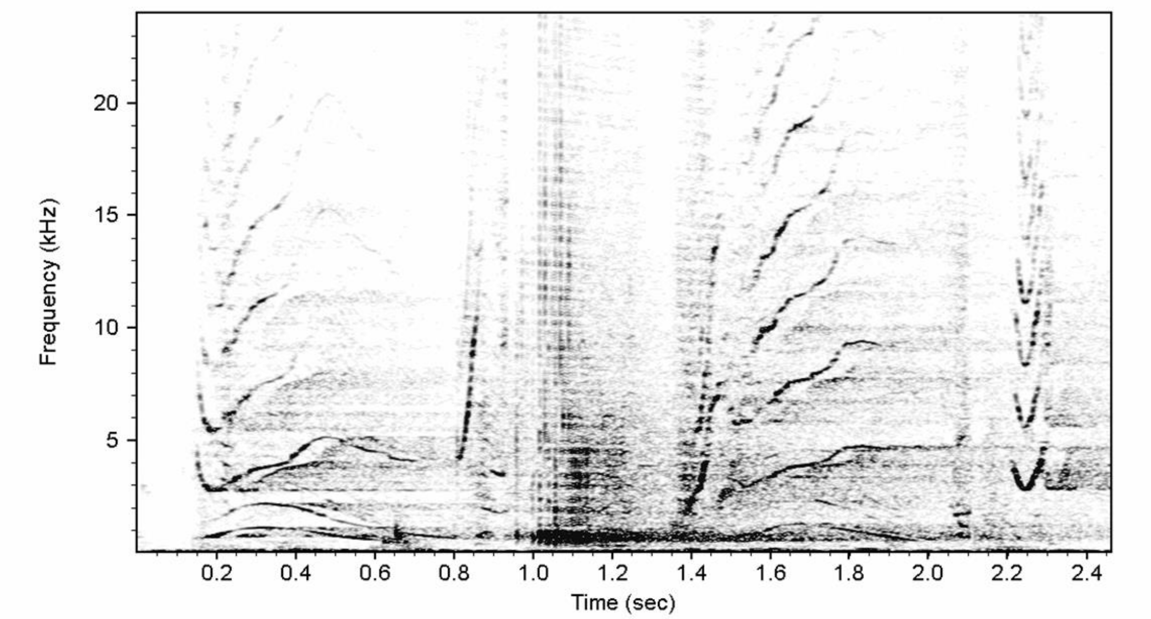


Figure 7-6. Spectrograms of call type combination recorded during salmon feeding, call type NKW-15ii which started the other call type combinations (see Figs. 7-3 to 7-5) is embedded here by different call types (42), and short unknown calls (x).

C) Spectrogram of exclusive herring feeding vocalisations:

- **Buzzes and tail slap during herring herding and feeding**

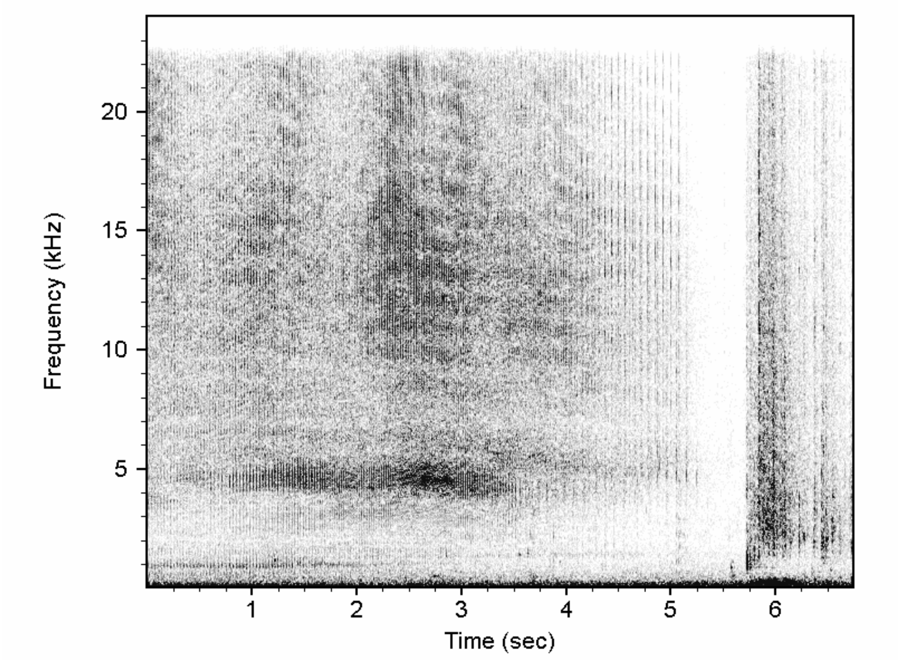
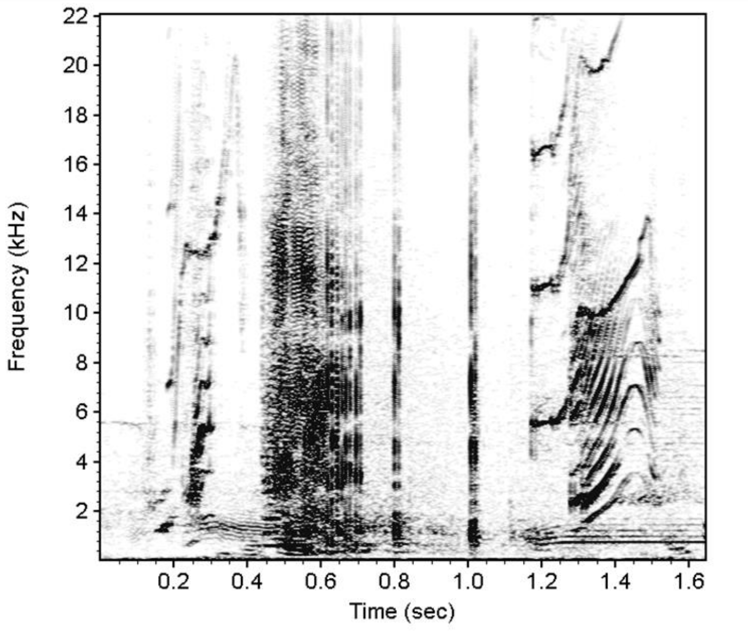


Figure 7-7. Spectrogram of typical sounds produced during carousel feeding: first there are buzzes for echolocation to detect herring but probably also to help herd the herring into tight groups and chase it under the surface, then the gap of silence indicates the animal turning around and hitting the herring with its tail. Spectrogram parameters: FFT size 1024, overlap 75%.

