

Vocal repertoire of long-finned pilot whales (*Globicephala melas*) in northern Norway

Heike Vester^{a),b)}

Cognitive Ethology Lab, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany

Sarah Hallerberg^{b)}

Faculty of Engineering and Computer Science, Hamburg University of Applied Sciences, Berliner Tor 21, 20099 Hamburg, Germany

Marc Timme

Network Dynamics, Max Planck Institute for Dynamics and Self-Organization (MPIDS), Am Fassberg, 37077 Göttingen, Germany

Kurt Hammerschmidt

Cognitive Ethology Lab, German Primate Center, Kellnerweg 4, 37077 Göttingen, Germany

(Received 7 December 2016; revised 22 April 2017; accepted 4 May 2017; published online 9 June 2017)

The knowledge of the vocal repertoire of pilot whales is very limited. In this paper, the vocal repertoire of long-finned pilot whales recorded during different encounters in the Vestfjord in northern Norway between November 2006 and August 2010 are described. Sounds were analysed using two different methods: (1) an observer-based audio-visual inspection of FFT-derived spectrograms, with which, besides a general variety of clicks, buzzes, nonharmonic sounds, and whistles, 129 different distinct call types and 25 subtypes were distinguished. These call types included pulsed calls and discrete structured whistles varying from simple to highly complex structures composed of several segments and elements. In addition, ultrasonic whistles previously not described for pilot whales were found. In addition to the diversity of single calls, call sequences consisting of repetitions and combinations of specific call types were recorded and (2) a parametric approach that permitted the confirmation of the high variability in pilot whale call structures was developed. It is concluded that the pilot whale vocal repertoire is among the most complex for the mammalian species and the high structural variability, along with call repetitions and combinations, require a closer investigation to judge their importance for vocal communication. © 2017 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>).

[<http://dx.doi.org/10.1121/1.4983685>]

[JFL]

Pages: 4289–4299

I. INTRODUCTION

Social toothed whales evolved to live in different social communities in which females often build the core element with strong and long lasting female bonds (Mann, 2000). In these matrilineal societies, group composition is stable over many years or generations and maternal care is often long, sometimes lasting a lifetime (Bigg *et al.*, 1990). According to the social complexity hypothesis of communication, the vocal repertoire of a species should become more diverse the more complex their social system (McComb and Semple, 2005; Freeberg *et al.*, 2012). Complex group-specific vocalizations are characteristic of matrilineal “social whales,” learned from members of the group and transmitted culturally (e.g., Deecke *et al.*, 2000; Yurk *et al.*, 2002; Rendell and Whitehead, 2003). In contrast, more solitary baleen whales use fewer vocalizations with some geographical differences,

such as blue whales (*Balaenoptera musculus*) (Berchok *et al.*, 2006) or fin whales (*Balaenoptera physalus*) (Edds, 1988). Of the matrilineal social odontocete species, the killer whale (*Orcinus orca*) is the most studied, regarding particularly their vocal behaviour. There are several populations of killer whales worldwide and it has been demonstrated that resident killer whales in the eastern North Pacific live in natal philopatric matrilineal societies, where offspring from both sexes stay a lifetime within their natal pod (Bigg *et al.*, 1990).

In another population of resident killer whales in British Columbia, group-specific dialects were first discovered in the early 1980s (Ford and Morton, 1991). 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, 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).

^{a)}Electronic mail: heike_vester@ocean-sounds.org

^{b)}Also at: Network Dynamics, Max Planck Institute for Dynamics and Self-Organization (MPIDS) 7, 37077 Göttingen, Germany.

In this study, we investigated the vocalizations of long-finned pilot whales (*Globicephala melas*) that migrated into the Vestfjord in Northern Norway. Long-finned pilot whales belong to the dolphin family and represent the second largest dolphin species after killer whales, with adult males reaching 6.5 m and females 5.5 m in length (Bloch and Lastein, 1993). They are widely distributed and live in circumpolar regions in both the northern and southern hemispheres and in the Mediterranean (Rice, 1998). Long-finned pilot whales mainly occur in waters deeper than 100 m, often at the edge of a geographical drop-off, and migrating between offshore and inshore waters, which correlates with the distribution of their main prey, cephalopods. In the North Atlantic they feed on squid species (*Gonatus* spp. and *Todarodes sagittatus*), but occasionally on fish as well (Desportes and Mouritsen, 1993).

The general social structure of long-finned pilot whales seems to be similar to that of resident killer whales of the eastern North Pacific (De Stephanis *et al.*, 2008). They form groups with core social units consisting of 11–14 animals, which represent a matriline of a mother and her direct offspring. These matrilineal units are often seen travelling together with other related matrilineal units in groups described as pods that commonly include up to 100 animals. Large temporary aggregations of several pods can exceed 150 animals, called super pods, with social interactions described as both casual acquaintances and constant companions for at least 5 years (Ottensmeyer and Whitehead, 2003; De Stephanis *et al.*, 2008).

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 in the northwest Atlantic (Ottensmeyer and Whitehead, 2003). Genetic investigations have shown that pilot whales that were killed in the Faroe hunts are all related and that males in the group do not father offspring (Amos *et al.*, 1993a). It was therefore postulated that long-finned pilot whales in the northeast Atlantic live in close matrilineal units but whether these matrilineal units 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. In our study we focused on long-finned pilot whales that migrated into the Vestfjord in northern Norway and spend several days or weeks there, for which migration behaviour and population size are unknown.

In general, long-finned pilot whales produce typical dolphin sounds, such as clicks, buzzes, and a variety of pulsed calls and whistles (Taruski, 1979; Weilgart and Whitehead, 1990; Nemiroff and Whitehead, 2009). Pulsed calls of the species are similar in structure to killer whale calls. They are complex with different structural components, such as elements and segments, calls can be two-voiced with a lower-frequency component (LFC) and a higher-frequency component (HFC) (Yurk, 2005; Nemiroff and Whitehead, 2009). However, in contrast to discrete killer whale call types, pilot whales seem

to use a more graded call repertoire (Nemiroff and Whitehead, 2009).

To shed more light on the structure of pilot whale vocal repertoires, here we focused on the vocal repertoire of the long-finned pilot whale population found in northern Norway. To describe the vocal repertoire of pilot whales we performed an observer-based audio-visual inspection of recorded sounds (Yurk *et al.*, 2002; Scheer, 2013). This method has proven to be reliable for classifying marine mammal sounds and is often used as a baseline for further automated classification analysis (Janik, 1999; Filatova *et al.*, 2012). In addition, we combined the observer-based classification with a fast-Fourier-transformation- (FFT-) based acoustic analysis, estimating different acoustic features such as fundamental frequency (F0) and peak frequency (PF). FFT-based analyses are widely used in acoustic studies of marine mammals as well as terrestrial mammals such as monkeys or apes (e.g., Crockford *et al.*, 2004; Maciej *et al.*, 2013).

