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### Moving in concert: Social and migratory behaviour of dolphins and whales in the North Atlantic Ocean

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## Chapter 3. Silent crowds: the socio-behavioural context of long-finned pilot whale vocalisations

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### Abstract

Vocalisations form a key component of the social interactions and foraging behaviour of cetaceans. We investigated the interplay between the vocal, diving and group behaviour of long-finned pilot whales by combining concurrent recordings of the soundscape and diving depth of tagged individuals with surface observations of group-level behaviour. During deep dives, which are generally associated with foraging, the pilot whales showed much higher vocal activity than during shallow dives. The strong increase in echolocation clicks and buzzes was indicative of prey detection and capture attempts. In addition, pilot whales more often produced complex whistles during deep dives, which suggests intensified and more complex social communication. Simple whistles were used consistently throughout the behavioural spectrum, irrespective of social context and depth, indicating that these calls may function to signal presence to group members. Long-finned pilot whales were more silent in larger, more closely spaced groups with a higher degree of surface active behaviour (spyhops). This indicates that higher levels of social cohesion may release the function of vocalising in pilot whales. Relationships between clicks and group-level behaviour during periods of shallow diving showed that these echolocation signals were produced not only during foraging but might also have a social function, possibly to locate conspecifics at lower degrees of social cohesion. Combined, our results create new insights into the functionality of long-finned pilot whale vocalisations, tuned to the socio-behavioural context in which they are produced.

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## Introduction

Animal vocalisations are related to the socio-behavioural context in which they are produced. Specific call types function in courtship and mating behaviour (Wells 1977, Eriksson & Wallin 1986), territorial defence (Brantley & Bass 1994, Marler & Slabbekoorn 2004), foraging behaviour (Griffin 1953, Johnson et al. 2004, Miller et al. 2004a), social interaction (Poole et al. 1988) and the signalling of identity (Yurk et al. 2002, Curé et al. 2011). Vocalisation and hearing is of particular importance for cetaceans, as their marine environment often limits the use of visual cues. In contrast, sounds can be detected over long distances in marine systems (Payne & Webb 1971). Consequently, many cetaceans rely on vocalisations for finding prey, navigation, social interaction and coordination of behaviour (Richardson et al. 1995, Nummela et al. 2004).

Long-finned pilot whales (*Globicephala melas*) are highly social cetaceans that live in long-term stable, matrilineal groups (Amos 1993, Ottensmeyer & Whitehead 2003, de Stephanis et al. 2008). They mostly occur in tightly spaced, behaviourally coordinated groups of about 10 individuals, often within larger aggregations of 60-100 whales (Cañadas & Sagarminaga 2000, de Stephanis et al. 2008, Visser et al. Chapter 2 in this thesis). Pairs of long-finned pilot whales can perform highly synchronous movements, at less than one body length apart (Senigaglia & Whitehead 2012). Long-finned pilot whales forage during deep dives, up to 800 m depth. Foraging periods consist of a series of deep foraging dives and intermittent shallow dives (Baird et al. 2002, Sivle et al. 2012). Pilot whales employ a social foraging strategy whereby group members to a large degree synchronise the timing of their foraging periods, although they do not necessarily synchronise their individual dives (Aoki et al. 2013, Visser et al. Chapter 2 in this thesis).

Long-finned pilot whales have a highly complex vocal repertoire, consisting of echolocation clicks and a wide variety of tonal calls (whistles) and pulsed calls (Taruski 1979, Nemiroff & Whitehead 2009). Deep-diving cetaceans use echolocation clicks to localise prey during bio-sonar based foraging (Soto et al. 2008, Madsen et al. 2013). The long-finned pilot whale whistles and pulsed calls are social communication signals, formed along an apparent continuum from simple to highly complex calls (Taruski 1979, Nemiroff & Whitehead 2009). This complexity in the calling behaviour of long-finned pilot whales may function to allow communication of different socio-behavioural contexts. For instance, pilot

whale groups produce more, and more complex, whistles at higher levels of arousal and with more groups present (Taruski 1979, Weilgart & Whitehead 1990).

Apart from these broad patterns, it remains unclear how the different vocalisations function within the interplay of social and behavioural contexts. Pilot whales perform a large part of their behaviours out of sight, which limits the ability to associate vocalisation patterns with direct observations of their behaviour using traditional observation techniques. However, recently developed archival tags make it feasible to monitor the movements and vocal behaviour of individual pilot whales (Johnson & Tyack 2003). These data can be used to identify behavioural patterns (e.g. foraging; Madsen et al. 2013) of the tagged individuals and can be matched to surface observations of group behaviour.

Here, we investigate the socio-behavioural context of long-finned pilot whale vocalisations, by integrating tag recordings of vocal and diving behaviour of individuals with concurrent visual observations of group-level behaviour at the water surface. We analysed whether vocalisation patterns varied between (i) periods of foraging and non-foraging dives, and (ii) as a function of group-level behaviour.

## Materials and Methods

The behaviour of long-finned pilot whales was monitored from the research vessel *M/S Strønstad* (29 m, engine driven) in the Vestfjord basin off Lofoten, Norway (67°00'N, 11°50'E to 68°30'N, 17°00'E). The study was conducted from May 17 to June 5, 2009, and from May 23 to June 6, 2010. We collected three types of concurrent behavioural data: vocalisation and dive parameters collected from individuals tagged with non-invasive tags, and focal follow observations of group-level behaviour at the water surface.

### *Tag recordings*

Following initial sighting of a group of pilot whales, an individual was tagged at the first available opportunity, using a handheld, 6 m pole from a small tagging vessel. We used archival DTAGs, sensors that are attached on the animals with suction cups, to record sound and diving depth (two channels, 192 kHz sampling rate per channel, 16-bit resolution; Johnson & Tyack 2003) of seven tagged individuals. The tag contained a built-in beacon transmitting a radio

signal when the tagged whale was at the surface. All data recorded from 30 minutes after the tagging vessel left the tagged animal up to the release of the tag or the start of sound exposure experiments (reported in Miller et al. 2012) were included in our analysis.