- **Combination of call types during herring feeding**

NKW-15ii-20-P-2005



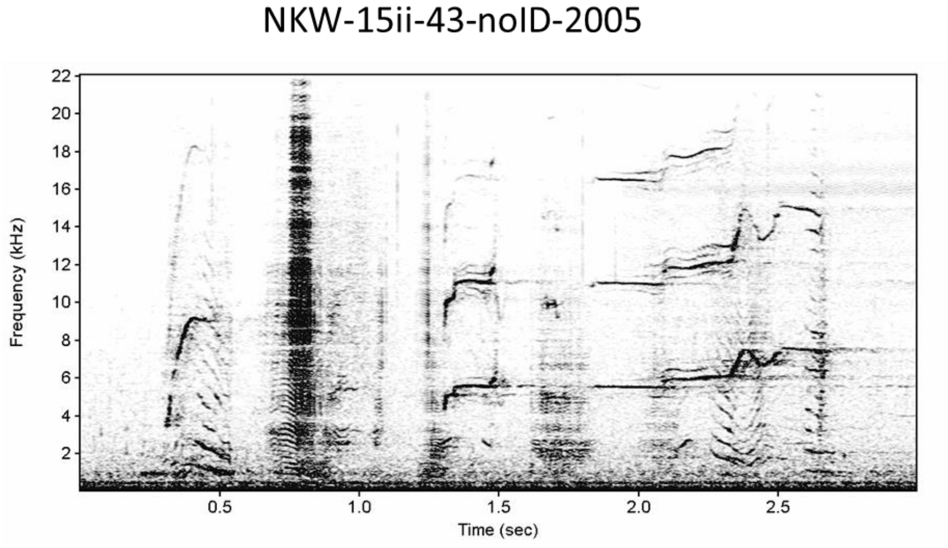


Figure 7-8. Two spectrograms of examples of call type combinations recorded during herring carousel feeding. Note that the first call type (NKW-15ii) was also used during salmon feeding contexts in combination with new call types.

Call type NKW-15i (without HFC) was recorded alone on 15 occasions mostly during carousel feeding (N=12), and rarely during travelling (N=1) or socialising (N=2). Call subtypes NKW-15 (N15ii with HFC or N15iii with a different-shaped element) and combinations with NKW-15 were only recorded during carousel feeding of herring or during salmon feeding (see Figs. 7-3 to 7-6). Call type NKW-15i was combined with NKW-02 by two groups (group P N=14; group T N=2), subtype NKW-15ii was combined with NKW-20 by one group (group P N=11) and NKW-43 by one group (noID N=3), and subtype NKW-15iii was combined with NKW-20 by one group (group T N=12), with NKW-46 by one group (group T N=4), with 1x (unknown call) +NKW-20 by one group (group T N=6) and combined with x2 (second unknown call) by one group (group AB N=1).

Food-associated call: long duration tonal call similar to herding calls in Iceland?

A three–second-long low-frequency tonal call type was recorded during carousel feeding from six different groups (NKW-56, see Fig. 7-8). This call was rare, in total only produced 18 times, but differed from all other call types due to its tonal frequency band (700–950Hz, one variable version 650Hz; see Fig. 7-11) and extreme length (2.6–3.7 seconds, one variable version with 1.6 seconds; see Fig.7-11). The same call was detected from group AN+AP during non-feeding contexts in the summertime when the main prey was salmon, not herring (see Fig. 7-10, N=1). From the literature a similar call type was known on killer whale populations in Iceland and Shetland; this call was directly connected to herring feeding and often recorded directly prior to tail slaps, leading to its description as a herding call (Deecke et al., 2011; Samarra, 2015; Simon et al., 2006). Upon request Dr. Filipa Samarra kindly provided several samples of herding calls from Iceland (see Fig. 7-12), similar in frequency and duration to NKW-56, which I recorded during this study (see Figs. 7-8 and 7-9). As in Iceland, NKW-56 was mainly recorded during carousel feeding but not prior to tail slaps and on one occasion it was recorded during travelling.

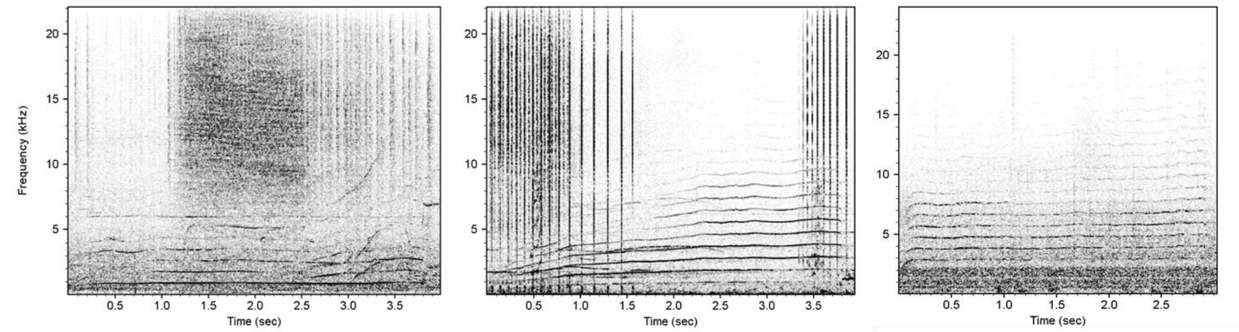


Figure 7-9. Three spectrograms of call type NKW-56 from group K (N=3), group P (N=6), and group AD (N=2) with main frequency 840–950Hz and duration 3–3.7 seconds, recorded during carousel feeding. This call type is similar to a call type recorded in Icelandic killer whales during carousel feeding. Spectrogram parameters: FFT size 1024, overlap 75%.