Based on these two approaches, we aimed to describe the structural complexity of pilot whales' vocal repertoires. We expected to find a similarly complex vocal repertoire to that known for killer whales, with discrete call types.

II. MATERIALS AND METHODS

A. Ethics statements

All observations and recordings reported here were made in the Vestfjord, northern Norway. In general, no permission is required for non-invasive research on marine mammals along the Norwegian coast. To ensure our research was conducted according to Norwegian ethical guidelines, the Animal Test Committee (Forsøksdyrutvalget) of Norway was contacted, who confirmed our studies do not require any permission (approval paper ID 6516).

B. Study site and field data collection

All recordings and observations were made between November 2006 and August 2010 in the Vestfjord in northern Norway. The Vestfjord connects the mainland and the Lofoten islands archipelago, has many side fjords and is more than 140 km long. It reaches 300–600 m deep in the middle, with the deepest side fjord having a depth of almost 900 m. This represents a good foraging site for pilot whales, which are known to preferentially prey on squid such as *Gonatus* spp. and *Todarodes sagittatus* in the northeast Atlantic (Desportes and Mouritsen, 1993). Records were made in an area more than 150 km in range, mainly in waters deeper than 200 m and over a period of 2–6 weeks. Our 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 main land side of the Vestfjord (Fig. 1). Boat tracks and starting/ending waypoints of a whale encounter were recorded using a Raymarine E80 chart plotter mounted on the boat. During the course of the day, recording track numbers and data on the whales' behaviour were written down in a notebook. Behavioural categories of surface behaviour such as “traveling” when all animals moved in the same general direction, “resting” when

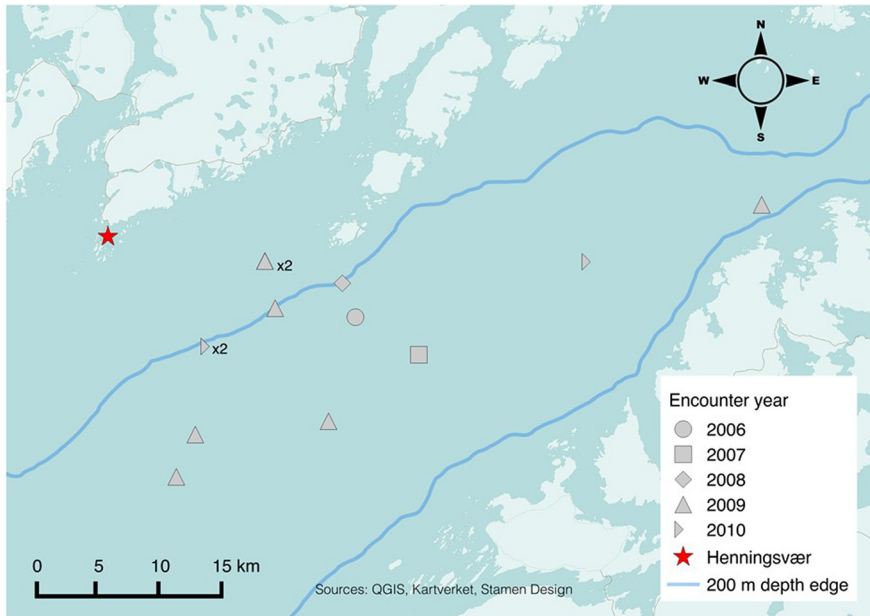


FIG. 1. (Color online) Map of encounters with long-finned pilot whale groups in the Vestfjord (Northern Norway) between 2007 and 2010. Symbols represent the positions of pilot whale recordings considered in the present study.

all animals were at the surface with little or no movements, this included “logging” when animals were laying at the surface with tails down, looking like logs, “milling” when all animals were remaining in the same area, moving slowly back and forth, and “socializing” when animals showed high surface activities with body contacts and increasing events. Long synchronised dives with a sudden increase in click production were considered “feeding dives,” for which sounds produced were recorded in continuous or *ad libitum* sampling (Altmann, 1974). In addition, short term behaviour were noted as events, for example: “jumps,” “spy hopping,” “body contacts,” “flipper touching,” “aerial vocalisations,” and “mother and offspring meeting” (Mann, 2000).

C. Photo-ID

Photo identification of individual whales has been used for over three decades to identify individual whales and monitor them over several years (Bigg, 1982). During single pilot whale encounters we took as many pictures (Fig. 2) of individuals as possible. In 2006–2009 we used a Canon EOS-D30 and in 2010 a Canon EOS-D1 Mark IV camera,

with either a Canon EF 70–200mm or a Canon EF 100–400mm lens, depending on the light conditions. We aimed to photograph both sides of the whales’ dorsal fin and, when possible, the whole body (during jumps) in order to search for identity scars, pigmentations and nicks that distinguish individual pilot whales (Auger-Menthe and Whitehead, 2007). However, pilot whales tend to occur in very large aggregations, often consisting of several matriline, and can move fast over a large area. Since the present animals were no exception, this prevented us from taking pictures of all individuals. Therefore, we focused on photographing whales within 150 m of the boat and those closely associated. When whales moved out of the 150 m radius, we approached them again until sufficient pictures were taken and repeated this procedure as long as possible.

D. Sound recording

We used one or two Reson TC4032 hydrophones (frequency range 5 Hz–120 kHz with a linear range from 10 Hz to 80 kHz, receiving sensitivity: ± 2.5 dB, -170 dB re $1 \text{ V}/\mu\text{Pa}$, omnidirectional ± 2 dB at 100 kHz), lowered at 18 m from a



FIG. 2. (Color online) Example of long-finned pilot whale Photo-ID-pictures. The figures show left and right sides of individual #10, group D. Photos were taken in 2009 during a pilot whale group encounter in the Vestfjord, Lofoten, Norway.

7 m Zodiac boat with engine turned off, when in close proximity (50–100 m) to the whales. Sound was amplified with a custom built Etec amplifier (DK) and recorded with 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. Recordings lasted as long as the whales were within 500 m of the boat and as soon as they moved out of range and the signals became weak, we stopped the recordings and moved closer to the whales. At the first sign of disturbance of the whales (e.g., leaving area at our approach, sudden change of swimming direction or behaviour), we ceased sampling and waited 30 min before resuming it. If whales repeatedly showed to be disturbed, we terminated the encounter.

E. Sound analysis for visual categorization

The sound recordings (PCM-24 format) were analysed using Avisoft-SASLab Pro 5.2 (R. Specht, Berlin, Germany). First, we examined the recordings and identified different vocalizations based on audio-visual inspection of the sounds and FFT-based spectrograms. Then we tested the inter-observer reliability of the classification by two trained reviewers. They independently rated the 4572 calls with only 7 misclassifications. The total vocal repertoire, including clicks, buzzes, tonal and pulsed sounds, was described by analysing spectrograms. Due to the differences in recording equipment and the lower frequency structure of pulsed calls, we used a sampling rate of 48 kHz, resulting in a 24 kHz frequency range. We also analysed the 2009–2010 recordings with a higher sampling rate (192 kHz) in order to look for vocalizations in the ultrasonic frequency domain (24 to 96 kHz). To compute spectrograms we used a sliding Hamming window with a length of 1024 time steps and 87.5% overlap unless otherwise noted (Avisoft, 2016).

