

RESEARCH ARTICLE

Signal-specific amplitude adjustment to noise in common bottlenose dolphins (*Tursiops truncatus*)

Ida M. Kragh¹, Katherine McHugh², Randall S. Wells², Laela S. Sayigh^{3,4}, Vincent M. Janik⁵, Peter L. Tyack⁵ and Frants H. Jensen^{3,6,*}

ABSTRACT

Anthropogenic underwater noise has increased over the past century, raising concern about the impact on cetaceans that rely on sound for communication, navigation and locating prey and predators. Many terrestrial animals increase the amplitude of their acoustic signals to partially compensate for the masking effect of noise (the Lombard response), but it has been suggested that cetaceans almost fully compensate with amplitude adjustments for increasing noise levels. Here, we used sound-recording DTAGs on pairs of free-ranging common bottlenose dolphins (*Tursiops truncatus*) to test (i) whether dolphins increase signal amplitude to compensate for increasing ambient noise and (ii) whether adjustments are identical for different signal types. We present evidence of a Lombard response in the range 0.1–0.3 dB per 1 dB increase in ambient noise, which is similar to that of terrestrial animals, but much lower than the response reported for other cetaceans. We found that signature whistles tended to be louder and with a lower degree of amplitude adjustment to noise compared with non-signature whistles, suggesting that signature whistles may be selected for higher output levels and may have a smaller scope for amplitude adjustment to noise. The consequence of the limited degree of vocal amplitude compensation is a loss of active space during periods of increased noise, with potential consequences for group cohesion, conspecific encounter rates and mate attraction.

KEY WORDS: Cetacean, Signature whistle, Communication, Anthropogenic noise, Masking, Lombard response

INTRODUCTION

Marine environments have seen a steady increase in anthropogenic underwater noise over the past century (Andrew et al., 2002; Hildebrand, 2009; McDonald et al., 2006; Merchant et al., 2016), and noise is now recognized as an environmental pollutant of global concern (Van der Graaf et al., 2012). Many marine animals have evolved to rely on hearing as one of their primary senses, and sound

has come to play a fundamental role in vital behaviours as diverse as foraging, predator detection, communication and navigation (King and Janik, 2015; Simpson et al., 2005; Vasconcelos et al., 2012). With this in mind, there is growing concern among the scientific community, regulatory agencies and the public as to how anthropogenic noise pollution might affect marine animals (Boyd et al., 2011; Erbe et al., 2018).

At present, there is substantial evidence that anthropogenic noise can have detrimental effects on a variety of marine animals (Slabbekoorn et al., 2010; Weilgart, 2007). High-intensity sound sources can have serious consequences including fatal injury or strandings (Frantzis, 1998; Parsons et al., 2008; Simmonds and Lopez-jurado, 1991) or lead to temporarily or permanently elevated hearing thresholds (Kastak et al., 2005; Mooney et al., 2009; Smith et al., 2004). At lower exposure levels, anthropogenic noise may affect behavioural patterns (Nowacek et al., 2007; Samson et al., 2016), which can be associated with fitness consequences and eventually population-level effects (Nabe-Nielsen et al., 2018; New et al., 2014). Anthropogenic noise may also interfere with the ability of marine animals to detect biologically relevant sounds – an effect termed masking (American National Standards Institute, 2008; Erbe et al., 2016b). Studies have shown that masking by anthropogenic noise can cause failure to detect and discriminate a range of important sounds used for localization of prey (Schaub et al., 2008), parent–offspring interactions (Lucass et al., 2016) and predator recognition (Templeton et al., 2016), among others. Thus, increasing noise may compromise detection of acoustic signals and effectively reduce the conspecific detection range or active space (Marten and Marler, 1977).

Masking is a universal feature of all sensory systems. Underwater soundscapes typically consist of noise generated by wind, waves and precipitation as well as biological sounds, such as fish choruses or snapping shrimp (Erbe et al., 2016a), all of which can vary greatly with both time and location. Consequently, many species have evolved mechanisms to mitigate effects of masking and ensure efficient communication across a wide span of ambient noise levels (Erbe et al., 2016b). Among these are vocal adaptations of the sender, including changes in signal type (Dunlop et al., 2010), changes in signalling activity such as timing or redundancy, or modifications of certain signal features such as frequency or amplitude (Hotchkiss and Parks, 2013; Tyack and Janik, 2013). One such modification is the increase of signal amplitude in response to a perceived increase in ambient noise – a mechanism known as the Lombard response (Brumm and Zollinger, 2011; Lombard, 1911). In humans, the magnitude of the Lombard response has been shown to vary according to experimental design, but increases in vocal amplitude generally range from 0.05 to 0.4 dB per 1 dB increase in noise level (Table 1; Garnier et al., 2010; Hotchkiss and Parks, 2013). A similar Lombard response magnitude in the range of 0.2 to 0.8 dB per 1 dB increase in noise level has been demonstrated for

¹Zoophysiology, Department of Bioscience, Aarhus University, C. F. Moellers Allé, 8000 Aarhus C, Denmark. ²Chicago Zoological Society's Sarasota Dolphin Research Program, c/o Mote Marine Laboratory, 1600 Ken Thompson Pkwy, Sarasota, FL 34236, USA. ³Woods Hole Oceanographic Institution, 266 Woods Hole Rd, Woods Hole, MA 02543, USA. ⁴Hampshire College, 893 West Street, Amherst, MA 01002, USA. ⁵Sea Mammal Research Unit, Scottish Oceans Institute, School of Biology, University of St Andrews, St Andrews, KY16 8LB, UK. ⁶Aarhus Institute of Advanced Studies, Aarhus University, Hoegh-Guldbergs Gade 6B, 8000 Aarhus C, Denmark.

*Author for correspondence (frants.jensen@gmail.com)

DOI: 10.1242/jeb.216606; I.M.K., 0000-0002-6433-3483; K.M., 0000-0002-6948-5427; R.S.W., 0000-0001-9793-4181; L.S.S., 0000-0001-8334-1326; V.M.J., 0000-0001-7894-0121; P.L.T., 0000-0002-8409-4790; F.H.J., 0000-0001-8776-3606

Table 1. The Lombard response magnitude measured across taxonomic groups

Taxonomic group	Species	Lombard response magnitude (dB/dB)	Reference
Primates	Human [speech]	0.05–0.2	Lane and Tranel, 1971
		0.12–0.38	Garnier et al., 2010
		0.14–0.41	Cynx et al., 1998
	Long-tailed macaque (<i>Macaca fascicularis</i>)	0.2	Sinnott et al., 1975
	Pig-tailed macaque (<i>Macaca nemestrina</i>)	0.2	Sinnott et al., 1975
	Common marmoset (<i>Callithrix jacchus</i>)	0.3–0.75	Brumm et al., 2004
	Cotton-top tamarin (<i>Saguinus oedipus</i>)	0.35–0.63	Egnor and Hauser, 2006
	Grey mouse lemur (<i>Microcebus murinus</i>)	0.2–0.22	Schopf et al., 2016
Bats	Free-tailed bat (<i>Tadarida brasiliensis</i>)	0.43 (echolocation)	Tressler and Smotherman, 2009
	Pale spear-nosed bats (<i>Phyllostomus discolor</i>)	0.1 (echolocation)	Luo et al., 2015
Cetaceans	Humpback whale (<i>Megaptera novaeangliae</i>)	0.9	Dunlop et al., 2014
		0.81	Fournet et al., 2018
	Right whale (<i>Eubalaena glacialis</i>)	1	Parks et al., 2011a
	Killer whale (<i>Orcinus orca</i>)	1	Holt et al., 2009
	Beluga whale (<i>Delphinapterus leucas</i>)	0.88	Scheifele et al., 2005
	Bottlenose dolphin (<i>Tursiops truncatus</i>)	0.1–0.3	This study
Birds	Zebra finch (<i>Taeniopygia guttata</i>)	0.3–0.49	Cynx et al., 1998
	Great tits (<i>Parus major</i>)	0.28	Zollinger et al., 2017
	Nightingale (<i>Luscinia megarhynchos</i>)	0.2–0.66	Brumm and Todt, 2002
	Budgerigars (<i>Melopsittacus undulatus</i>)	0.16	Osmanski and Dooling, 2009
	Canaries (<i>Serinus canaria</i>)	0.1	Hardman et al., 2017
	Mallard (<i>Anas platyrhynchos</i>)	0.18–0.75	Dorado-Correa et al., 2018
	Tinamou (<i>Eudromia elegans</i>)	0.75	Schuster et al., 2012
	Domestic fowl (<i>Gallus gallus domesticus</i>)	0.41	Brumm et al., 2009
Sirenians	West Indian manatee (<i>Trichechus manatus</i>)	n.s.	Miksis-Olds and Tyack, 2009

An overview of the documented Lombard response magnitude (measured as dB change in signal amplitude per dB change in noise) in mammals and birds. For both bat species, the Lombard response was measured for echolocation signals. n.s., not significant.

other primates (Brumm et al., 2004; Egnor and Hauser, 2006) as well as bats (Tressler and Smotherman, 2009) and several different bird taxa (Brumm and Todt, 2002; Cynx et al., 1998; Dorado-Correa et al., 2018). Thus, many highly vocal terrestrial animals display a Lombard response that helps to partially offset the reduction in active space, yet none of them fully compensate for increased ambient noise and, therefore, face a loss of active space during periods of increased noise.

