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Calling under pressure: short-finned pilot whales make social calls during deep foraging dives

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Toothed whales rely on sound to echolocate prey and communicate with conspecifics, but little is known about how extreme pressure affects pneumatic sound production in deep-diving species with a limited air supply. The short-finned pilot whale (*Globicephala macrorhynchus*) is a highly social species among the deep-diving toothed whales, in which individuals socialize at the surface but leave their social group in pursuit of prey at depths of up to 1000 m. To investigate if these animals communicate acoustically at depth and test whether hydrostatic pressure affects communication signals, acoustic DTAGs logging sound, depth and orientation were attached to 12 pilot whales. Tagged whales produced tonal calls during deep foraging dives at depths of up to 800 m. Mean call output and duration decreased with depth despite the increased distance to conspecifics at the surface. This shows that the energy content of calls is lower at depths where lungs are collapsed and where the air volume available for sound generation is limited by ambient pressure. Frequency content was unaffected, providing a possible cue for group or species identification of diving whales. Social calls may be important to maintain social ties for foraging animals, but may be impacted adversely by vessel noise.

Keywords: communication; sound production; social organization; pilot whales; acoustic tags; ecophysiology

1. INTRODUCTION

Environmental conditions affect the production and propagation of sound and hence play a role in the evolution of acoustic signalling in animals. Ambient temperature influences the sound production of poikilotherm animals, and changes in frequency, duration and amplitude of calls in response to temperature variations have been documented for various phyla such as insects [1,2], frogs [3,4] and fishes [5]. Some endotherm mammals may have juveniles that are unable to maintain a constant body temperature, and where temperature variations may influence the production of signals such as the isolation calls of vespermillionid bat pups [6]. However, most birds and mammals are functionally homeothermic and their sound production system is consequently unaffected by local temperature variations. In these species, signal characteristics mainly reflect adaptations to environmental differences in sound attenuation, reverberation and ambient noise levels that optimize the transmission distance of the signal [7,8]. However, some mammals have adapted to habitats of extreme pressure that may also affect their sound production. Toothed whales, comprising around 72 extant species, produce a variety of acoustic signals to communicate with conspecifics as well as to navigate and find prey at depths that may exceed 1000 m [9]. This raises the question of how the large span in hydrostatic

pressure might affect air-driven sound production in these marine mammals that rely on sound for foraging and communication in the deep sea [10].

Most toothed whales produce dedicated tonal signals for communication and clicks for echolocation. Echolocation clicks are produced pneumatically by forcing pressurized air from ventral nasal passages past the phonic lips [11,12]. Each time the phonic lips separate, a small volume of air is passed through the phonic lips into vestibular air sacs [13]. When whales are submerged, they must recycle air in their nasal system to maintain continued sound production [14]. In contrast to echolocation signals, little is known about how tonal sounds are generated and coupled to the environment. It may be speculated that tonal sounds arise when phonic lips vibrate continuously instead of separating in discrete instances as in click generation [12,15]. This has been corroborated by studies showing that, at least at atmospheric pressure, a higher nasal pressure and more air volume are required to generate tonal sounds compared with echolocation clicks [16,17].

As a whale dives, hydrostatic pressure increases with depth and air volumes in the body are compressed following Boyle's Law. Alveolar collapse is estimated to occur in bottlenose dolphins around 70–100 m depth [18,19], and the remaining compressed air volume is shunted to the less compressible nasal passages where it is available for sound production [14,20] and where it continues to be further compressed as the whale descends. Diving

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toothed whales therefore face the challenge of producing echolocation clicks, and possibly communication sounds, with a dwindling supply of air available for pneumatic sound production. Several tag studies have demonstrated that the production of echolocation clicks can be maintained during very deep dives [20–22], but whales seem to recycle air more often at depth where remaining air volume is smaller [23]. Tonal sounds are longer and require a greater nasal pressure to produce than do echolocation clicks [16,17]. It would therefore follow that tonal sounds would more likely be affected by depth. In the only study addressing the production of communication sounds at depth so far, Ridgway *et al.* [10] found that whistle amplitude generally decreased with depth for two beluga whales trained to emit a response whistle, and that one animal was seemingly unable to produce whistles at 300 m. This suggests that deep-diving social toothed whales may have difficulty producing whistles and maintaining acoustic communication during deep dives.