In general, whistles were described as narrow band tonal structured calls with or without harmonic bands, and could be variable or distinct in structure (Thomsen *et al.*, 2001). We used the term “whistle” only for sounds that were tonal in structure but with a variable or aberrant contour and we sorted them in audible (0–20 kHz) and two ultrasonic (20–60 and above 60 kHz) frequency categories. Narrow band tonal sounds that had a distinct structure were considered another call type since many of the pulsed calls were tonal in structure or mixed with buzzes, pulsed/noisy elements, making a clear distinction between a whistle and pulsed call impossible.

Distinctive spectral features within a call are LFCs, HFCs, amount of segments, and structure and amount of elements (Fig. 3). Segments are units within a call type separated by a short silent gap, whereas elements are units within the segments separated by abrupt frequency shifts similar to the description of killer whale calls (Yurk, 2005). We described elements according to their main frequency structures and grouped them into eight different structures: an ascending frequency sideband, descending frequency sideband, U-shape, \cap -shape (inverted U), buzzes (clicks in rapid repetition), noise or broadband parts (no sideband structure visible), whistles (variable inflection points), and constant

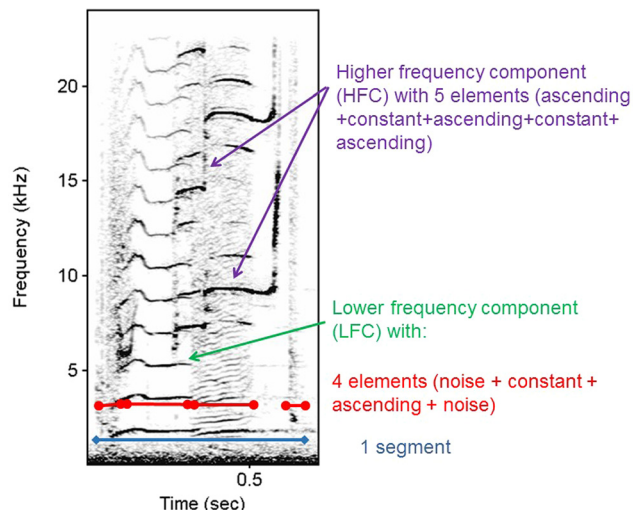


FIG. 3. (Color online) Spectrogram example of a long-finned pilot whale two-voiced call type with LFC and HFC, one segment and four elements.

frequency sidebands. The calls were then classified into different call types based on their similar acoustic features, such as fundamental and main frequency contours, two-voiced components, segments, and especially same elements within a call type, and duration. We categorized subtypes of the same call type, whether the call type varied in duration, had an HFC, or varied slightly in the amount of elements.

During call type scanning of our recordings we noticed several patterns in the alignments of calls. Certain call types seemed to be repeated more often than others and repeated over a long period of time. Yet other call types seemed to be combined in different variations, thus adding to the complexity of call type production in pilot whales. In this study we only describe an example of call type repetitions and combinations.

F. FFT-based spectral analysis

In a first step we selected 541 calls which had sufficient signal-to-noise ratio and did not overlap with other sounds or calls. As a second step we sorted the calls dependent on the possibility of estimating the fundamental frequency (F0). We established four call categories: Category 1, “tonal calls,” for which F0 could be calculated over whole call; category 2, “mixed tonal calls,” for which F0 could be calculated but calls have segments with different structures; category 3, “tonal calls no estimates,” for which calls presented tonal structure but F0 could not be estimated; category 4, “noisy calls,” for which no tonal parts can be found. A tonal call is a harmonic series which consist of the original waveform and higher harmonics. The frequencies of the harmonic waveforms are integer multiples of the frequency of the original waveform, called the fundamental frequency (F0).

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 estimates. We saved the binary spectrogram of the calls (1024 pts FFT) and exported them

into the acoustic analysis software LMA 2013. We used an 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 F0 by visual cues. LMA permits the user to adjust the possible F0 range with a harmonic cursor. The harmonic cursor consists of indicator lines spaced as multiple integers of the first (bottom) line. This also makes it possible to get F0 estimates for weak or few harmonics (Fischer *et al.*, 2013). Besides different F0 estimates, the program calculates peak frequency (PF), the frequency with the highest amplitude in a given time segment. Descriptions of the acoustic parameters considered here are given in Table I.

We used a two-step cluster analysis on the selected acoustic variables (Table I), which has proved useful in evaluating acoustic structure in other studies (Hammerschmidt *et al.*, 2012; Maciej *et al.*, 2013). We used the log-likelihood distance measure to calculate different cluster solutions and the Schwarz's Bayesian criterion (BIC) to estimate the best solution. In addition, we used silhouette values (Rousseeuw, 1987) to assess the quality of cluster solutions. A silhouette value represents the summarized distance of all cases, calculated from the similarity between all objects within a cluster, in relation to all objects of the closest cluster not containing the object. The result is a coefficient varying between -1 and 1 , with values above 0.5 being considered solid solutions (Rousseeuw, 1987). 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 cluster solutions. Analyses were performed using IBM SPSS STATISTICS 20 (SPSS, 2016).

III. RESULTS

During the observation period we had 13 pilot whale encounters, with a total observations time of 35:15 h and 16:47 h of suitable sound recordings. During this time we could identify 187 whales through photo-ID using distinguishing markings on individual pilot whales.

TABLE I. Description of call parameter used in the analysis.

Parameter	Description
Duration [ms] ^{a,b}	Time between onset and offset of call
F0start [Hz] ^b	F0 at the beginning of a call
F0end [Hz] ^b	F0 at the end of a call
F0mean [Hz] ^b	Mean F0
F0max [Hz] ^b	Maximum F0
F0maloc [(1/duration) ^b loc] ^b	Location of F0 max in relation to total call duration
F0slope ^b	Factor of linear trend of the course of F0
PFstart [Hz] ^a	PF at the beginning of a call
PFend [Hz] ^a	PF at the end of a call
PFmax [Hz] ^a	Maximum PF
PFmaloc [(1/duration) ^b loc] ^a	Location of PF max in relation to total call duration
PFmaxdiff [Hz] ^a	Maximum difference in PF between successive bins

^aUsed for global cluster structure.

^bUsed for tonal cluster structure.

