Vocal repertoire and group specific vocal variations in long-finned pilot whales (*Globicephalus melas*) in northern Norway

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1 Abstract

This is the first description of group specific vocalizations of long-finned pilot whales. Sounds were recorded and analyzed from seven different social groups of long-finned pilot whales in the Vestfjord in northern Norway between November 2006 and August 2010. We analyzed the sound recordings by three different methods: First, we created a baseline data-set by doing a classical observer-based call categorization and classification, using observer-based audio-visual inspections. We found 154 different call types including 16 sub-types of calls and we observed complex structures of call type combinations, call and whistle combinations and repetitions. Second, to confirm the variation of call types and identify possible group specific vocalizations we measured selected acoustic features. We observed that in contrast to call types the broader composed call categories were used by all groups. Third, we proposed and applied a new method for studying group specificity of vocalizations via cepstral distributions: We constructed comparable ensembles of calls, representing each group and compared distributions of sound features of entire ensembes rather than comparing individual call occurrences. Quantifying the differences of group specific ensembles by measuring differences of feature distributions, we demonstrated that group specific differences in vocalizations are significantly larger than intra-group differences. By using this unique three-fold combination of analysis we showed that the vocal behavior of long-finned pilot whales is complex and group specific. Additionally, the pilot whale’s vocal repertoire contains among others, vocalizations known from other dolphin species such as whistles in bottlenose dolphins or discrete calls and call combinations in killer whales.

Keywords: long-finned pilot whales, *Globicephala melas*, Norway, vocal repertoire, discrete call types, group specific vocalization, sound analysis, cepstral distribution, bag of words.

2 Introduction

Social toothed whales evolved to live in social communities in which females build the core element with often strong and long lasting female bonds e.g. [1]. In these societies, group composition is stable over many years or generations and maternal care is long, sometimes lasting for a lifetime. According to the social function hypothesis, the vocal repertoire of a species should become more diverse the more complex its social system is [2, 3]. Complex, group specific vocalizations are characteristic for matrilineal social whales, and are learned from members of the group and transmitted culturally (e.g. [4–6]). In contrast, more solitary baleen whales such as blue whales (*Balaenoptera musculus*) (see e.g. [7]) or fin whales (*Balaenoptera physalus*) [8] use fewer vocalizations with some geographical differences. Regarding all the
matriarchal social odontocetes, killer whales (*Orcinus orca*) are the most studied, with a particular focus on the study of their vocal behavior. There are several populations of killer whales and most of them live in natal philopatric matrilineral societies where offspring from both sexes stay a lifetime within their natal pod. In a population of resident killer whales in British Columbia, group specific dialects were first discovered in the early 1980ies. Most calls were transmitted vertically from mother to offspring and dialects evolved through accumulated copying errors, which results in similar dialects in closely related pods. However, killer whales are capable of vocal mimicry and learning and therefore horizontal (intra-pod, between adult animals) transmission of vocal traditions is also likely to create repertoire changes in dialects, which will add more diversity to their vocal repertoire.

In this contribution, we study the vocalizations of long-finned pilot whales (*Globicephala melas*). Long-finned pilot whales belong to the dolphin family and represents the second largest dolphin species after the killer whales, with adult males reaching 6.5 m and females 5.5 m in length. The species is widely distributed and is found in circumpolar regions both in the northern and southern hemispheres and in the Mediterranean (see and refs. therein). Long-finned pilot whales mainly occur in deeper waters (deeper than 100 m), often at the edge of a geographical drop off, with migrations between offshore and inshore waters, correlating with the distribution of squid, their main prey. In the North Atlantic they mainly feed on squid *Gonatus spp* and *Todarodes sagittatus*, but occasionally they may feed on fish as well.

The social structure of long-finned pilot whales seem to be similar to the resident type of killer whales from the eastern North Pacific, as they live and travel in groups with core social units consisting of 11-14 animals, representing a matriline of a mother and her direct offspring of both sex. These matrilines often travel together with other related matrilineral groups, described as pods, and up to 100 animals gathered together are a common sight. Large temporary aggregations of several pods can exceed 150 animals and social interactions are described as both short-term and long-term relationships (lasting at least 5 years). The distribution of long-finned pilot whales in the north-eastern Atlantic ranges from the Norwegian coast in the east to the Faroe Islands, Iceland and Greenland in the west. The north-east Atlantic population of pilot whales is not well studied, but it is likely that they live in stable matrilineral groups throughout their lives, such as other pilot whale populations in Gibraltar and the North West Atlantic. Genetic investigations have shown that pilot whales killed in the Faroe hunts are all related and that the males in the group do not father the offspring. It was therefore postulated that long-finned pilot whales in the north-eastern 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, it is likely that the pods seen in Norway migrate to the Faroe Islands and therefore belong to the same population. In our study we investigated the long-finned pilot whales that migrated into the Vestfjord in Northern Norway and which stayed there for several days or weeks. The migration pattern and population size of pilot whales in northern Norway are to this date unknown.

Long-finned pilot whales produce typical dolphin sounds, such as clicks, buzzes, grunts, and a variety of pulsed calls including whistles. 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, and a fifth of the calls can be bi-phonal with a lower (LFC) and an upper frequency component (UFC). In contrast to discrete killer whale call types, pilot whales have been reported to use graded calls. However, the recordings of pilot whales analyzed in this study did show discrete call types.

So far, no attempt has been undertaken to investigate group specific vocalization among long-finned pilot whales. Observer based audio-visual (or perceptual) inspection of sounds has proven to be a reliable method for dolphin vocal classification analysis and it is often used as baseline for further automated classification analysis. Although observer based methods result in fine scale categorizations, they are
subjective due to the limitations of human sensory physiology and human experiences and expectations. A human observer will not be able to compensate for the physical properties of sound in water (e.g., 5 times faster than in air), where whales have adapted to faster resolution both in hearing and sound processing, as well as sound production (see e.g., 25). Therefore we amend human based categorization by including automated categorization and a new automated method to study group specificity (cepstral distributions). Early approaches to automated categorization were done by Spong and colleagues 26 and Deecke and colleagues 27 and these studies used artificial neural networks to classify and compare pulsed vocalizations of killer whales. These artificial neural network approaches were combined with specific methods such as dynamic time warping to extract important features of marine mammal sounds 28,29. Other studies applied methods known from human speech analysis, such as that of Shapiro and Wang 30 who used an FFT based pitch detection algorithm, or of Kaufman and colleagues 31 who favored a so-called HAL (Hyperspace Analog to Language) model to describe the structure of humpback whale songs.

We use FFT features (cepstral coefficients) which are used in similar ways in speech processing 32. Focusing on statistical properties of ensembles of vocalizations and not on single calls, allows us to investigate group specific differences. Investigating ensembles of calls rather than identifying individual call types is conceptually similar to the bag-of-words-model 33 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. We investigate group specific vocalizations by comparing “bags of calls” (ensembles) that contain calls made by 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. Using histograms of automatically computed sound features, has also been suggested to attribute bird songs to bird species 34.

In this contribution we describe the previously unknown vocal repertoire of the long-finned pilot whale population in northern Norway. Additionally we present the complex vocal behavior of long-finned pilot whales with emphasis on group specific differences. Furthermore we compare different methodological approaches to analyze whale vocalizations and test if and how these methods can mutually complement.