A series of studies have examined the Lombard response in marine mammals. In 2005, Scheifele and colleagues first described a Lombard response of 0.9 dB per 1 dB increase in ambient noise in beluga whales (*Delphinapterus leucas*) (Scheifele et al., 2005). Subsequently, Lombard responses of ~0.8–1 dB per 1 dB increase in noise have been reported for groups of killer whales (*Orcinus orca*) (Holt et al., 2009), North Atlantic right whales (*Eubalaena glacialis*) (Parks et al., 2011a,b) and humpback whales (*Megaptera novaeangliae*) (Dunlop et al., 2014; Fournet et al., 2018). Thus, cetaceans seem to almost match increases in ambient noise with increases in signal amplitude, at least within the range of ambient noise levels measured in the respective studies.

This variation in the Lombard response warrants further investigation. The acoustic communication range will decrease for animals that only partially compensate for increases in ambient noise, which can affect group cohesion, encounter rates and mate attraction (Clark et al., 2009). However, if cetaceans are able to compensate fully for increased ambient noise within a reasonable span of ambient noise levels, their active space remains constant and they only have to manage any potential energetic demands associated with increased signalling effort (Holt et al., 2015, but see also Pedersen et al., 2020).

Here, we tested the hypothesis that dolphins compensate for increasing ambient noise in a 1 dB to 1 dB manner as reported for larger cetaceans. We investigated this using acoustic tags deployed on free-ranging common bottlenose dolphins, *Tursiops truncatus* (Montagu 1821), which is one of the best-studied cetacean species because of its cosmopolitan distribution and prevalence in marine parks and aquariums (Wells and Scott, 2018). Bottlenose dolphins are known to produce individually distinctive signature whistles (Caldwell and Caldwell, 1965; Caldwell et al., 1990; Sayigh et al., 2007) that are important for facilitating group cohesion (Janik and Slater, 1998; King et al., 2016; Quick and Janik, 2012). As such, signature whistles may be especially important in situations of increased separation, especially in typically murky estuarine habitats, where maintaining active space is more critical. Therefore, we tested whether vocal amplitude compensation was different for signature and non-signature whistles.

MATERIALS AND METHODS

Study animals and location

The study was conducted with the long-term resident community of common bottlenose dolphins in Sarasota Bay, FL, USA (Wells, 2014). This is an urbanized coastal area where dolphins are exposed to a vessel passing within 100 m every 6 min on average during daylight hours (Nowacek et al., 2001). As such, this habitat involves highly fluctuating noise levels with frequent increases in masking noise (Fig. 1) within frequencies used for signature whistles (Fig. S1).

As part of a long-term study (Irvine et al., 1981; Wells, 1991), resident dolphins have been handled and examined during periodic capture–release sessions conducted since 1970, taking advantage of the shallow waters of the dolphins' range. Early efforts emphasized marking animals for future identification for behavioural studies,

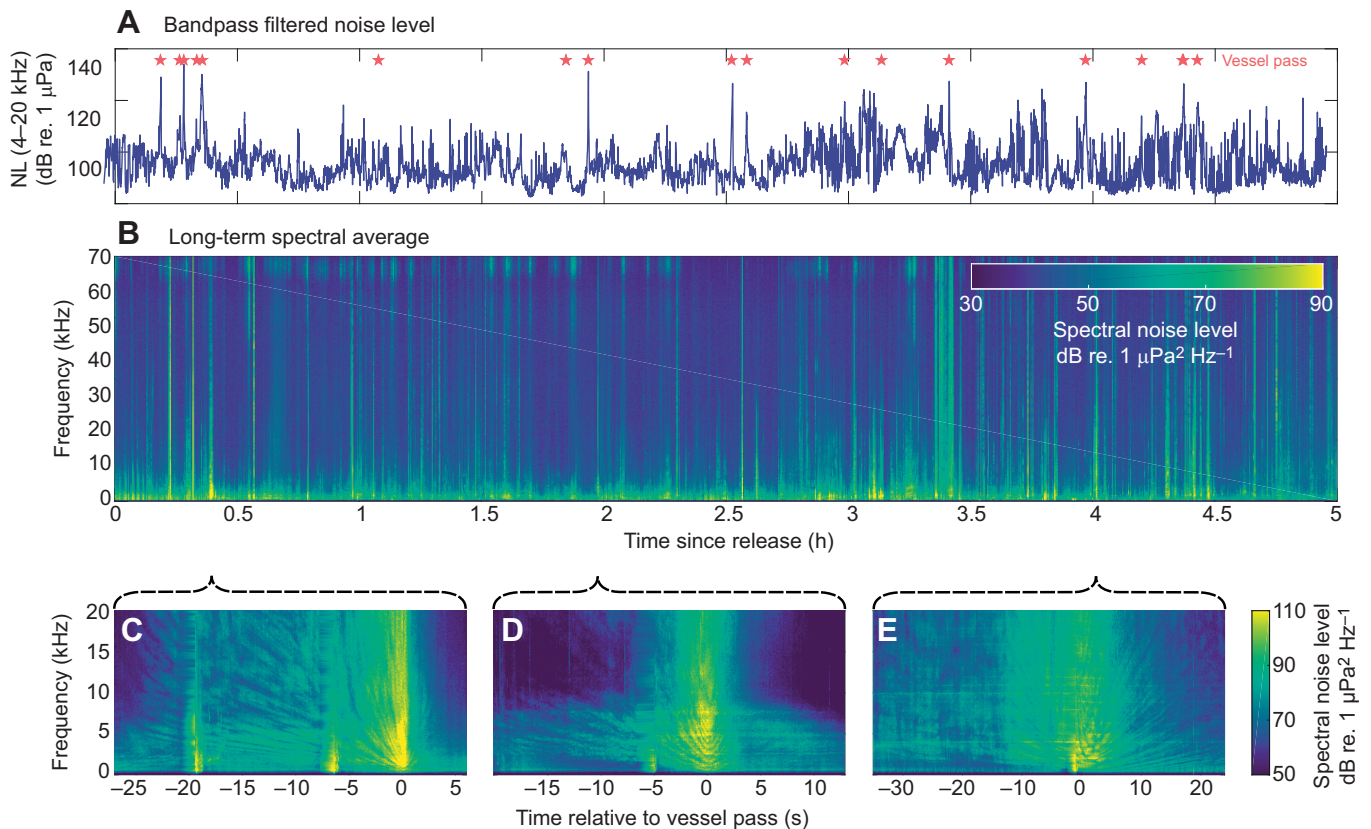


Fig. 1. Example of ambient noise exposure for a bottlenose dolphin in Sarasota Bay. (A,B) Ambient noise throughout a 5 h tagging period immediately following release, calculated as either ambient noise level (NL) within a 4–20 kHz analysis band (A) or as spectral noise level (B). Long-term spectral noise level was calculated for each 2 s block by subdividing the block into 0.1 s analysis windows with 90% overlap, identifying the analysis window with the lowest bandpass-filtered noise level, then calculating the power spectral density using Welch's method (FFT size 4096, sample rate 240 kHz). Surfacing periods within 0.2 m of the surface were identified and removed using linear interpolation of both bandpass-filtered noise level and spectral noise level. Aurally identifiable close vessel approaches were manually labelled within the dataset (red stars) and a spectrogram calculated for three example vessel passes (C–E) to show the broadband noise generated by cavitation.

and obtaining life history and genetic information on each resident dolphin to facilitate interpretation of behaviour; since 1988, health parameters have been examined as well (Wells, 2009; Wells et al., 2004). During capture–release sessions, a large seine net (500×4 m in size) was deployed from a motorboat to encircle a small group of dolphins in shallow water. Once enclosed in a net corral, experienced handlers could safely handle and support the animals. A suite of morphological, physiological and behavioural data were collected, partly in water and partly on an adjacent sampling boat with a shaded, padded deck. Behaviour and respiratory patterns were closely monitored by veterinarians throughout the process, and water was repeatedly washed over the dolphins when on deck. The whole process typically required 1–2 h, after which the dolphins were ready to be released on site.

Permits

Fieldwork was carried out under National Marine Fisheries Service Scientific Research Permit no. 15543 to R.S.W. as well as through IACUC approvals through Woods Hole Oceanographic Institution, Mote Marine Laboratory and the University of St Andrews Animal Welfare and Ethics Committee.