Vocalisations were classified into five categories: simple whistles, intermediate whistles, complex whistles (call types), click trains and buzzes (echolocation clicks; Fig. 1A-E). This broad classification of call types was applied as long-finned pilot whales produce an apparent continuum of tonal and pulsed calls, which makes it difficult to categorise discrete calls. Moreover, the complexity of discrete calls may vary in relation to behavioural state (Taruski 1979, Nemiroff & Whitehead 2009). Hence, we did not discriminate between discrete tonal calls, but investigated the level of complexity of calls. Simple whistles, intermediate whistles and complex whistles were defined as calls with no inflections, 1 or 2 inflections, or more than 2 inflections, respectively (Fig. 1A-C), based on the classifications by Taruski (1979) and Weilgart & Whitehead (1990). Echolocation clicks were series of short broadband signals classified as click trains or buzzes. Consecutive but distinct broadband clicks recorded less than 2 s apart were classified as a click train (Fig. 1D). Buzzes were defined as rapid successions of clicks that fused together on the spectrogram (Fig. 1E).

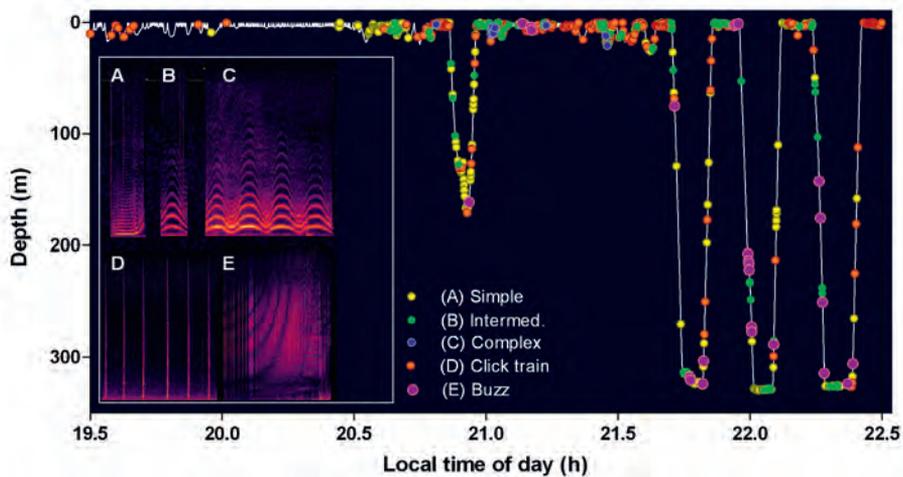


Figure 1. Long-finned pilot whale dive profile and associated soundscape, showing a period of shallow diving followed by a period with deep-diving foraging behaviour. Inset: Spectrograms of the five vocalisation types: A) simple whistle, B) intermediate whistle, C) complex whistle, D) click train and E) buzz. Call duration: A) 0.43 s, B) 0.42 s, C) 1.35 s, D) 1.52 s and E) 1.13 s.

The start and stop time of each vocalisation was recorded by two independent observers by visual and aural inspection of the spectrogram (Blackman-Harris window, 4096 sample FFT, 75% overlap) in Adobe Audition 2.0. Calls that were less than 0.2 s apart were classified as one call. Overlapping tonal calls that could not be classified individually were classified as a composite call (e.g. simple + complex whistle). All vocalisations that were clearly audible and/or visible on the spectrograms were included in our analysis. The vocal behaviour hence represents the soundscape of the tagged individual, here defined as all vocalisations produced by the tagged individual and nearby vocalising conspecifics.

In addition, we identified periods of silence. We used a log-frequency analysis of time intervals between consecutive vocalisations to determine the threshold between silent periods and periods of vocalisations with naturally occurring pauses (Sibly et al. 1990, Miller et al. 2004b). We fitted a one-process model (no distinction between vocal and silent periods), two-process model (distinction between vocal and silent periods) and three-process model (multiple distinctions between vocal and silent periods) to the log-frequency distribution. The best of these three models was selected with the Akaike Information Criterion (AIC).

Diving depth of the tagged whales was obtained by calibrated conversion of the values from the pressure sensor on the tags. Vocalisations and silent periods were matched to the depth of the tagged individual at the time of the start of the vocalisation or silent period. Dives were assigned to either deep diving bouts or shallow diving bouts, to distinguish between periods of foraging (associated with deep dives; Baird et al. 2002) and non-foraging behaviour. Log-frequency analysis of the tag data (Sibly et al. 1990) indicated a threshold depth of 34 m to separate shallow from deep dives, and a maximum time interval of 14.5 min between consecutive deep dives within the same diving bout. Following Visser et al. (Chapter 2 in this thesis), a deep diving bout was therefore defined as the period from the first dive >34 m up to 14.5 min after the end of the last deep dive.

#### *Visual observations of group behaviour*

Visual observations of group behaviour were made from the research vessel, at 6 m above water level. The focal group consisted of the tagged individual and associated individuals. The research vessel aimed to maintain a distance of 100 – 400 m to the focal group. Behavioural data were collected by two dedicated

observers, alternating in 6-hour shifts, assisted by a second person recording the data. The distance estimates of the two observers were calibrated by laser range finder, and by comparison of their estimates of a range of distances to a gps-equipped buoy. Sampling was conducted during all hours of the day, as the high latitude provided 24-hour daylight conditions.

Group-level behaviour parameters of focal groups were recorded during focal follows using a pre-defined ethogram (Table 1). The focal group was defined as the group of individuals in closer proximity to the tagged whale and each other than to other individuals in the area, following Visser et al. (Chapter 2 in this thesis). The focal area was defined as the 200 m radius around the tagged individual. Group size, group geometry (individual spacing, line swimming) and proximity to other groups (number of individuals and groups in the focal area, distance to nearest other group) were determined by scanning the area around the tagged animal. Non-focal groups were defined in a similar way as the focal group, as all individuals in closer proximity to each other than to other individuals in the area. Synchronicity parameters (surfacing synchrony, milling index) were quantified from the timing or orientation of surfacing of the associates relative to the tagged animal using traditional scan sampling (Altmann 1974). The events in the focal group (loggings and spyhops) were recorded for each sampling interval using incident sampling (Mann 1999). Parameters were recorded at 2-minute intervals, or at first surfacing of the tagged individual following dives longer than 2 minutes. Hence, group-level behaviour was sampled when the tagged individual was visible at the surface. This sampling interval was shorter than the time scale at which the state parameters were expected to change (Martin & Bateson 2007), and ensured observation of the tagged individual. Additional background information on our sampling protocol is provided in Visser et al. (Chapter 2 in this thesis).