1) An observer-based visual classification of spectrograms: This method is widely spread in classification of marine mammal sounds 5,11,35, and allows a fine graded description of differences in vocal structure. However, the objectivity of this way of categorization remains debatable.

2) Classification based on FFT-derived acoustic features, such as fundamental frequency or peak frequency: This method is also widely spread in marine mammals as well as terrestrial mammal studies, like monkeys or apes (e.g., 36,37). Often one can find a combination between observer-based audio-visual classification combined with FFT measurements. The FFT measurements are well-suited to describe structural differences in vocal repertoires and can contribute to more objective categorizations. However, the method requires good a-priori knowledge of important acoustic features.

3) Cepstral Distributions: We study group specificity of vocalization by comparing statistical properties of sound features computed for ensembles of recordings. This new automated method circumvents the limitation of the first two approaches in so far that it is not dependent on the observer or on the selection of features. Consequently, it is a valuable extension in the description of vocal repertoires and group specific differences.

3 Materials and Methods

3.1 Ethics Statements

All observations and recordings reported in this contribution were made in the Vestfjord in northern Norway (see GPS coordinates in Tab. 1). In general no permission is needed for non-invasive research
on marine mammal along the Norwegian coast. To ensure that we conducted our research according to Norwegian ethical laws, we asked the Animal Test Committee (Forsksdyrutvalget) of Norway for permission, and they confirmed that our studies do not require any permission (approval paper ID 6516).

3.2 Study site and field data collection

![Map of encounters with long-finned pilot whale groups in the Vestfjord (Northern Norway). Symbols mark the places where the different groups have been encountered. More details about the different encounters can be found in Tab. 1.](image)

Figure 1: Map of encounters with long-finned pilot whale groups in the Vestfjord (Northern Norway). Symbols mark the places where the different groups have been encountered. More details about the different encounters can be found in Tab. 1.

All recordings and observation were made between November 2006 and August 2010 in the Vestfjord in northern Norway over 10 encounters with seven different groups of long-finned pilot whales. The Vestfjord connects the mainland and the Lofoten islands archipelago, has many side fjords and is more than 140 km long. It runs deep in the middle 300-600 m, with the deepest side fjord being almost 900 m deep. This represents a good foraging site for pilot whales, which are known to select for squid such as *Gonatus spp.* and *Todarodes sagittatus* in the Northeast Atlantic [14]. We found the pilot whales in an area in over 150 km of range, mainly in waters that are deeper than 200 m, and over a period of 2-6 weeks. Our study site covered most of the Vestfjord, on the Lofoten side of the Vestfjord as far south as Reine and North-East to Lodingen and from Stegen to Tysfjord on the main land side of the Vestfjord (see Fig. 1). Over a period of 4 years, 33 hours of behavioral observation and 16:32 hours of sound recordings were collected in total (see Tab. 1). On all boat trips the entire track and waypoints at the beginning
Table 1: Sightings, Recordings and Encounters

| group | Date         | location [ N/E ] | group size | photo ID's | obs. time [hr:min] | sound rec. [hr:min] | behavior                                      |
|-------|--------------|------------------|------------|------------|--------------------|--------------------|------------------------------------------------|
| B     | 03/07/2010   | 68°04.870'/14°25.130' | 45         | 43         | 05:33              | 03:17              | slow traveling, socializing                    |
| C     | 10/11/2006   | 68°06.146'/14°42.088' | 13         | 7          | 00:43              | 00:13              | milling, slow traveling, boat friendly         |
| D     | 10/08/2009   | 68°06.532'/14°32.771' | 100        | 60         | 04:50              | 01:07              | milling, slow traveling, socializing          |
|       | 11/08/2009   | 68°10.997'/15°29.205' | 100        | 60         | 04:50              | 02:25              | milling, slow traveling, socializing, foraging, resting |
| F     | 28/06/2007   | 68°04.517'/14°49.436' | 20         | 9          | 00:50              | 00:23              | milling, boat friendly                         |
| G     | 14/07/2008   | 68°07.612'/14°40.562' | 7          | 4          | 02:10              | 00:49              | milling, socializing, boat friendly            |
| H     | 22/05/2009   | 68°08.578'/14°31.581' | 50         | 32         | 04:00              | 02:45              | milling, socializing, resting                  |
|       | 24/05/2009   | 68°01.636'/14°38.966' | 50         | 22         | 02:00              | 01:20              | milling, resting                               |
| I     | 13/07/2009   | 68°01.053'/14°23.519' | 60         | 17         | 05:48              | 03:10              | milling, resting socializing, boat friendly     |
| J     | 08/06/2010   | 68°08.540'/15°09.330' | 60         | 19         | 01:40              | 01:06              | first fast traveling -avoided boat, later calmed down slow traveling, |
|       | 03/07/2010   | 68°04.870'/14°25.130' | n/a        | 4          | 02:00              | 01:08              | traveling and milling with group B            |

Table of all encounters. Note that the group sizes are estimated by visual observation on site, whereas the number of photo ID’s refer to animals identified aposteriori from pictures taken.
and end of an encounter of whales were recorded using a Raymarine E80 chart plotter mounted on the boat. The course of the day, recording track numbers and data on the whales’ behaviour were written down in a notebook. Behavioral categories, such as traveling, resting, socializing, and feeding dives were collected using continuous or ad libitum sampling, and short term behavior such as jumps, spy hops, mother and offspring meeting were sampled as events.

3.3 Photo-ID

Figure 2: Examples for Photo-ID-pictures Shown are the left side and the right side of individual 10 from group D. The photos were taken in 2009.

Photo identification of individual whales has been used for over three decades and is a non-invasive and inexpensive method to identify individual whales and monitor them over several years. In our study we tried to take as many pictures (see e.g. Fig. 2) of individuals in a group as possible using different equipment. In 2006-2009 a Canon EOS-D30 and in 2010 a Canon EOS-D1 MarkIV camera was used, with either a Canon EF 70-200 mm or a Canon EF 100-400 mm lens, depending on the light conditions. Whales were photographed from both sides of the dorsal fin, as well as of the whole body to search for identity scars, pigmentation and nicks that distinguish individual pilot whales. However, pilot whales tend to occur in very large groups and often move fast, which makes it difficult to take pictures of all individuals in a large group (see Tab. 1).

3.4 Study Population

We studied seven different groups of long-finned pilot whales in the Vestfjord in northern Norway in the time period from 2006-2010. It appears that some animals and their natal pods return from year to year, and spend some time in the same locations inside the Vestfjord (e.g. group J in Tab. 1). This finding suggests that long-finned pilot may exhibit migration patterns and site fidelity to potential resource rich feeding grounds. Seven groups have been encountered in the Vestfjord from 2006 to 2010. Using naturally occurring distinguishing markings on individual pilot whales, we identified 262 whales through Photo-ID. Pilot whale group size varied from 7 to 60 animals, with one matriline typically consisting of 7-20 animals and several matrilines traveling together creating super pods, which contained up to 200 animals. Out of the seven groups, one group was re-sighted in the Vestfjord twice within an interval of one and two years (see Tab. 1). Data collection was not able to conduct continuously over the whole year due to weather conditions and resources and as a result several groups of pilot whales visiting the Vestfjord were missed. From opportunistic and scientific observations, we know that typically at least one pod of pilot whales
enters the Vestfjord every month. Peak occurrences (several pods and matrilines at the same time) are reported from April to September when food (squid but also fish, such as mackerel) availability is highest.