A. Visual categorization

The following description of long-finned pilot whales' vocal repertoires is based on 1007 min of recording time and 4572 selected calls. We found a variety of clicks and buzzes in different frequency ranges [Figs. 4(a)–4(c)]. In addition, we found low-frequency pulsed calls which have a broadband nonharmonic frequency structure with varying distribution of

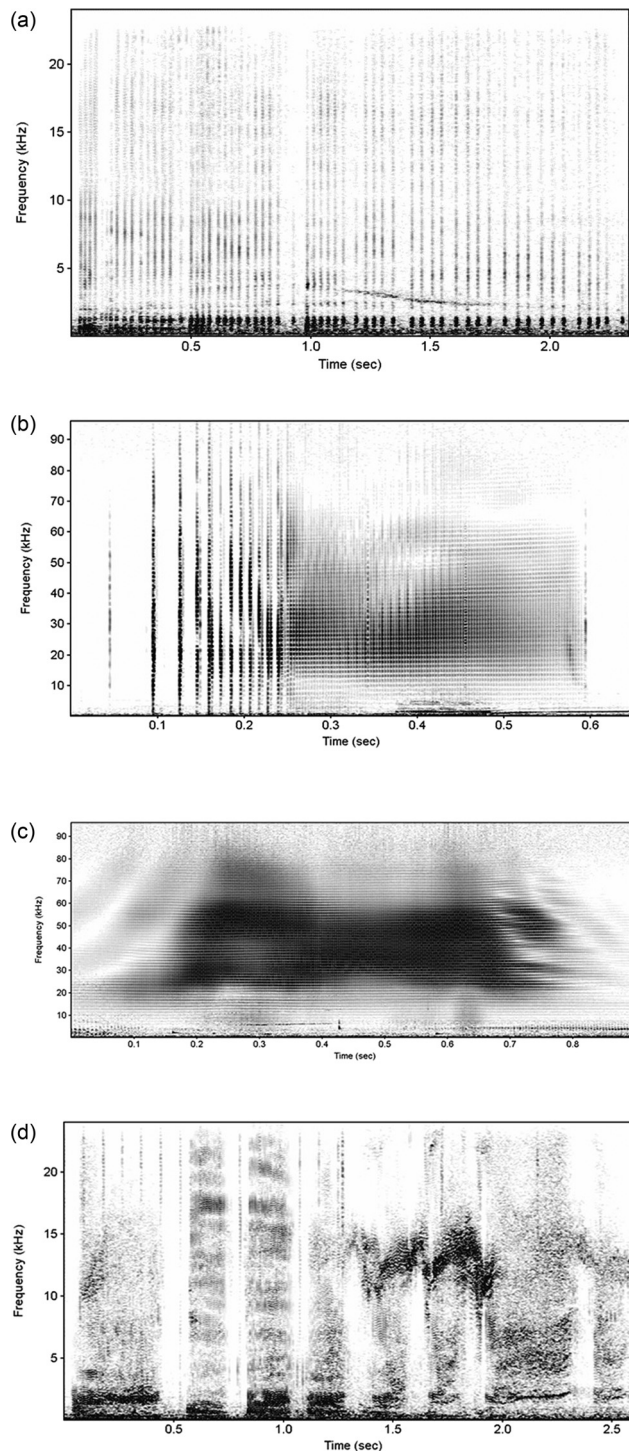


FIG. 4. Spectrogram examples of different long-finned pilot whale sounds: (a) Low-frequency clicks main energy below 2 kHz; (b) high-frequency clicks and buzzes main energy above 20 kHz; (c) high-frequency buzzes, main frequencies between 20–60 kHz; (d) low-frequency broadband calls with varying energy content are often produced in sequences (rasp-like sounds).

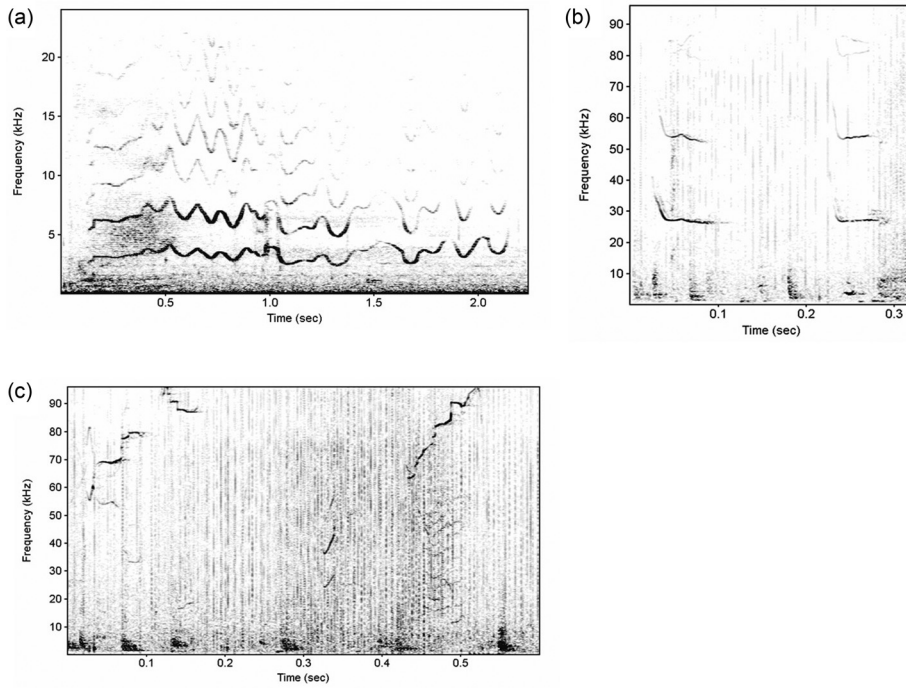


FIG. 5. Spectrogram examples of long-finned pilot whale whistles: (a) whistle with main energy below 20 kHz; (b) whistles in the lower ultrasonic range, main energy above 25 kHz; (c) two ultrasonic whistles above 60 kHz.

frequency amplitudes and were difficult to assign to distinct call types. These calls were often produced in sequences [Fig. 4(d)].

Norwegian pilot whales produce whistles in sonic [Fig. 5(a)] and ultrasonic frequency ranges [Figs. 5(b) and 5(c)]. We classified these whistles in three categories: whistles with main energy below 20 kHz [Fig. 5(a)]; whistles in the lower ultrasonic range 25–40 kHz [Fig. 5(b)]; and ultrasonic whistles above 60 kHz [Fig. 5(c)]. In total we recorded 794 low-frequency whistles (below 20 kHz), 65 whistles in the lower ultrasonic range (between 25 and 40 kHz), and two whistles in the higher ultrasonic range (above 60 kHz).