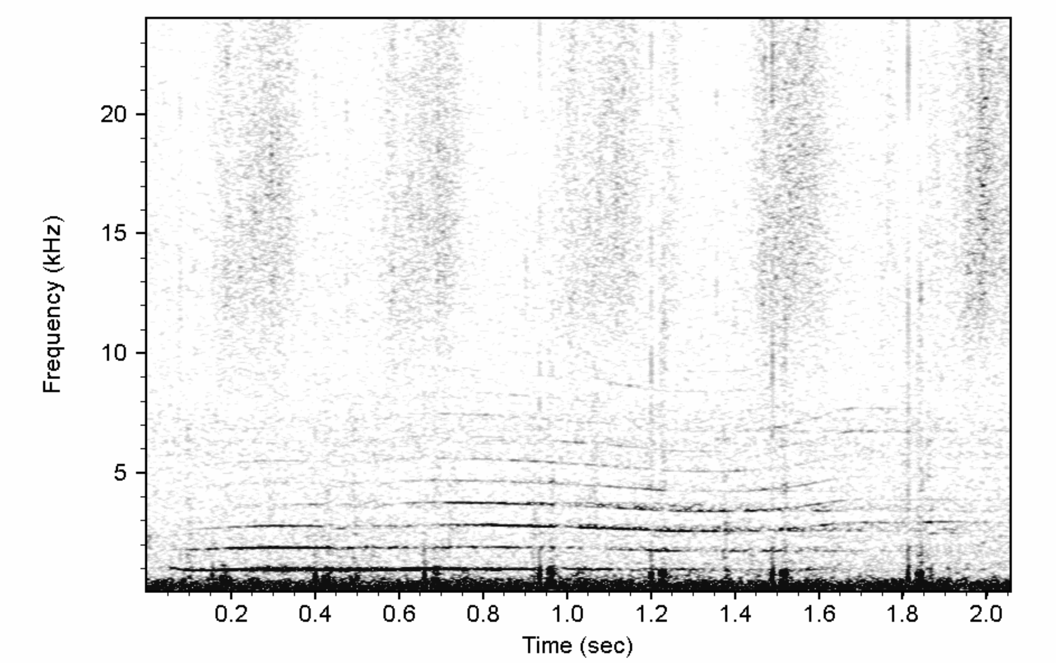


Figure 7-10. Spectrogram of NKW-56 recorded during non-feeding from group AN+AP but only on one occasion. Main frequency 890 Hz, duration 2 seconds.

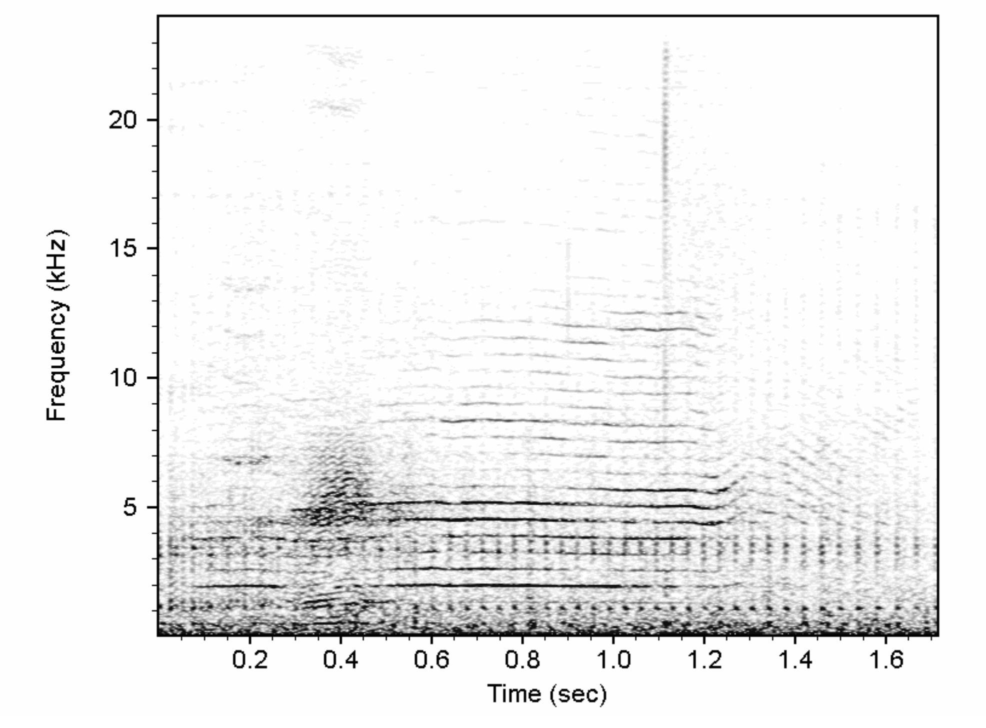


Figure 7-11. Spectrogram of variable version of NKW-56 recorded during carousel feeding from group Q (N=4). Main frequency 650 Hz, duration 1.6 seconds.

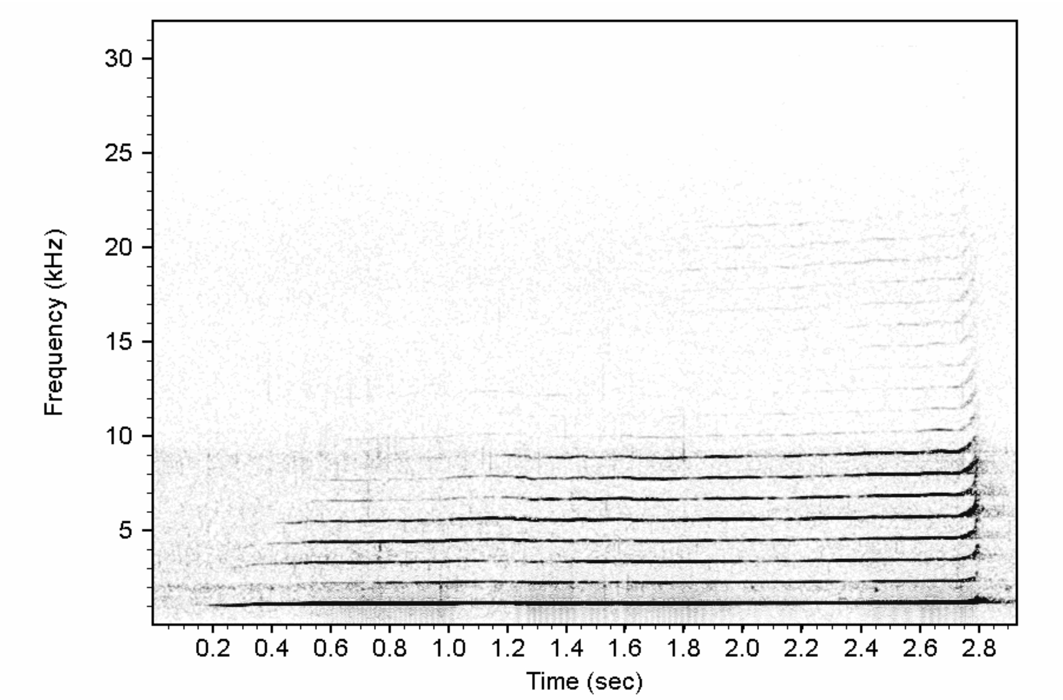


Figure 7-12. Spectrogram of call type from Iceland recorded during herding of herring. Note the similarity to NKW-56: both have their main energy around 1 kHz and are about 3 seconds long (call type kindly provided by Dr. Filipa Samarra). Spectrogram parameters: FFT size 1024, overlap 75%.

