Cetaceans roam through a vision-limited underwater habitat and are highly reliant on sound for navigation, communication, and foraging (Au, 1993). Individuals benefiting from social group living need communication signals to maintain or regain contact with their group members when group individuals are not in sight of each other (Tyack, 2000). Except for the non-whistling odontocetes, delphinid vocalizations are generally divided into the categories of clicks (often used for echolocation), burst-pulses, and whistles (both used for communication) (see Janik, 2009, for a review). To facilitate recognition and cohesion among individuals of a social group which share their home range with other groups, social delphinids were shown to use stereotyped whistles and calls which can be stable over years and even decades (bottlenose dolphins [Tursiops truncatus]; Sayigh et al., 1990; killer whales [Orcinus orca]; Ford, 1991; Filatova et al., 2007).

Short-finned pilot whales (Globicephala macrorhynchus) are part of the Delphinidae family, which also includes bottlenose dolphins and killer whales. They are a deep-diving species (Aguilar Soto et al., 2008), and the social structure of sympatric groups was observed to be long-lasting and resembles group structures observed for matri- lineal cetaceans (Kasuya & Marsh, 1984; Marsh & Kasuya, 1984; Heimlich-Boran, 1993; Alves et al., in press). Studies of their tonal or tonal-like signals have mostly focused on the description of physical characteristics of pure-tone whistles (Rendell et al., 1999; Oswald et al., 2003; Baron et al., 2008). Other reports described pulsed signals with tonal properties such as calls, squeals, or whistle-like vocalizations (Schevill, 1964; Evans, 1967; Fish & Turl, 1976; Taruski, 1976; Higashi et al., 1992; Matthews et al., 1999; Scheer, 1999; Nakahara & Amano, 2001; Jensen et al., 2011). The function of these calls is unclear. De Ruiter et al. (2013) showed that pilot whales may mimic mid-frequency active sonar, but this study did not have any implication for the function of calls. Sayigh et al. (2013) showed that they produce stereotyped calls and suggested that these may facilitate individual or group recognition. Information derived from tags (Jensen, 2011; Jensen et al., 2011) suggests that calls play a role in maintaining or re-establishing contact between group members, in particular after foraging dives. It was shown that some calls seem to be stereotyped, both for captive (Caldwell & Caldwell, 1969) and wild (Sayigh et al., 2013) animals, and this might suggest a role in identification of individuals or groups (Sayigh et al., 2013).

This study was initiated to analyse the structure of call vocalizations recorded among short-finned pilot whale groups off Tenerife. To further examine whether these animals produce stereotyped vocalizations, the spectrographic time-frequency contours of recorded calls were compared.

Observations were made in August-September 1996 and June-July 2001 off the southwest coast of Tenerife between 27° 56’ 36” N to 28° 08’ 56” N and 16° 42’ 21” W to 16° 52’ 50” W (Figure 1). The 6 m, fiberglass-bottomed m/v Caldéron was used as a research platform in 1996; and the fiberglass-bottomed, 10 m s/v Delfín with an auxiliary diesel engine in 2001. During 37 d in 1996 and 2001, a total of 162 h 5 min was spent at sea. Recordings were obtained during five recording sessions in 1996 and ten in 2001. A recording session was defined as a recording made among a group of animals found in the same place. Group individuals all showed the same behavioural movement pattern (e.g., all individuals travelled in the same direction) and inter-individual distances ranged 0.5 to < 20 m. Recordings were made with the engines turned off. To obtain recordings with a good signal-to-noise ratio, we recorded relatively stationary groups of animals engaged in resting, milling, or socializing close to the boat. However,
some recordings were obtained during travelling and diving behaviour. A single hydrophone was lowered to a depth of approximately 25 m. During the 1996 field season, the flat frequency response of the recording systems was 20 to 20,000 Hz using a Sea Mike SM-1000 hydrophone (sensitivity: -180 dB re 1V/µPa or greater; frequency response: 20 to 20,000 Hz ± 1 dB) from Deepsea Power and Light, San Diego, California, with a portable Sony TCD3 digital audiotape recorder (sample rate: 48,000/s). In 2001, an Offshore Acoustics standard hydrophone (manufactured by Beverly Ford, North Vancouver, British Columbia) (sensitivity: -154 dB re 1V/µPa at 100 Hz; frequency response: 6 to 14,000 Hz ± 3 dB and 5 to 40,000 Hz ± 10 dB) with a portable Tascam DA-P1 digital audiotape recorder (sample rate: 48,000/s) was used, resulting in a frequency response of 5 to 24,000 Hz (± 10 dB) (flat: 6 to 14,000 Hz [± 3 dB]). Both recording systems contained the same customized pre-amplifier (+30 dB).