Pulsed-type calls contained extensive 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 [Figs. 6(a)–6(d)]. In an observer-based analysis we identified 4572 discrete pulsed calls during 111 recording sessions (total observation time 35:57 h, usable recording time 16:47 h). We classified these calls into 129 different

call types and 25 subtypes according to their similar vocal structure. Most call types (127 call types, $N = 3264$) only consist of LFCs, whereas 27 call types ($N = 1308$) contained both LFC and HFC. Further, most calls ($N = 3648$) consist of only one segment: 87% of only LFC calls ($N = 2832$) and 62% of LFC + HFC calls ($N = 816$), however, 13% ($N = 584$) of the calls have more than one (between two and six) segment [Figs. 6(a)–6(c)]. 33% of the LFC call types are simple in structure ($N = 1075$), containing just one element [Fig. 6(a)]; the other call types contained 2–8 elements [Figs. 6(b) and 6(c)]. Most of the LFC + HFC call types contain two elements (52%; $N = 675$), 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 ($N = 2$) [Fig. 6(d)]. A detailed breakdown of the calls is shown in the supplementary material.¹

Within the calls we described eight different element structures according to their contour as ascending, descending, U-shape, \cap -shape, noisy, buzz, warble, and constant sidebands. Within the 154 different call types we found over

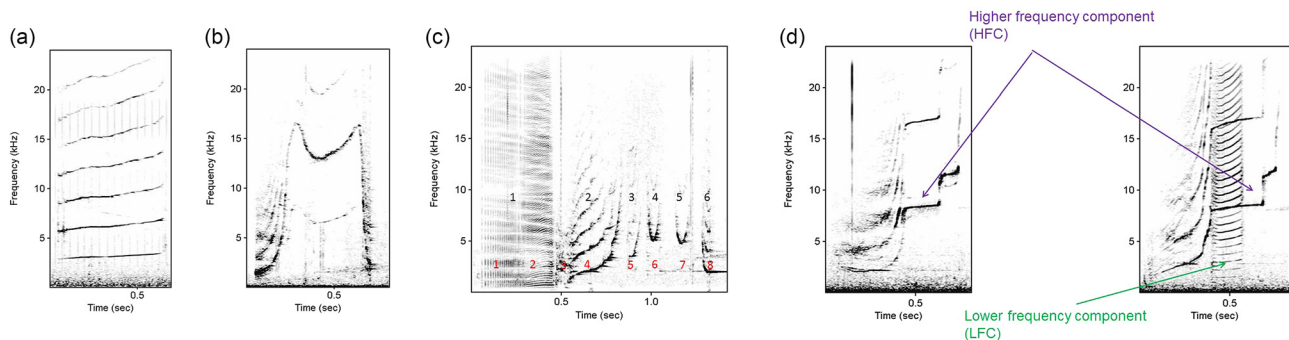


FIG. 6. (Color online) Spectrogram examples of long-finned pilot whale pulsed calls: (a) simple structure with one segment and one element; (b) complex structure with one segment and three elements; (c) more complex structure with six segments and eight elements; and (d) call type consisting of only a HFC and of two-voiced components (HFC+LFC).

444 elements. Most of the elements appear to be similar in structure; 36% of the elements consist of ascending sidebands ($N=156$), followed by a constant frequency band structure (20%, $N=87$), and 18% are descending elements ($N=81$), the remaining 26% are either U-shaped, \cap -shaped, noise, buzzes, or whistles (supplementary material).

As part of the vocal repertoire we recognised several combinations of calls and call types that were repeated more than once. Broadband nonharmonic calls that did not have a distinct structure were often repeated with variable time gaps giving them a rhythmical nature [Fig. 4(d)]. In addition to the broadband nonharmonic call sequences, we found call type combinations in which some call types were combined in different variations [Fig. 7(a)]. 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 [Fig. 7(b)].

B. Categorization based on acoustic features

Based on the estimates of FFT-based acoustic analysis we conducted two different cluster approaches to find out how many call categories could be established by an objective analytical method. When using acoustic parameters which could be calculated for all selected calls ($N=541$), we found a two- and three-cluster solution, using five peak frequency parameters and duration, as the best solutions. For both two-cluster and three-cluster solutions, we achieved a silhouette value, a measure describing the quality of the

respective cluster solution, of 0.5. Additional acoustic features 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: mean = 9452 Hz, SE = 67.3 Hz, $N=292$, low-pitched calls: mean = 4899 Hz, SE = 75.8 Hz; $N=249$). The three-cluster solution established a third cluster mainly on the difference in “PFend” (high-pitched, high-end calls: mean = 7726 Hz, SE = 197.5, low end calls: mean = 2434 Hz, SE = 93.5).

When focusing on tonal vocalizations, and excluding noisy calls and tonal calls for which we could not get F0 estimates, cluster analysis using F0 parameters found as the most effective a four-cluster solution with a silhouette value of 0.6. A subsequent DFA showed that single calls could be well assigned to the correct cluster (correct assignment = 98%, cross-validated = 97.1%; Fig. 8). Similar to the results of the first cluster solution we found two high-pitched clusters which differ in location of the F0 maximum, CL1: high “F0start,” with “F0maloc” (mean = 0.17, SE = 0.02), “F0max” (mean = 4484 Hz, SE = 70); CL3: high “F0end” with “F0maloc” (mean = 0.94, SE = 0.01), “F0max” (mean = 5389 Hz, SE = 103.9); and two low-pitched clusters, CL2: low “F0end” with “F0maloc” (mean = 0.82, SE = 0.02), “F0max” (mean = 2921 Hz, SE = 94); CL4: low “F0start” with “F0maloc” (mean = 0.12, SE = 0.01), “F0max” (mean = 2590 Hz, SE = 29 Hz). Based on this result we identified five categories, four tonal and one noisy call type.

The four tonal vocal types and the atonal noisy call category are not randomly distributed over the different pilot