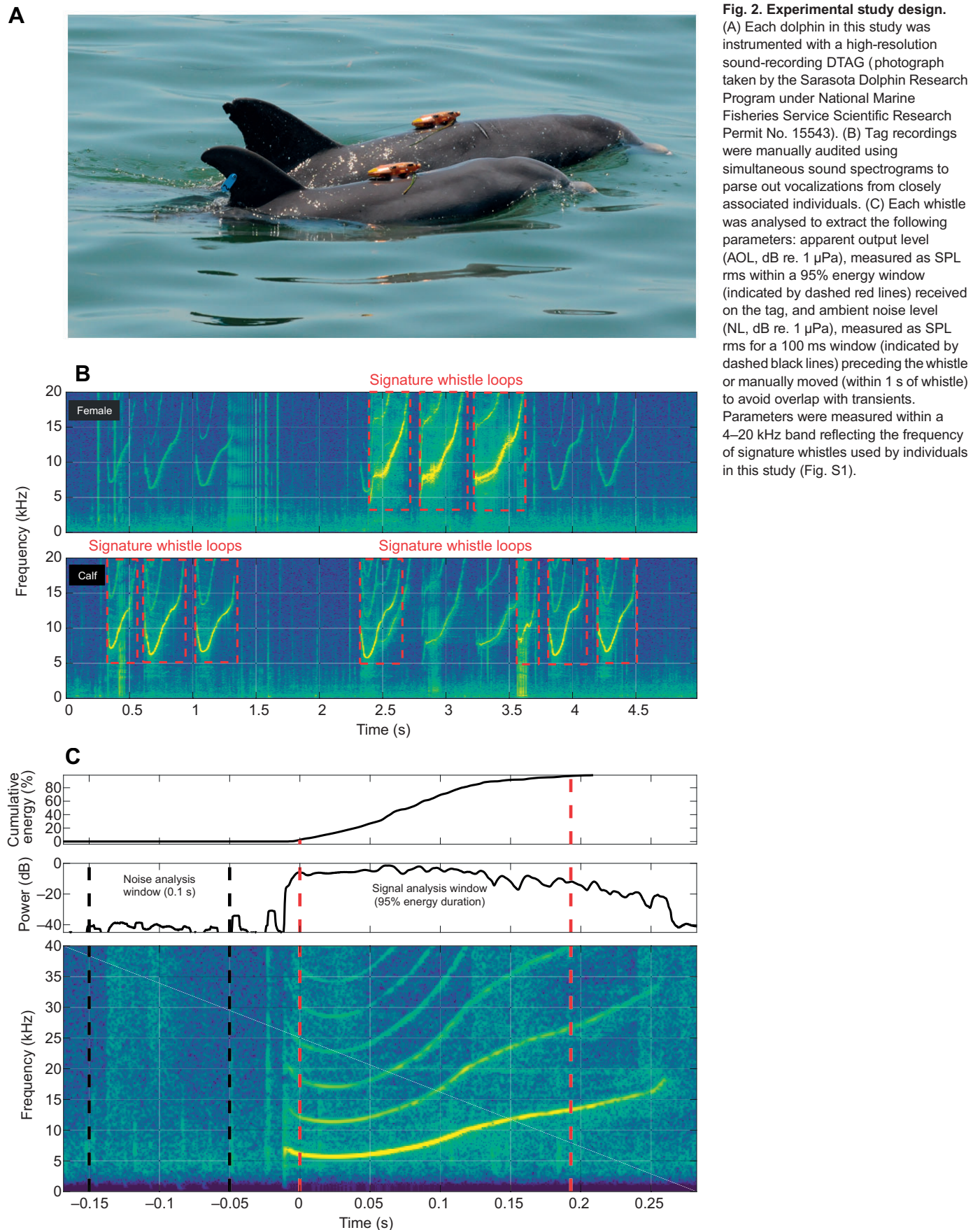
Experimental design

Before release, some dolphins were instrumented with a high-resolution sound and movement recording DTAG3 (Johnson and Tyack, 2003), which was positioned roughly halfway between the

blowhole and the dorsal fin, approximately 0.5 m from the melon (Fig. 2A). The skin of the dolphin was gently scrubbed with a piece of paper towel to remove algae and dead skin cells, and the tag was attached with four small (approximately 48 mm diameter) sterilized suction cups. The tag continuously recorded 16-bit sound on two hydrophones at a sample rate of 240 kHz and with a flat frequency response within ± 2 dB between 0.5 and 80 kHz. A pressure sensor, tri-axial accelerometer and magnetometer were sampled at 200–250 Hz after passing through an analog low-pass filter with a -3 dB cut-off frequency of one-third of the sampling rate. Preceding the experiment, tag sensitivities were measured by relative calibration in an anechoic tank (1.5 m diameter, Aarhus University) to a clip level of 179 dB re. 1 μ Pa (± 1.2 dB between tags). The tags were programmed to release after a specified time period (up to 24 h), but many came off before this programmed release (see Table S1) as a result of high-energy activities of the dolphins, including repeated breaching, fast sprints or energetic interactions with conspecifics. After detachment, the tags floated to the surface to be retrieved using boat-based tracking of their VHF beacons with a Yagi antenna and an R1000 VHF receiver (Communication Specialists, Inc.).

Obtaining whistle parameters from tag recordings

All tag recordings were audited in MATLAB R2013b (The MathWorks, Inc., Natick, MA, USA) using DTAG-toolbox scripts (<https://www.soundtags.org/>). In this process, each recording was manually inspected in sequential 10 s segments. For each period,



acoustic data were downsampled to 60 kHz, and amplitude envelopes and spectrograms (Hamming window, FFT size 512, 50% overlap, 80 dB dynamic range) were displayed in concert with a synchronized dive profile.

Individual vocalizations were labelled manually along with a start time and duration cue according to the following definitions: uninterrupted tonal sounds with a narrowband fundamental frequency were labelled as either whistles (exceeding 100 ms in duration) or chirps (durations of less than 100 ms; Caldwell and Caldwell, 1968), with chirps ignored for the purpose of this paper. Whistles produced by the tagged individual were distinguished from those of non-focal individuals based on (i) intensity comparisons between two tags deployed on tightly associated pairs (mother–calf or male alliances) and (ii) a stereo angle of arrival within $\pm 10^\circ$ of echolocation clicks produced by that animal.

Signature whistles of each tagged individual were identified and differentiated from non-signature whistles by comparison with the dominant whistle obtained from suction-cup hydrophone recordings during health assessments, where signature whistles account for the majority of emitted whistles (Sayigh et al., 2007). No signature whistle copies (Janik, 2000b; Tyack, 1986) were included in this study, as these are generally rare.

For the subsequent analysis, accurate measures of both whistle amplitude and ambient noise were required. Therefore, we manually removed all whistles that had overlapping extraneous sound components, such as flow noise (during high-energy activities), surfacing noise, clicks or other whistles from either the tagged individual or nearby conspecifics. All remaining whistles were analysed individually to extract a range of parameters (Fig. 2B). First, each extracted sound period was filtered with a 4–20 kHz 6-pole Butterworth filter. This frequency range adequately captured the energy in the fundamental frequency of signature whistles of the recorded animals in our study while removing low-frequency flow noise that did not overlap with dolphin signals (Fig. S1).

We first estimated the ambient noise level (NL, dB re. 1 μ Pa) in the 4–20 kHz band as the root-mean-square sound pressure level (SPL_{rms}) within a 100 ms window preceding each whistle: $NL = 10 \log_{10}(I_N)$, where the noise intensity I_N is the mean of the squared pressure values throughout the noise analysis window. If loud transients (often echolocation clicks of the tagged animal or a nearby conspecific) preceded the whistle, the background noise window was manually shifted to a period without clicks within 1–2 s before the whistle, possibly generating a small but negligible time gap between the NL and apparent output level (AOL) measurements.

We then estimated the AOL (dB re. 1 μ Pa) of the whistle as received on the tag (Madsen et al., 2005). To do this, we calculated a time window containing 95% of the signal energy (Fig. 2; Madsen et al., 2005). We then measured the SPL_{rms} within the 95% energy window after correcting for noise intensity: $AOL = 10 \log_{10}(I_S - I_N)$, where signal intensity I_S is the mean of the squared pressure values over the 95% energy window and I_N is the noise intensity as defined above. The signal-to-noise ratio was then calculated as the difference between AOL and NL. These AOL measurements enabled the subsequent analysis of relative changes in output level as a function of ambient noise.

Statistics

To investigate the effect of noise level on signal amplitude, we used a subset of whistles that were filtered to have a signal-to-noise ratio greater than 6 dB and a minimum of six signature and six non-signature whistles per individual. The former criterion was

implemented because measurements of signal intensity become steadily more unreliable at increasingly small signal-to-noise ratios. Given the close proximity of the tag to the sound source, this criterion affected very few signals (5% of all recorded whistles).

We performed a linear mixed-effects analysis of the relationship between AOL and NL using the *lme4* toolbox (Bates et al., 2015) in R (<http://www.R-project.org/>). We modelled NL, whistle type and an interaction term between the two as fixed effects to examine their importance in explaining AOL. We accounted for differences between individuals by including a random effect on both intercept and slope for each tagged dolphin.

As a model selection method, we generated four nested models: a null model with only random effects and three extending models where each new model was identical to the previous except for the addition of a fixed effect. A stepwise likelihood-ratio test was performed to evaluate the importance of each of the fixed effects and to determine which model was best fitted to the data. We visualized the marginal effect (ignoring random factors) of NL on AOL for each whistle type using parametric bootstrapping with 1000 replicates within the *bootpredictlme4* toolbox (<http://www.remko Bruinsma.com/post/2017-06-15-bootpredictlme4/>) in R. Subsequently, we constructed a separate linear mixed-effect model for each whistle type and then tested whether NL had a significant effect on AOL using the same likelihood-ratio test, by comparison with a model without NL.

RESULTS

In total, 26 individual tag recordings of 23 different individuals were analysed for this study, including data from nine mother–calf pairs and four male alliance pairs in the years 2012–2016 (see Table S1 for the full data overview). Individual tag recordings ranged in duration from 0.58 h to 24.24 h (mean \pm s.d., 10.95 ± 7.72 h), amounting to a total of 284.82 h. From these recordings, we manually audited and analysed 222.42 h (see Table S1) and identified a total of 4151 whistles with no overlapping extraneous sounds. After filtering for a signal-to-noise ratio greater than 6 dB (removing 209 whistles, equal to 5% of all whistles) and a minimum of 6 signature and 6 non-signature whistles per individual (removing 7 tag recordings with a total of 87 whistles, equal to 2% of the total), our remaining dataset for statistical treatment consisted of 19 individuals (6 mothers, 8 calves, 5 males) and a total of 3855 whistles (2750 signature and 1105 non-signature whistles). Measured NL ranged from 80 to 147 dB re. 1 μ Pa, while the range of AOL was from 105 to 164 dB re. 1 μ Pa, which is compatible with previous studies of output levels for this species (Janik, 2000a; Jensen et al., 2012; Tyack, 1986).

The linear mixed-effects model showed that the addition of NL, whistle type and an interaction term between the two factors significantly improved model fit (see ΔAIC and ΔBIC ; Table 2) and that all three of these fixed effects had a significant effect on AOL (Table 2).