The short-finned pilot whale (*Globicephala macrorhynchus*) is an example of a social, deep-diving toothed whale with long-lasting inter-individual associations within their social group [24]. It has been hypothesized that these groups are similar to the matriarchal groups found in the related long-finned pilot whales [25,26] and resident killer whales [27,28]. Recent studies using acoustic tags have shown that short-finned pilot whales make deep daytime foraging dives exceeding 1000 m [29], and indicate that the whales forage individually or in small groups [30]. Although pilot whales are known to be highly vocal when socializing at the surface, nothing is known about the effects of extreme pressure on pneumatic sound production and how the deep-diving ecology of pilot whales may have shaped the evolution of their acoustic communication capacity. The study by Ridgway *et al.* [10] suggests that deep-diving toothed whales are impeded in their ability to produce tonal communication sounds at depth and may even be unable to produce tonal communication signals below a certain depth, like one individual in the study. Here, we test this hypothesis by analysing data from sound and orientation recording DTAGs [31] on short-finned pilot whales in the wild. We show that short-finned pilot whales produce communication calls during deep foraging dives down to depths greater than 800 m. We demonstrate that the energy output of calls at great depths is reduced by an order of magnitude, and that the calls are shorter at depth compared with shallow calls, but do not seem to be restricted in frequency content. We discuss these findings in the light of models for pneumatic sound production, and address implications of these effects on the function of acoustic communication and foraging ecology at depth in this highly social delphinid.

2. MATERIAL AND METHODS

Two tagging cruises were conducted in the spring of 2006 and 2008 off the southwest coast of Tenerife, Canary Islands, where there is a resident population of *G. macrorhynchus* [24]. DTAGs [31] were attached with suction cups to record sound (two channels, 96 or 192 kHz sampling rate per channel, 16-bit resolution), three-dimensional orientation

(derived from three-axis accelerometers and magnetometers) and depth of the tagged pilot whales.

Sound recordings were analysed using MATLAB 6.5 (Mathworks) to identify the time and depth of vocalizations from the tagged animal. Vocalizations were broadly classified into tonal, intermediate and pulsed sounds [32] based on visual inspection of the waveforms and spectrograms of each call. Vocalizations from the tagged animal were discriminated from conspecific vocalizations based on their increased low-frequency content (propagating through the body of the tagged whale but poorly coupled to the surrounding water) and generally higher received levels [9]. Subsequently, each call was cross-correlated between the two tag hydrophones (separation 23 mm) to get an estimate of the angle-of-arrival of the call. If conspecific clicks or extraneous noise sources overlapped with the call, an angle-of-arrival was found using interference-free parts of calls for cross-correlation. Calls were accepted only if the angle-of-arrival could be measured unambiguously. For each whale, vocalizations initially classified as tagged whale sounds but with an angle-of-arrival of more than 10° from the mean angle-of-arrival of calls produced by that whale were discarded from the analysis to reduce the possibility of including calls from conspecifics [9,33]. Despite these analytical steps, it cannot be entirely excluded that some conspecific calls may have been erroneously classified as tagged whale calls. However, the high received levels of these calls indicate that they were produced near the tagged whale and so would be subject to similar depth effects. Furthermore, given the number of calls investigated here, it is unlikely that a few misclassifications would change the overall conclusions.

All tonal calls interpreted as produced by the tagged whale during deep dives were filtered with a 6-pole variable high-pass filter (low-frequency cut-off between 500 and 2000 Hz, but always well below the minimum fundamental frequency) to reduce flow noise from the recording. A root mean square (r.m.s.) noise measure was derived from a 0.1 s window following each call, and the call duration was then defined as the length of a window containing 95 per cent of the total signal energy after subtracting the noise power. The signal-to-noise ratio was calculated as the difference in r.m.s. signal amplitude and r.m.s. noise amplitude on a decibel scale, and signals with less than 10 dB signal-to-noise ratio were excluded from further analysis. Within the signal window, the r.m.s. pressure was corrected for the nominal tag hydrophone sensitivity (-182 dB re 1 V μPa^{-1}) to compute the received sound level (r.m.s.) at the tag, then squared and multiplied by the window length to find the energy flux density (EFD) of the call. As tag placement differed between whales, the received level was taken as an uncorrected estimate of the sound level of the calls produced by each whale, termed the apparent output ($\text{AO}_{\text{r.m.s.}}$ and AO_{EFD} , respectively) following Madsen *et al.* [34]. Calls sampled at 192 kHz were decimated by a factor of 2, after which a spectrogram was computed with 5 ms Hanning windows (480 samples, zero-padded to 4096 samples for fast Fourier transform (FFT) computation) with 50 per cent overlap for a spectral resolution of 200 Hz and a temporal resolution of 2.5 ms. A supervised trace of the fundamental frequency contour [35] was used to derive the fundamental minimum (F_{min}), mean (F_{mean}) and maximum (F_{max}) frequency over the 95 per cent energy window. Spectral power distribution was estimated using the Welch method [36] by summing power spectra within the 95 per cent energy