3.5 Sound Recording

We used one or two Reson TC4032 hydrophones (frequency response 5 Hz - 120 kHz, omnidirectional), which were lowered directly ca. 18 m into the water from a 7 m Zodiac boat, when in close proximity (less than 50 m) to the whales. Sound was amplified with a custom built Etec amplifier (DK) and recorded with different mobile recording devices; in 2006-2008 we used an Edirol-R09 (Roland) with a sampling frequency of 48 kHz, and in 2009-2010 we used a Korg MR-1000 with a sampling frequency of 192 kHz. GPS coordinates were taken of the beginning and end of an encounter, and notes of the whales’ behavior were continuously taken during recordings. Recordings lasted as long as the whales were within a 500 m range of the boat, as soon as they moved out of range and the signals became weak, we stopped the recordings and moved closer to the whales. At first sign of disturbance of the whales, we ceased the studies and waited 30 min before resuming our studies. If the whales were repeatedly disturbed we terminated the field encounter. In most cases, however the whales became quickly habituated to the presence of our boat and data collection was possible for longer periods.

3.6 Sound Analysis for Visual Categorization

The sound recordings (PCM-24 format) were analyzed using Avisoft-SASLab Pro 5.2 (R. Specht, Berlin, Germany). First a human observer examined all the recordings and identified different vocalizations based on audio-visual inspection of the sounds and FFT based spectrograms. The total vocal repertoire, including clicks, buzzes, tonal and noisy sounds, was described by analysing spectrograms from recordings looking at two frequency ranges: 0-24 kHz and 0-96 kHz (only for 2009-2010 recordings). We considered high frequency (24-96 kHz) clicks, buzzes and whistles, in addition to the lower frequency sounds in order to investigate a wider range of sounds used by pilot whales. To compute spectrograms we used a window length of 1024 time steps and a Hamming window with 87,5% overlap unless otherwise noted.

In general, whistles of dolphinids were described as narrow band tonal structured calls with or without harmonic bands, and could be variable or distinct in structure [41]. We used the term whistle only for call types that were tonal in structure but with a variable or aberrant contour or shape. Tonal sounds that had a stereo-typed contour were considered a call type. Whistles were further sorted in audible (0-20 kHz) and ultrasonic (20-90 kHz) frequency categories.

To distinguish and describe different call types, calls were analyzed and categorized using their spectral features. Distinctive features within a call are UFCs, LFCs, segments, and elements (see Fig. 4). Segments are separated by a silent part, whereas elements are parts of a call that are separated by abrupt frequency shifts (see Fig. 4 (d) and (e)). We further described elements in their frequency contour over time, e.g. up-sweep, down-sweep, parallel sidebands, noisy parts, u-shapes, and A-shapes (see Fig. 4(e)). The calls where then classified into different call types based on their similar acoustic features, such as fundamental and main frequency, bi-phononal components, segments and elements within a call type, and duration. We categorized sub-call types within the same call type, if the call type either varied in duration or had appendices, either in the beginning or at the end of a call. Call types with the same core element but additional elements have been categorised as sub-call types in other studies (e.g. [9, 35, 42]). To give a more objective description of the vocal repertoire, we consider these combinations of elements as a new call type. In addition to call types, repetitive call type combinations and repetitions of the same call types were described.

The quality of the recordings were very different due to background noise and distance of the animals to our hydrophones. Therefore we sorted all calls and whistles into 4 different categories depending on the signal to noise ratio. Calls in category A are all all clear, contain no background noise or overlap; category B calls have some background noise, with at least one of the harmonic bands entirely visible on
Figure 3: **Spectrograms of examples of typical long-finned pilot whale sounds recorded in northern Norway**: Examples of different clicks, buzzes, and variable or non-stereotyped calls. (a) Low frequency clicks, highest power below 2 kHz. (b) High frequency clicks and buzzes, highest power above 20 kHz. (c) High frequency buzzes with frequencies 20-60 kHz. (d) Other calls that appeared infrequently, such as whining sounds, are aberrant non-stereotyped structured which are variable in frequency and duration. (e) Noisy calls low frequency sounds with no distinct frequency band often produced in sequences (rasps or pig like sounds).

The spectrogram; category C calls had high background noise and calls were not entirely visible on the spectrogram; category D calls had a weak signal and high background noise and calls could barely be seen on the spectrogram, but could still be heard by the examiner. Calls from all four categories could be used for call type categorisation; calls that could not be identified were excluded from the analysis. To test whether vocalizations are group specific we only used call types with the quality category A and B without overlap of other calls.
Figure 4: Examples of different pulsed calls, including main types of whistles (calls with one or few frequency bands, stereotyped or aberrant structure, variable in frequency and duration) and stereotyped calls. (a) Lower frequency (LF) whistles below 20 kHz: all nine groups produced LF whistles (N=623). (b) Medium high frequency (MHF) whistles 20-30 kHz (from 4 different groups, B, D, H, J; N=77). (c) High frequency (HF) whistles above 60 kHz (from one group H; N=6). Stereotyped calls: (d) with simple structure (one segment, one element) (e) more complex, with one segment, several elements (f) one segment, 3 elements and multiple frequency components (LFC + UFC) (g) one segments, 6 elements and multiple frequency components (LFC+UFC).
Figure 5: (a) Spectrogram of combinations of different call types and (b) repetition of a call type. The labeling in (a) refers to the respective call type numbers.
3.7 FFT based Spectral Analysis

Differences in recording distances and background noise made it necessary to select recorded calls regarding their sufficient quality for spectral analysis. In a second step we sorted the calls dependent on the possibility to estimate the fundamental frequency $f_0$. We established four categories: Call category 1, tonal calls: $f_0$ can be calculated over whole call; category 2, mixed tonal calls: $f_0$ can be calculated but calls have segments with different structures; category 3, tonal calls no estimates: Calls with tonal structure but $f_0$ cannot be estimated; category 4, noisy calls: No tonal parts could be found.

| Acoustic parameters | Description                                      |
|---------------------|--------------------------------------------------|
| Duration [ms]‡      | Time between onset and offset of call            |
| $f_0$ start [Hz] *  | $f_0$ at the beginning of a call                |
| $f_0$ end [Hz] *    | $f_0$ at the end of a call                      |
| $f_0$ mean [Hz] *   | Mean $f_0$                                       |
| $f_0$ max [Hz] *    | Maximum $f_0$                                    |
| $f_0$ max-loc [(1/duration)* loc]* | Location of $f_0$ max in relation to total call duration |
| $f_0$ slope *       | Factor of linear trend of the course of $f_0$   |
| PF start [Hz]‡      | PF at the beginning of a call                   |
| PF end [Hz]‡        | PF at the end of a call                         |
| PF max [Hz]‡        | Maximum PF                                       |
| PF max-loc [(1/duration)* loc] † | Location of PF max in relation to total call duration |
| PF maxdiff [Hz] †   | Maximum difference in PF between successive bins|

‡ = used for global cluster structure
* = used for tonal cluster structure

We used Avisoft-SAS Lab Pro 5.2 (R. Specht, Berlin, Germany) to visually assess the quality of calls and to adjust the sampling frequencies to 24 kHz to get an appropriate frequency resolution for further estimations. We saved the binary spectrogram of the calls (1024 pts FFT) and exported them into the acoustic analysis software LMA 2013. We used a LMA procedure which allowed us to estimate the tonality of a time segment based on the outcome of an autocorrelation, and supported the estimation of $f_0$ by visual cues. The user adjusts the possible $f_0$ range with a harmonic cursor. Harmonic cursor consists of indicator lines spaced as multiple integer of the first (bottom) line. This makes it possible to get $f_0$ estimates also for weak or few harmonics \[43\]. Beside different $f_0$ estimates the program calculates the peak frequency (PF), the frequency with the highest amplitude in a given time segment. Details of all acoustic parameters are given in Tab. 2.