#### *Statistical analysis of vocalisation patterns*

The data gathered in our study enabled a comparison between vocalisations of tagged individuals, their diving behaviour and the group-level behaviour at the water surface. For each 2-minute sampling interval of group-level behaviour, we determined the proportion of time that vocalisation types and silent periods were recorded in the soundscape, and the maximum diving depth and diving state (deep or shallow diving) of the tagged individual. In total, the input data comprised time series from seven tagged individuals in seven different focal groups.

Table 1. The ethogram with group sampling parameters and their definitions.

Parameter	Definition (s = state; e = event) <sup>1</sup>	Quantification
Group size	Number of animals most closely associated with the tagged individual and with each other (s)	Number of individuals
Individual spacing	Distance between individuals in the focal group (in body lengths (BL)) (s)	Very tight: < 1 BL Tight: 1 – 3 BL Loose: 3 – 15 BL Very loose: >15 BL and within focal area Solitary: no other individual in focal area and/or distant from nearest neighbour
Number of individuals in focal area	Number of individuals within 200 m of the tagged individual (s)	Number of individuals
Number of groups in focal area	Number of groups within 200 m of the tagged individual (s)	Number of groups
Distance to nearest other group	Distance between the focal group and the nearest other group (s)	Distance in meters
Surfacing synchrony	The % of individuals in the focal group surfacing during the surfacing of the tagged individual (s)	% of individuals
Milling index	Presence of individuals in the focal group surfacing with different orientation as the tagged individual (s)	Presence / absence
Line swimming	Presence of lined-up geometry of the focal group (s)	Presence / absence
Display events	Number of events per display type in the focal group (e)	Number of loggings, spyhops

<sup>1</sup>State: characteristic of the focal group as a whole. Events: behaviours, mostly of short duration, displayed by one or several individuals in the focal group.

As a first step, we used redundancy analysis (RDA) to identify relationships between the vocalisations of the long-finned pilot whales and the set of diving and group-level behaviours. To investigate whether patterns in the vocalisations were different between the two diving states (deep or shallow diving), we first analysed the complete data set. We then conducted the RDA analysis separately for periods of deep diving and periods of shallow diving. Significance testing

was conducted using a permutation test. RDA does not require input data to be normally distributed and permits potential collinearity between explanatory variables. RDA assumes that underlying parameter relations are linear, which was supported by our data-exploration. RDA analyses were conducted using Brodgar 2.5.1 ([www.brodgar.com](http://www.brodgar.com)).

Second, differences in vocal behaviour between periods of deep and shallow diving, and between the different group-level behaviours, were quantified using Generalised Estimating Equations (GEEs; Hardin & Hilbe 2003). GEEs form an extension to Generalized Linear Models (GLMs). They are specifically designed to model autocorrelated data, such as time series. GEEs account for residual autocorrelation within individual time series (panels) while assuming independence between time series, and return predicted values for the average response across the entire dataset.

We investigated 1) whether vocalisation patterns varied between periods of deep and shallow diving, and 2) whether vocalisation patterns varied as a function of group-level behaviour. For this purpose, each vocalisation type was modelled as a binomial response variable in the GEE with a logit link function. For each sample, the seconds during which this vocalisation type was recorded were assigned as “successes” while the total number of seconds during the sampling interval was treated as “trials”. Because GEE models can handle only a limited number of explanatory parameters, we restricted the GEE model to those group behaviour parameters that had a significant effect on the pattern of vocalisations in the RDA. Display events and milling were treated as binary data, while all other group behaviours were treated as continuous data. We applied a backward model selection by removing one group behaviour parameter at a time and selecting the best model based on the lowest QIC-value (GEE model equivalent of Akaike Information Criterion (AIC); Hardin & Hilbe 2003).

GEE models were fitted using the time series of the tagged animal as panel variable within the GENMOD procedure in SAS 9.3 (Zeger et al. 1988, Kauermann & Carroll 2001, SAS 2011). In the absence of support for a particular autocorrelation structure in the data, the empirical standard errors were used to quantify uncertainty in the GEE model estimates. In GENMOD, empirical standard errors are calculated directly from the model residuals and are robust to any misspecification of the working correlation.

*Classification of diving behaviour from vocal behaviour*

We used random forest (RF) analysis (Breiman 2001) to further assess whether vocalisations were different between deep and shallow diving bouts. RFs consist of a series of unpruned classification trees generated from one dataset. We used the vocal parameters as predictors to classify deep versus shallow diving bouts, with Conditional Inference Forests to account for the different categories of predictors (e.g., binary, continuous; Holthorn et al. 2006, Strobl et al. 2007). The model was run with 1000 trees. For each tree, two-thirds of the data set was randomly selected without replacement, and run down the tree. At each node of a tree, two predictors were randomly selected, and the predictor that yielded the best split was chosen. Weights were assigned to deep and shallow diving bouts, inversely proportional to their occurrence. Each sample was then classified based on the majority vote from all trees. The error estimate of the model was determined internally with the remaining one-third of the data set as test data. The predictors with the lowest variable importance were removed one by one from the model, until further removal did not improve the error rate of the new model. The relative importance of each of the predictors was calculated using conditional computation of variable importance (Strobl et al. 2008). The RF analysis was performed using the package 'party' in R version 2.14.1 (R development core team 2011).

## Results

We conducted seven focal follows comprising concurrent vocal, diving and group behaviour of long-finned pilot whale tagged individuals and their focal groups. Focal follow duration ranged from 0.8 – 8.9 h, during a total of 32.5 h. The tagged individuals were three medium-sized individuals associated with a calf, three medium-sized individuals without a calf and one large adult. The data comprised a total of 10393 vocalisations and 556 samples of group-level behaviour.