We found a much lower degree of amplitude compensation compared with previous studies on cetaceans, despite a large variation within individual datasets. Representative relationships between AOL and noise level are shown for both signature and non-signature whistles of a representative mother, calf and male in Fig. 3. AOL within each whistle type varied greatly, with significant variation in the estimated Lombard response magnitude across datasets (Fig. 4A,B). Despite these confounding factors, all datasets showed a Lombard response magnitude far less than the ~ 0.9 –1 dB per 1 dB noise found in previous cetacean studies (Table S1).

Table 2. Model selection using likelihood-ratio test

Model		d.f.	Δ AIC	Δ BIC	χ^2	P-value
Full model:	AOL~NL+WT+NL×WT+(1+NL ID)	8	0	0	37.62	<0.0001
Model 2:	AOL~NL+WT+(1+NL ID)	7	35	29	1050.22	<0.0001
Model 1:	AOL~NL+(1+NL ID)	6	1084	1071	22.32	<0.0001
Null model:	AOL~(1+NL ID)	5	1104	1085		

Four linear mixed-effects models (fixed effects in bold, random effects in italics) were tested hierarchically, with χ^2 and P-values for each model representing a test against the model one level down. The results show that the addition of each fixed effect significantly improved the model. Thus, all three fixed effects had a significant effect on apparent output level (AOL: dB re. 1 μ Pa) ($P<0.0001$). The full model showed that signature whistles were 8.6 dB higher output than non-signature whistles, with a shallower slope (0.14 ± 0.03 dB per 1 dB noise level) compared with non-signature whistles (0.14 ± 0.03 dB per 1 dB noise level). NL, noise level (dB re. 1 μ Pa); WT, whistle type; ID, individual.

We also found significant differences in the output level of signature and non-signature whistles (for the entire dataset: signature whistle mean \pm s.d. AOL: 133 \pm 7.5 dB re. 1 μ Pa, non-signature whistle AOL: 127 \pm 9.3 dB re. 1 μ Pa). Thus, the AOL of signature whistles was generally greater than that of non-signature whistles, with a difference of 8.6 dB after accounting for individual differences and the simultaneous effect of noise.

Finally, we found that the effect of NL on AOL was significantly lower for signature whistles (0.14 ± 0.03 dB per 1 dB noise) than for non-signature whistles (0.32 ± 0.03 dB per 1 dB noise). These results were robust to different acoustic measures of AOL, irrespective of whether models were run using rms output level, 200 ms peak rms level or energy flux density (Table S2). A separate linear mixed-effects model with only signature whistles demonstrated that the AOL of these whistles was significantly correlated with NL despite a low slope ($\chi^2_1=11.214$, $P=0.0008$).

DISCUSSION

Animals that communicate acoustically need to solve the challenge of successfully transmitting signals in varying conditions of ambient noise. In this paper, we show that bottlenose dolphins demonstrate a Lombard response by adjusting signal amplitude in

response to variation in ambient noise levels. We found that the magnitude of this response is consistent with studies of terrestrial species, yet much lower than reported by previous studies on larger cetaceans. Furthermore, the response magnitude was on average consistently lower for signature whistles (0.1 dB increase in AOL per 1 dB increase in NL) than for non-signature whistles (0.3 dB increase in AOL per 1 dB increase in NL), demonstrating the utility of separating signals with different functions when studying vocal compensation in wild animals.

The lower amplitude adjustments seen for signature whistles may be a consequence of these whistles inherently operating at higher output levels than non-signature whistles, rendering a smaller potential scope for the Lombard response. Similar arguments have been presented to explain why some species of frogs (Schwartz and Bee, 2013) and tokay geckos (Brumm and Zollinger, 2017) do not exhibit a Lombard response. While signature whistles were emitted on average at 9 dB higher output levels compared with non-signature whistles, this difference depended on noise level, and the two signal types gradually converged on similar output levels at high noise levels. Maximum source levels of wild bottlenose dolphins have been estimated to be approximately 162–169 dB re. 1 μ Pa SPL_{rms} (Janik, 2000a; Jensen et al., 2012), which is

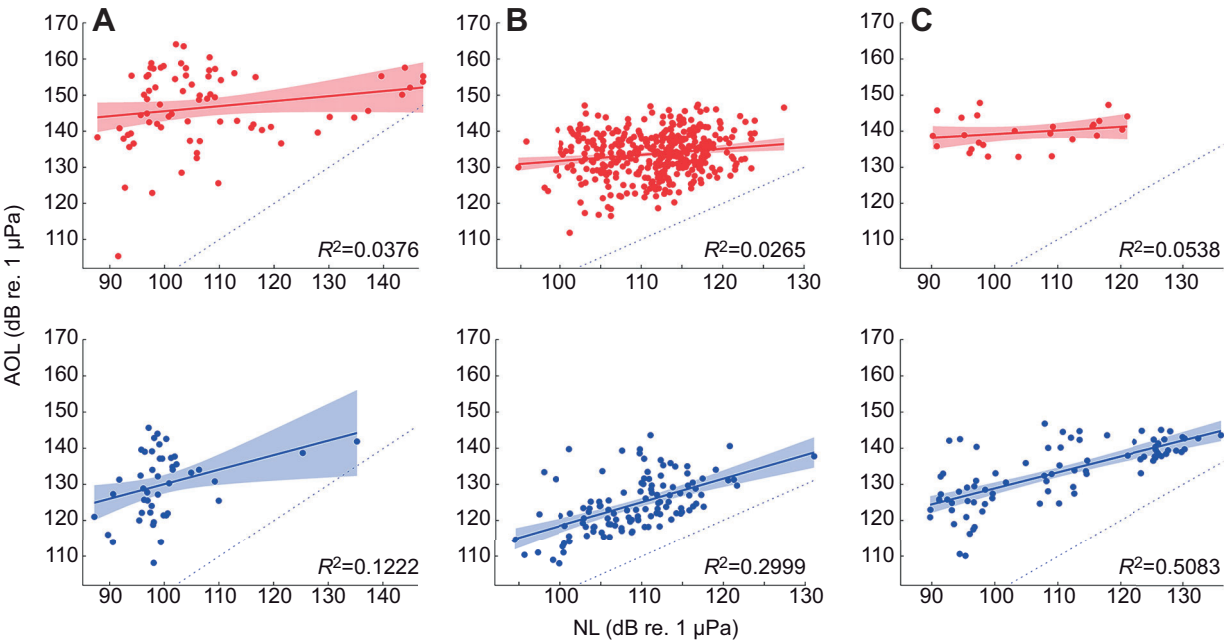


Fig. 3. Variation in amplitude adjustment to noise. The relationship between AOL and NL for signature (top row, red) and non-signature (bottom row, blue) whistles for a representative mother (A), calf (B) and male (C). Filled circles represent whistles, whereas solid line and shaded area represent a linear regression and 95% regression confidence interval. A signal-to-noise ratio where signal amplitude equals noise amplitude is shown as a dotted line in each plot.