We used a two-step cluster analysis on the selected acoustic variables (Tab. 2), which has been proven useful to evaluate the acoustic structure in other studies \[36, 44\]. We used the log-likelihood distance measure and the Schwarz criterion/ Bayes information criterion (BIC) to calculate and compare differently clustered solutions. In addition, we used silhouette values \[45\] to assess the quality of cluster solutions. A silhouette value represents the summarized distance of all cases, calculating the similarity to all objects in its own cluster, in relation to all objects of the closest cluster not containing the object. The result is a coefficient varying between $-1.0$ and $1.0$; values above 0.5 are considered to be solid solutions \[45\]. To test the assignment quality of the found cluster solutions we ran a discriminant function analysis (DFA) using the same acoustic parameters we used to calculate clusters solutions. The analysis was performed using SPSS 20 \[46\].
3.8 Preparing Ensembles of Recordings for intra- and inter-Group Comparisons

For the following analysis we considered 1056 short cut recordings of whale calls having quality A or B according to their signal to noise ratio (see above). These short recordings have been cut from continuous data, such that each of them contains one call of a pilot whale. The lengths of the cut recordings varied between 0.14 s and 6.27 s. The total length of all recordings used for this intra- and inter-group comparison was 31 min. and 23 s. All recordings used in this part of the study have a sampling interval $\Delta t = 1/48000$ s.

| group | B  | D  | F  | G  | H  | J  |
|-------|----|----|----|----|----|----|
| B     | 27, 45, 79, 84, 110 | 79 | 27 | 45 | 84 | 110 |
| D     | 79 | 27, 45, 79 | 27 | 45 | 79 | 79 |
| F     | 27 | 27, 45, 79 | 27 | 45 | 27 | 27 |
| G     | 45 | 45 | 27 | 27, 45 | 45 | 45 |
| H     | 84 | 79 | 27 | 45 | 27, 45, 79, 84 | 84 |
| J     | 110 | 79 | 27 | 45 | 27, 45, 79, 84 | 27, 45, 79, 84, 110 |
| available recordings $N$ | 221 | 159 | 54 | 90 | 168 | 337 |

In order to compare group specific differences in vocalizations, we constructed several ensembles of calls, each representing a sample of recordings made for one group of whales. The number of calls within each ensemble is adjusted according to the later usage of that ensemble. In other words, for each pairwise comparison of groups four ensembles of equal size were constructed. The choice of the calls featured in each ensemble is made by a random number generator.

The detailed procedure of constructing ensembles is described as follows: Suppose we have $N_i$ recordings of calls of whale group $i$ and $N_j$ recordings of group $j$. We then drew an ensemble $E_i(n) = \{C_1, C_2, \ldots, C_n\}$ of $n$ calls $C_i$, by randomly choosing $n$ out of $N_i$ recordings for group $i$. Analogously we drew a second ensemble $E_j(n)$ consisting of $n$ out of $N_j$ recordings of group $j$. For each pairwise comparison of groups, the size of the ensembles $n$ was adjusted according to the smaller number of available recordings, i.e., to the largest integer smaller than half of the smaller number of available recordings, $n = \lfloor \frac{1}{2} \min(N_i, N_j) \rfloor$. Considering e.g., group $J$ and $B$, there were 337 recordings of group $J$ and 221 recordings of group $B$ available. Consequently the size of the ensembles generated for comparing groups $J$ and $B$ should e.g., be $n = 110$. We then compared group $i$ and $j$ by comparing properties of the ensembles $E_i(n)$ and $E_j(n)$. In order to check whether the resulting differences can be attributed to the difference in group, we also compared pairs of two random ensembles drawn from the same group, using the $N_i - n$ or $N_j - n$ remaining recordings (i.e., recordings not used for the previous comparison of two different groups). In other words, we generated additional ensembles $\tilde{E}_i(n)$ of size $n$ using now only the recordings that are not part of ensemble $E_i(n)$. The differences in distribution within group $i$ were then estimated by comparing properties of $E_i(n)$ and $\tilde{E}_i(n)$.

3.9 Computing Cepstral Coefficients

Several features have been proposed and studied in order to characterize bioacoustic signals. Bias can be introduced by selectively choosing features that the observer considers to be relevant. We tried to reduce this bias by completing the previous findings with a study based on (relatively) unselected features. Therefore we considered cepstral coefficients [32] as relevant sound features. Cepstral coefficients were in a similar form often used in speech processing as suitable generic features. Unlike so called hand crafted
Figure 6: Spectrograms (left) and Cepstrosgrams (right). The colour coding of the cepstrosgrams refers to $\ln(c(q,t)/\max(c(q,t)))$ with $t = 0, ..., T$ and $T$ being the length of the call and $q = 1, ..., 128$ being the index of each cepstral coefficient. Spectrograms were computed with a window length of $w = 512$, allowing to estimate $\frac{w}{2}$ spectral coefficients and $\frac{w}{4} = 128$ cepstral coefficients for each time step.

features, they are computed for any arbitrary input signal, without requiring knowledge about the sounds under study. The only bias that is inherent to cepstral coefficients is the choice of the representation (FFT-based) and the choice of the window lengths. Mel Cepstral Coefficients \[47\], often used to describe human vocalizations, project cepstral coefficients onto the Mel scale \[48\] to emphasize the frequencies most relevant for human communication. We, however, did not project onto the Mel scale, since frequencies that are most relevant for humans might not be \textit{a priori} suitable for analyzing communication among pilot whales. In more detail, we used the coefficients $c(q,t)$ of the power cepstrum

$$c(q,t) = \left\| \mathcal{F} \left\{ \log \left( \frac{\|\mathcal{F}[x(t)]\|^2}{2\pi g_N} \right) \right\} \right\|^2$$

as features. Here, $\mathcal{F}$ denotes the Fourier transform and the normalization factor $g_N = \max(\mathcal{F}[x(t)])$ with $t = 0, ..., T$ is given by the maximum of the power spectral density of each cut recording of length $T$. For a discrete time signal $x(t_n)$ with $t_n = t_0 + n\Delta t$, the discrete fourier transforms were realized using a Hanning window of $w = 512$ time steps and an overlap of 511 time steps. The audio files used for
this study have a sampling rate of $\Delta t = 1/48000$ s of. The resulting $w/4$ cepstral coefficients $c_{q,t}$, with $q = 1, 2, ..., w/4$ characterize prominent frequencies in the signal at a given time instance $t$. Adapting the suitable window lengths for computing spectrograms, we obtained a high resolution in quefrency space, i.e., we worked with $w/4 = 128$ cepstral coefficients. This resolution is relatively large compare to human speech processing, using 13 cepstral coefficients and their temporal derivatives. Fig. 6 shows a visualization of the coefficients $c_{q,t}$, in form of a ceprogram in comparison to the typical spectrograms. Due to the second Fourier transformation, peaks in the spectrum indicate the (reciprocal) difference between peaks in the spectrum. Loosely speaking, a line in the ceprogram (representing large values of $c_{q,t}$) is shifted upwards (towards larger $q$), whenever two lines in the spectrogram (representing high values of the power spectral density) approach each other. The fundamental frequency can be determined from the first (non-trivial) line in the ceprogram.