*Characteristics of vocal behaviour*

In total, pilot whale vocalisations were recorded during 40% of time (Table 2). Click trains comprised the predominant part of the time spent vocalising (Table 2). Of the call types, simple whistles were produced most often, followed by

whistles of intermediate complexity. Complex whistles were relatively rare. Log-frequency analysis of the intervals between vocalisations indicated that a threshold duration of 24.5 s of continuous silence distinguished between vocal periods with naturally occurring pauses and silent periods (Fig. 2; AIC two-process model: 32597; three-process model: 32679; one-process model: 37903). Silence was recorded during 430 silent periods, with durations ranging from 24.6 s to 39.2 min, covering 39% of the time (Table 2).

Table 2. Number, length and percentage of time recorded for each vocalisation type, for short pauses and for silent periods.

Vocalisation type	Number*	Mean length (SD) (s)	Percentage of time*
Total vocalisations	10393	-	40.2
- Click trains	2883	15.3 (37.3)	37.4
- Buzzes	747	3.02 (5.0)	1.7
- Simple whistles	4929	0.79 (1.1)	3.1
- Intermediate whistles	2643	0.95 (1.4)	1.9
- Complex whistles	676	1.23 (0.7)	0.7
Short pauses**	4980	4.6 (4.6)	20.8
Silent periods**	430	106.1 (195.6)	39.0

\* Including single and composite vocalisation types

\*\* Short pauses were < 24.5 seconds; silent periods were > 24.5 seconds

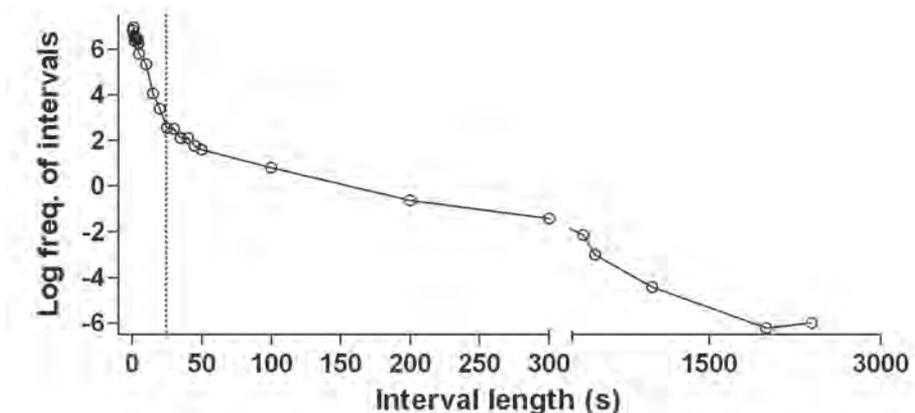


Figure 2. Log-frequency distribution of intervals between vocalisations. The vertical dashed line indicates the interval length that was used to distinguish between vocal periods with naturally occurring pauses (intervals < 24.5 s) and silent periods (intervals > 24.5 seconds).

The seven tagged whales spent the great majority of time in the upper 10 m of the water column (76%; Fig. 3A). Vocal activity peaked between 30 and 100 m depth (Fig. 3B-G). Silent periods were nearly absent at these diving depths. Moreover, silence was never recorded during dives beyond 300 m depth (Fig. 3B). The frequency of initiation of click trains was highest in the top 50 m of the water column and steadily decreased with depth (Fig. 3C). The presence of simple and intermediate whistles in the soundscape showed limited variability with depth between 50 and 500 m (Fig. 3E,F). Complex whistles were most often recorded at depths of 31 to 100 m and their occurrence steadily decreased with depth (Fig. 3G). Buzzes were present throughout the depth range (Fig. 3D). Interestingly, the highest occurrence of buzzes, at 550 m depth, coincided with a decrease in the occurrence of simple and intermediate whistles, and with an increase in the occurrence of complex whistles (Fig. 3D-G).

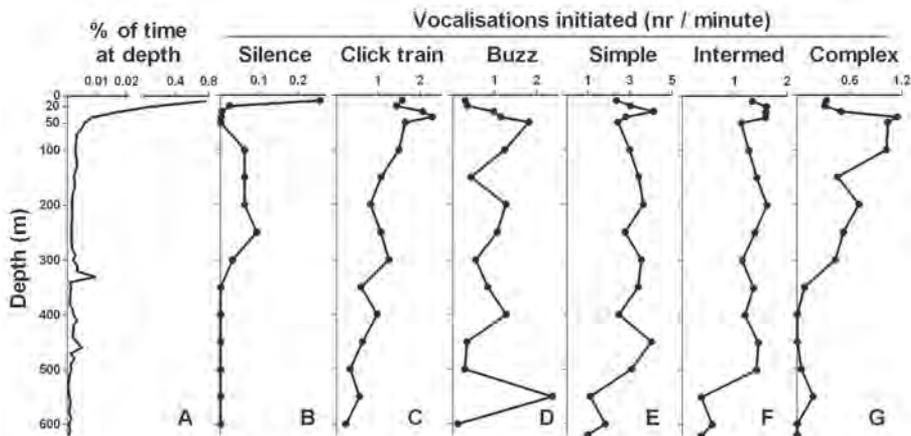


Figure 3. Time spent at depth and vocal activity in the soundscape in relation to diving depth. A) The proportion of time spent at depth by the tagged whales. B-G) The number of silent periods, click trains, buzzes, simple whistles, intermediate whistles and complex whistles per minute as a function of depth. Intermed = intermediate.

#### *Vocal behaviour during deep and shallow diving bouts*

All tagged whales performed both shallow and deep dives, except for one individual that performed shallow dives only. The maximum depth per diving bout ranged from 4 – 34 m for shallow bouts (17 bouts) and from 46 – 617 m for deep bouts (16 bouts). The tagged individuals were engaged in deep and shallow diving bouts during 27% and 73% of the behavioural samples. Redundancy analysis results revealed that the vocal behaviour differed between

shallow and deep diving bouts of the tagged individuals (Table 3A). This was confirmed by the GEE analysis, which showed that the occurrence of click trains was significantly higher during deep diving bouts than during shallow diving bouts, concordant with a significantly lower occurrence of silence (Fig. 4A,B; Table 4). There was also a tendency for higher occurrences of buzzes and whistles during deep diving bouts (Fig. 4C-F), although these differences were only marginally significant after Bonferroni correction (Table 4).