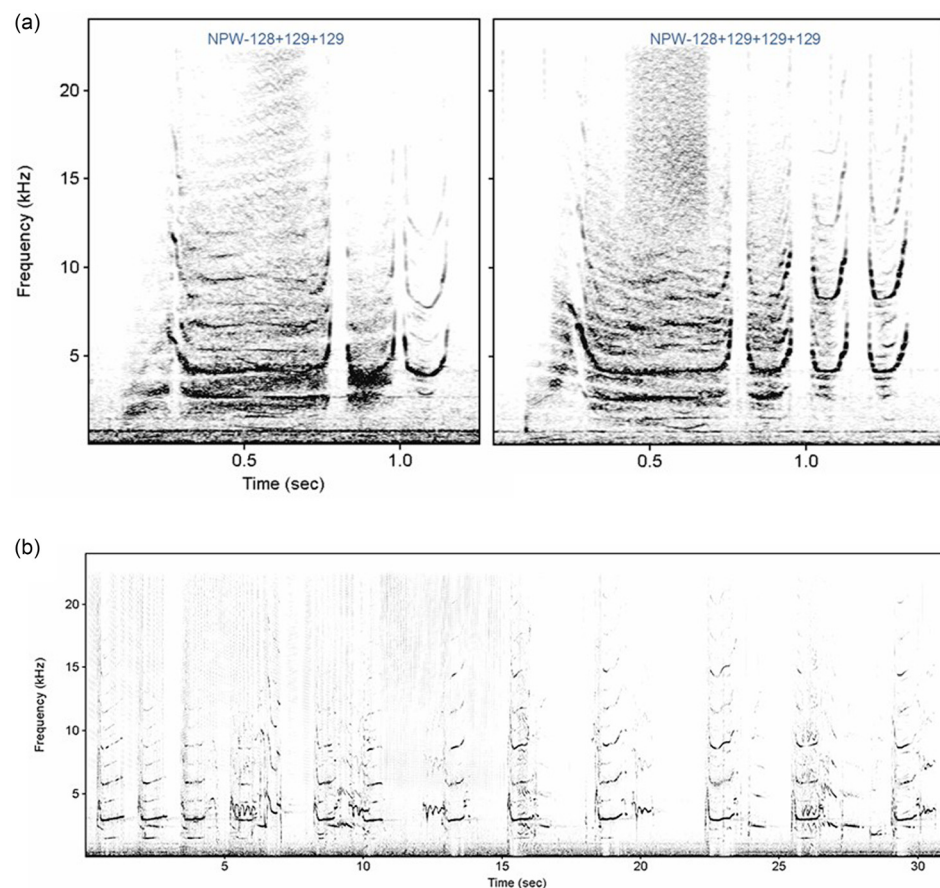


FIG. 7. (Color online) Example of long-finned pilot whale pulsed call sequences with two typical call type combinations (a), note that the order of the call types remains the same with NPW-128 being the leading call type, followed by variable amounts of NPW-129 call types. Certain call types often appear in call type repetitions (b).

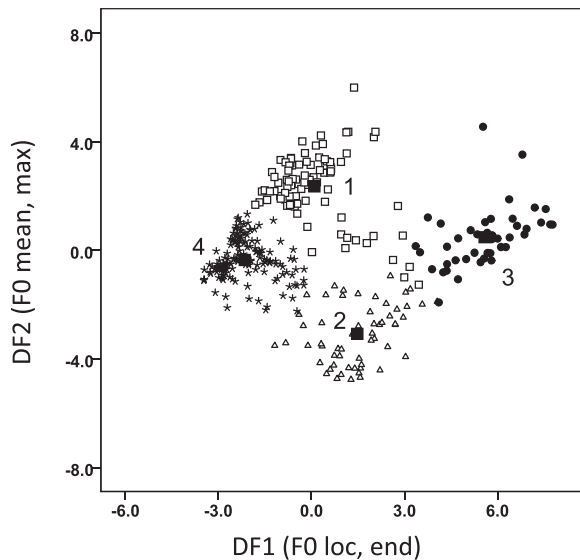


FIG. 8. Assignment of tonal vocalizations to the four established vocal clusters: Figure displays a projection of the first and second discriminating functions (DF1, DF2). Important acoustic parameters are given in brackets. Squares represent elements of cluster 1, triangles represent elements of cluster 2, filled circles represent cluster 3, and elements of cluster 4 are plotted as asterisks.

whale aggregations (Table II). However, none of these categories were exclusively used by one or two aggregations indicating the global characteristics of the categories found by the analysis.

IV. DISCUSSION

A. Vocal repertoire

Similar to the description of the vocal repertoire of long-finned pilot whales in the northwest Atlantic by Nemiroff and Whitehead (2009), we found that 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, we found minor differences: Nemiroff and Whitehead described most pulsed calls as simple, consisting of only one segment (93% in versus 87% in our study). In addition to the higher number of pulsed calls with several segments and

TABLE II. Distribution of call category in relation to the different pilot whale units (% number of calls).

Units	Tonal 1	Tonal 2	Tonal 3	Tonal 4	Noisy
1	11 (20.8)	2 (3.8)	30 (56.6)	4 (7.5)	6 (11.3)
2	2 (66.7)	0 (0)	0 (0)	1 (33.3)	0 (0)
3	15 (25.9)	12 (20.7)	0 (0)	13 (22.4)	18 (31)
4	11 (45.8)	9 (37.5)	0 (0)	4 (16.7)	0 (0)
5	1 (2.6)	5 (12.8)	0 (0)	2 (5.1)	31 (79.5)
6	42 (25.3)	23 (13.9)	3 (1.8)	98 (59)	0 (0)
7	8 (12.9)	6 (9.7)	11 (17.7)	36 (58.1)	1 (1.6)

elements, we also found more two-voiced calls than in the former study (29% versus 20%). Nemiroff and Whitehead found no discrete patterns in the structures of pulsed calls, instead the calls were described as graded. In our study based on observer analysis we could identify discrete calls and classified them into 129 different call types, however, the 25 subtypes are of graded structure. 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 study of Nemiroff and Whitehead, 2009 and 4572 calls in our study) and the different analysing approach, an automatic classification compared to an observer-based classification, might account for such differences. Sayigh *et al.* (2013) 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. Consequently, these different findings emphasize the importance of developing a common methodological approach.

Additionally, we found ultrasonic whistles with frequencies above 20 kHz and even above 60 kHz in the northern Norwegian long-finned pilot whale population, which were previously not described for this species. In general, the use of whistles in long-finned pilot whales seems to be highly context dependent (Weilgart and Whitehead, 1990). During our observations, we noticed that simple structured whistles seemed more apparent during resting behaviour such as milling and during times when the matriline were spread out in the fjord over an area of many kilometres. More complicated structured whistles 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. We also noticed that whistle activity seemed to increase during multi-pod meetings, and when Atlantic white-sided dolphins joined the group. This supports the hypothesis that whistles act as contact vocalization as well as coordination of movements of the whole group (Weilgart and Whitehead, 1990).

Killer whales are known to produce whistles with ultrasonic frequencies ranging up to 75 kHz (Samarra *et al.*, 2010; Andriolo *et al.*, 2015). 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 dolphin species 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 (Samarra *et al.*, 2010; Andriolo *et al.*, 2015).

In summary, the vocal repertoire of long-finned pilot whales in northern Norway is highly variable and among the most complex repertoires found in mammalian species. Similarly, complex vocal repertoires are known in killer whales, with discrete call types, aberrant and low frequency calls, stereotyped and aberrant whistles, clicks and buzzes, as well as two-voiced calls with lower- and higher-frequency components (Ford, 1989; Ford and Morton, 1991). Both

killer whales and long-finned pilot whales are long-lived marine mammals living in small matrifocal groups with natal group philopatry (Amos *et al.*, 1991; Amos *et al.*, 1993a; Amos *et al.*, 1993b; Sayigh *et al.*, 2013), and vocal complexity may reflect their similarity in social intra- and inter-group interactions (Ford and Morton, 1991; Deecke *et al.*, 2010). 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 (1979), then by Weilgart and Whitehead (1990), and more recently by Sayigh and colleagues (Sayigh *et al.*, 2013), that pilot whales may use stereotyped individual whistles, similar to bottlenose dolphin signature whistles. In 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 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 matriline meetings in summer in the Vestfjord. During these meetings, social contacts between groups and breeding behaviour (mating, calving, and nursing) were commonly observed. In such super pod meetings individual signalling 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 and Sayigh, 2013; Sayigh *et al.*, 2013).