3.10 Comparing Distributions of Features

As described in the previous section, each cut recording contains one call and is characterized by the ceprogram $c_{q,t}$, with $t = 0, ..., T$ and $T$ being the length of the recording. To study differences in vocalization between and within groups, we did not compare features between individual calls as this would require a large number of recordings of each call type to ensure statistical significance. Instead, we compared features of ensembles of calls of one vs. another group, disregarding from which individual call a given feature originates. In addition, we neglected the time dependencies within each call and only considered the collection of all features within a given ensemble. We thus proposed that properties of the ensemble $E_i(n)$ are represented by the distribution $p_{q,i}$ of the values of each coefficient $c_{q,t}$ of group $i$. We then asked in how far the 128 distributions (one for each cepstral coefficient $c_{q,t}$, $q = 1, 2, ..., w/4$) for ensemble $E_i(n)$ were different from the distributions of another ensemble $E_j(n)$. Fig. 7 showed four examples for distributions of cepstral coefficients estimated for ensembles of calls recorded from different groups of whales. For some coefficients, in particular for coefficients with smaller $q$, [e.g., Fig. 7 (a)] the differences between distributions were even noticeable by visual inspection, whereas, many higher order coefficients, representing small scale fluctuations in the spectrum have more similar distributions.

To quantify this observation, we used common measures for the difference in distribution, such as the (symmetrized) Kullback Leibler divergence [49] or the Hellinger distance [50]. The (discrete) Kullback Leibler divergence

$$D(p_{q,i}||p_{q,j}) = \sum_k \ln \left( \frac{p_{q,i,k}}{p_{q,j,k}} \right) p_{q,i,k} ,$$

with $k$ referring to the $k$-th bin of the distribution $p_{q,i}$ and the values $p_{q,i,k}$ are normalized s. t. $\sum_k p_{q,i,k} = 1$, is a non-symmetric measure for the difference of two distributions. Note, that $D(p_{q,i}||p_{q,j})$ is only defined if both distributions are normalized and if $p_{q,i,k} = 0$ implies $p_{q,j,k} = 0$ for all $k$. Here, we used a symmetrized version of the Kullback Leibler divergence

$$S(p_{q,i}||p_{q,j}) = D(p_{q,i}||p_{q,j}) + D(p_{q,j}||p_{q,i}) ,$$

to quantify the difference between distributions $p_{q,i}$ and $p_{q,j}$, representing group $i$ and group $j$. Similarly one can compute $S(p_{q,i}||\tilde{p}_{q,i})$ to measure intra- group differences by comparing the distributions $p_{q,i}$ and $\tilde{p}_{q,i}$ referring to ensembles of equal size drawn from recordings of the same group $i$, as explained above.

To summarize and quantify the difference between inter- and intra- group comparisons we introduced coefficients

$$v_{ij} = \sum_q \left[ S(p_{q,i}||p_{q,j}) - S(p_{q,i}||\tilde{p}_{q,i}) \right] ,$$

with $i, j$ referring to the compared groups. Inter- group differences are larger than intra- group differences is $v_{ij}$ is positive and vice versa if $v_{ij}$ is negative. Since smaller coefficients reflect large scale structures
in spectra, differences in distributions of small coefficients can be considered to be more relevant than differences in higher order coefficients that can be due to small scale fluctuations and noise. Therefore, we additionally introduced linearly weighted coefficients

$$ w_{ij} = \sum_q \frac{1}{q} [S(p_{q,i}||p_{q,j}) - S(p_{q,i}||\tilde{p}_{q,i})] , $$

as a second measure for comparing inter- and intra-group differences. The relevance of the coefficients with smaller index $q$ is emphasized through larger weights $1/q$. 

Figure 7: Four examples for distributions of cepstral coefficients $c_{n,t}$: (a), $p_{2,i}$, (b), $p_{6,i}$, (c) $p_{57,i}$ and (d) $p_{88,i}$ estimated for groups $i = \{B, D, F, G, H, I\}$. The number of calls used to estimate these distributions were chosen to be the largest number used for ensemble comparisons, as specified in Tab. 5.
To test whether the calculated values of $v_{ij}$ and $w_{ij}$ are statistically significant we estimated confidence intervals for both coefficients by comparing random ensembles $E_r(n)$. In more detail, we constructed $m$ random ensembles by randomly drawing $n$ recordings out of all available recordings (not sorted by group) without repetition. Note that these mixed random ensembles used to estimate confidence intervals contained recordings from different groups. Any 3-tuple of random ensembles, $E_r$, $E_r'$ and $E_r''$, could serve to simulate a comparison of inter- and intra-group differences. Consequently, two random ensembles, e.g. $E_r$ and $E_r''$, were interpreted as representing the same group, whereas the third one ($E_r'$) was assumed to represent a different group. For each 3-tuple of random ensembles, we computed the coefficients $v_{rr'}$, $v_{rr''}$ and $w_{rr'}$, $w_{rr''}$. We then used the distributions of $g(m) = \sum_{k=0}^{m-1} a(k)$ values for each coefficient (with $a(k)$ referring to triangular numbers) to estimate confidence intervals according to Student’s distribution. Additionally, we introduced the inverse of the weighted coefficient, $s_{ij} = 1/w_{ij}$ as a measure for the similarity in vocalization.

4 Results

4.1 Vocal Repertoire

We found that the vocal repertoire of long-finned pilot whales in northern Norway includes a variety of clicks and buzzes (Fig. 3(a)-(c)), low frequency calls that are noisy and irregular (Fig. 3(d)-(e)), three types of whistles, which are below and above 20 kHz, (Fig. 3(a)-(c)), as well as different types of pulsed calls that range from simple and short to highly complex structures (Fig. 4 (a)-(c)). Through the observer based analysis we categorized 154 different call types including 16 sub-call types. In total we classified 4624 stereo-typed calls (Category A-D) into 154 different call types. Most call types (122 call types, $N = 3227$) only consist of LFCs, whereas 32 call types ($N = 1397$) contained both LFC and UFC. Further, most calls ($N = 4040$) consist of only one segment: 68% of only LFC calls ($N = 2759$) and 32% of LFC+UFC calls ($N = 1281$). However 14% ($N = 584$) of the calls had more than one segment (between two and eight segments) and more than one element (between two and eight elements) and some calls were very complex in structure ($N = 54$). We found 301 elements in the 154 call types and most of them were up-sweep ($N = 95$), less were down-sweep ($N = 63$) or parallel ($N = 48$) in structure, 33 elements were U-shaped, 19 elements were Λ-shaped, and 43 elements were noisy parts.

In addition, we found stereotyped call type combinations of certain call types with different variations (Fig. 5(a)). Some call types (such as NPW-56i) were repeated more often than others. The durations of call repetitions ranged from several milliseconds to over 2 minutes (Fig. 5(b)). Out of the total of 16:32 hours of recordings, 4624 calls could be categorized. However only 1037 categorized A-B calls (from 126 call types) without overlap with other calls could be used for further analysis.