Table 3. Results of redundancy analysis (RDA) for the effects of A) diving behaviour and B) group behaviour during shallow diving bouts and during deep diving bouts, on the vocal behaviour of long-finned pilot whales. The F-test score and P-value are shown for each parameter. \*Parameters significant at  $P < 0.05$  were included in subsequent GEE analysis.

Explanatory variable	<i>F</i>	P-value	<i>F</i>	<i>P</i> -value
A)	(all)	(all)		
Deep vs. shallow diving	32.48	0.001*	-	-
Maximum depth	1.88	0.11	-	-
B)	(shallow)	(shallow)	(deep)	(deep)
Group size	18.96	0.001*	0.77	0.55
Spyhops	11.73	0.001*	0.99	0.37
Individual spacing	7.72	0.001*	1.21	0.31
Distance to other group	4.97	0.005*	2.60	0.03*
Surfacing synchrony	5.08	0.001*	1.35	0.22
Milling index	2.46	0.05*	2.79	0.02*
Nr of individuals in focal area	1.75	0.13	8.39	0.001*
Nr of groups in focal area	1.83	0.11	1.20	0.32
Logging	1.30	0.26	1.70	0.12
Line swimming	0.79	0.51	2.45	0.08

Table 4. Results of the Generalised Estimating Equation model for differences in vocalisations between deep diving bouts and shallow diving bouts. The parameter estimate, empirical standard error, Z-test score and P-value are shown for each parameter. \*Significant after Bonferroni correction at  $P < 0.05/6 = 0.008$ .

Dependent variable	Parameter	Estimate	SE	Z-score	P-value
Silence	Intercept	0.07	0.20	0.35	0.723
	Deep vs. shallow diving	-1.55	0.31	-5.05	< 0.0001*
Click train	Intercept	-1.06	0.28	-3.82	0.0001
	Deep vs. shallow diving	1.10	0.15	7.16	< 0.0001*
Buzz	Intercept	-4.37	0.33	-13.12	< 0.0001
	Deep vs. shallow diving	0.80	0.35	2.32	0.020
Simple whistle	Intercept	-3.63	0.23	-16.04	< 0.0001
	Deep vs. shallow diving	0.57	0.24	2.36	0.018
Intermediate whistle	Intercept	-4.12	0.30	-13.95	< 0.0001
	Deep vs. shallow diving	0.54	0.30	1.79	0.073
Complex whistle	Intercept	-5.46	0.29	-19.06	< 0.0001
	Deep vs. shallow diving	0.98	0.46	2.11	0.035

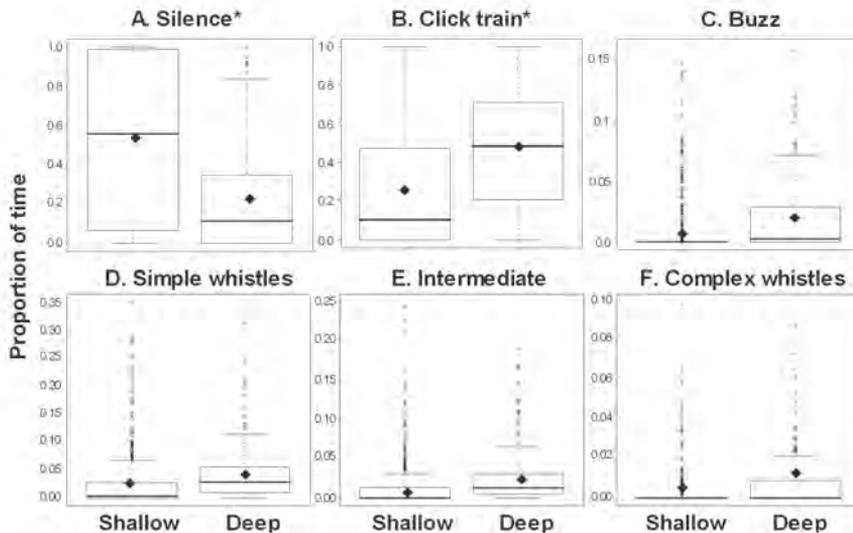


Figure 4. Vocal activity during periods of deep and shallow diving. The proportion of time pilot whales A) were silent, or produced B) click trains, C) buzzes, D) simple whistles, E) intermediate whistles and F) complex whistles during shallow diving and deep diving bouts. Diamonds indicate the mean proportion of time the vocalisation was recorded; boxes indicate interquartile range (IQR); whiskers extend to the lowest and highest data point within 1.5 IQR of the lower and upper quartile. \*Significant in the GEE model after Bonferroni correction at  $P < 0.05 / 6 = 0.008$  (Table 4).

Random forest analysis could distinguish between deep and shallow diving bouts on the basis of the vocal data with an error rate of 17.1%, and confirmed the role of buzzes and whistles. Complex whistles, buzzes and intermediate whistles were the most important vocal parameters distinguishing between shallow and deep diving bouts (Fig. 5).

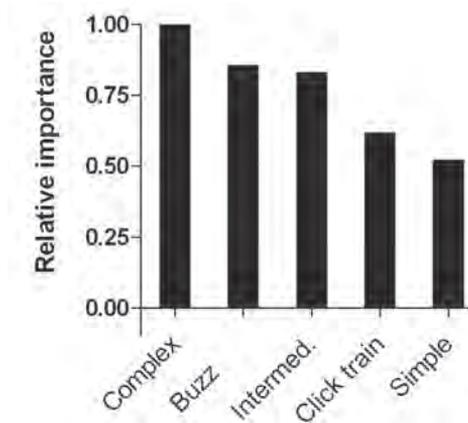


Figure 5. Relative importance of the vocal parameters in the random forest classification of deep versus shallow diving bouts.