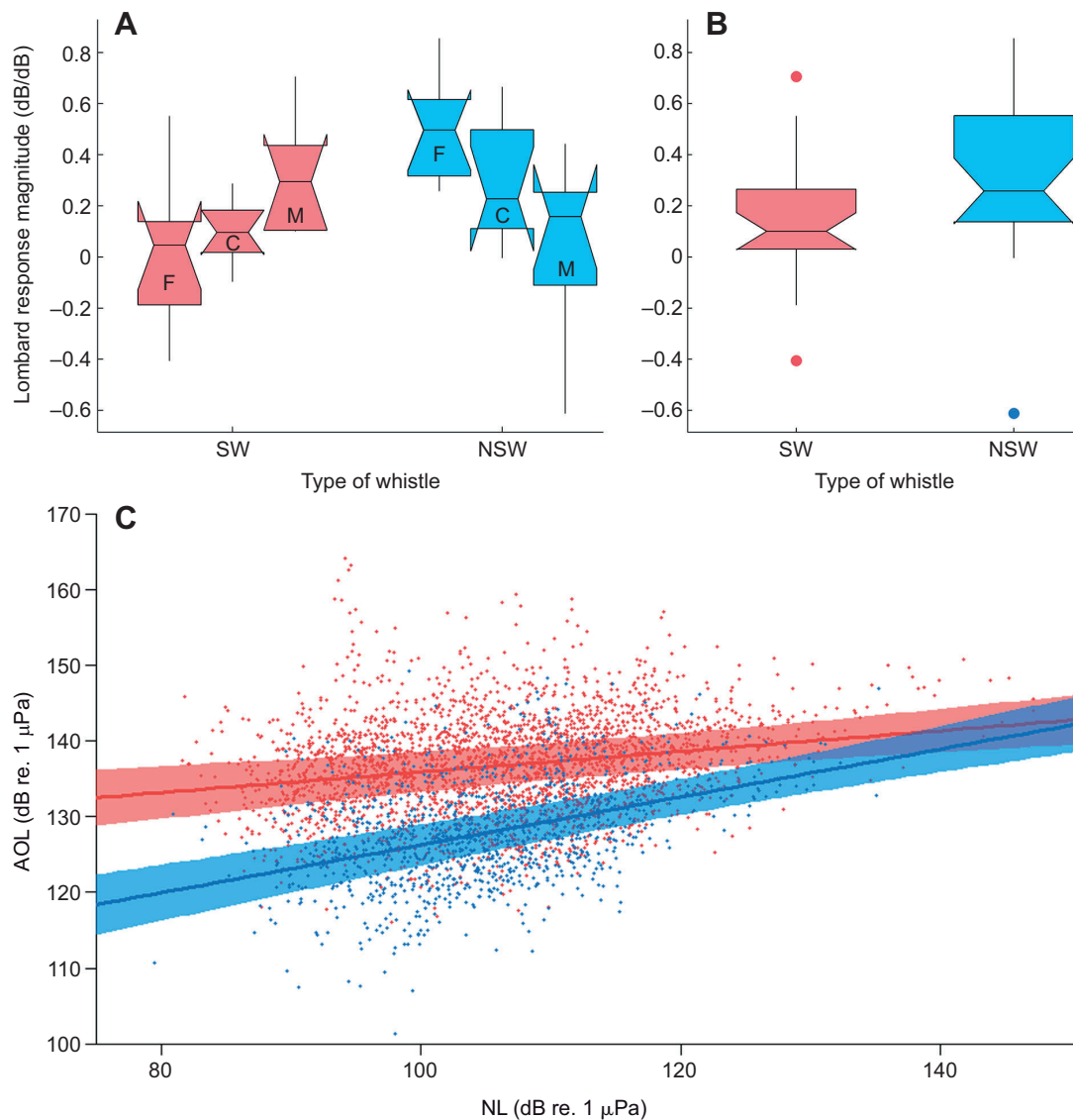


Fig. 4. Signal-specific Lombard response magnitude. (A) Boxplot showing the distribution of Lombard response magnitudes (dB whistle/dB NL) obtained from linear regression on signature whistles (SW) and non-signature whistles (NSW) for each individual animal, based on whether it was a female (F), a calf (C) or an allied male (M). (B) Boxplot showing differences between signature and non-signature whistles pooled across individuals. Slopes were generally larger for non-signature whistles (median: 0.3 dB whistle/dB NL) than for signature whistles (median: 0.1 dB whistle/dB NL) but with large variation between individuals. For both plots, boxes represent upper and lower quartiles, horizontal middle lines indicate medians, and notches represent 95% confidence interval of the median. Whiskers extend to the most extreme data point within 1.5 \times interquartile range (IQR), and points beyond 1.5 \times IQR (probably outliers) are marked as coloured circles. (C) The marginal effect (ignoring random factors) of NL (dB re. 1 μ Pa) on AOL (dB re. 1 μ Pa) for signature whistles (red) demonstrated a significantly lower Lombard response magnitude than for non-signature whistles (blue). Coloured dots represent whistles, whereas solid lines and shaded areas represent the linear mixed-effects model prediction and 95% confidence intervals.

comparable to the maximum output levels measured in this study, especially considering that tag-recorded AOLs need to be corrected for tag placement and directivity to be directly comparable with an on-axis source level at 1 m distance. Higher output levels of signature whistles are probably tied to differences in function between the two signal types. Signature whistles are used to broadcast individual identity (Sayigh et al., 1999) and facilitate group cohesion (Janik and Slater, 1998), including when separate groups meet at sea (Quick and Janik, 2012) or when mother–calf pairs need to reunite (King et al., 2016; Smolker et al., 1993). These functions are likely to benefit from a higher output level and the larger detection range that comes with it. In contrast, while much less is known about the functions of non-signature whistles, the

9 dB lower output levels for non-signature whistles would result in a threefold smaller detection range (Jensen et al., 2012; Quintana-Rizzo et al., 2006). This smaller active space supports the notion that many non-signature whistles may be used in more discreet short-range communication contexts, which could serve many potential functions (Gustison and Townsend, 2015). At the same time, the lower output levels of non-signature whistles compared with the physiological peak output levels allow a larger scope for changing amplitude in response to noise.

The Lombard response magnitudes of signature and non-signature whistles in this study are similar to those demonstrated for terrestrial mammals (Egnor and Hauser, 2006; Garnier et al., 2010; Tressler and Smotherman, 2009), but lower than shown for

other cetaceans across a similar span of noise levels (90–150 dB re. 1 μ Pa SPL_{rms}) (Holt et al., 2009; Parks et al., 2011a; Scheifele et al., 2005). Part of the reason for the different results might be ascribed to socio-behavioural differences among the cetacean species being studied and the contexts in which they were studied. We know from humans that the Lombard response may depend on social context as well as speaker task (Garnier et al., 2010; Lu and Cooke, 2008), though this is less well understood for animals. One study of Bengalese finches found a Lombard effect in undirected song but not in directed singing (Kobayasi and Okanoya, 2003), but the evidence was inconsistent across individuals, and several other studies of the closely related zebra finch have found a Lombard response during undirected singing (Cynx et al., 1998; Zollinger et al., 2011). In this study, all tagged dolphins were closely associated pairs, either mothers with a dependent calf or allied males (Connor and Krützen, 2015; Wells, 2003). It is possible that the majority of the recorded whistles were exchanges between the tagged individuals and, thus, used in relatively short-range communication where range was not limited by noise. Studies on this dolphin population have shown that pairs often stay within communication range of each other while moving through their acoustically complex habitat (Quintana-Rizzo et al., 2006), which might lessen the motivation to maintain their active space and lead to a smaller Lombard response if this is cognitively modulated. At the same time, animals might change overall cohesion in response to increasing noise (Buckstaff, 2004), thus offsetting the need to increase vocal output. It is possible that communication within larger social groups or with distant conspecifics is more sensitive to changes in detection range, necessitating a tighter coupling of signal output level and noise level. However, this argument breaks down for animals communicating to distant animals at an unknown range, where a better option may just be to vocalize as loudly as possible.

There are several methodological differences between studies that may also help explain our different results. Studies of the Lombard response require reliable measurements of both signal output levels and any simultaneous changes in background noise (or experimentally manipulated noise), but this is quite difficult to obtain for cetaceans in the wild. Scheifele et al. (2005), Holt et al. (2009) and Dunlop et al. (2014) used hydrophone arrays to obtain estimates of output levels of whale signals and concurrent fluctuations in noise levels. This method has two problems. First, the spatial offset between the animals and the hydrophone means that the noise level experienced by the animals may be considerably different from the noise level recorded. While this problem may be less important in the case of noise generated primarily by wind and waves rather than shipping (Dunlop et al., 2010), changes in depth of the whale or bathymetry at and around the location of the whale still affect the resulting noise level. Second, because the signal-to-noise ratio of each signal has to be sufficiently high to enable a reliable measurement of the signal, this method also biases analysed signals toward higher amplitude signals. As signal-to-noise ratio also depends on transmission range, this filtering introduces a further bias towards higher amplitude signals (or signals recorded at shorter range) at higher ambient noise levels, thus potentially driving a larger apparent vocal adaptation to noise.

On-animal tag recordings (Parks et al., 2011a; this study) offer some advantages with respect to both of these issues. If calls from the tagged individual can be determined confidently, the spatial offset between noise recorded and noise experienced by the animals is minimal, as estimates of concurrent noise levels can be recorded at the location of the animal. At the same time, signals are recorded at a constant distance close to the sound-production apparatus of the

animal and at a relatively high received level compared with more distant recordings. However, there are still some difficulties for recording signals on the tag. These tags are almost always positioned behind the sound generator and, as a consequence, signal features received on tags are likely to be different from those that would be recorded at 1 m in front of the animal, i.e. the source level (Johnson et al., 2009). However, because of the relatively omnidirectional nature of the fundamental frequency of bottlenose dolphin whistles (Branstetter et al., 2012), any relative changes in AOL will probably mirror changes in source level. Another problem is flow noise from animal movement on tags. We were able to eliminate flow noise by excluding noise below 4 kHz. This is justified because the main noise sources were small boat engines that produce considerable high-frequency noise (Fig. 1), because whistles do not contain energy below 4 kHz (Fig. S1), and because dolphin hearing sensitivity is poor at low frequencies (Johnson, 1968). This problem would be harder to solve in an area where most noise comes from large vessels producing primarily low-frequency noise and where animals communicate and hear in those lower frequency bands, as is the case for large whales.

Furthermore, when using tags to assess noise-dependent vocal adjustments, the experimental design has to ensure that signals produced by the tagged individual can be readily discerned from signals from other individuals – even at very close range. In this study, we used stereo angle-of-arrival estimates and amplitude comparisons between pairs of tagged animals to accomplish this, with known signature whistles of tagged individuals providing additional certainty. A corresponding level of certainty is more difficult to accomplish in studies of the larger baleen whales. Acoustic signals generated by baleen whales are low frequency and can propagate over relatively large distances, which makes it challenging to ensure that signals are from the tagged animal. While Parks et al. (2011a,b) minimized this problem by visually ensuring that the tagged animal was alone at the surface, other studies have used high-resolution accelerometers on tags to detect low-frequency vibrations on the surface of fin whales as an indication of vocal activity (Goldbogen et al., 2014), which might be an interesting method for future studies of vocal amplitude compensation in large cetaceans. Similarly, clicks from tagged animals are often much easier to identify because of their off-axis distortion, and thus species that communicate with click-based signals, such as some delphinids (Pérez et al., 2016) or narrow-band high-frequency species (Martin et al., 2018; Sorensen et al., 2018), may be good species in which to examine Lombard response magnitude.

The lower Lombard response magnitude found in this study is important to consider in the assessment of how anthropogenic noise may affect acoustic communication, as it means that animals will experience a loss of active space during periods of increased ambient noise. Decreases in potential communication range can be estimated in situations when noise levels, sound propagation conditions and source characteristics of communication signals are known or measured (Jensen et al., 2009). Several studies have modelled changes in detection range as a consequence of large-scale and long-term anthropogenic noise in marine environments, aiming both to understand contributions of different noise sources and to decrease impacts through improved management (Clark et al., 2009; Hatch et al., 2012). However, none of these models account for potential compensatory mechanisms and thus they may be overestimating loss of communication space. In the long run, these efforts may help us evaluate long-term population-level effects of anthropogenic noise (Nabe-Nielsen et al., 2014; New et al., 2014) and thus enable better data-driven conservation and marine planning

(Hatch et al., 2016). However, there are still many poorly understood aspects of acoustic masking, such as the extent of spatial release from masking (Erbe et al., 2016b), or potential compensation mechanisms that should be incorporated into models of masking.