4.2 FFT derived Call Repertoire

Additionally to the categorization and classification done manually, we clustered the calls based on selected features. In a general description using acoustic parameters which can be calculated for all calls (Tab. 2) we found a two- and three-cluster solution, using five peak frequency parameters and duration, as the best solutions. In both cases we achieved a silhouette value of 0.5. Different numbers or combinations of parameters could not improve the result. In both cluster solutions PFmax was the most important acoustic parameter dividing high pitched and low pitched calls into two distinctive clusters [high pitched calls: $(9452 \pm 67.3)$ Hz (mean ± SEM), low pitched calls: $(4899 \pm 75.8)$ Hz; $N = 525$]. The three-cluster solution established a third cluster mainly on the difference in PFend frequency [high pitched, high end calls: $(7726 \pm 197.5)$ Hz; low end calls: $(2434 \pm 93.5)$ Hz].

In a second step we took a more subtle view of the repertoire structure. Therefore, we excluded the noisy calls and the tonal calls for which we had no $f_0$ estimates. The cluster analysis focused on $f_0$
parameters found as a best solution a four-cluster solution with a silhouette value of 0.6. A subsequent DFA analysis showed that single calls can be well assigned to the correct cluster (correct assignment = 98%, cross-validated = 97.1%; Fig. 9). Similar to the results of the general cluster solution we found two high pitched clusters which differ in location of the $f_{0,\text{max}}$ CL1 (high $f_0$ at start): $f_{0,\text{loc}} = 0.17 \pm 0.02$, $f_{0,\text{max}} = 4484 \pm 70$ Hz; CL3 (high $f_0$ at end): $f_{0,\text{loc}} = 0.94 \pm 0.01$, $f_{0,\text{max}} = 5389 \pm 103.9$ Hz) and two low pitched clusters (CL2 (low $f_0$ at end): $f_{0,\text{loc}} = 0.82 \pm 0.02$, $f_{0,\text{max}} = 2921 \pm 94$ Hz; CL4 (low $f_0$ at start): $f_{0,\text{loc}} = 0.12 \pm 0.01$, $f_{0,\text{max}} 2590 \pm 29$ Hz). Based on this result it is possible to build up five categories, four tonal and one noisy call type.

The usage of the four tonal vocal types, noisy calls and the rest group of presumably tonal calls is given in Tab. 4. The six vocal categories or vocal types are not randomly distributed over the six groups of pilot whales. However none of these categories were exclusively used by one or two groups indicating the global character of the categories found by the analysis.
Figure 9: Clustering of pilot whale vocalizations results in four different tonal categories: Shown is a projection onto the plane spanned by the first and second discriminating functions (DF1, DF2). Colour coding refers to the respective cluster: blue symbols represent cluster 1, green symbols are elements of cluster 2, gold symbols represent cluster 3, and elements of cluster 4 are plotted as purple symbols.

4.3 Using Cepstral Distributions to test for Group Specific Differences in Distribution

To study group specificity we considered 6 of the 7 observed groups of pilot whales, namely group B, group D, group F, group G, group H and group J. Group C was omitted, since we have only few recordings of sufficient quality (quality category A and B) from this group. Fig. 8 illustrates the number of calls used for this study. As explained above, the number of calls used for each pairwise comparison depends
Table 4: Usage of the six vocal types within seven groups of pilot whales.

| group | Cluster | tonal 1 | tonal 2 | tonal 3 | tonal 4 | noisy | presumable tonal |
|-------|---------|---------|---------|---------|---------|-------|------------------|
|       |         | m       | %       | m       | %       | m     | %               | m     | %               |
| B     |         | 10      | 9.7%    | 0       | 0.0%    | 28     | 27.26%          | 1     | 1.0%            |
| D     |         | 15      | 19.5%   | 12      | 15.6%   | 0      | 0.0%            | 13    | 16.9%           |
| F     |         | 11      | 33.3%   | 9       | 27.3%   | 0      | 0.0%            | 4     | 12.1%           |
| G     |         | 1       | 2.3%    | 5       | 11.6%   | 0      | 0.0%            | 2     | 4.7%            |
| H     |         | 42      | 22.7%   | 23      | 12.4%   | 3      | 1.6%            | 98    | 53.0%           |
| J     |         | 8       | 9.9%    | 5       | 6.2%    | 11     | 13.6%           | 33    | 40.7%           |

Usage of the six vocal types, characterized by the number of observation \( m \) and the relative usage in percent.

Usage of the six vocal types, characterized by the number of observation \( m \) and the relative usage in percent.

on the number of calls available for the group with lesser recordings. Table 3 shows the number of calls used for intra- and inter-group comparisons.

We quantified the difference in vocalizations uttered by different groups of pilot whales by comparing their distributions of sound features (cepstral coefficients). As noted earlier, the distributions \( p_{q,i} \) and \( p_{q,j} \) were estimated using ensembles \( E_i(n) \) of \( n \) calls and differences in distributions are quantified using the Kullback-Leibler divergence. To compare the obtained similarity measures to a null model, we computed similarities for intra-group comparisons. Therefore, we constructed ensembles of calls of equal size \( E_i(n) \), \( E_j(n) \) for each pairwise intra-group comparison, and computed distributions of coefficients for these ensembles \( \tilde{p}_{q,i} \) and \( \tilde{p}_{q,j} \). To compare call features within groups, we computed the differences \( S(p_{q,i}, \tilde{p}_{q,i}) \), \( S(p_{q,j}, \tilde{p}_{q,j}) \) as defined in Eq. (2). We found that the differences in distributions for inter-group comparisons (blue solid lines) are larger than the ones estimated for intra-group comparisons (red dashed and orange dotted lines) for most coefficients (see Fig. 10). Note that the Kullback-Leibler divergence in Fig. 10 is visualized using logarithmic scales. Visual inspection of Fig. 10 yields that inter-group differences are clearly larger than intra-group differences for 10 out of 15 comparisons, i.e., when comparing groups B and D, groups B and D, groups B and G, groups B and H, groups D and F, groups D and G, groups D and H, groups F and G, groups F and H and groups F and J. More attention to details is needed to interpret the results of the comparison between groups B and J, groups D and J, groups G and H, groups G and J, and groups H and J. Comparing groups G and H (Fig. 10 (m)), we found large difference in distributions for the first coefficients than for higher order coefficients. The smaller coefficients (\( c_2, ..., c_70 \)) reflect large scale structures in the spectrum, whereas higher order coefficients capture fluctuations on a small scale, e. g. , noise. Thus, the results displayed in Fig. 10 (m) indicate that the inter-group difference of group G and H is larger than intra-group differences concerning the more relevant large scale structures in the spectrum. Comparing groups B and J, there are many coefficients (especially in the vicinity of \( c_{40} \) and \( c_{50} \)) for which we found inter-group differences to be larger than intra-group differences; similar for group H and J. In the comparison of groups D and J, the inter-group differences (blue line in Fig. 10 (i)) are about one order of magnitude larger than the intra group differences of group D (red line). However, they are in the same order of magnitude as the intra-group differences of group J (orange line) for small \( q \), whereas the difference was again larger for higher order coefficients. More precisely, there are 12 out of 128 coefficients for which the intra-group difference of group J exceed the inter-group difference, whereas 116 out of 128 coefficients indicate that inter-group difference is larger. Summarizing one can therefore conclude that the overall inter-group difference between group J and D is larger than group J’s intra-group difference.