#### *The social context of vocal behaviour*

All seven focal groups were part of larger aggregations of 60-100 pilot whales, generally composed of several groups spread out over a larger area. Focal group size ranged from 1 to 30 individuals, with a median of 11 individuals and an interquartile range of 7-13 individuals. Individuals in the focal group were mostly tightly spaced (57% of samples). Loosely spaced (18%), very tightly spaced (14%) and very loosely spaced (10%) individuals were also observed regularly. Observations of solitary individuals were rare (1%).

The pattern of vocalisations varied with group behaviour (Table 3B). Moreover, the relationships between vocalisations and group behaviour differed between shallow and deep diving bouts (Figs. 6 & 7). Redundancy analysis indicated that, during shallow diving bouts, vocal behaviour was affected by group size, individual spacing within the group, distance to the nearest other group, surfacing synchrony, milling, and the occurrence of spyhops (Table 3B).

The relationships between vocal and group behaviour were confirmed by the GEE models (Fig. 6; Table 5A). During shallow diving bouts, whales were more silent in larger, more tightly spaced groups with a lower surface activity

Table 5. Results of the Generalised Estimating Equation model for differences in vocalisations between group behaviours during A) shallow diving bouts and B) deep diving bouts. \*Significant after Bonferroni correction at  $P < 0.05/6 = 0.008$ .

Dependent variable	Parameter	Estimate	SE	Z-score	P-value
A) Shallow diving					
Silence	Intercept	-0.52	0.30	-1.72	0.08
	Group size	0.15	0.04	4.12	< 0.0001*
	Individual spacing	-0.44	0.15	-2.94	0.003*
	Spyhop	-1.63	0.19	-8.55	< 0.0001*
Click train	Intercept	-0.58	0.41	-1.43	0.15
	Group size	-0.17	0.03	-4.98	< 0.0001*
	Individual spacing	0.51	0.10	5.07	< 0.0001*
	Spyhop	1.28	0.17	7.62	< 0.0001*
Buzz	Intercept	-6.63	0.69	-9.58	< 0.0001
	Surfacing synchrony	0.92	0.37	2.5	0.013
	Spyhop	1.69	0.45	3.79	0.0002*
Simple whistle	Intercept	-3.64	0.23	-15.5	< 0.0001
	Milling	-0.87	0.23	-3.81	0.0001*
	Spyhop	0.48	0.21	2.29	0.022
Intermediate whistle	Intercept	-3.10	0.74	-4.19	< 0.0001
	Distance to other group	-0.31	0.18	-1.75	0.080
Complex whistle	Intercept	-5.43	0.28	-19.43	< 0.0001
	Milling	-1.97	0.47	-4.16	< 0.0001*
B) Deep diving					
Silence	Intercept	-3.11	0.12	-26.99	< 0.0001
	Nr of individuals in focal area	0.11	0.01	9.26	< 0.0001*
	Milling	-1.57	0.39	-4.04	< 0.0001*
Click trains	Intercept	0.62	0.14	4.38	< 0.0001
	Distance to other group	0.12	0.03	3.71	0.0002*
	Nr of individuals in focal area	-0.06	0.01	-6.85	< 0.0001*
Buzz	Intercept	-3.74	0.12	-30.71	< 0.0001
	Milling	0.95	0.20	4.7	< 0.0001*
Simple whistles	Intercept	-2.77	0.24	-11.58	< 0.0001
	Nr of individuals in focal area	-0.02	0.02	-1.27	0.20
Intermed. whistles	Intercept	-3.58	0.08	-46.13	< 0.0001
	Nr of individuals in focal area	0.00	0.01	-0.05	0.96
Complex whistles	Intercept	-4.40	0.33	-13.4	< 0.0001
	Milling	-0.95	0.41	-2.29	0.02

(fewer spyhops) (Fig. 6A,B,D). In contrast, the occurrence of click trains was higher when the pilot whales were organised in smaller groups, with more loosely arranged individual spacings and more spyhops (Fig. 6E,F,H). The production of buzzes was also positively correlated with the presence of spyhops (Fig. 6L). Simple and complex whistles were negatively associated with the presence of milling (Fig. 6O; Table 5A).

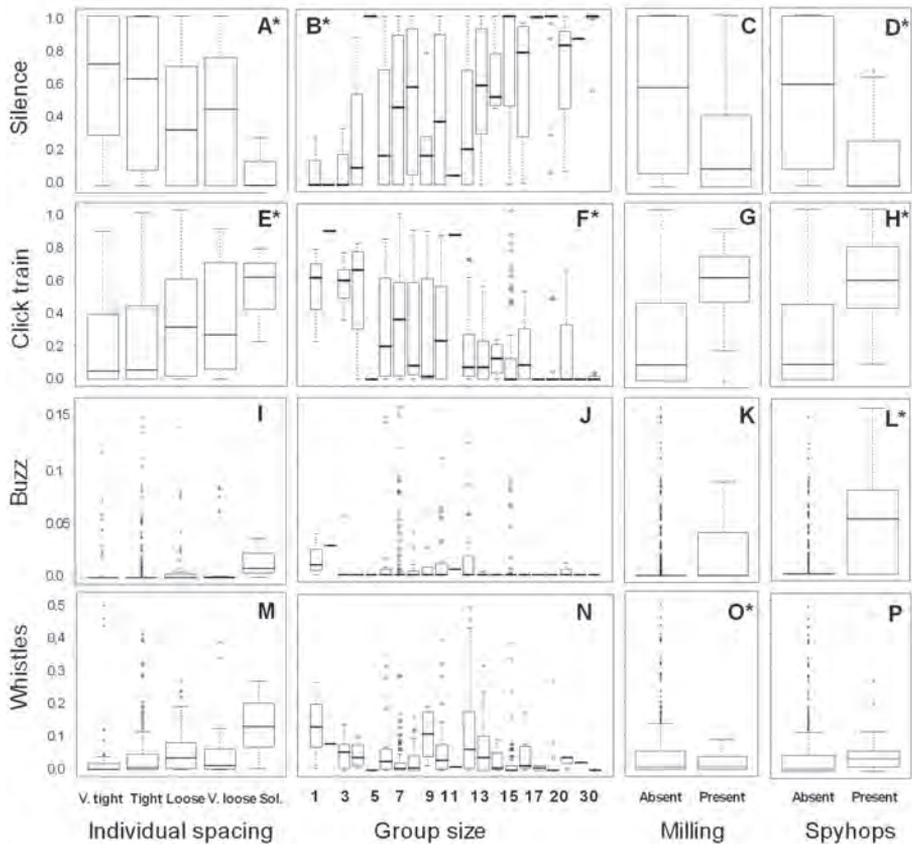


Figure 6. Vocal activity in relation to group-level behaviour during shallow diving bouts. The proportion of time whales were silent or produced click trains, buzzes and whistles (simple, intermediate and complex) in relation to individual spacing in the focal group (A,E,I,H), group size (B,F,J,N), the presence of milling (C,G,K,O) and the presence of spyhops (D,H,L,P). Only those group-level behaviours are shown for which at least one vocalisation type was significant (indicated by \*) in the GEE model after Bonferroni correction at  $P < 0.05 / 6 = 0.008$  (Table 5A).