Discussion

The occurrence of two groups of killer whales inside a protected fjord in northern Norway for up to six months gave me a unique opportunity to study killer whale behaviour in more detail. The fact that they were mainly hunting and feeding on salmon added a new context to the existing data catalogue. For the first time, I could record and assess the vocal repertoire of these two groups over a long period of time, thus probably recording the entire vocal repertoire. The recordings revealed over 59 different call types, 25 sub call types, and 35 different call type combinations for two groups; these are similar results to the multiple shorter-duration recordings I have analysed from 11 different groups in over 5 years (see chapter 4). Strager described 34 discrete and 20 call subtypes from 9 groups and claimed that the repertoire was fully described after around 200 recorded calls (Strager, 1995).

My results (both from chapter 4 and chapter 8) show that the vocal repertoire is much larger and more complex than previously expected and highlights the need to gather data from individual groups of killer whales over a longer period of time and in repetitive series in order to access the full vocal repertoire.

Further, I found differences in overall vocal communication in the structure and usage of call types between different foraging contexts, whereas differences in call type usage between groups was low (see chapter 4 on call type sharing). Both groups of killer whales observed feeding on salmon were often recorded together and it was not possible to determine call sharing or group specific call types for these recordings. Pooled together, the two groups produced 29 call types exclusively during salmon foraging and 13 call types only during non-feeding contexts, while 15 call types were produced during both contexts. One could argue that these exclusively produced call types may be dialect differences between the groups. Certain call types (e.g. NKW-15) were already recorded from groups feeding on herring, which shows that they belong to the same acoustic clan. Most of the herring feeding groups had a small group specific repertoire (1 to 3 CT), but only group P showed the largest proportion of call types not shared with other groups (10 CT); even groups AN and AP not sharing many calls could not account for the large number of call types produced exclusively during one context. In conclusion, even if part of the call types were group specific and had nothing to do with context, the majority seem to be correlated with context.

Two-voiced calls were not exclusively produced in any of the two contexts and it is difficult to explain their role in whale communication. However, I found intriguing call type combinations during salmon feeding, which were not produced in non-feeding contexts. The combination with call type NKW-15 shows that killer whales can combine discrete call types in different orders, but may also add the same call types in variable versions. While the first example looks like similarly described multisyllable calls in killer whales from Iceland (Filatova et al., 2015) the second combination seems more similar to the description of increased call rates in nonhuman primates (Clay et al., 2012). Clay et al., discussed that most food association calls in nonhuman primates are non-referential and proposed that call rate may carry information about food quantity whereas call variations encode food quality (Clay et al., 2012). For example, bonobos (*Pan paniscus*) produce a series of calls which are related to the food available; in a study of captive bonobos five different food association calls were determined, and these calls were combined in a different order according to the caller’s food item. No increase in calling rates was detected, instead composition of the call sequences was significantly correlated to the caller’s preferred food item (Clay & Zuberbühler, 2009). In a more recent study the combinations of two long distance calls in wild bonobos where described to facilitate and regulate intergroup movements of foraging groups. (Schamberg, et al., 2016).

While my findings suggest that certain distinct call type combination may carry information about context such as feeding or quality and quantity of the food, and that call type combination with repeated variable calls might encode the degree of arousal of the caller, I cannot test this at this stage. Information about the sender is necessary to study context specific communication.

On the other hand, when looking into the cultural evolution of killer whale calls, Filatova et al. suggested that killer whale compound calls may develop into stereotyped calls with multi syllables, then some syllables may be reduced, eventually forming simple calls with few syllables, which may then again be combined to create compound calls to complete the cycle analogous to the “linguistic cycle” in human language using the reduction/fusion principle (Filatova et al., 2015; Van Gelderen, 2011). The main difference is that most of the labelled syllables of compound calls in Filatova et al. are classified as actual call types in my study because they were recorded independently from the combined other calls or in combination with other call types. In this way my results represent a mixture of flexible call type combinations similar to those of bonobos and the multi syllable stereotyped calls of killer whales described by Filatova et al. However, if the development of call types in killer whales follows the linguistic reduction/fusion cycle the importance of food association calls would give killer whales a suitable situation for building complex stereotyped and flexible call combinations, from which new call types and combinations can be developed.

Vocal behaviour depending on group behaviour in killer whales has been described earlier in the Norwegian and Icelandic population by Simon et al. (Simon, et al., 2007). Besides echolocation clicks and tail slaps used to debilitate herring, no food-specific vocalisation—in particular calls—have been isolated for the Norwegian population (Domenici, et al., 2000; Simon, et al., 2007; Van Opzeeland et al., 2005). However, in Iceland and Shetland a long tonal low-frequency call was described as a herding call, used during herring feeding, mostly prior to tail slaps (Deecke et al., 2011; Samarra, 2015; Simon et al., 2006). I found a very similar call in Norway, during carousel feeding but also once during a non-feeding context. It seems these calls are not very commonly produced by killer whales in Norwegian waters and their function might not be the same as in Iceland and Shetland.

In summary, I have found call types that were exclusively produced during feeding and non-feeding situations in killer whales. Among these, many different call type combinations were produced. But at this stage of my study I am not able to conclude whether some of the call types and combinations are referential signalling and/or which calls may carry information about the emotional state of the callers and/or if this is just part of the repertoire (e.g. group dialects).

CHAPTER 8 GENERAL DISCUSSION

Vocal repertoires

The study of vocal repertoires of animals can serve as a necessary fundamental baseline to further investigate vocal communication. For example, vocal repertoire studies combined with good-quality identification of individual whales and their behaviour can be used to understand social structure and organisation and will make it possible to investigate group specific vocalisations (Ford, 1991). We know from several studies that species' vocal repertoire can change dramatically from one population to another, even from group to group within a population (Filatova et al., 2012; Filatova et al., 2015; Weilgart & Whitehead, 1997).

Although I was only able to describe part of the entire vocal repertoires of long-finned pilot whales and killer whales from the Norwegian population, I could create baseline data, which clearly shows the variety and complexity of their vocal communication. Possible factors influencing the vocal repertoires could not sufficiently be determined, which is due to the low samples size used for this study. However a trend in my study shows that a minimum of one hour of useable sound recording is necessary to compare data, larger group sizes result in a higher number of calls but not call types, and behavioural stages seem to influence vocal activity.