The example of the comparison of group J and group D indicates that the interpretation of Fig. 10...
has to be done with care. Therefore, we additionally quantified inter- and intra-group differences by computing the coefficients $v_{ij}$ and $w_{ij}$, introduced in Eqs. (3) and (4). When comparing two groups, each coefficient $v_{ij}$ and $w_{ij}$ can be evaluated in two different ways: with respect to the intra-group difference of the group with a higher number of totally available recordings and with respect to the intra-group difference of the group with a smaller number. Note that the number of calls in the respective ensembles $n = \lfloor \frac{1}{2} \min(N_i, N_j) \rfloor$ is still the same for inter- and intra-group comparison, although the number of calls available for creating the ensembles $(N_i, N_j)$ can differ. As shown in Fig. (11), $v_{ij}$ is larger than zero for all comparisons made in this study. Although $w_{ij}$ emphasizes the influence of smaller coefficients, all values of $w_{ij}$ computed in this contribution are also positive. For all but one out of 15 group comparison (group B and J), the values of $v_{ij}$ and $w_{ij}$ are also clearly larger than the confidence bounds estimated using random ensembles of similar sizes $n$. Since group B has been only observed while traveling and milling with group J, we tested whether the measured similarity in vocalization could be influenced by the fact that the recordings were made at the same location. Therefore we repeated the comparison of group B and group J but excluded all recordings of group J that were made during the common encounter of group B and J (03/07/2010). These additional results are shown as two single points (green triangles) in Fig. (11) and they are in the same order of magnitude as the previous comparison of group J and B, using also calls of group J that were made during the common encounter. Consequently we conclude that features of the vocalizations of group B and J are very similar, as far as we can estimate on the bases of cepstral distributions. Using the inverse of the weighted coefficients $s_{ij} = 1/w_{ij}$ as a measure for the similarity in vocalization, we visualized the results of all comparisons in terms of a network. In more detail, the different values of $s_{ij}$ were arranged to form an adjacency matrix of a network as it is shown in Fig. (12) The distance between edges in this network corresponds to the values of $s_{ij}$, e.g., a high similarity in vocalizations of group B and J is represented by a small distances between edge B and J.

Additionally to the comparison of distributions through the KLD we also compared all distributions using the Hellinger distance. The results obtained using the Hellinger distance (not shown) are qualitatively very similar to results for the KLD. In conclusion, comparing different ensembles is robust with respect to the measure for similarity in distribution.

In summary, it is thus possible to distinguish ensembles of calls representing different groups of pilot whales by simply comparing the statistics of their cepstral coefficients without referring to individual properties of single calls or comparing single call occurrences.
Symmetrized Kullback-Leibler indicate differences in distribution of cepstral coefficients. The blue solid lines represent intra-group comparisons, whereas the red dotted and orange dashed lines represent inter-group comparisons. Each panel shows the result for the pairwise comparison of two groups as indicated in each panel's legend. The number of calls in ensembles created for pairwise group comparisons, was chosen to be the same for inter- and intra group comparisons (see Tab. 3 for details).
Figure 11: Quantifying inter- and intra-group differences. (a) the numbers of calls used to create Ensembles (b) the coefficients $w_{ij}$ as introduced in Eq. (4). (c) the coefficients $v_{ij}$ as introduced in Eq. (3). Inter group differences are larger than intra-group differences if the coefficients $v_{ij}$ and $w_{ij}$ are positive. Both coefficients were evaluated with respect to the intra-group differences of the group for which more recordings were available, and for the group for which less recordings were available. Confidence Intervals are estimated by comparing randomly generated, not group specific ensembles and assuming that the resulting values follow Student’s distribution. To test whether the similarity of group B and J is due to recordings made during the common encounter of group B and J, we repeated the analysis excluding all calls of group J that were recorded during the common encounter.
Figure 12: **Visualization of the similarity in vocalization.** Using the inverse of the weighted coefficients $s = 1/w$ as a measure for similarity in vocalizations, the results of all 15 comparisons can be visualized in form of a similarity network. The distance between edges in the network represents the value of $s$. i.e., the similarity in vocalization.
5 Discussion

Using different methods to analyze pilot whale calls, we found a complex vocal repertoire in the northern Norwegian population. The audio-visual analysis of spectrograms revealed up to 154 different call types for Norwegian long finned pilot whales, different whistles as well as call combinations and repetitions. Using spectral measurements we found that the different call types can belong to the same broad vocal categories. The observer based call categorization also revealed only a low overlap in the usage of the same call types between the six different pilot whale groups. We further quantified these results by an automated quantitative comparison (cepstral distributions) of group specific ensembles of calls. Based on cepstral distributions we found that it is possible to distinguish groups of pilot whales by difference in their vocalizations. More generally, our results suggest that usage of different methodological approaches may yield a more complete overview of vocal repertoire structures.

5.1 Cepstral Distributions as a Method to investigate Group specific Vocalizations

Many automated approaches to analyzing whale vocalizations focus on the automated categorization and classification of single sounds, such as types of calls and whistles [26-31]. Group specific usage of vocalizations is then discussed by comparing the repertoire (which sounds are used) and whether there are variations of sounds. In the first part of this contribution we followed this well established approach by conducting an observer based categorization and classification of all recorded sounds. Secondly, we complemented this method with spectral measurements and clustering in the second part. In the third part of this article we proposed and tested a new method of automated testing for group dependent difference in vocalizations. The main idea of the latter approach is that we omit separating and sorting vocalizations into call types, but compare ensembles of vocalizations produced by each group. This idea is conceptually similar to the bag-of-words-approach used in text analysis [33]. Additionally, we did not select specific (hand-crafted) features, but use all information contained in the cepstral coefficients [32,34] of sounds. Furthermore we realized that we can even neglect the temporal ordering of these features and each group is well represented by their statistical distributions estimated for each ensemble of sounds. We then quantified differences in vocalization among six groups of pilot whales by computing differences in distribution. To reason whether the calculated differences in distribution were relevant, we compared magnitudes of inter- and intra-group differences. In more detail, we introduced two types of coefficients that summarize the relation between inter- and intra-group differences. For all but one out of 15 inter-group comparisons we found that inter-group differences were significantly larger than intra-group differences. Interestingly, group B and J, the two groups with no significant difference in vocalizations, have also been observed traveling and milling together. One possible explanation for their similarity in vocalization is that they are related or that they are sub-groups of a bigger group (acoustic clan).

5.2 Vocal Repertoire

Similar to the description of the vocal repertoire of long-finned pilot whales in the northwest Atlantic by Nemiroff and Whitehead [21], we found that the repertoire of long-finned pilot whales in the northeast Atlantic comprise a variety of clicks and buzzes, low frequency calls that are noisy and irregular, different types of whistles, as well as different types of pulsed calls that range from simple, single element calls to calls of highly complex structures composed of up to eight elements. Most pulsed calls consisted of only one element (93% in Nemiroff & Whitehead versus 86% in our study). In addition to the higher number of pulsed calls with several elements, we also found more bi-phonial calls than in Nemiroff’s study. Nemiroff and colleagues did not describe discrete patterns in the structure of their pulsed calls, whereas we had no problems identifying discrete calls and categorizing them. It is questionable whether these very different findings can be explained by structural differences in the repertoire of northwest and northeast Atlantic
long-finned pilot whales. The smaller number of recordings (419 calls in the study of Nemiroff et al., 4627 calls in our study) is also not very likely to cause such different results. Another, more likely explanation for these different findings is the usage of the different methodological approaches to analyze and describe vocal repertoires. Consequently, these contrasting findings emphasize the importance of analyzing vocal repertoires with different methodological approaches.