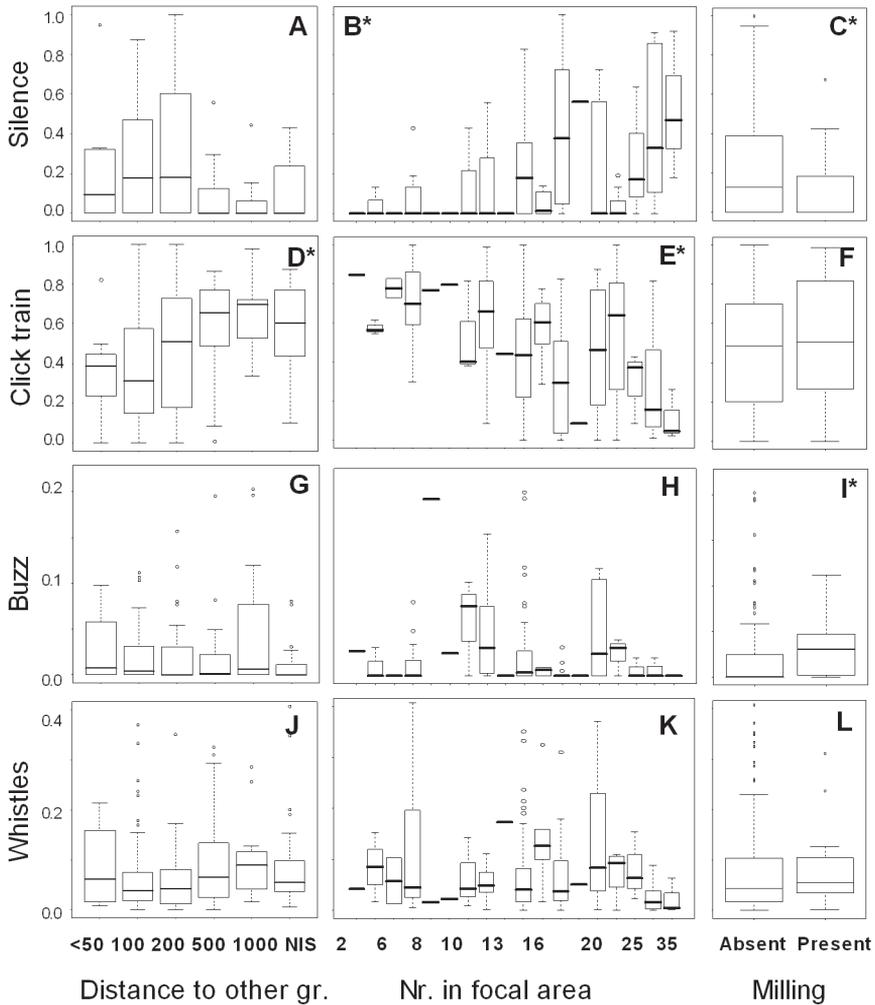


Figure 7. Vocal activity in relation to group-level behaviour during deep diving bouts. The proportion of time whales were silent or produced click trains, buzzes and whistles (simple, intermediate and complex) in relation to the distance to the nearest other group (A,D,G,J), the number of individuals in the focal area (B,E,H,K) and the presence of milling (C,F,I,L). Only those group-level behaviours are shown for which at least one vocalisation type was significant (indicated by \*) in the GEE model after Bonferroni correction at  $P < 0.05 / 6 = 0.008$  (Table 5B). NIS = none in sight.

The redundancy analysis revealed that, during deep diving bouts, vocal behaviour was affected by the number of individuals in the focal area, distance to the nearest other group, and milling (Table 3B). This was confirmed by the GEE analysis, which showed that whales were more silent when there were more individuals in the focal area and when the presence of milling was low

(Fig. 7B,C; Table 5B). The occurrence of click trains was negatively correlated with the number of individuals in the focal area, and increased at larger distances between groups (Fig. 7D,E). Buzzing activity was positively correlated with the presence of milling (Fig. 7I). The whistle types did not show a relationship with group behaviour during periods of deep diving (Fig. 7J-L).

## Discussion

Our results provide new insights in the functionality of long-finned pilot whale vocalisations. We identified a series of relationships between vocalisations, the social context of individuals, and their diving behaviour. Long-finned pilot whales were relatively silent during shallow dives but strongly increased their vocal activity during deep-diving bouts. Long-finned pilot whales reduced their vocal activity in the presence of larger numbers of individuals, at closer distances to others and with a higher degree of surface active behaviour. During periods of shallow diving, this association occurred at the level of the group (individual spacing within the group, group size). In contrast, during periods of deep diving, the association between vocal and group behaviour occurred at the level of the focal area (distance to the nearest other group, number of individuals within 200 m).

### *Vocal signature of foraging behaviour*

Deep dives of long-finned pilot whales are associated with foraging on their major prey species, deep-sea squid, which generally occur at several hundred meters depth (Baird et al. 2002). Periods of deep diving behaviour were characterised by more vocal activity, with more echolocation clicks as well as whistles, than shallow diving bouts. Click trains showed the largest increase, whereas buzzes and complex whistles were the most important vocalisation types in the random forest classification of foraging versus non-foraging behaviour. These results are consistent with the use of bio-sonar (click trains and buzzes) during foraging. The consistent presence of simple and intermediate whistles and increased levels of clearly audible complex whistles during periods of deep diving indicate that foraging individuals stayed within audible ranges of each other. Moreover, it shows that during foraging, social communication was intensified in terms of the number of whistles and their complexity.