For spectrographic analyses, Canary 1.2.4. software (Cornell University, Ithaca, New York) was used. Sound sequences were digitized at 48 kHz (16 bit). A low-pass filter (-3 dB cutoff at 24 kHz) was applied to prevent aliasing errors. Spectrograms (512 pt FFT, 75% overlap, Hamming window) resulted in a time resolution of 1.33 ms and a frequency resolution of 93.75 Hz. The spectrographic analysis concentrated on tonal or tonal-like, non-echolocation signals termed *calls*. Based on signal-to-noise (S/N) quality, calls were qualitatively graded on a scale of 1 to 5 (adopted from Chmelnitsky & Ferguson, 2012): 1 = very high S/N ratio (call was clear: no background noise or overlapping calls), 2 = high S/N ratio (call was relatively clear and all spectrographic call details contrasted from the background: minor background noise or slightly overlapping calls), 3 = moderate S/N ratio (call was less clear: relatively faint with some background noise or overlap), 4 = low S/N ratio (call was not clear: relatively faint with background noise or overlapping calls), and 5 = very low S/N ratio (call was not clear: either faint and/or too much background noise or overlap to measure call properties). All calls graded 4 and 5 were excluded from analyses. For each call, duration as well as initial, end, minimum, and maximum frequency were measured. All calls had a tonal quality to the analyst. However, these sounds showed different spectrographic appearances. Calls showed (1) non-harmonic, narrow sideband structures with abrupt frequency shifts which were presumed to be pulsed sounds (see Watkins, 1967) or to have originated from non-linear phenomena during sound production (according to Wilden et al., 1998); (2) harmonic bands at integer multiples of the fundamental frequency and thus being tonal in nature; and (3) a mixture of tonal and nontonal segments. For this study
all these calls were considered for analysis. Call measurements were derived from the fundamental frequency band. As shown for bottlenose dolphin whistles, the identity information is conveyed by the signal shape and does not depend on voice features (Janik et al., 2006). It might be assumed that this also can be applied for pilot whale calls. Furthermore, delphinid fundamental frequency contours are unaffected by hydrostatic pressure and thereby depth (Madsen et al., 2012). Pulsed call measurements were derived from the fundamental sideband of the pulse repetition rate (Sjare & Smith, 1986). For the comparison and classification of calls, the author visually inspected their overall spectrographic contour (time vs frequency). According to Taruski (1980) and Weilgart & Whitehead (1990), for long-finned pilot whales (Globicephala melas), calls were grouped into seven broad and simplified contour types: S1 = level frequency; S2 = falling frequency; S3 = rising frequency; S4 = frequency first rises, then falls; S5 = frequency first falls, then rises; S6 = at least three symmetrical frequency inflections; and S7 = at least three asymmetrical frequency inflections.