window. The peak frequency, F_p (defined as the frequency with highest spectral power) and the centroid frequency, F_c (defined as the frequency separating the power spectrum into two halves with the same amount of total energy) were computed from the power spectrum [37].

Analysis of covariances (ANCOVAs) between depth and apparent output, duration and frequency were performed using JMP v. 7.0 (SAS Institute), treating tag ID as a covariate to account for differences in tag placement and potential inter-individual differences in call characteristics. Normality of error and homogeneity of variance were improved by log-transforming depth, duration and frequency, and by using apparent output on a log-based decibel scale. Correlations of signal parameters against depth were further tested by randomization using R (R Development Core Team, Vienna, Austria). Vocalizations from all whales were indexed against $\log(\text{depth})$. For each response variable, a generalized linear model with random intercept and random slopes for individual whales was constructed. The linear regression test statistic t was calculated as the slope of the regression divided by the standard error of the slope. The test statistic was computed for 10 000 permutations of the depth vector, where the response variable vector was associated with a permutation of the depth vector for each individual whale. A significance value was obtained as the fraction of permutation test statistics exceeding the test statistic for the original dataset [38].

3. RESULTS

Tagging of 12 whales provided a total of 58.8 h of recordings (table 1) including 58 deep foraging dives (defined as exceeding 300 m) with a median depth of 685 m. In addition to previously described echolocation clicks and buzzes [29], short-finned pilot whales produced harmonically rich tonal sounds throughout many of their deep foraging dives (figure 1). The call rate per dive differed greatly between dives and across whales (table 1) with an overall decrease in call rate with depth (figure 2) and most (66%) calls produced in the ascent phase of the dive. Deep calls were found in all tagged whales except one (not included in the analysis as calls were produced only at <170 m depth), with two calls as deep as 800 m (figure 2).

Calls produced during deep dives ($n = 474$) had median peak frequencies of 3.9 kHz (5–95th percentiles: 1.8–12.3 kHz) and higher median centroid frequencies of 7.3 kHz (5–95th percentiles: 3.7–13.3 kHz) owing to the multiple call harmonics. Even though the centroid frequency increased with depth (table 2; $p = 0.001$), only 2 per cent of the variance was explained and the pattern was not a simple increase with depth (figure 3). By contrast, peak frequency tended to decrease somewhat, but depth had an equally low explanatory power (table 2; $p = 0.002$). Frequency parameters based on the fundamental frequency contour also showed little difference across depths (table 2). In randomization tests, peak frequency ($p = 0.0054$) and maximum contour frequency ($p = 0.0271$) were significantly correlated with depth. The remaining frequency parameters were not significantly correlated with depth ($p > 0.05$), and the centroid frequency was highly insignificant ($p = 0.82$).

Calls were significantly shorter when produced at depth, with call duration halved for every 10-fold

Table 1. Overview of tags contributing to analysis. (The asterisks indicate significant negative correlation between AO_{EFD} and $\log(\text{depth})$: $p < 0.01$.)

tag	year	sample rate (kHz)	duration (h)	deep dives	tonal calls in dives
Pw06_081e	2006	96	8.15	11	87*
Pw06_081g	2006	96	3.74	2	23*
Pw06_082c	2006	96	4.80	2	33*
Pw06_085h	2006	96	6.29	5	8
Pw08_108d	2008	192	8.00	8	18*
Pw08_110b	2008	96	4.26	5	69*
Pw08_110c	2008	192	7.40	2	9
Pw08_110d	2008	192	7.49	9	63*
Pw08_112b	2008	96	2.81	6	28
Pw08_112e	2008	192	1.12	3	11
Pw08_113b	2008	96	2.58	2	44
Pw08_113e	2008	192	2.18	3	81*

increase in depth (table 2; $p < 0.0001$). Even though the 95 per cent energy duration was correlated to the signal-to-noise ratio and hence signal amplitude ($r^2 = 0.27$), a negative correlation persisted even if $AO_{\text{r.m.s.}}$ was included in the model as an additional explanatory variable.