In particular long-finned pilot whales, with over 150 specific call types, ultrasonic whistles, and diverse call type combinations, seem to have the largest and most diverse vocal repertoires described so far of any mammalian species. I found that group call type sharing is in general low, which could be an indication of group specific call types, signature whistles, or even dialects. Call type combinations, sequences, and repetitions make their repertoire even larger and more flexible; all of these aspects should be investigated in more detail in future studies.

Killer whales' vocal repertoire from 11 groups revealed over 85 specific call types and 33 call type combinations. With 25 calls per group, this is much higher than previously described (Strager, 1995). When comparing it to studies of longer duration and more effort, it seems that the vocal repertoire of killer whales in Norway is larger than in Canada, where a stable vocal repertoire of 7–17 call types per group was established (Ford, 1991). I used a slightly different method to classify and describe call types, therefore the subtypes were differently classified and this might partially account for the differences. On the other hand, other vocal repertoire contents such as percentage of two-voiced calls and use and structure of ultrasonic whistles do not differ from earlier studies (Andriolo et al., 2015; Filatova et al., 2009; Filatova et al., 2012; Samarra et al., 2010).

However, more information on different groups is necessary to assess and describe the entire vocal repertoire of killer whales in the Norwegian population and possible factors influencing it. As a next step, comparison studies should be conducted with other killer whale populations in the Northeast Atlantic and in other parts of the world to reveal vocal behaviour on the group level as well as population differences, and this might help us to understand how different dialects have evolved.

The large, complex vocal repertoires of pilot whales and killer whales combined with their capacity for vocal learning makes them prime candidate species for investigation into the structure and mechanism behind vocal repertoire evolution in light of language evolution.

Both species are matrilineal, socially organised with small core units consisting of a mother and offspring of both gender (Amos et al., 1993; Barrett-Lennard, 2000). Both species share similar call type structures (in the frequency time domain) and they produce ultrasonic whistles and certain call type combinations. However there are subtle differences in social organisation and behaviour (e.g. different hunting strategies, deep dives—squid in pilot whales and shallow cooperative feeding on fish in killer whales) that result in large differences in the vocal repertoire.

In my study I found that pilot whales have a larger vocal repertoire than killer whales, with more graded and nonharmonic low frequency calls. This might be a reflexion of the larger group sizes and more complex social organisations than observed in killer whales.

Killer whales, on the other hand, show a higher biphonation and a more distinct set of call types, which are often combined. Their smaller social units and specific cooperative hunting methods might partly account for this difference compared to pilot whales.

Context specific vocalisation

In this study I have found 29 call types exclusively produced during salmon feeding and 13 call types during non-feeding situations in two killer whale groups. Among these, many different call type combinations (e.g. more than seven combinations of NKW-15 call type) were produced, of which some combination were also produced during herring feeding. But at this stage of my study I am not able to conclude whether some of the call types and combinations found are referential signalling, and/or which calls may carry information about the emotional state of the callers, and/or if this is just part of the repertoire (e.g. group dialects). However, we know that the prerequisite for referential signalling, vocal learning, is present in killer whales: they can copy sounds of con-specifics but from different populations in captivity (e.g. (Crance et al., 2014)), or sounds of other species (Foote et al., 2006; Musser et al., 2014), or artificial sounds (the sound of an engine was imitated by the abandoned juvenile “Luna” in B.C.). This makes killer whales, like other dolphin species, good candidates to study referential signalling in animals.

As my study shows, care has to be taken when explaining and comparing vocal behaviour. The example of the “herding call” show us that even if a call type can be associated with a specific behaviour in two sub-populations of killer whales (Iceland and Shetland), the same call might mean/be used less and in a somewhat different way in a neighbouring sub-population (Norway).

In general underwater passive acoustic investigations are a good tool for studying vocal behaviour and activity patterns of whales. However, without being able to localise individual callers and or assess underwater behaviour of the whales it is difficult to address context specific vocal activity.

In this study the investigation of behavioural context effects on vocal communication could only be conducted in killer whales, due to the larger pilot whale groups and their subsurface foraging techniques. It is relatively easy to detect feeding and foraging behaviour in killer whales. During carousel feeding on herring, as buzzes and tails slaps as well as specific surface behaviour are clear indicators, whereas in salmon feeding the whole group is spread out and is echolocating along an entire fjord until salmon is found. Then the behaviour changes suddenly with high-speed charges and loud calling, indicating a salmon pursuit, and then feeding can be detected through either visual confirmation of the fish in the whales’ mouths or salmon parts floating in the sea and being picked up by seagulls.

Detecting feeding behaviour in pilot whales becomes much more difficult, because the groups are much larger and often do not feed in synchrony—one has to be very close to a feeding matriline, however they can move vertically more than 600m and sounds from neighbouring groups may influence recording. Typically during foraging dives the animals increase their clicking and are submerged for up to 10 minutes. Since they hunt their prey in deep waters so no surface behaviour can observed while hunting, there is no confirmation except for the odd piece of squid floating on the surface after the hunt. The study of behavioural context in vocal communication in pilot whales remains challenging when using only a boat with a pair of hydrophones as a research platform.

In some whale populations solid baseline data exists on group size and dynamics or individuals through Photo-ID, vocal repertoires, genetic relations, and often habitat use or migration behaviour. And as technology advances, the study of whale behaviour soon may see a breakthrough; for example, hydrophone arrays have become more accurate and easy to use, and D-tags are more commonly used to localise and study calling animals. Drone development will particularly help study whales from the air over longer periods of time, revealing group behaviour as well as interactions between animals, and automatic analysis of big data is continuously evolving and combined with detailed long-term field observations, can reveal many new insights into the lives of these social yet elusive animals.

CONCLUSION & OUTLOOK

It seems like decades of promising studies of vocalisation in nonhuman primates and discovering the origins of human language may have come to a sobering end, largely due to the lack of vocal production learning in nonhuman primates (Fischer 2016).

Some whales and dolphins have the ability for vocal learning and vocal as well as gestural mimicry, which gave rise to vocal traditions, and many live in cultural societies (review Whitehead & Rendell). These animals have the prerequisite needed to develop a sophisticated language and may be better candidates than primates for studying early language evolution in humans. However, there is one major difference: these are marine mammals living in a sound environment and sound has become their primary sensory modality, compared to humans in whom vision has taken on this role. Cetaceans can sense and “see” their environment with all sounds; their echolocation is the best developed system in the animal kingdom. All sounds give them rich information about topography and sea states, other animals including prey or con-specifics, orientation to others, even the distance and composition of objects or other animals. In other words, even their social sounds must be seen in light of echolocation. Modern humans lack this ability or are at best quite poor at deciphering environmental information in vocal signals, instead developing a cryptic written language, which is unique.