Conclusion

In this study, we have shown that bottlenose dolphins partially compensate for increased noise by adjusting signal amplitude, with higher output levels and lower compensation for signature whistles that are associated with group cohesion than for non-signature whistles of unknown function. These findings underline the need for further investigations of the interaction between signal types, masking and how the social function of calls may be used to predict range of communication. Further studies are needed to investigate how dolphins modulate the intensity of their whistles in order to tailor their effective range to the function of the whistle, varying noise levels and varying propagation loss in different habitats such as the sand flats, open bays and sea grass meadows (Quintana-Rizzo et al., 2006). These analyses are required to understand and evaluate socio-behavioural consequences of increased noise, including maintenance of contact between mother and calf, changes in overall structure and connectivity of a fission–fusion society, decreased encounter rates with conspecifics, lost mating opportunities, and possible shifts in time and energy budgets, as potential consequences of behavioural compensation mechanisms.

Acknowledgements

The authors gratefully acknowledge the support of the Chicago Zoological Society's Sarasota Dolphin Research Program, as well as the many researchers and volunteers that enable the health assessments of the Sarasota dolphin community, especially N. Macfarlane, J. Van Der Hoop, R. Tyson and A. Barleycorn for their support with the tagging project. Tag support and logistics were provided by A. Bocconcelli, T. Hurst, D. Bogorff and R. Swift. M. Johnson provided tag analysis software and expertise. We also express our gratitude to P. Madsen for support, encouragement and helpful comments on this manuscript and to O. N. Larsen and two anonymous reviewers for constructive feedback.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: I.M.K., F.H.J.; Methodology: F.H.J.; Software: F.H.J.; Formal analysis: I.M.K.; Investigation: I.M.K., K.M., R.S.W., L.S.S., V.M.J., P.L.T.; Resources: K.M., R.S.W., L.S.S., V.M.J., P.L.T.; Data curation: I.M.K.; Writing - original draft: I.M.K.; Writing - review & editing: I.M.K., K.M., R.S.W., L.S.S., V.M.J., P.L.T., F.H.J.; Visualization: I.M.K., F.H.J.; Supervision: F.H.J.; Project administration: I.M.K., F.H.J.; Funding acquisition: R.S.W., P.L.T., F.H.J.

Funding

Fieldwork in Sarasota was funded by the Grossman Foundation, the Office of Naval Research, and Woods Hole Oceanographic Institution. Health assessments were funded by Dolphin Quest, Inc. I.M.K. received support from the Danish Acoustical Society (Dansk Akustisk Selskab). P.L.T. received funding from the University of St Andrews, the Office of Naval Research (N00014-19-1-2560) and the MASTS pooling initiative (The Marine Alliance for Science and Technology for Scotland). F.H.J. was supported by the Office of Naval Research (N00014-14-10410) and an AIAS-COFUND fellowship from Aarhus Institute of Advanced Studies under the FP7-PEOPLE programme of the EU (agreement no. 609033). All support is gratefully acknowledged.

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.216606.supplemental>

References

- American National Standards Institute** (2008). *Bioacoustical Terminology* (ansi S2.20-1995, R 2008). New York: Acoustical Society of America.
- Andrew, R. K., Howe, B. M., Mercer, J. A. and Dzieciuch, M. A.** (2002). Ocean ambient sound: Comparing the 1960s with the 1990s for a receiver off the California coast. *Acoust. Res. Lett. Online* **3**, 65–70. doi:10.1121/1.1461915
- Bates, D., Maechler, M., Bolker, B. and Walker, S.** (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Soft.* **67**, 1–48. doi:10.18637/jss.v067.i01
- Boyd, I. L., Frisk, G., Urban, E., Tyack, P., Ausubel, J., Seeyave, S., Cato, D., Southall, B., Weise, M., Andrew, R. et al.** (2011). An international quiet ocean experiment. *Oceanography* **24**, 174–181. doi:10.5670/oceanog.2011.37
- Branstetter, B. K., Moore, P. W., Finneran, J. J., Tormey, M. N. and Aihara, H.** (2012). Directional properties of bottlenose dolphin (*Tursiops truncatus*) clicks, burst-pulse, and whistle sounds. *J. Acoust. Soc. Am.* **131**, 1613–1621. doi:10.1121/1.3676694
- Brumm, H. and Todt, D.** (2002). Noise-dependent song amplitude regulation in a territorial songbird. *Anim. Behav.* **63**, 891–897. doi:10.1006/anbe.2001.1968
- Brumm, H. and Zollinger, S. A.** (2011). The evolution of the Lombard effect: 100 years of psychoacoustic research. *Behaviour* **148**, 1173–1198. doi:10.1163/000579511X605759
- Brumm, H. and Zollinger, S. A.** (2017). Vocal plasticity in a reptile. *Proc. R. Soc. B* **284**, 20170451. doi:10.1098/rspb.2017.0451
- Brumm, H., Voss, K., Köllmer, I. and Todt, D.** (2004). Acoustic communication in noise: regulation of call characteristics in a New World monkey. *J. Exp. Biol.* **207**, 443–448. doi:10.1242/jeb.00768
- Brumm, H., Schmidt, R. and Schrader, L.** (2009). Noise-dependent vocal plasticity in domestic fowl. *Anim. Behav.* **78**, 741–746. doi:10.1016/j.anbehav.2009.07.004
- Buckstaff, K. C.** (2004). Effects of watercraft noise on the acoustic behavior of bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Mar. Mamm. Sci.* **20**, 709–725. doi:10.1111/j.1748-7692.2004.tb01189.x
- Caldwell, M. C. and Caldwell, D. K.** (1965). Individualized whistle contours in bottle-nosed Dolphins (*Tursiops truncatus*). *Nature* **207**, 434–435. doi:10.1038/207434a0
- Caldwell, M. C. and Caldwell, D. K.** (1968). Vocalization of naive captive dolphins in small groups. *Science* **159**, 1121–1123. doi:10.1126/science.159.3819.1121
- Caldwell, M. C., Caldwell, D. K. and Tyack, P. L.** (1990). Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In *The Bottlenose Dolphin* (ed. S. Leatherwood and R. R. Reeves), pp. 199–234. New York: Academic Press.
- Clark, C. W., Ellison, W. T., Southall, B. L., Hatch, L., Van Parijs, S. M., Frankel, A. and Ponirakis, D.** (2009). Acoustic masking in marine ecosystems: intuitions, analysis, and implication. *Mar. Ecol. Prog. Ser.* **395**, 201–222. doi:10.3354/meps08402
- Connor, R. C. and Krützen, M.** (2015). Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Anim. Behav.* **103**, 223–235. doi:10.1016/j.anbehav.2015.02.019
- Cynx, J., Lewis, R., Tavel, B. and Tse, H.** (1998). Amplitude regulation of vocalizations in noise by a songbird, *Taeniopygia guttata*. *Anim. Behav.* **56**, 107–113. doi:10.1006/anbe.1998.0746
- Dorado-Correa, A. M., Zollinger, S. A. and Brumm, H.** (2018). Vocal plasticity in mallards: multiple signal changes in noise and the evolution of the Lombard effect in birds. *J. Avian Biol.* **49**. doi:10.1111/jav.01564
- Dunlop, R. A., Cato, D. H. and Noad, M. J.** (2010). Your attention please: increasing ambient noise levels elicits a change in communication behaviour in humpback whales (*Megaptera novaeangliae*). *Proc. R. Soc. B Biol. Sci.* **277**, 2521–2529. doi:10.1098/rspb.2009.2319
- Dunlop, R. A., Cato, D. H. and Noad, M. J.** (2014). Evidence of a Lombard response in migrating humpback whales (*Megaptera novaeangliae*). *J. Acoust. Soc. Am.* **136**, 430–437. doi:10.1121/1.4883598
- Egnor, S. E. R. and Hauser, M. D.** (2006). Noise-induced vocal modulation in cotton-top tamarins (*Saguinus oedipus*). *Am. J. Primatol.* **68**, 1183–1190. doi:10.1002/ajp.20317
- Erbe, C., McCauley, R. D. and Gavrilov, A.** (2016a). Characterizing marine soundscapes. In *The Effects of Noise on Aquatic Life II* (ed. A. D. Hawkins and A. N. Popper), pp. 265–271. New York City, NY: Springer.
- Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K. and Dooling, R.** (2016b). Communication masking in marine mammals: A review and research strategy. *Mar. Pollut. Bull.* **103**, 15–38. doi:10.1016/j.marpolbul.2015.12.007
- Erbe, C., Dunlop, R. and Dolman, S.** (2018). Effects of noise on marine mammals. In *Effects of Anthropogenic Noise on Animals* (ed. H. Slabbekoorn, R. J. Dooling, A. N. Popper and R. R. Fay), pp. 277–309. New York, NY: Springer New York.
- Fournet, M. E. H., Matthews, L. P., Gabriele, C. M., Haver, S., Mellinger, D. K. and Klinck, H.** (2018). Humpback whales *Megaptera novaeangliae* alter calling behavior in response to natural sounds and vessel noise. *Mar. Ecol. Prog. Ser.* **607**, 251–268. doi:10.3354/meps12784
- Frantz, A.** (1998). Does acoustic testing strand whales? *Nature* **392**, 29–29. doi:10.1038/32068
- Garnier, M., Henrich, N. and Dubois, D.** (2010). Influence of sound immersion and communicative interaction on the Lombard effect. *J. Speech Lang. Hear. Res.* **53**, 588–608. doi:10.1044/1092-4388(2009)08-0138
- Goldbogen, J. A., Stimpert, A. K., DeRuiter, S. L., Calambokidis, J., Friedlaender, A. S., Schorr, G. S., Moretti, D. J., Tyack, P. L. and Southall, B. L.** (2014). Using accelerometers to determine the calling behavior of tagged baleen whales. *J. Exp. Biol.* **217**, 2449–2455. doi:10.1242/jeb.103259
- Gustison, M. L. and Townsend, S. W.** (2015). A survey of the context and structure of high- and low-amplitude calls in mammals. *Anim. Behav.* **105**, 281–288. doi:10.1016/j.anbehav.2015.04.021