AO amplitude ($AO_{\text{r.m.s.}}$) and energy (AO_{EFD}) decreased significantly with depth in seven of 12 individual whales (individual regression of AO_{EFD} against $\log(\text{depth})$ with $p < 0.01$ marked with an asterisk in table 1), including the whales producing the most calls. To pool data from all whales, it was necessary to correct for tag differences by subtracting individual tag means. Unfortunately, this inevitably removed some variance that would have been explained by depth as the mean depth of vocalizations varied between whales. After correcting for tag means, $AO_{\text{r.m.s.}}$ and AO_{EFD} were nonlinearly correlated with $\log(\text{depth})$, seen as an initial increase followed by a subsequent decrease over the depth examined (figure 3a). To test the apparent nonlinear relationship between call level and $\log(\text{depth})$, we included a second-order term of $\log(\text{depth})$ as an additional explanatory variable. This second-order dependency between AO_{EFD} and $\log(\text{depth})$ was significant (effects test of $(\log(\text{depth}))^2$: $F = 41.9$, $p < 0.0001$) with a peak around 80 m, corresponding to the approximate depth of alveolar collapse of bottlenose dolphins [18,19]. Calls produced below this depth were isolated and further analysed to quantify the effects on sound production after lung collapse. Calls produced below 80 m decreased in amplitude and energy content with increasing depth (table 2; $p < 0.0001$). Depth accounted for 20–24% of the variance and was responsible for a 100-fold decrease in energy per 10-fold increase in depth (table 2).

4. DISCUSSION

(a) Tonal calls are produced at great depth throughout deep foraging dives

Animals living in cohesive associations undergoing temporary changes in group structure during foraging activities are expected to communicate to maintain group cohesion and coordinate activities [39,40]. Short-finned