By searching for stereotyped spectrographic patterns, most calls showed structurally unique features and occurred in varying repetition rates during recording sessions. Calls occurring more than once were labelled repetitive calls. Based on their spectrographic distinctiveness, repetitive calls were grouped into call types. Similar to killer whale calls (Ford, 1987, 1991), some call types were slightly rendered in form, nevertheless they showed homologous structural features. These call type variants were defined as call subtypes and were labelled with a lower-case Roman suffix (see Ford, 1987). Calls occurring just once were preliminarily labelled non-repetitive calls. Such calls were only classified as a repetitive call when an identical call was recorded during another recording session. All call (sub-) type labels start with a “T” indicating the place of recording (i.e., Tenerife). To test interobserver reliability, all spectrograms were printed on A4 paper and presented to two further independent observers naïve to spectrographic analysis. Each observer was asked to perform his own call type classification, and their results were compared with the initial categorization made by the author. There was an agreement among all three observers for more than 90% on call type classification. For the call subtype classification, there was less agreement (about 65%). Disagreements were discussed among all three observers until a consensus was achieved. In case of a nonconfirmation of a call subtype by one observer, this subtype was finally classified as an independent call type.

A total of 4 h 57 min 6 s of audio recordings were obtained which contained 3,063 audible call vocalizations (Table 1). Of these, 779 call vocalizations were spectrographically analysed. Table 2 summarizes measured call frequency and duration values. The distribution of calls among the seven contour types was S1 = 9% (n = 71), S2 = 7% (n = 51), S3 = 45% (n = 348), S4 = 30% (n = 231), S5 = 5% (n = 38), S6 = 4% (n = 28), and S7 = 2% (n = 12).

Twenty-nine (3.7%) calls were heard just once, whereas 750 (96.3%) of all identified calls were repeated 2 to 34 times (6.94 ± 7.09 [mean ± SD]) during a recording session. These repetitive calls were grouped in 55 different call types. Though repetitive calls belonging to one call type showed strong structural similarities and differed from others, for some calls, subtle structures were sometimes added, subtracted, or modulated in duration or frequency. Repetitive calls belonging to the same call type, but showing some of these subtle differences, were grouped into call subtypes. Of the 55 call types, 33 showed two to five subtypes (2.52 ± 0.83). As an example, Figure 2 shows spectrograms of call type T-15 with its four subtypes T-15i-iv. A complete spectrographic overview of call types and subtypes identified in this study is given in Scheer (2012). Twenty-three out of 55 call types were recorded across two to five different sessions (see Figure 2), but with only two instances of the same call subtype recorded on different occasions. Call subtype T-10i was matched between two recording sessions in 2001 (recording session 7 and 9); and as a match between years, call subtype T-20i was recorded three times on 1 September 1996 and twice on 19 June 2001 (Figure 3). This indicates that although the majority of calls in this study were repeated several times over a recording session, calls recorded between sessions differed in slight ways, resulting in categorization into different subtypes of similar calls. It is difficult to know whether the two instances of call subtypes recorded across several recording sessions represent a chance recording of the same group or individual. During 15 recording sessions, a mean rate of 7.20 ± 3.21 (range: 3 to 13) of different call (sub-) types was observed (see Table 1).

Results showed that most analysed calls of short-finned pilot whales off Tenerife were repetitive, and these calls could be grouped into exclusive call types with and without subtypes. Some call subtypes contained variant components or a component itself showed varying spectrographic features such as increased numbers of sidebands (see call subtypes T-15i-iv in Figure 2). However, these subtypes retained the identifiable aural quality and basic component structure of that call type.
Table 1. Overview of data and results obtained from 15 acoustic recording sessions (1996 and 2001) of short-finned pilot whales off Tenerife