From my study it seems that pilot whales and killer whales are suitable candidates for studying semantics in animals to a limited extent. Even though the methods for studying whales are still rather simple and time consuming and deliver limited results, there is fast development in this area of study. New technology like the use of D-tags and more sophisticated hydrophone arrays let us localise individual callers, and new generations of drones and underwater cameras can reveal more detailed information about whale behaviour when they are out of sight of human observers on a boat—and I am sure there will be more. In addition, automatic analysis of the big data collected is needed. This requires interdisciplinary cooperation between branches of science and technology, and most of all scientists in the field, in order to find common ground and share results.

However, we should not favour new technology while underestimating the value of field biologists and naturalists, who spend hours, days, even years observing and building a core of understanding wild animals, and later applying lab results to the wild.

In fact while I spent the last 10 years trying to decipher whale sounds, I also spent long hours and days at sea recording whales’ behaviour and recording their sounds. All during this time I was trying to figure how and what they were communicating to better understand their

behaviour, especially when they were submerged. One of the major sounds they produced while foraging at sea, often in deep depths, were echolocation clicks to search for prey. Trying to imagine the dark deep Vestfjord being “illuminated” by loud and plentiful whale echolocating clicks, I realised that all sounds they use actually produce an echo. What information can the whales possibly extract from these echoes?
Can certain social calls encode information about the underwater soundscape? Depth, distance, space, seascapes such as mountains, ridges, and other topography, sound speed, and transmission or temperature and salinity could all be transmitted with certain echoes given off frequency parts of calls. Could for example subtypes of call types encode directional information, e.g. on where to go or where animals come from? This information could be retrieved from the presence or absence of more directional higher-frequency components in a call type. Other information could be created to form a picture, however this concept requires a good understanding of the species’ vocal repertoire, and for most species, even though we’ve already spent more than 40 years, we are only beginning this study.

There are still many open questions (old and new), and in my opinion, the aspect of whether and how cetaceans use social sounds in their echolocation skills should be included in future vocal communication studies. In other words, we should find a way to study cetacean capacity to hear and see sounds and also send vocal communication with “images” created by the echo of their projected signals. This additional information creates a new space in communication and without adding this dimension, we might not be able to fully understand their vocal communication and how these animals use and utilise sounds in their environment.

In conclusion, with this thesis I hope to be able to present a useful baseline study and contribute to future studies on the mysterious topic of vocal communication in cetaceans. I am very excited to move on to the next level of this exciting topic.

List of peer reviewed publications published during my PhD time

Bold publications are relevant to this thesis

1) *"Vocal repertoire of long-finned pilot whales (Globicephala melas) in northern Norway"*. Heike Vester, Marc Timme, Sarah Hallerberg, & Kurt Hammerschmidt, 2017, re-submitted to JASA.

2) *"Quantifying group specificity of animal vocalizations without specific sender information"*. Heike Vester, Kurt Hammerschmidt, Marc Timme, & Sarah Hallerberg, 2016. Physical Review E 93, 022138.

3) *"Whale watching in Norway caught between the more traditional hunting canons and the lucrative promising seismic airguns"*. Giovanna Bertella & Heike Vester, 2015. Tourism in Marine Environments Vol 11, p. 1.

4) *"First record of killer whales (Orcinus orca) feeding on Atlantic salmon (Salmo salar) in northern Norway suggest a multi-prey feeding type"*. Heike Vester & Kurt Hammerschmidt, 2013. Marine Biodiversity Records, Vol 6, pp. 1–5.

5) *"Dietary variation within and between populations of northeast Atlantic killer whales Orcinus orca inferred from 13C and 15N analyses"*, Andrew D. Foote, Heike Vester, Gisli A. Vikingsson, & Jason Newton, 2012. Marine Mammal Science. DOI: 10.1111/j.1748-7692.2012.00563.

6) *"Call for cooperation to contain damage by Chile's salmon farms"*, Heike Vester & Marc Timme, 2010. Nature, Vol. 465, 17 June 2010, p. 869.

7) *"Genetic differentiation within a North Atlantic killer whale ecotype"*, Andrew D. Foote, Julia Vilstrup, Renaud de Stephanis, Philippe Verborgh, Sandra C. Abel Nielsen, Morten Rasmussen, Robert J. Reid, Kelly M. Robertson, Lars Kleivane, Nils Øien, Tiu Similä, Heike Vester, Gísli A. Vikingsson, Robert Deaville, Emer Rogan, Eske Willerslev, M. Thomas P. Gilbert, and Stuart B. Piertney, 2010. Molecular Ecology, Vol 20 (3), pp. 629–641.

8) *"Southernmost distribution of common Bottlenose dolphins (Tursiops truncatus) in the eastern South Pacific"*, Carlos Olavarría, Jorge Acevedo, Heike I. Vester, José Zamorano-Abramson, Francisco A. Viddi, Jorge Gibbons, Emma Newcombe, Juan Capella, A. Rus Hoelzel, Marcelo Flores, Rodrigo Hucke-Gaete, & Juan Pablo Torres-Flórez, 2010. Aquatic Mammals, Vol 36 (3), pp. 288–293.

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Supplement 1

Supplement 1. Structural description of Norwegian long-finned pilot whale call types: The call types are broken down according to their content of segments and elements and whether they consist of only lower frequency components (LFC), or two frequency components (LFC and higher frequency components (UFC)). Within the segments, elements are described by their shape and we identified 8 different structures of which the most common were ascending and constant frequency sidebands. Most calls were simple in structure with just one segment and one element, with ascending or descending elements. But a high variety of element structures can be seen with all call types, showing the complexity of the vocal repertoire of long-finned pilot whales in northern Norway.