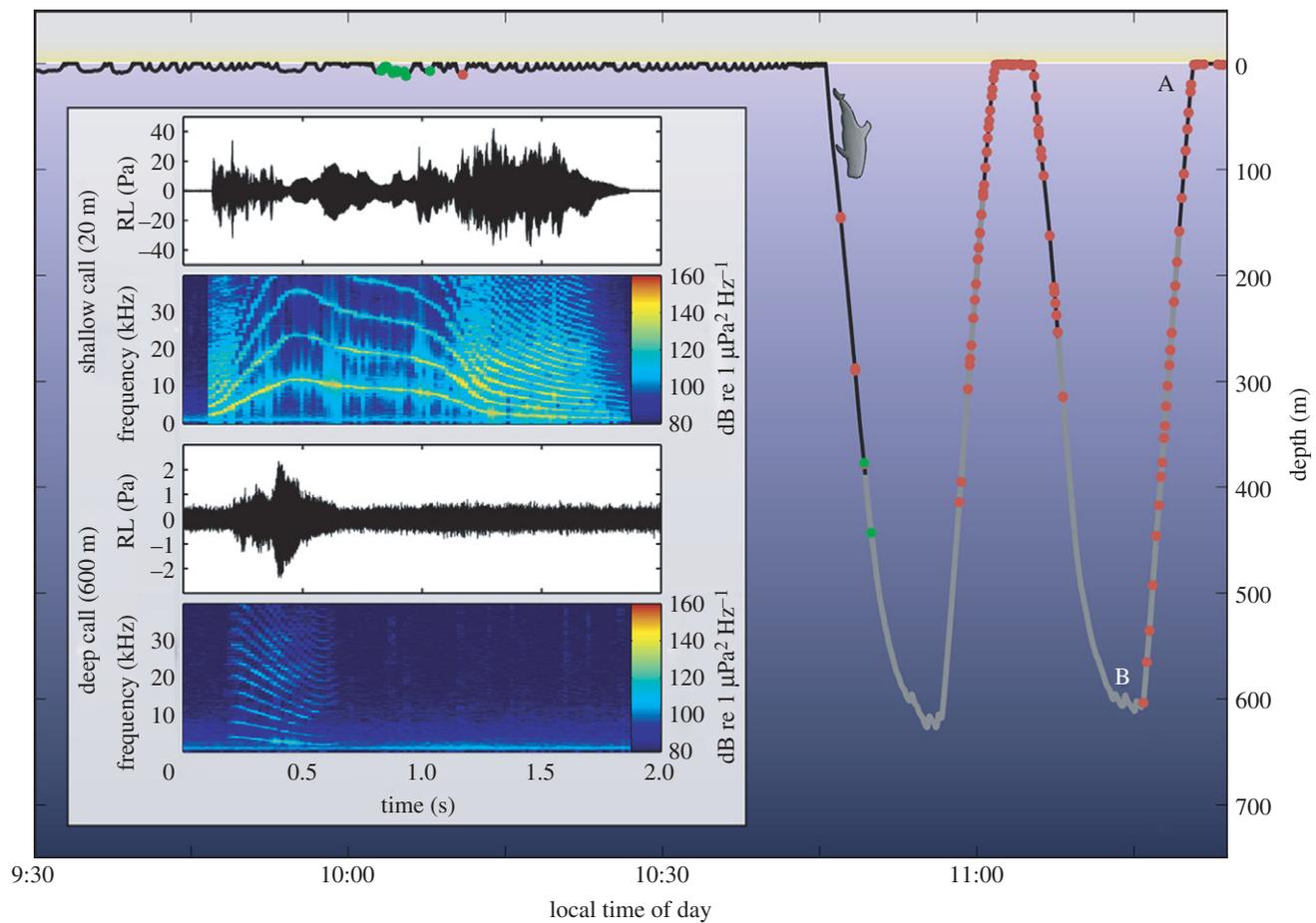


Figure 1. Annotated dive profile of a tagged short-finned pilot whale comprising a period of surface resting or socializing followed by two deep foraging dives. Two tonal calls from the last ascent (see letters in dive profile) are shown as inset waveforms and spectrograms (sampling rate 192 kHz, FFT size 4096 samples, 50% overlap): call A was produced by the tagged whale near the end of the dive, close to the surface and call B was produced at the bottom of the dive. Note the lower amplitude and shorter duration of the deep call. Grey lines, regular clicking; red dots, tonal call; green dots, pulsed call.

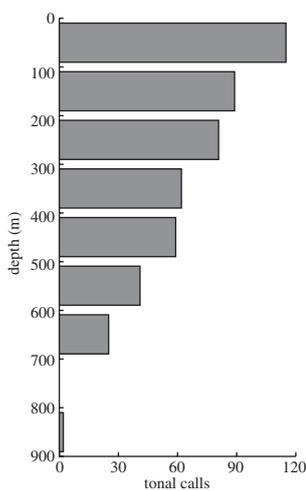


Figure 2. Histogram showing the number of tonal calls produced during deep dives by 12 tagged short-finned pilot whales (*Globicephala macrorhynchus*) as a function of depth.

pilot whales have a cohesive long-term group structure [24] and regularly leave their social group during deep foraging dives to depths exceeding 1000 m [29]. While previous studies suggest that whales might be unable or reluctant to make calls at these depths [10], this study shows that deep-diving pilot whales regularly produce tonal calls

throughout deep foraging dives (figure 1) interspersed with previously described echolocation clicks and buzzes [29]. Tagged pilot whales were able to produce tonal calls at more than twice the depths tested by Ridgway *et al.* (figure 2). Taken together with another concurrent study reporting whistles at great depths in a Blainville's beaked whale [41], this demonstrates that toothed whales from different families can make tonal sounds during very deep dives and suggests that there may be no strict physiological depth limit on tonal sound communication in cetaceans.

The calls of pilot whales described here were made at depths of up to 600 m, and in two cases as deep as 800 m. As these calls occur in foraging dives, it is tempting to consider that they may serve similar roles as bottlenose dolphin bray calls that have been hypothesized to alter the behaviour of prey, to call attention to patches of food or to coordinate foraging with group members [42]. However, pilot whales seem to hunt for large, caloric squid during the day, where bursts of high vertical speeds are necessary to catch the prey [29]. It is unlikely that any acoustic manipulation of prey behaviour is taking place as squid do not seem to detect the pressure component of a sound field [43,44]. Given the general decrease in calling activity of tagged whales at foraging depths (figures 1 and 2) and the apparent lack of dive synchrony in this population [30], calls at depth do not seem

Table 2. Results of ANCOVA regression against log(depth).