Additionally we found ultrasonic whistles with frequencies above 20 kHz in the northern Norwegian long-finned pilot whale population, which were previously not described for this species. The usage of whistles seems to be highly context dependent [20]: simple structured whistles are produced more often during resting behavior such as milling, whereas more complicated structured whistles and pulsed calls occurred more frequently during active surface behavior (probably including feeding behavior). Vocal activity was highest during multi-pod meetings and when the whales were spread out over a large area. This supports the hypothesis that whistles act as contact vocalization as well as coordination of movements of the whole group [20]. Killer whales in Norway are known to produce whistles with ultrasonic frequencies (ranging up to 75 kHz) [51]. The whistles we found for the long-finned pilot whales were similar in frequency range but different in structure and length. It seems that ultrasonic whistles are more commonly used by different delphinids than earlier reported. 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 [51].

In summary the vocal repertoire of long-finned pilot whales in northern Norway seems to be one of the most complex found in the animal kingdom. Similarly complex vocal repertoires are known from killer whales, for which also discrete call types have been described, aberrant and low frequency calls, stereotyped and aberrant whistles, clicks and buzzes as well as bi-phonol calls with lower and upper frequency components [9][52]. Both killer whales and pilot whales are long lived marine mammals living in small matrifocal groups with bisexual natal group philopatry [17][53][55] and vocal complexity may reflect their similarity in social intra- and inter-group interactions [10][56]. However in contrast to killer whales, pilot whales produce a larger variety of whistles, which are more similar in structure to whistles of Bottlenose dolphins. It has been suggested by Taruski [19] and Caldwell [57], and more recently by Sayigh [58] that pilot whales may use stereo-typed individual whistles, similar to the Bottlenoses 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 are mostly traveling only with their natal pod and therefore individuals may be easily recognized. In contrast to this, we observed large groups of long finned pilot whales often containing 8-12 pods to meet during summer time in the Vestfjord (Table 1). During these meetings social contacts between groups and breeding behavior (mating, calving and nursing) were commonly observed. In such super pod meetings individual signaling could help to maintain close contact to members of the natal pod, to announce each individual and to recognise/find each other again after separation [58][59]. It could be that whistles are also important during encounters with other species. We have observed Atlantic white sided dolphins (Lagenorhynchus acutus) traveling and foraging together with long-finned pilot whales; during these encounters the whistle rates increased.

Temporal organization in call sequences, as we observed for pilot whales, has rarely been reported and up to this day seems a rather rare event outside our own species. Arnold and Zuberbhler published an example of call sequences in male putty-nosed monkeys (C. nictitans martini) [60][61]. Fitch and Hauser [62] tested cotton-top tamarins (Saguinus Oedipus) with different sound sequences. Their results showed that the monkeys are capable of discriminating context-free grammars from finite state grammars, but not the other way around. Many studies on marine mammals behavior have shown that they are highly cognitive [63], capable of vocal learning [64] and mimicry [65]. In particular, dolphins have evolved advanced communication and sound production flexibility, which ranges from signature whistles, group specific calls to different combination of calls [57][66][67]. Vocal exchange of matching call types has been demonstrated in whales and dolphins. Southern right whales (Eubalaena australis) exchange one
call during approach of each other and react to playback with calling and approaching [68]; bottlenose dolphins match whistles within 3 seconds in the wild, which seem a response to the initial caller [69]; and resident killer whales exchange stereotyped calls with call type matching [70]. Compound calls, which are call combinations were first described by Strager in 1995 [67] from Norwegian killer whales, in addition unpublished data from recordings of killer whales in Norway shows that combinations of certain call types build a large part of their vocal repertoire (Vester unpublished data). Call type matching has been described for short-finned pilot whales which comprised a large part of their vocal activity [58]. Killer and pilot whales live in stable matrilineal groups with social bonds lasting for an entire lifetime. To be successful in such highly complex societies it is probably necessary to have profound cognitive skills and an adequate communicative flexibility. In contrast to killer whales, pilot whales often meet in super pods, which is more similar to the fission-fusion societies of dolphins. This may explain the higher complexity in vocal repertoire in comparison to killer whales, and also the higher whistle content, which is typical for dolphin societies.

We found stereo-typed whistles in long-finned pilot whales, however due to the nature of our field studies we could not investigate whether these whistles were used as signature whistles. Our finding of call type repetitions and combinations of calls were previously not described in long-finned pilot whales but it seems to be a common feature in killer and pilot whales vocal communication. This, in addition to the probability of signature whistle production in long-finned pilot whales, calls for a closer investigation. In summary, long-finned pilot whales communicate with a high variety of vocal signals, social complexity is high, and their cognitive abilities range from vocal learning to mimicry and they show sound production flexibility.

5.3 Group specific vocalization

Both, observer based classification of calls and the analysis of cepstral coefficients showed clear differences in used call types between the 6 groups of pilot whales recorded in Norway. Although all groups shared some call types, other call types were exclusively used by only one group. This finding is supported by the results obtained through cepstral distributions. Comparing group specific ensembles of vocalizations, we clearly saw that inter-group differences were far larger than intra-group differences for all but one of the 15 group comparisons made in this study. Although the concordance between relatedness and vocal similarity cannot be finally answered without genetic studies, group specific vocalizations may be advantageous in several ways: In a multi-dimensional aquatic environment that favors matrilineal social organizations among mammals, it becomes important to recognize group members for offspring care, protection against predators and cooperative social and feeding behavior. For roving males in those societies, group specific vocal repertoires may help to distinguish between relatives and non-relatives to avoid inbreeding and to increase their fitness. In case of female choice, they will be able to distinguish between related and non-related mates by their vocal dialect.

The degree of shared vocalizations does reflect kinship in killer whale call types and sperm whale codas [10, 71]. The possibility to share more or less vocal types seems to be evolved via vocal learning, as social systems became more complex and the complexity of signals increased to recognize individuals, kin, or other social partners [72]. Killer whales in many places of the world have dialects; first discovered in Canada in a resident population where groups use seven to 17 distinct call types [9]. These repertoires remain stable over time, but subtle changes could occur in call type structure supporting the fact that killer whales have a high vocal flexibility [10, 9]. The question is whether the group specific differences of vocal types found in our pilot whale population is also the result of similar social organizations and vocal learning. In a recent study Alves and colleagues [73] found that long-finned pilot whales 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.

Group specific vocalizations are also known from other mammal societies, but the mechanism behind the specification seem to be different. Studies in nonhuman primates, gibbons and leaf monkeys, com-
Bining genetic and acoustic analysis of the same groups have shown a high concordance between genetic relatedness and acoustic similarity of their loud calls [74, 75]. But their loud calls are innate and no vocal learning is involved. In addition the degree of difference seems to be more influenced by sexual selection and not by social organization. This is also true for some subtle group differences found in vocal repertoires of other nonhuman primates, like macaques [76] or chimpanzees [37]. Again there is no evidence for a concordance between vocal repertoire complexity and complexity in social structure. Therefore, it seems that the prerequisite of response to more complex social requirements with a more complex vocal repertoire found in a high flexibility of vocal production in marine mammals. It would be interesting to investigate whether other mammal species with higher vocal flexibility than nonhuman primates, like bats [77] or elephants [78], have developed such concordance between social and vocal complexity.

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