Call type structures			**Element structures**										
	Segments	Elements	Ascending	Descending	U-shape	∩-shape	Noise	Buzz	Whistle	Constant	Different elements (N)	Calls (N)	Call types (N)
LFC	1	1	13	12	5	2	0	0	3	8	42	1075	46
LFC	1	2	33	10	13	6	7	3	2	16	90	936	44
LFC	1	3	14	10	9	3	3	0	1	10	51	591	15
LFC	1	4	8	5	1	0	0	0	0	6	20	100	5
LFC	1	5	2	1	0	0	0	0	1	1	5	4	1
LFC	1	6	2	4	1	0	0	0	0	0	6	126	1
LFC	2	2	3	3	0	0	1	0	1	0	8	40	4
LFC	2	3	2	1	0	0	0	0	0	0	3	2	1
LFC	2	4	3	2	1	1	2	0	1	2	12	332	3
LFC	3	3	3	3	0	1	0	0	0	0	6	8	2
LFC	3	4	1	1	0	0	2	0	0	0	4	6	1
LFC	4	4	1	2	0	0	0	0	1	0	4	7	1
LFC	5	6	0	4	0	0	1	0	0	1	6	22	1
LFC	5	8	4	1	1	0	1	0	0	0	7	11	1
LFC	6	8	2	1	1	0	1	1	0	1	8	4	1
total			91	60	32	13	18	4	10	45	272	3264	127
LFC+UFC	1	1	6	1	1	1	0	0	1	2	12	97	5
LFC+UFC	1	2	7	1	1	0	1	2	1	3	15	675	5

LFC+UFC	1	3	4	1	0	1	1	0	1	2	10	25	2
LFC+UFC	1	5	5	4	3	0	0	0	0	8	20	5	3
LFC+UFC	1	6	6	4	6	0	0	0	1	7	24	9	3
LFC+UFC	1	7	7	5	4	1	0	0	1	8	27	5	3
LFC+UFC	2	3	6	3	0	0	3	0	0	1	13	56	3
LFC+UFC	2	4	2	0	0	0	2	0	0	1	5	427	1
LFC+UFC	2	5	1	0	1	1	3	0	0	1	7	7	1
LFC+UFC	4	4	1	1	0	3	0	0	0	0	5	2	1
UFC*	1	1	11	0	0	0	0	0	0	0	11		
UFC*	1	2	9	1	0	0	0	0	0	8	18		
UFC*	1	3	1	0	0	0	0	0	1	1	3		
UFC*	2	2	1	0	0	1	0	0	0	0	2		
total			67	21	16	8	10	2	6	42	172	1308	27

* Upper frequency components (UFC) are described independent of their lower frequency components (LFC) but are part of the same LFC+UFC calls and therefore the total calls and call types are not listed twice.

Supplement 2

Supplement 2. Structural description of Norwegian killer whale call types: The call types are broken down according to their content of segments and elements and whether they consist of only lower frequency components (LFC), or two frequency components (LFC and higher frequency components (HFC)). Within the segments, elements are described by their shape and we identified 9 different structures of which the most common were ascending and constant frequency sidebands. Most calls were simple in structure with just one segment and two elements. But a high variety of element structures can be seen with all call types, showing the complexity of the vocal repertoire of killer whales in northern Norway.

					Element structure											
Call type	LFC	LFC + HFC	HFC	Segment	Ascending	Descending	U-shape	∩-shape	Noise	Buzz	Whistle	Constant	Hook	Total elements	Groups (number of calls, all categories)	Total calls
1	1	0	0	1	0	1	0	0	0	0	0	0	1	2	AD (17); AV (4)	21
2	0	1	0	1	2	0	1	1	0	0	0	2	0	6	P (23); T (9); BI+AA (6)	38
3	0	1	0	1	1	1	0	0	0	0	0	1	0	3	AN (4); AP (17); AP+AN (42)	63
4i	0	1	0	1	2	0	1	0	0	0	0	0	1	4	n/a (27); K (13); P (6); T (3); BI+AA (8); AV (11); E (1)	69
4ii	0	1	0	1	1	0	1	1	0	0	0	0	1	4	K (2); P (129); T (22); BI-AA (16); AV (1)	170
4iii	0	1	0	1	2	0	1	0	0	0	0	0	1	4	P (76); T (10); (BI+AA (2)	88
4iv	0	1	0	1	2	1	1	0	0	0	0	1	1	6	P (22); Z (3); BI+AA (62); AV (3)	90
5i	1	0	0	1	0	0	0	0	0	0	0	1	0	1	n/a (4); K (3); T (4); AV (1)	12
5ii	0	1	0	1	0	0	0	0	0	0	0	2	0	2	P (12)	12
6i	1	0	0	1	1	0	1	0	0	0	0	0	0	2	n/a (28); Q (22)	50
6ii	1	0	0	1	1	0	1	0	0	0	0	0	0	2	n/a (76); K (2); P (3); H (3)	84
6iii	1	0	0	2	2	0	0	0	0	1	0	2	0	5	Q (4)	4
7	0	1	0	1	0	1	0	0	0	0	1	0	0	2	n/a (12);	12
8	1	0	0	1	0	0	0	1	0	0	0	0	0	1	n/a (1); K (3)	4
9	1	0	0	1	0	0	0	0	0	0	0	1	0	1	n/a (20)	20
10	1	0	0	2	2	0	0	0	0	0	0	2	0	4	P (21); T (3)	24
11i	1	0	0	1	0	0	0	0	0	0	0	1	0	1	K (2); P (35); AB (30); BI+AA (7); H (2)	76
11ii	1	0	0	1	0	0	0	0	0	0	0	1	0	1	n/a (7); K (17); T (11); AB (3); AV (7)	45
11iii	0	1	0	1	2	0	0	0	0	0	0	1	1	4	P (48); T (24); BI+AA (9)	81