effect	slope	95% CI	<i>n</i>	<i>r</i> ²	<i>F</i>	<i>p</i>
all calls						
log(<i>F</i> _c)	0.06	(0.02 : 0.09)	474	0.02	10.6	0.001
log(<i>F</i> _p)	-0.10	(-0.15 : -0.03)	474	0.02	9.63	0.002
log(<i>F</i> _{min})	0.03	(-0.01 : 0.07)	474	0.01	2.37	0.125
log(<i>F</i> _{mean})	-0.05	(-0.09 : -0.01)	474	0.01	6.59	0.011
log(<i>F</i> _{max})	-0.08	(-0.12 : -0.04)	474	0.03	12.9	0.0004
log(Dur _{95%})	-0.31	(-0.39 : -0.22)	474	0.11	56	<0.0001
calls below 80 m						
AO _{r.m.s.}	-18.2	(-21.5 : -14.8)	387	0.24	115	<0.0001
AO _{EFD}	-20.5	(-24.6 : -16.3)	387	0.20	94.2	<0.0001

to serve in cooperative foraging with other diving animals either. An alternative and more parsimonious explanation given the predominance of calls in the ascent phase would be that calls primarily serve to maintain or re-establish social ties during individual foraging periods when the whale is far from its social group at the surface. This has already been hypothesized for long-finned pilot whales [45] and resembles how acoustic signals are believed to mediate social cohesion and group structure in other toothed whales [32,46] and other group-living animals such as birds [47] and primates [48,49].

(b) Call frequency content is robust to changes in depth

Little is known about the production of tonal sounds in toothed whales or how these sounds are coupled into water, but it has been hypothesized that resonances in the nasal passages or vestibular air sacs may be involved [13]. As these air spaces probably shrink with depth to accommodate the reducing air volume, higher resonance frequencies or emphasis of higher harmonics would be expected at depth. A significant shift of energy towards higher harmonics, and consequently higher centroid and peak frequency, was noted for trained belugas whistling at depth [10]. Ridgway *et al.* argued that changing air density affecting the flow of air might explain the change in frequency [10]. However, we found poor correlations between frequency content and depth for the free-ranging pilot whales studied here (table 2 and figure 3). Both high- and low-frequency calls were produced at depth (figure 3), suggesting that the slight shift in frequency may have a behavioural explanation rather than a biophysical one. Hence, our results do not support the notion that toothed whales should be limited to high-frequency signals when diving deep but demonstrate that pilot whales contrary to trained belugas are capable of maintaining frequency content even at great depths.

(c) Call duration and output is physically limited by hydrostatic pressure

Calls produced at depth were generally shorter and contained much less energy when compared with shallower calls (figure 3). Average call duration was halved for every ten-fold increase in depth, while AO_{EFD} decreased 100 times (20 dB) for similar depth increases below about 80 m. Given that there is little evidence for synchronous diving in this population [30], the most

plausible receivers of calls made during dives would be members of the social group remaining at the surface. During these regular separations from their group, foraging whales have to transmit information over greater distances the deeper they descend, and would need to produce calls with more energy to compensate for the increased distance to the social group. This might be achieved by producing higher amplitude calls, as communication distance increases, or longer calls as has been shown in both macaques and squirrel monkeys [50,51]. The observed reduction in pilot whale vocal output and duration at great depth is in sharp contrast with these predictions. During foraging at depth, more air might be invested in echolocation signals at the cost of potentially decreasing duration, amplitude or number of calls at depth. However, the prevalence of calls during the ascent phase of foraging dives, after most foraging events and where echolocation click series are more sporadic, makes it difficult to explain our results by an increased focus on foraging efforts with depth. Instead, the decrease in call amplitude and duration in spite of an increasing communication range is consistent with the hypothesis that the pneumatic sound generator is limited by the high ambient pressure at depth [10].

In contrast with our results, Ridgway *et al.* [10] did not find any changes in the duration of whistles with increasing depth. However, this might be a consequence of the training procedure if the animals perceived the duration of the response whistle as important to receive a reward [52]. Furthermore, it is noteworthy that whistles in the Ridgway study were already short (duration approx. 0.1 s and approx. 0.3 s for the two belugas) and that the beluga producing the longer whistles switched to a pulse train instead of a whistle at 300 m depth. Trained beluga whales did decrease their whistle amplitude with depth much like the pilot whales studied here [10]. Ridgway *et al.* argued that this might indicate a biophysical constraint on sound communication related to the increasing density of air used for sound production at depth. If this were the case, the call amplitude should decrease inversely with increasing hydrostatic pressure as whales dive. However, this hypothesis is not supported by our data (figure 3). Rather, the gradual reduction in sound level beginning around 80 m depth suggests that the air volume available for sound generation in the nasal passages is limiting the output of the whale, rather than air density. While the total air volume in the body of the whale is compressed from the very beginning of the deep dive, air from the