- Hardman, S. I., Zollinger, S. A., Koselj, K., Leitner, S., Marshall, R. C. and Brumm, H. (2017). Lombard effect onset times reveal the speed of vocal plasticity in a songbird. *J. Exp. Biol.* **220**, 1065–1071. doi:10.1242/jeb.148734
- Hatch, L. T., Clark, C. W., Van Parijs, S. M., Frankel, A. S. and Ponirakis, D. W. (2012). Quantifying loss of acoustic communication space for right whales in and around a U.S. national marine sanctuary. *Conserv. Biol.* **26**, 983–994. doi:10.1111/j.1523-1739.2012.01908.x
- Hatch, L. T., Wahle, C. M., Gedamke, J., Harrison, J., Laws, B., Moore, S. E., Stadler, J. H. and Van Parijs, S. M. (2016). Can you hear me here? Managing acoustic habitat in US waters. *Endanger. Species Res.* **30**, 171–186. doi:10.3354/esr00722
- Hildebrand, J. A. (2009). Anthropogenic and natural sources of ambient noise in the ocean. *Mar. Ecol. Prog. Ser.* **395**, 5–20. doi:10.3354/meps08353
- Holt, M. M., Noren, D. P., Veirs, V., Emmons, C. K. and Veirs, S. (2009). Speaking up: Killer whales (*Orcinus orca*) increase their call amplitude in response to vessel noise. *J. Acoust. Soc. Am.* **125**, EL27–EL32. doi:10.1121/1.3040028
- Holt, M. M., Noren, D. P., Dunkin, R. C. and Williams, T. M. (2015). Vocal performance affects metabolic rate in dolphins: implications for animals communicating in noisy environments. *J. Exp. Biol.* **218**, 1647–1654. doi:10.1242/jeb.122424
- Hotchkiss, C. and Parks, S. (2013). The Lombard effect and other noise-induced vocal modifications: insight from mammalian communication systems. *Biol. Rev.* **88**, 809–824. doi:10.1111/bvr.12026
- Irvine, A. B., Scott, M. D., Wells, R. S. and Kaufmann, J. H. (1981). Movements and activities of the Atlantic bottlenose dolphin, *Tursiops truncatus*, near Sarasota, Florida. *Fish. Bull.* **79**, 671–688.
- Janik, V. M. (2000a). Source levels and the estimated active space of bottlenose dolphin (*Tursiops truncatus*) whistles in the Moray Firth, Scotland. *J. Comp. Physiol. A* **186**, 673–680. doi:10.1007/s003590000120
- Janik, V. M. (2000b). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science* **289**, 1355–1357. doi:10.1126/science.289.5483.1355
- Janik, V. M. and Slater, P. J. (1998). Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim. Behav.* **56**, 829–838. doi:10.1006/anbe.1998.0881
- Jensen, F. H., Bejder, L., Wahlberg, M., Aguilar de Soto, N., Johnson, M. and Madsen, P. T. (2009). Vessel noise effects on delphinid communication. *Mar. Ecol. Prog. Ser.* **395**, 161–175. doi:10.3354/meps08204
- Jensen, F. H., Beedholm, K., Wahlberg, M., Bejder, L. and Madsen, P. T. (2012). Estimated communication range and energetic cost of bottlenose dolphin whistles in a tropical habitat. *J. Acoust. Soc. Am.* **131**, 582–592. doi:10.1121/1.3662067
- Johnson, C. S. (1968). Masked tonal thresholds in bottlenosed porpoise. *J. Acoust. Soc. Am.* **44**, 965–967. doi:10.1121/1.1911236
- Johnson, M. P. and Tyack, P. L. (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Ocean. Eng.* **28**, 3–12. doi:10.1109/OJEO.2002.808212
- Johnson, M., Aguilar de Soto, N. and Madsen, P. T. (2009). Studying the behaviour and sensory ecology of marine mammals using acoustic recording tags: a review. *Mar. Ecol. Prog. Ser.* **395**, 55–73. doi:10.3354/meps08255
- Kastak, D., Southall, B. L., Schusterman, R. J. and Kastak, C. R. (2005). Underwater temporary threshold shift in pinnipeds: Effects of noise level and duration. *J. Acoust. Soc. Am.* **118**, 3154–3163. doi:10.1121/1.2047128
- King, S. L. and Janik, V. M. (2015). Come dine with me: food-associated social signalling in wild bottlenose dolphins (*Tursiops truncatus*). *Anim. Cogn.* **18**, 969–974. doi:10.1007/s10071-015-0851-7
- King, S. L., Guarino, E., Keaton, L., Erb, L. and Jaakkola, K. (2016). Maternal signature whistle use aids mother-calf reunions in a bottlenose dolphin, *Tursiops truncatus*. *Behav. Process.* **126**, 64–70. doi:10.1016/j.beproc.2016.03.005
- Kobayashi, K. I. and Okanoya, K. (2003). Context-dependent song amplitude control in Bengalese finches. *Neuroreport* **14**, 521–524. doi:10.1097/00001756-200303030-00045
- Lane, H. and Tranel, B. (1971). The Lombard sign and the role of hearing in speech. *J. Speech Hear. Res.* **14**, 677–709. doi:10.1044/jshr.1404.677
- Lombard, E. (1911). Le signe de l'élévation de la voix. *Annales des Maladies de L'Oreille et du Larynx* **37**, 101–119.
- Lu, Y. and Cooke, M. (2008). Lombard speech: effects of task and noise type. *J. Acoust. Soc. Am.* **123**, 3072–3072. doi:10.1121/1.2932849
- Lucass, C., Eens, M. and Müller, W. (2016). When ambient noise impairs parent-offspring communication. *Environ. Pollut.* **212**, 592–597. doi:10.1016/j.envpol.2016.03.015
- Luo, J. H., Goerlitz, H. R., Brumm, H. and Wiegrebe, L. (2015). Linking the sender to the receiver: vocal adjustments by bats to maintain signal detection in noise. *Sci. Rep.* **5**, 18556. doi:10.1038/srep18556
- Madsen, P. T., Johnson, M., de Soto, N. A., Zimmer, W. M. X. and Tyack, P. (2005). Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J. Exp. Biol.* **208**, 181–194. doi:10.1242/jeb.01327
- Marten, K. and Marler, P. (1977). Sound transmission and its significance for animal vocalization. *Behav. Ecol. Sociobiol.* **2**, 271–290. doi:10.1007/BF00299740
- Martin, M. J., Gridley, T., Elwen, S. H. and Jensen, F. H. (2018). Heaviside's dolphins (*Cephalorhynchus heavisidii*) relax acoustic crypsis to increase communication range. *Proc. R. Soc. B* **285**, 20181178. doi:10.1098/rspb.2018.1178
- McDonald, M. A., Hildebrand, J. A. and Wiggins, S. M. (2006). Increases in deep ocean ambient noise in the Northeast Pacific west of San Nicolas Island, California. *J. Acoust. Soc. Am.* **120**, 711–718. doi:10.1121/1.2216565
- Merchant, N. D., Brookes, K. L., Faulkner, R. C., Bicknell, A. W. J., Godley, B. J. and Witt, M. J. (2016). Underwater noise levels in UK waters. *Sci. Rep.* **6**, 36942. doi:10.1038/srep36942
- Miksis-Olds, J. L. and Tyack, P. L. (2009). Manatee (*Trichechus manatus*) vocalization usage in relation to environmental noise levels. *J. Acoust. Soc. Am.* **125**, 1806–1815. doi:10.1121/1.3068455
- Mooney, T. A., Nachtigall, P. E. and Vlachos, S. (2009). Sonar-induced temporary hearing loss in dolphins. *Biol. Lett.* **5**, 565–567. doi:10.1098/rsbl.2009.0099
- Nabe-Nielsen, J., Sibly, R. M., Tougaard, J., Teilmann, J. and Sveegaard, S. (2014). Effects of noise and by-catch on a Danish harbour porpoise population. *Ecol. Model.* **272**, 242–251. doi:10.1016/j.ecolmodel.2013.09.025
- Nabe-Nielsen, J., van Beest, F. M., Grimm, V., Sibly, R. M., Teilmann, J. and Thompson, P. M. (2018). Predicting the impacts of anthropogenic disturbances on marine populations. *Conserv. Lett.* **11**, e12563. doi:10.1111/conl.12563
- New, L. F., Clark, J. S., Costa, D. P., Fleishman, E., Hindell, M. A., Klanjšček, T., Lusseau, D., Kraus, S., McMahon, C. R., Robinson, P. W. et al. (2014). Using short-term measures of behaviour to estimate long-term fitness of southern elephant seals. *Mar. Ecol. Prog. Ser.* **496**, U99–U344. doi:10.3354/meps10547
- Nowacek, D. P., Thorne, L. H., Johnston, D. W. and Tyack, P. L. (2007). Responses of cetaceans to anthropogenic noise. *Mammal. Rev.* **37**, 81–115. doi:10.1111/j.1365-2907.2007.00104.x
- Nowacek, S. M., Wells, R. S. and Solow, A. R. (2001). Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Mar. Mamm. Sci.* **17**, 673–688. doi:10.1111/j.1748-7692.2001.tb01292.x
- Osmanski, M. S. and Dooling, R. J. (2009). The effect of altered auditory feedback on control of vocal production in budgerigars (*Melopsittacus undulatus*). *J. Acoust. Soc. Am.* **126**, 911–919. doi:10.1121/1.3158928
- Parks, S. E., Johnson, M., Nowacek, D. and Tyack, P. L. (2011a). Individual right whales call louder in increased environmental noise. *Biol. Lett.* **7**, 33–35. doi:10.1098/rsbl.2010.0451
- Parks, S. E., Seaby, A., Célérier, A., Johnson, M. P., Nowacek, D. P. and Tyack, P. L. (2011b). Sound production behavior of individual North Atlantic right whales: implications for passive acoustic monitoring. *Endanger. Species Res.* **15**, 63–76. doi:10.3354/esr00368
- Parsons, E. C. M., Dolman, S. J., Wright, A. J., Rose, N. A. and Burns, W. C. G. (2008). Navy sonar and cetaceans: Just how much does the gun need to smoke before we act? *Mar. Pollut. Bull.* **56**, 1248–1257. doi:10.1016/j.marpolbul.2008.04.025
- Pedersen, M. B., Fahlman, A., Borque, A., Teglbjerg Madsen, P. and Jensen, F. H. (2020). Whistling is metabolically cheap for communicating bottlenose dolphins (*Tursiops truncatus*). *J. Exp. Biol.* [in press]. doi:10.1242/jeb.212498
- Pérez, J. M., Jensen, F. H., Rojano-Doñate, L. and Aguilar de Soto, N. (2016). Different forms of acoustic communication in deep-diving short-finned pilot whales (*Globicephala macrorhynchus*). *Mar. Mamm. Sci.* doi:10.1111/mms.12344
- Quick, N. J. and Janik, V. M. (2012). Bottlenose dolphins exchange signature whistles when meeting at sea. *Proc. R. Soc. B Biol. Sci.* **279**, 2539–2545. doi:10.1098/rspb.2011.2537
- Quintana-Rizzo, E., Mann, D. A. and Wells, R. S. (2006). Estimated communication range of social sounds used by bottlenose dolphins (*Tursiops truncatus*). *J. Acoust. Soc. Am.* **120**, 1671–1683. doi:10.1121/1.2226559
- Samson, J. E., Mooney, T. A., Gussekloo, S. W. S. and Hanlon, R. T. (2016). A brief review of cephalopod behavioral responses to sound. In *The Effects of Noise on Aquatic Life II* (ed. A. N. Popper and A. Hawkins), pp. 969–975. New York, NY: Springer New York.
- Sayigh, L. S., Esch, H. C., Wells, R. S. and Janik, V. M. (2007). Facts about signature whistles of bottlenose dolphins, *Tursiops truncatus*. *Anim. Behav.* **74**, 1631–1642. doi:10.1016/j.anbehav.2007.02.018
- Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D. and Irvine, A. B. (1999). Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Anim. Behav.* **57**, 41–50. doi:10.1006/anbe.1998.0961
- Schaub, A., Ostwald, J. and Siemers, B. M. (2008). Foraging bats avoid noise. *J. Exp. Biol.* **211**, 3174–3180. doi:10.1242/jeb.022863
- Scheifele, P. M., Andrew, S., Cooper, R. A., Darre, M., Musiek, F. E. and Max, L. (2005). Indication of a Lombard vocal response in the St. Lawrence River beluga. *J. Acoust. Soc. Am.* **117**, 1486–1492. doi:10.1121/1.1835508
- Schopf, C., Schmidt, S. and Zimmermann, E. (2016). Moderate evidence for a Lombard effect in a phylogenetically basal primate. *PeerJ* **4**, e2328. doi:10.7717/peerj.2328
- Schuster, S., Zollinger, S. A., Lesku, J. A. and Brumm, H. (2012). On the evolution of noise-dependent vocal plasticity in birds. *Biol. Lett.* **8**, 913–916. doi:10.1098/rsbl.2012.0676
- Schwartz, J. J. and Bee, M. A. (2013). Anuran acoustic signal production in noisy environments. In *Animal Communication and Noise* (ed. H. Brumm), pp. 91–133. Berlin, Germany: Springer-Verlag.