In a former study based on cepstral coefficients comprising vocalizations of different pilot whales' aggregations recorded in the Vestfjord, we were able to show that calls within the aggregations of pilot whales were significantly more similar than between the different aggregations (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 audio-visual inspection (Vester *et al.*, 2016). 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.

The results presented above of our parametric acoustic analysis do not contrast these findings. All observed aggregations of pilot whales use vocalizations with generally the same structural complexity. Within this complex vocal repertoire it seems that smaller units, perhaps even matriline, use specific variants of these general structural patterns. 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 aggregations.

B. Temporal organization

Many studies on marine mammals' behaviour have shown that they are highly cognitive (Kuczaj *et al.*, 2009),

capable of vocal learning (Foote *et al.*, 2006) and mimicry (Richards *et al.*, 1984). In particular, dolphin species have evolved advanced communication and sound production flexibility, ranging from signature whistles and group-specific calls to different combinations of calls (Caldwell and 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 and Clark, 1980); bottlenose dolphins match whistles within 3 s in the wild, which seems to be a response to the initial caller (Janik, 2000); 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 part of these whales' vocal repertoire. It is also known that killer whales repeat call types and exhibit call-type matching, however, the function remains unknown (Miller *et al.*, 2004). Killer and pilot whales live in stable groups with strong social bonds between individuals, in the case of resident killer whales often lasting for a lifetime (Bigg *et al.*, 1990; Ottensmeyer and Whitehead, 2003; De Stephanis *et al.*, 2008). In such highly complex societies, individuals may develop 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 of vocal repertoire found here for long-finned pilot whales in comparison to killer whales, and also the higher variation in whistles, which is typical for dolphin societies. 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 description of the call types is similar to our present findings, in addition they considered call types that were produced more than 10 times and found that these predominant call types are often repeated. We 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 our recordings we 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 and Whitehead, 2017). The amount and variety of call combination found in our study lead to the suggestion that call repetition in pilot whales is similar common in killer whales. A closer investigation of their function promises further insight into their complex communication abilities.

This study on the vocal communication of long-finned pilot whales in northern Norway may contribute a step to our overall understanding of complex communication in social whales.

ACKNOWLEDGMENTS

We would like to thank Ellyne Hamran and Megan Doxford for helping to classify the calls. We also thank Felipe Matos for providing a map of Vestfjorden and Fredrik Broms; Lotta Borg, Kerstin Haller, Denny Fliegner, and Madita Zetzsche for field assistance, computational support, and photo-identification; and Gabi Reichert, Marten Brill, and Fredrik Broms for photographs. We thank Irene Barnard and Karl Inne Ugland for proofreading and Theo Geisel and Jan Nagler for helpful discussions. This study was mainly funded by Ocean Sounds, with additional support granted by the WWF Sweden and the Max Planck Society.

¹See supplementary material at <http://dx.doi.org/10.1121/1.4983685> for structural descriptions of pilot whale call types with the amount of segments and elements.