11iv	1	0	0	1	1	0	0	0	0	0	0	1	0	2	n/a (54); K (12); P (60); Z (5); BI+AA (4); AD (2); Q (3)	140
11var	1	0	0	1	2	0	0	0	0	0	0	1	0	3	n/a (1)	1
12i	1	0	0	1	1	0	0	0	0	0	0	0	0	1	n/a (8); BI+AA (25)	33
12ii	0	1	0	1	2	0	0	0	0	0	0	0	1	3	P (5)	5
13	1	0	0	1	0	1	0	0	0	0	0	1	0	2	P (36); H (12)	48
14	0	1	0	1	0	1	1	0	0	0	0	1	1	4	P (4); n/a (18); BI+AA (17); AV (1)	40
15i	1	0	0	2	1	0	0	0	0	1	0	0	0	2	P (24); T (2); AV (1); BI+AA (2)	29
15ii	0	1	0	2	2	0	0	1	0	1	0	1	0	5	n/a (3); P (14)	17
15iii	1	0	0	2	0	1	0	0	0	1	0	0	0	2	AB (1); T (21)	22
16	1	0	0	1	0	0	0	0	1	0	0	1	0	2	n/a (46); K (8); P (3); T (4); BI+AA (1); H (3); Q (30); ANAP (4); AN (2); AP (22)	123
17	0	1	0	1	2	1	0	0	0	0	0	2	0	5	P (35); BI+AA (1)	36
19	1	0	0	3	0	1	0	0	0	0	0	2	0	3	n/a (13); P (19)	32
20	0	1	0	1	4	1	0	0	0	0	0	1	1	7	P (11), T (18)	29
21	0	1	0	1	0	0	1	2	0	0	1	0	0	4	K (1); P (1)	2
22	1	0	0	1	1	1	0	0	0	0	0	0	0	2	n/a (3); P (3)	6
23	1	0	0	1	1	1	0	0	0	1	0	0	0	3	n/a (2)	2
24	1	0	0	1	1	0	0	0	0	0	0	1	0	2	P (21)	21
25	1	0	0	1	1	0	0	0	0	0	0	0	0	1	P (1); n/a (14)	15
26	1	0	0	1	1	0	0	1	0	1	0	0	0	3	n/a (2)	2
27	0	1	0	1	2	0	0	0	1	0	0	0	1	4	P (3)	3
28i	1	0	0	1	1	0	1	0	0	0	0	0	0	2	n/a (77); AD (49), P (20); Q (3); K (7)	156
28ii	1	0	0	2	2	0	1	0	0	0	0	0	0	3	n/a (94); K (45); P (3)	142
28iii	1	0	0	1	2	0	1	0	0	0	0	0	0	3	K (39); P (24); BI+AA (10); E (13)	86
28iv	1	0	0	1	2	0	1	0	0	0	0	0	0	3	P (20)	20
29i	1	0	0	1	2	0	0	0	0	0	0	1	0	3	n/a (11); K (4); BI (11)	26
29ii	0	1	0	1	3	0	0	0	0	0	0	1	1	5	K (2); P (3)	5
30	0	1	0	1	3	0	0	0	0	0	0	2	1	6	n/a (15); T (19)	34
31	1	0	0	1	0	0	0	0	0	0	0	1	0	1	n/a (21); P (6)	27
32	1	0	0	1	1	0	1	0	0	0	0	0	0	2	n/a (2); BI+AA (15)	17

33i	1	0	0	1	0	1	0	0	0	0	0	0	0	1	n/a (34); P (43); AV (65); BI (1); BI+AA (2); AD (8); H (23), Q(1)	177
33ii	1	0	0	1	0	1	0	0	0	0	0	0	0	1	BI+AA (33)	33
33iii	1	0	0	1	0	1	0	0	0	0	0	0	0	1	Q (1)	1
34	0	1	0	1	2	1	0	0	0	0	0	0	1	4	P (15)	15
35	1	0	0	3	4	0	0	0	0	1	0	3	0	8	n/a (17); P (11); T (2); BI (12); BI+AA (7); AD (8); H (1)	58
36	0	1	0	3	3	0	1	0	2	1	1	1	0	9	P (1)	1
37	1	0	0	1	1	0	1	0	0	1	0	0	0	3	AN+AP (6)	6
38	1	0	0	1	1	0	0	1	0	0	0	1	0	3	Q (4)	4
39	1	0	0	1	1	1	0	0	0	0	0	1	0	3	n/a (49); K (27); AD (68); E (6)	150
40i	0	0	1	1	1	0	0	0	0	0	0	1	0	2	n/a (66); P (2); BI+AA (1); Q (3)	72
40ii	0	1	0	1	1	0	0	0	0	0	0	2	0	3	n/a (8)	8
41i	0	1	0	1	2	0	0	0	0	0	0	0	1	3	P (22); T (19)	41
41ii	0	1	0	1	4	0	0	0	0	0	0	0	1	5	P (3)	3
42i	0	1	0	2	1	1	1	0	0	0	0	0	1	4	n/a (25); K (4); P(58); BI+AA (15)	102
42ii	0	0	1	2	1	0	1	0	0	0	0	0	1	3	n/a (25); K(7); P (7)	39
43	0	1	0	1	1	1	2	1	0	0	1	0	1	7	P (8); n/a (4); AB (4)	16
44	1	0	0	1	0	1	1	1	0	0	0	1	0	4	n/a (1)	1
45i	1	0	0	1	1	0	0	0	0	0	0	1	0	2	n/a (67)	67
45ii	1	0	0	1	2	0	0	0	0	0	0	1	0	3	T (4)	4
46	0	1	0	1	3	0	0	0	0	0	0	1	1	5	n/a (17); P (243); T (44); BI+AA (31); AV (1)	336
47i	0	1	0	1	1	0	0	0	0	0	0	1	1	3	P (54), T (2)	56
47ii	0	1	0	1	0	1	0	0	0	0	0	2	0	3	BI+AA (3)	3
48	1	0	0	1	0	0	1	0	0	0	0	1	0	2	P (1); BI+AA (9)	10
49	1	0	0	1	1	1	0	0	0	0	0	0	0	2	K (1); T (7)	8
50	0	1	0	1	3	0	0	0	0	0	0	1	0	4	T (3)	3
51	1	0	0	1	0	1	1	0	0	0	0	1	0	3	AD (5)	5
52	0	1	0	2	1	0	0	0	0	0	0	2	1	4	P (12); BI+AA (3); AN+AP (11); AP (1); AN (1)	28
53	0	1	0	5	2	1	3	1	0	2	1	0	0	10	P (5)	5
54	0	1	0	1	0	1	2	1	0	1	2	0	0	7	AV (4)	4
55i	1	0	0	1	0	0	0	0	0	0	0	2	0	2	K (2); AB (1)	3

55ii	0	1	0	1	3	0	0	0	0	0	0	3	0	6	AB (4)	4
56	1	0	0	1	0	0	0	0	0	0	0	1	0	1	K (3); P (6); T (2); n/a (1); AD (2); Q (4)	18
57	0	1	0	1	1	0	1	1	0	0	0	1	1	5	K (1)	1
58	0	1	0	1	2	0	0	0	0	0	0	1	1	4	H (17)	17
59	1	0	0	1	1	0	0	0	0	0	0	0	0	1	n/a (22); P (1); BI+AA (1)	24
61	0	1	0	2	0	1	0	0	0	2	0	1	0	4	AN+AP (185);	185
62	0	1	0	2	1	0	0	0	0	1	0	0	1	3	AN+AP (53); AN (8); AP (80)	141
	46	37	2	106	101	26	29	13	4	15	7	62	24	281		**3731**