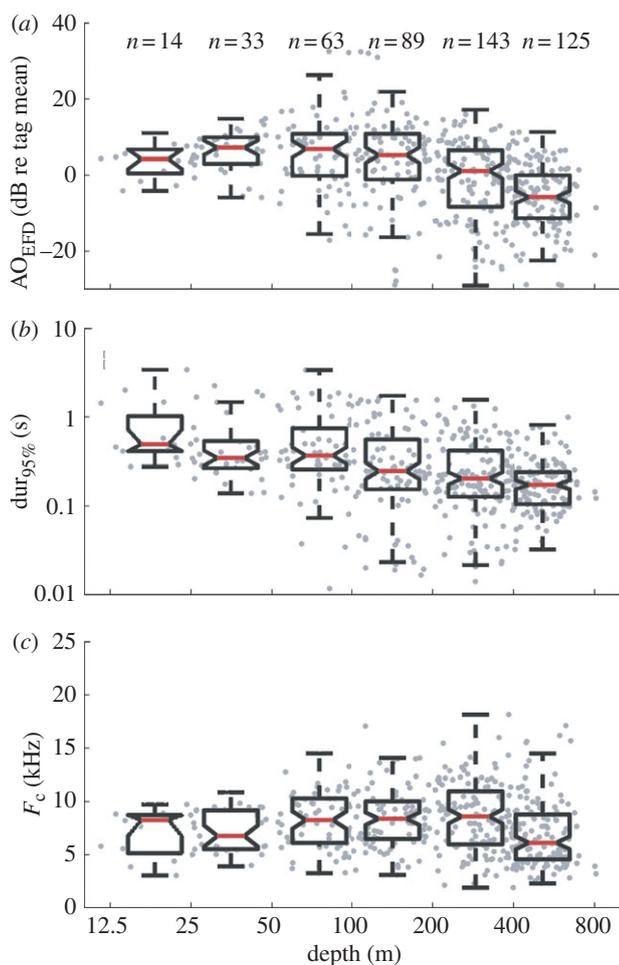


Figure 3. Acoustic parameters of tonal calls produced during deep dives by 12 tagged short-finned pilot whales (*Globicephala macrorhynchus*) as a function of depth: (a) energy flux density (AO_{EFD}) corrected for tag differences by subtracting mean tag values; (b) 95% energy duration ($dur_{95\%}$) and (c) centroid frequency (F_c). Pooled data points from all whales (grey) have been grouped into geometrically increasing depth bins (demarcated by depth-axis values) to form notched box plots, showing the 25th, 50th (median) and 75th percentile (lower, mid and upper lines in the box) of the calls within each depth bin. Whiskers mark the lowest and highest datum within 1.5 interquartile range. Notched boxes are centred on the mean depth of calls produced in each depth bin.

lungs is gradually shunted to less compressible nasal passages throughout the first part of the dive until the lungs are collapsed [18]. At shallow depths, the lungs of the toothed whale may therefore act as a reservoir of air for the nasal system, ensuring that sound production is unaffected by pressure until lungs are collapsed. Beyond that point, the volume of air available for sound production decreases, leading to progressively weaker calls.

One possible way to alleviate restrictions on vocal output owing to the limited air in nasal passages might be to switch to click-based communication signals [32] that require less nasal pressure and consequently less air volume to produce [10,16]. However, high-frequency clicks are more directional than low-frequency signals radiated from the same aperture [37,53], meaning that a switch to click-based signals would come at the cost of restricting the possible audience [54]. The fact that tonal calls are produced by pilot whales even at depths

of 800 m suggests that these calls carry information or reach an audience that would be unavailable with clicks, and that they are important enough to produce despite biophysical limitations in output.

However, the weak calls at depth will have a much lower detection range than calls produced close to the surface. AO_{EFD} of calls decreased to $20.5 \log(\text{depth})$ below 80 m, which means that a whale diving from 80 to 800 m depth would produce calls approximately 20 dB lower and with less than 10 per cent of the active space of shallow calls depending on propagation conditions [55]. These weak, short-range signals, addressed to distant conspecifics, are especially susceptible to masking from increased ambient noise [56] that may be introduced by motorized vessels approaching the whales for prolonged, short-range encounters as in whale watching [57]. Since the signals may serve a role in group coordination [46,58], noise from vessels navigating close to the surface group may delay or impede the contact between foraging animals and their social group [57], potentially influencing group coordination and cohesion in these social animals.