- Altmann, J. (1974). "Observational study of behavior: Sampling methods," *Behaviour* **49**, 227–267.
- Amos, B., Schlotterer, C., and Tautz, D. (1993a). "Social structure of pilot whales revealed by analytical DNA profiling," *Science* **260**, 670–672.
- Amos, J. A., Barrett, J., Bancroft, D. R., Majures, T. M. O., Bloch, D., Desportes, G., and Dover, G. A. (1993b). "A review of molecular evidence relating to social organization and breeding system in the long-finned pilot whale," in *Report of the International Whaling Commission*, Special Issue 14: pp. 219–231.
- Amos, J. A., Barrett, J., and Dover, D. A. (1991). "Breeding system and social structure in the Faroese pilot whale as revealed by DNA fingerprinting," *Heredity* **67**, 49–55.
- Andriolo, A., Reis, S. S., Amorim, T. O. S., Sucunza, F., and De Castro, F. R. (2015). "Killer whale (*Orcinus orca*) whistles from the western South Atlantic Ocean include high frequency signals," *J. Acoust. Soc. Am.* **138**, 1696–1701.
- Auger-Menthe, M., and Whitehead, H. (2007). "The use of natural markings in studies of long-finned pilot whales (*Globicephala melas*)," *Marine Mammal Sci.* **23**, 77–93.
- Avisoft (2016). "Avisoft, S. A. S. Lap Pro user guide for version 5.2."
- Berchok, C. L., Bradley, D. L., and Gaborielson, T. B. (2006). "St. Lawrence blue whale vocalizations revisited: Characterization of calls detected from 1998 to 2001," *J. Acoust. Soc. Am.* **120**, 2340–2354.
- Bigg, M. (1982). "An assessment of killer whales (*Orcinus orca*) sticks off Vancouver Island, British Columbia," in *Report of the International Whaling Commission*, 32: pp. 655–666.
- Bigg, M. A., Olesiuk, P. F., Ellis, G. M., Ford, J. K. B., and Balcom, K. C. (1990). "Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State," in *Report of the International Whaling Commission*, Special Issue 12: pp. 383–405.
- Bloch, D., Heide-Jørgensen, M. P., Stefansson, E., Mikkelsen, B., Ofstad, L. H., Dietz, R., and Andersen, L. W. (2003). "Short-term movements of long-finned pilot whales *Globicephala melas* around the Faroe Islands," *Wildlife Biol.* **9**, 47–58.
- Bloch, D., and Lastein, L. (1993). "Morphometric segregation of long-finned pilot whales in the eastern and western north Atlantic," *Ophelia* **38**, 55–68.
- Caldwell, M. C., and Caldwell, D. K. (1965). "Individualized whistle contours in bottlenose dolphins (*Tursiops truncatus*)," *Nature* **207**, 434–435.
- Clark, C. W., and Clark, J. M. (1980). "Sound playback experiments with southern right whales (*Eubalaena australis*)," *Science* **207**, 663–665.
- Crockford, C., Herbinger, I., Vigilant, L., and Boesch, C. (2004). "Wild chimpanzees produce group-specific calls: A case for vocal learning?," *Ethology* **110**, 221–243.
- De Stephanis, R., Verborgh, P., Prez, S., Esteban, R., Minville-Sebastia, L., and Guinet, C. (2008). "Long-term social structure of long-finned pilot whales (*Globicephala melas*) in the strait of Gibraltar," *Acta Etholog.* **11**, 81–94.
- Deecke, V. B., Barrett-Lennard, L. G., Spong, P., and Ford, J. K. B. (2010). "The structure of stereotyped calls reflects kinship and social affiliation in resident killer whales (*Orcinus orca*)," *Naturwissenschaften* **97**, 513–518.
- Deecke, V. B., Ford, J. K. B., and Spong, P. (2000). "Dialect change in resident killer whales: Implications for vocal learning and cultural transmission," *Animal Behav.* **60**, 629–638.
- Desportes, G., and Mouritsen, R. (1993). "Preliminary results on the diet of long-finned pilot whales off the Faroe Islands," in *Report of the International Whaling Commission*, Special Issue 14: pp. 305–324.
- Edds, P. (1988). "Characteristics of finback *Balaenotera physalus* vocalizations in the St. Lawrence estuary," *Bioacoustics* **1**, 131–149.
- Filatova, O. A., Deecke, V. B., Ford, J. K. B., Matkin, C. O., Barrett-Lennard, L. G., Guzeev, M. A., Burdin, A. M., and Hoyt, E. (2012). "Call diversity in the north Pacific killer whale populations: Implications for dialect evolution and population history," *Animal Behav.* **83**, 595–603.
- Fischer, J., Noser, R., and Hammerschmidt, K. (2013). "Bioacoustic field research: A primer to acoustic analyses and playback experiments with primates," *Am. J. Primatol.* **75**, 643–663.
- Foote, A. D., Griffin, R. M., Howitt, D., Larsson, L., Miller, P. J. O., and Hoelzel, A. R. (2006). "Killer whales are capable of vocal learning," *Biol. Lett.* **2**, 509–512.
- Ford, J. K. B. (1989). "Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia," *Can. J. Zool.* **67**, 727–745.
- Ford, J. K. B., and Morton, A. B. (1991). "Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia," *Can. J. Zool.* **69**, 1454–1483.
- Freeberg, T. M., Dunbar, R. I. M., and Ord, T. J. (2012). "Social complexity as a proximate and ultimate factor in communicative complexity," *Philos. Trans. R. Soc. B: Biol. Sci.* **367**, 1785–1801.
- Hammerschmidt, K., Reisinger, E., Westekemper, K., Ehrenreich, L., Strenze, N., and Fischer, J. (2012). "Mice do not require auditory input for the normal development of their ultrasonic vocalizations," *BMC Neurosci.* **13**, 40.
- Janik, V. M. (1999). "Pitfalls in the categorization of behaviour: A comparison of dolphin whistle classification methods," *An. Behav.* **57**, 133–143.
- Janik, V. M. (2000). "Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*)," *Science* **289**, 1355–1357.
- Janik, V. M., and Sayigh, L. S. (2013). "Communication in bottlenose dolphins: 50 years of signature whistle research," *J. Comp. Physiol. A* **199**, 479–489.
- Kuczaj, S. A., Gory, J. D., and Xitco, M. J. (2009). "How intelligent are dolphins? A partial answer based on their ability to plan their behavior when confronted with novel problems," *Jpn. J. Animal Psychol.* **59**, 99–115.
- Maciej, P., Ndao, I., Hammerschmidt, K., and Fischer, J. (2013). "Vocal communication in a complex multi-level society: Constrained acoustic structure and flexible call usage in Guinea baboons," *Front. Zool.* **10**, 58.
- Mann, J. (2000). "Unraveling the dynamics of social life: Long-term studies and observational methods," in *Cetacean Societies: Field-Studies of Dolphins and Whale*, edited by J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead (University of Chicago, Chicago), pp. 45–64.
- McComb, K., and Semple, S. (2005). "Coevolution of vocal communication and sociality in primates," *Biol. Lett.* **1**, 381–385.
- Miller, P. J. O., Shapiro, A. D., Tyack, P. L., and Solow, A. R. (2004). "Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*," *Animal Behav.* **67**, 1099–1107.
- Nemiroff, L., and Whitehead, H. (2009). "Structural characteristics of pulsed calls of long-finned pilot whales *Globicephala melas*," *Int. J. Animal Sound Record.* **19**, 67–92.
- Ottensmeyer, C. A., and Whitehead, H. (2003). "Behavioural evidence for social units in long-finned pilot whales," *Can. J. Zool.* **81**, 1327–1338.
- Rendell, L. E., and Whitehead, H. (2003). "Vocal clans in sperm whales (*Physeter macrocephalus*)," *R. Soc.* **270**, 225–231.
- Rice, D. W. (1998). "Marine mammals of the world: Systematics and distribution," *Soc. Marine Mammol., Special Publication* **4**, 1–231.
- Richards, D. G., Wolz, J. P., and Herman, L. M. (1984). "Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*," *J. Comp. Psychol.* **98**, 10–28.
- Rousseuu, P. J. (1987). "Silhouettes: A graphical aid to the interpretation and validation of cluster analysis," *J. Comp. Appl. Math.* **20**, 53–60.
- Samarra, F. I. P., Deecke, V. B., Rasmussen, M. H., Swift, R. J., and Miller, P. J. O. (2010). "Killer whales (*Orcinus orca*) produce ultrasonic whistles," *J. Acoust. Soc. Am.* **128**, EL205–EL210.
- Sayigh, L. S., Quick, N., Hastie, G., and Tyack, P. (2013). "Repeated call types in short-finned pilot whales, *Globicephala macrorhynchus*," *Marine Mammal Sci.* **29**, 312–324.

- Scheer, M. (2013). "Call vocalizations recorded among short-finned pilot whales (*Globicephala macrorhynchus*) off Tenerife, Canary Islands," *Aquat. Mammals* **39**, 306–313.
- SPSS (2016). "IBM_SPSS_Statistics_Base."
- Strager, H. (1995). "Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca linnaeus*, 1758, in the waters of northern Norway," *Can. J. Zool.* **73**, 1037–1047.
- Taruski, A. G. (1979). "The whistle repertoire of the north Atlantic pilot whale (*Globicephala melaena*) and its relationship to behavior and environment," in *Behavior of Marine Animals, Vol. 3: Cetaceans*, edited by H. E. Winn and B. L. Olla (Springer, New York), pp. 345–368.
- Thomsen, F., Franck, D., and Ford, J. K. B. (2001). "Characteristics of whistles from the acoustic repertoire of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia," *J. Acoust. Soc. Am.* **109**, 1240–1246.
- Vester, H., Hammerschmidt, K., Timme, M., and Hallerberg, S. (2016). "Quantifying group specificity of animal vocalizations without specific sender information," *Phys. Rev. E* **93**, 022138.
- Weilgart, L. S., and Whitehead, H. (1990). "Vocalizations of the north Atlantic pilot whale (*Globicephalus melas*) as related to behavioral contexts," *Behav. Ecol. Sociobiol.* **26**, 399–402.
- Yurk, H. (2005). *Vocal Culture and Social Stability in Resident Killer Whales (*Orcinus orca*)* (University of British Columbia Press, Vancouver), pp. 1–114.
- Yurk, H., Barrett-Lennard, L., Ford, J. K. B., and Matkin, C. O. (2002). "Cultural transmission within maternal lineages: Vocal clans in resident killer whales in southern Alaska," *Animal Behav.* **63**, 1103–1119.
- Zwamborn, E. M., and Whitehead, H. (2017). "Repeated call sequences and behavioural context in long-finned pilot whales of Cape Breton, Nova Scotia, Canada," *Bioacoustics* **26**, 169–183.