- Simmonds, M. P. and Lopez-jurado, L. F.** (1991). Whales and the military. *Nature* **351**, 448–448. doi:10.1038/351448a0
- Simpson, S. D., Meekan, M., Montgomery, J., McCauley, R. and Jeffs, A.** (2005). Homeward sound. *Science* **308**, 221–221. doi:10.1126/science.1107406
- Sinnott, J. M., Stebbins, W. C. and Moody, D. B.** (1975). Regulation of voice amplitude by the monkey. *J. Acoust. Soc. Am.* **58**, 412–414. doi:10.1121/1.380685
- Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C. and Popper, A. N.** (2010). A noisy spring: the impact of globally rising underwater sound levels on fish. *Trends Ecol. Evol.* **25**, 419–427. doi:10.1016/j.tree.2010.04.005
- Smith, M. E., Kane, A. S. and Popper, A. N.** (2004). Noise-induced stress response and hearing loss in goldfish (*Carassius auratus*). *J. Exp. Biol.* **207**, 427–435. doi:10.1242/jeb.00755
- Smolker, R. A., Mann, J. and Smuts, B. B.** (1993). Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behav. Ecol. Sociobiol.* **33**, 393–402. doi:10.1007/BF00170254
- Sorensen, P. M., Wisniewska, D. M., Jensen, F. H., Johnson, M., Teilmann, J. and Madsen, P. T.** (2018). Click communication in wild harbour porpoises (*Phocoena phocoena*). *Sci. Rep.* **8**. doi:10.1038/s41598-018-28022-8
- Templeton, C. N., Zollinger, S. A. and Brumm, H.** (2016). Traffic noise drowns out great tit alarm calls. *Curr. Biol.* **26**, R1173–R1174. doi:10.1016/j.cub.2016.09.058
- Tressler, J. and Smotherman, M. S.** (2009). Context-dependent effects of noise on echolocation pulse characteristics in free-tailed bats. *J. Comp. Physiol. A – Neuroethol. Sens. Neural Behav. Physiol.* **195**, 923–934. doi:10.1007/s00359-009-0468-x
- Tyack, P.** (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? *Behav. Ecol. Sociobiol.* **18**, 251–257. doi:10.1007/BF00300001
- Tyack, P. L. and Janik, V. M.** (2013). Effects of noise on animal signal production in marine mammals. In *Animal Communication and Noise* (ed. H. Brumm), pp. 251–272. Berlin, DE: Springer-Verlag.
- Van der Graaf, A. J., Ainslie, M. A., André, M., Brensing, K., Dalen, J., Dekeling, R. P. A., Robinson, S., Tasker, M. L., Thomsen, F. and Werner, S.** (2012). *European Marine Strategy Framework Directive - Good Environmental Status (MSFD GES): Report of the Technical Subgroup on Underwater noise and other forms of energy*. JRC Scientific and Technical Report. TSG Noise & Milieu Ltd. <https://www.iqoe.org/library/8061>
- Vasconcelos, R. O., Carriço, R., Ramos, A., Modesto, T., Fonseca, P. J. and Amorim, M. C. P.** (2012). Vocal behavior predicts reproductive success in a teleost fish. *Behav. Ecol.* **23**, 375–383. doi:10.1093/beheco/arr199
- Weilgart, L. S.** (2007). The impacts of anthropogenic ocean noise on cetaceans and implications for management. *Can. J. Zool.* **85**, 1091–1116. doi:10.1139/Z07-101
- Wells, R. S.** (1991). The role of long-term study in understanding the social structure of a bottlenose dolphin community. In *Dolphin Societies: Discoveries and Puzzles* (ed. K. Pryor and K. S. Norris), pp. 199–225. Berkeley, CA: University of California Press.
- Wells, R. S.** (2003). Dolphin social complexity: lessons from long-term study and life-history. In *Animal Social Complexity: Intelligence, Culture, and Individualized Societies* (ed. F. B. M. De Waal and P. L. Tyack), pp. 32–56. Cambridge: Harvard University Press.
- Wells, R. S.** (2009). Learning from nature: bottlenose dolphin care and husbandry. *Zoo Biol.* **28**, 635–651. doi:10.1002/zoo.20252
- Wells, R. S.** (2014). Social structure and life history of common bottlenose dolphins near Sarasota Bay, Florida: Insights from four decades and five generations. In *Primates and Cetaceans: Field Research and Conservation of Complex Mammalian Societies, Primatology Monographs* (ed. J. Yamagiwa and L. Karczmarski), pp. 149–172. Tokyo: Springer.
- Wells, R. S. and Scott, M. D.** (2018). Bottlenose dolphin: Common Bottlenose Dolphin (*Tursiops truncatus*). In *Encyclopedia of Marine Mammals* (ed. B. Würsig, J. G. M. Thewissen and K. Kovacs), pp. 118–125. San Diego, CA: Elsevier, Inc.
- Wells, R. S., Rhinehart, H. L., Hansen, L. J., Sweeney, J. C., Townsend, F. I., Stone, R., Casper, D. R., Scott, M. D., Hohn, A. A. and Rowles, T. K.** (2004). Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. *EcoHealth* **1**, 246–254. doi:10.1007/s10393-004-0094-6
- Zollinger, S. A., Goller, F. and Brumm, H.** (2011). Metabolic and respiratory costs of increasing song amplitude in zebra finches. *PLoS ONE* **6**, e23198. doi:10.1371/journal.pone.0023198
- Zollinger, S. A., Slater, P. J. B., Nemeth, E. and Brumm, H.** (2017). Higher songs of city birds may not be an individual response to noise. *Proc. R. Soc. B* **284**, 20170602. doi:10.1098/rspb.2017.0602