Complex whistles, which were relatively rare, were associated with deep foraging dives. Interestingly, these calls were nearly absent from the soundscape at deep diving depths (beyond 350 m), which may be related to pressure-induced restrictions of tonal call production at large depths (Jensen et al. 2011). The use of more complex whistles during foraging may indicate that calls need to convey more, or different, information or need different characteristics to transfer their information. The longer complex whistles have a higher energy content than the shorter simple whistles, and can therefore convey information over longer distances (Jensen et al. 2011). As group members potentially disperse much further from each other during deep foraging dives than during shallow diving, the production of complex whistles during deep dives could compensate for this strong increase in distance. Visser et al. (Chapter 2 in this thesis) suggested that the synchrony in foraging periods of long-finned pilot whales may be related to the signalling of good feeding opportunities by individuals with more local knowledge, for example at greater depths. Potentially, complex whistles could function to convey such information between the knowledgeable sender at depth and the receiver at the surface, or vice versa.

### *Silent crowds*

The soundscape of the long-finned pilot whales contained a rich repertoire of different vocalisations, and all vocalisation types could co-occur. For such a vocal species, periods of silence may be a highly informative characteristic of its vocal behaviour. The absence of vocalisations may indicate that the behavioural or social factor driving the production of the call has (temporarily) lost significance. Silence was recorded significantly more often during periods of shallow diving than during deep dives, when the whales rely on sound to find prey. The counter-intuitive, positive relationship between the number of nearby whales and the occurrence of silent periods indicated an active reduction in vocal activity at higher levels of social cohesion. This is consistent with the primary function of social calls in maintaining or re-establishing social ties, to mediate group cohesion of social animals (Palombit 1992, Tyack 2000). It also supports previous findings, which indicate that long-finned pilot whales produce more, and more complex, communication calls at larger spread of the aggregation and during more complex behaviours (Weilgart & Whitehead 1990). However, here, the presence of silence during shallow diving periods was mostly driven by a reduction of echolocation activity (click trains).

Silent periods may represent a resting state, during which whales move closer together and closely coordinate their behaviour to maintain group cohesion in the absence of vocal cues. Animals may be also silent as a cryptic behaviour, for example to avoid detection from predators or prey. While cetaceans are known to use this silencing strategy (Soto et al. 2011, Rankin et al. 2012), this is likely not the case for pilot whales. When the long-finned pilot whale groups of this study were exposed to playbacks of calls of their potential predators, killer whales (*Orcinus orca*), they did not respond with a cryptic behaviour, but actively approached the sound source (Curé et al. 2012). Moreover, given the high degree of vocal activity, it seems unlikely that silent periods of pilot whales at the scale of minutes would strongly reduce their acoustic detectability by predators.

#### *Vocalisations during non-foraging periods*

The ubiquitous presence and relatively limited relation with social context and diving depth of simple whistle types, combined with low importance in the random forest classification between deep and shallow diving periods, suggests that these simple calls are produced throughout the behavioural spectrum, without a specific association to a behavioural or social context. Several species of social cetaceans are known to use stereotyped calls to signal individual or group identity (e.g. Ford & Fisher 1983, Janik & Slater 1998). The closely related short-finned pilot whales (*Globicephala melas*), thought to have a comparable foraging strategy and social organisation, also regularly produce tonal calls, including at large depths (Jensen et al. 2011). Their simple whistles produced at depth likely serve to maintain or re-establish contact between group members when deep-diving individuals disperse from their associates. They may have sufficient information to signal group or species identity (Jensen et al. 2011). In long-finned pilot whales, the simple calls may have a comparable function, serving as an acoustic cue to signal presence and identity to group members throughout the behavioural and depth spectra, in an environment with many groups of conspecifics and where the use of visual cues is limited.

Click trains and buzzes were also recorded outside of the foraging period, and throughout the depth spectrum, indicating possible extended functionality of these vocalisations. Click trains in particular were regularly recorded during shallow diving periods (24% of recording time). Moreover, the intensity of clicking was associated with social context. The occurrence of clicking increased

in smaller, more widely spaced groups, displaying surface active behaviours. These clicks may originate from other individuals in the group which were foraging, while the tagged individual was shallow diving. Alternatively, it may indicate that long-finned pilot whales also use clicks outside of the foraging period, to gain information on the location of nearby conspecifics, and potentially as a social cue, serving to maintain group cohesion during less coordinated behavioural states. The function of clicks in communication and social cohesion has been recorded in several other odontocetes, such as sperm whales and Blainville's beaked whales (*Mesoplodon densirostris*). However, these species generally do not produce tonal calls (Dawson 1991, Weilgart & Whitehead 1993, Dunn et al. 2013).

#### *Future challenges*

The broad classification of tonal calls as applied here represents a major simplification of the social call repertoire of long-finned pilot whales (Taruski 1979). The relatively weak association between social context and simple and intermediate whistle types may be related to a restricted ability to separate different whistle types, and hence different functions, using this broad categorisation. Given the apparent continuum of call types, with potentially different functions at increasing complexity (Weilgart & Whitehead 1990), our classification was targeted at distinguishing different functionalities at both extremes of the spectrum, simple and complex whistle types. Future studies could benefit from additional classifications of the simple whistle types, such as the classification into frequency upsweeps or downsweeps (Weilgart & Whitehead 1990, McCowan & Reiss 2001).

#### *Conclusions*

Our results showed high vocal activity during the foraging dives of long-finned pilot whales, with a possible role for complex whistles in the communication between animals during the dives. Pilot whales strongly reduced their vocal activity at higher degrees of social cohesion, when they were at rest in tight groups at the water surface. These results relied on the combination of recordings of the soundscape and diving behaviour of tagged individuals with group-level observations. For vocal cetaceans such as pilot whales, which cannot be observed during their dives, increased understanding of their vocal repertoire may greatly enhance our ability to recognize their functional behaviour.

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