<table>
<thead>
<tr>
<th>Season</th>
<th>Date</th>
<th>No. of call (sub-) types</th>
<th>Total audible calls recorded</th>
<th>Nonrepetitive calls (%)</th>
<th>Repetitive calls (%)</th>
<th>Mean repetition rate per call (sub-) type (SD)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1996</td>
<td>27/8</td>
<td>13</td>
<td>193</td>
<td>4 (5.2)</td>
<td>73 (94.8)</td>
<td>5.62 (± 4.13)</td>
</tr>
<tr>
<td></td>
<td>31/8</td>
<td>6</td>
<td>110</td>
<td>1 (1.8)</td>
<td>55 (98.2)</td>
<td>9.17 (± 6.34)</td>
</tr>
<tr>
<td></td>
<td>1/9</td>
<td>12</td>
<td>285</td>
<td>7 (20)</td>
<td>28 (80)</td>
<td>2.33 (± 2.27)</td>
</tr>
<tr>
<td></td>
<td>1/9</td>
<td>8</td>
<td>110</td>
<td>1 (2.1)</td>
<td>47 (97.9)</td>
<td>6.71 (± 5.59)</td>
</tr>
<tr>
<td></td>
<td>17/9</td>
<td>3</td>
<td>316</td>
<td>2 (4.4)</td>
<td>43 (95.6)</td>
<td>5.38 (± 5.13)</td>
</tr>
<tr>
<td>2001</td>
<td>8/6</td>
<td>10</td>
<td>194</td>
<td>1 (2)</td>
<td>50 (98)</td>
<td>8.20 (± 6.83)</td>
</tr>
<tr>
<td></td>
<td>8/6</td>
<td>7</td>
<td>342</td>
<td>1 (1.2)</td>
<td>82 (98.8)</td>
<td>8.03 (± 6.65)</td>
</tr>
<tr>
<td></td>
<td>15/6</td>
<td>8</td>
<td>194</td>
<td>1 (2)</td>
<td>50 (98)</td>
<td>8.33 (± 9.00)</td>
</tr>
<tr>
<td></td>
<td>15/6</td>
<td>9</td>
<td>161</td>
<td>7 (13.5)</td>
<td>45 (86.5)</td>
<td>5.63 (± 10.39)</td>
</tr>
<tr>
<td></td>
<td>19/6</td>
<td>10</td>
<td>194</td>
<td>1 (2)</td>
<td>56 (98.2)</td>
<td>9.33 (± 6.65)</td>
</tr>
<tr>
<td></td>
<td>19/6</td>
<td>11</td>
<td>57</td>
<td>0 (0)</td>
<td>20 (100)</td>
<td>5.00 (± 4.08)</td>
</tr>
<tr>
<td></td>
<td>23/6</td>
<td>12</td>
<td>40</td>
<td>0 (0)</td>
<td>27 (100)</td>
<td>9.00 (± 12.12)</td>
</tr>
<tr>
<td></td>
<td>23/6</td>
<td>13</td>
<td>196</td>
<td>0 (0)</td>
<td>33 (100)</td>
<td>11.00 (± 12.17)</td>
</tr>
<tr>
<td></td>
<td>26/6</td>
<td>14</td>
<td>206</td>
<td>4 (6.5)</td>
<td>58 (93.5)</td>
<td>6.44 (± 7.55)</td>
</tr>
<tr>
<td></td>
<td>7/7</td>
<td>15</td>
<td>669</td>
<td>0 (0)</td>
<td>114 (100)</td>
<td>11.40 (± 9.91)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td>3,063</td>
<td>29 (3.7)</td>
<td>750 (96.3)</td>
<td></td>
</tr>
<tr>
<td>Mean (SD)</td>
<td></td>
<td></td>
<td>4:57:06</td>
<td></td>
<td>7.20 (± 3.21)</td>
<td>6.94 (± 7.09)</td>
</tr>
</tbody>
</table>

Table 2. Summary of acoustic measurements of calls (mean ± SD)