(d) Limited call duration at depth may impose constraints on information transfer

When social birds and mammals rejoin, a variety of different cues can help individuals recognize each other. For many animals, acoustic recognition systems are of prime importance. In situations where the risk of confusion is low, or where acoustic identification can be aided by visual or olfactory cues, acoustic cues can be relatively simple. Sheep and some species of penguins recognize individuals based on the frequency content of calls aided by olfactory and topographical cues [59,60]. In situations where risk of confusion is high, such as the large and dense colonies of some birds, acoustic recognition cues can be more sophisticated. For example, king and emperor penguins use a combination of spectral and temporal characteristics [61], and bats also seem to use time-frequency contours for individual recognition [62]. Given that acoustic signals propagate faster and with less attenuation in water compared with that in air [55], and that visual and especially olfactory cues are much less reliable, it would be expected that acoustic recognition systems in toothed whales were equally complex. In bottlenose dolphins, identity information is encoded in the time-frequency contour of highly diverse signature whistles [63]. If similar identity encoding is used by pilot whales, reduced call duration at depth must limit the diversity of potential individually specific signature calls. In fact, calls at depth tend towards simpler, shorter downsweeps (e.g. figure 1), whereas surface calls may be much more complex and modulated, indicating that deep calls may be restricted to more primal recognition cues. For some animals, individual-specific recognition cues may be no more beneficial than more basic cues for kin, group or even species recognition. For example, sperm whales have been hypothesized to primarily encode the identity of their social unit into coda clicks [64]. Furthermore, if cues for individual recognition are complex, an increased propagation distance might obscure those cues for a potential receiver. Studies of red-winged blackbirds have shown how complex song components revealing the identity of the singer attenuate quickly,

whereas simpler frequency cues reveal the species of the singer at greater distances [65]. As the primary social groups of short-finned pilot whales often cluster together in larger aggregations within one area [24], a deep-diving pilot whale may be within the hearing range of several social groups. It is therefore quite possible that the simpler calls used at depth may contain group-specific cues. If such cues were encoded in the overall frequency content of deep calls, they would be robust to changes in depth and therefore well suited to the deep-diving lifestyle of pilot whales.

(e) Selection acts on signal production, transmission and reception

This study has shown how environmental factors in the form of hydrostatic pressure affect the communication capacity of homeothermic deep-diving toothed whales by limiting the communication range and information transfer at great depths. However, the communication potential of pilot whales is not only affected by pneumatic limitations in their sound production system, but also shaped by other environmental factors such as absorption, reverberation and background noise [7]. Changes in the sound speed throughout a medium will result in refraction of sound waves that shapes the communication space of vertically moving animals [55]. In terrestrial environments, this can result in time periods or spatial locations that optimize sound propagation, creating effective signalling opportunities that different animals, such as birds or frogs, have evolved to exploit [66,67]. Models of the propagation of humpback whale song indicate that song depth can likewise be a major determinant in the propagation of songs in an aquatic environment [68]. Therefore, pilot whales trying to maximize their calling distance during a deep dive would have to account for both the physical sound transmission properties of the environment, such as sound refraction, absorption and background noise, as well as the biophysical constraints on their pneumatic sound generator.

5. CONCLUSION

We have shown that short-finned pilot whales use acoustic communication during deep foraging dives by producing harmonically rich tonal calls at depths of up to 800 m. Frequency content of deep calls is not shifted towards higher frequencies and does not seem to be limited by the mechanisms of pneumatic sound production under great ambient pressure, providing a possible depth-resilient cue for group or species recognition of deep-diving animals. However, despite an increasing distance to likely receivers at the surface that would dictate increased source levels, both call amplitude and duration is reduced at depth. This is probably a consequence of the diminishing air volume used to power pneumatic sound production, but may be further influenced by behavioural factors. The short and weak signals produced at depth may be difficult to detect for group members remaining at the surface, and will be especially prone to masking. Increases in ambient noise near the surface group owing to motorized vessels will therefore have implications for the acoustic contact between foraging individuals and their social group.

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