<table>
<thead>
<tr>
<th>Frequency (kHz)</th>
<th>Initial</th>
<th>End</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Duration (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>2.28 (1.66)</td>
<td>6.50 (4.99)</td>
<td>1.66 (0.97)</td>
<td>8.92 (4.94)</td>
<td>0.86 (0.28)</td>
</tr>
</tbody>
</table>
Figure 2. Call type T-15 with its subtypes T-15i \((n = 4;\) recorded on 31 August 1996), T-15ii \((n = 9;\) recorded on 1 September 1996), T-15iii \((n = 4;\) recorded on 17 September 1996), and T-15iv \((n = 12;\) recorded on 19 June 2001) observed among short-finned pilot whales off Tenerife. All these call subtypes have an equal aural appearance to the analyst. They consist of three or four distinctive elements which are separated by abrupt frequency shifts. For T-15ii to T-15iv, each subtype consists of three elements (2, 3, and 4). Elements show subtle differences such as the number of sidebands for element 2, the frequency contours for elements 3 and 4, and the durations of elements 2 through 4. Call subtype T-15i has a further element 1, which is not found in the other three subtypes.

Figure 3. Call (sub-) type repertoires recorded during recording session 4 (recorded on 1 September 1996 with 7 call types and 6 subtypes) and 10 (19 June 2001 with 6 call types and 4 subtypes); numbers in parentheses give repetition rates of call (sub-) types during each recording session. Call subtype T-20ii was heard during both recording sessions. Call type T-22 can be found with two subtypes (T-22i and ii) in recording session 4 and with one subtype (T-22iii) in recording session 10.
(as also observed for killer whale calls: Ford, 1987; Strager, 1995). Though repetitive in nature, most call (sub-) types were only found during a single recording session. Furthermore, the overall number of nonrepetitive calls was low. However, these observations might be biased due to the low sample size or restricted by a limited record of behavioural or social context.

Repetitive call vocalizations were also described by previous studies (Caldwell & Caldwell, 1969; Jensen et al., 2011). More precisely, Sayigh et al. (2013) found repeated and nonrepeated call types for this species in the Bahamas and this corresponds with repetitive and nonrepetitive calls (respectively) recorded during this study. Though Sayigh et al. (2013) had a much larger sample size, additional data might reveal that for both studies, nonrepetitive call types might be repetitive ones but emitted at lower repetition rates. As shown for killer whales, call use varied with behavioural context (Ford, 1989), and this also might be the case for short-finned pilot whales. Though a range of relative occurrence of nonrepetitive calls with 0 to 20% per recording session could be observed here (see Table 1), this aspect was neither systematically investigated during this study nor by Sayigh et al. (2013).

Rendell et al. (1999) spectrographically analysed 345 tonal calls recorded in the same area. In contrast to this study, they found shorter durations (mean: 0.59 s ± 0.33), a higher minimum frequency (mean: 6.16 kHz ± 2.37), and a higher maximum frequency (mean: 10.87 kHz ± 3.61). However, these differences might be explained by their lower sample size and by the fact that pulsed calls were excluded from their analysis.

The results found during this study contrast with those found for the phylogenetically closely related long-finned pilot whale (Globicephala melaena). Studies on this species’ whistles and calls reported a graded system (Taruski, 1980; Weiglart & Whitehead, 1990). However, both studies categorized signals into broad classes but did not examine whether distinctive signals were shown in repetition. Nemиров & Whitehead (2009) analysed 419 pulsed calls using visual and statistical techniques. They argued that these vocalizations could not be grouped into multiple discrete call types and suggested that signals are graded and may provide information on the status, motivation, and behavioural context of the sender. It remains unclear how members of sympatric long-finned pilot whale groups enable identification among group members. Graded signals might contain individual features which could enable identification. It may also be that distinct call types exist but were not observed due to the presence of multiple variable calls in the same sample. Biases might arise due to their relatively small sample size.

In conclusion, calls (including whistles) were shown to be a predominant vocalization type among short-finned pilot whales, and most of them were repeated within the same recording session. While the function of calls in this species remains unclear, it is possible that calls may serve an important role in identification of groups or individuals, or in maintaining acoustic contact between group members.

Acknowledgments

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Literature Cited


Call Vocalizations Among Short-Finned Pilot Whales

311


