

## RESEARCH ARTICLE

# Dynamic biosonar adjustment strategies in deep-diving Risso's dolphins driven partly by prey evasion

Frants H. Jensen<sup>1,2,\*</sup>, Onno A. Keller<sup>3,4,5,\*</sup>, Peter L. Tyack<sup>6</sup> and Fleur Visser<sup>3,4,7</sup>

## ABSTRACT

Toothed whales have evolved flexible biosonar systems to find, track and capture prey in diverse habitats. Delphinids, phocoenids and iniids adjust inter-click intervals and source levels gradually while approaching prey. In contrast, deep-diving beaked and sperm whales maintain relatively constant inter-click intervals and apparent output levels during the approach followed by a rapid transition into the foraging buzz, presumably to maintain a long-range acoustic scene in a multi-target environment. However, it remains unknown whether this rapid biosonar adjustment strategy is shared by delphinids foraging in deep waters. To test this, we investigated biosonar adjustments of a deep-diving delphinid, the Risso's dolphin (*Grampus griseus*). We analyzed inter-click interval and apparent output level adjustments recorded from sound recording tags to quantify *in situ* sensory adjustment during prey capture attempts. Risso's dolphins did not follow typical ( $20\log R$ ) biosonar adjustment patterns seen in shallow-water species, but instead maintained stable repetition rates and output levels up to the foraging buzz. Our results suggest that maintaining a long-range acoustic scene to exploit complex, multi-target prey layers is a common strategy amongst deep-diving toothed whales. Risso's dolphins transitioned rapidly into the foraging buzz just like beaked whales during most foraging attempts, but employed a more gradual biosonar adjustment in a subset (19%) of prey approaches. These were characterized by higher speeds and minimum specific acceleration, indicating higher prey capture efforts associated with evasive prey. Thus, tracking and capturing evasive prey using biosonar may require a more gradual switch between multi-target echolocation and single-target tracking.

**KEY WORDS:** Echolocation, Sensory ecology, Mesopelagic foraging, Deep-water environment, Biosonar strategies, Gain control

## INTRODUCTION

Bats and toothed whales have independently evolved a sophisticated biosonar system for navigation and to detect, discriminate and capture prey in a wide range of habitats (Denzinger et al., 2016;

Fenton et al., 2014; Jensen et al., 2018). Biosonar is an active sense where intense, high-frequency transients are emitted by the echolocating animal that then listens for the faint, returning echoes to extract information on identity and spatial distribution of objects and potential prey in its environment. The interaction between features of the outgoing echolocation signals and of the target determine the echoic information available, so echolocating animals can actively manipulate their sensory perception of the environment through dynamic changes in biosonar behavior or characteristics of echolocation signals (Moss and Surlykke, 2010; Moss et al., 2011).

Biosonar-based foraging in bats has typically been divided into three distinctive 'phases' consisting of a search, an approach, and a terminal or capture phase (Griffin et al., 1960). While searching for prey, bats emit echolocation signals at a slow, stable repetition rate and thus high inter-call or inter-click intervals (ICIs). The start of the approach phase is marked by a sudden turn towards a target and is further characterized by a gradual decrease in ICI as the distance between predator and prey decreases. Finally, the ICI is lowered rapidly when prey is at close distance, resulting in a foraging buzz during the capture phase that lasts either until prey is captured or prey pursuit is terminated (Griffin et al., 1960; Kothari et al., 2014; Simmons et al., 2001; Warnecke et al., 2015).

Dolphins have been shown to adopt a strikingly similar biosonar adjustment strategy where they gradually reduce ICIs when approaching a target, leading up to foraging buzz during prey interception (Wisniewska et al., 2014). Bats and delphinids working on single target detection tasks generally maintain an ICI that is above the two-way travel time (TWTT) in order to avoid range ambiguity (Au, 1993; Kalko, 1995), though dolphins can deviate from this mode at ranges above 25 m (Ladegaard et al., 2019). Hence, the reduction in ICI observed in bats and dolphins during the approach phase results from a decrease in distance between predator and prey. This adjustment provides the predator with a higher temporal resolution of the spatial relationship between predator, prey and its environment, thus lowering the odds of prey escape (Ladegaard et al., 2015; Wisniewska et al., 2014).

As echolocating bats and toothed whales approach a target and the range ( $R$ ) to target decreases, they generally decrease biosonar output levels following an approximately  $20\log R$  relationship, corresponding to a 6 dB decrease in source level per halving of distance ( $dh$ ). This biosonar adjustment is used by delphinids (Au and Benoit-Bird, 2003; Jensen et al., 2009; Ladegaard et al., 2017; Rasmussen et al., 2002), phocoenids (Linnenschmidt et al., 2012) and even iniids (Ladegaard et al., 2017), and thus seems to be a relatively common feature of aquatic as well as aerial biosonar systems (Hartley, 1992). Since the level of returning echoes from a single target changes as a function of the two-way transmission loss (approximately  $40\log R$ ) whereas volume reverberation from a fish school is predicted to vary as a function of the one-way transmission loss (approximately  $20\log R$ ), the observed adjustments in toothed whales were originally suggested to help stabilize echo levels originating from fish schools (Au and

<sup>1</sup>Aarhus Institute of Advanced Studies, Aarhus University, 8000 Aarhus C, Denmark. <sup>2</sup>Biology Department, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA. <sup>3</sup>Department of Coastal Systems, Royal Netherlands Institute for Sea Research and Utrecht University, P.O. Box 59, 1790 AB Den Burg Texel, The Netherlands. <sup>4</sup>Department of Freshwater and Marine Ecology, Institute for Biodiversity and Ecosystem Dynamics, University of Amsterdam, 1090 GE Amsterdam, The Netherlands. <sup>5</sup>Department of Animal Ecology, Utrecht University, 3584 CH Utrecht, The Netherlands. <sup>6</sup>Scottish Oceans Institute, School of Biology, University of St Andrews, East Sands, St Andrews KY16 8LB, UK. <sup>7</sup>Kelp Marine Research, 1624CJ Hoorn, The Netherlands.

\*Joint first authors

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

© F.H.J., 0000-0001-8776-3606; O.A.K., 0000-0002-3443-1234; P.L.T., 0000-0002-8409-4790; F.V., 0000-0003-1024-3244

Benoit-Bird, 2003). On the other hand, a full stabilization of the echo level from a single target might be achieved through partial transmission gain control complemented by adjustments on the auditory side of biosonar systems (Nachtigall and Supin, 2008) similar to bats (Hartley, 1992). The  $20\log R$  adjustment was thought to be a consequence of limitations imposed on the sound production system by increased repetition rates and was therefore termed automatic gain control. However, source levels are not limited by ICIs in bottlenose dolphins (Ladegaard et al., 2019) or harbor porpoises (Sørensen et al., 2018) and they seem to be under cognitive control at least in bottlenose dolphins (*Tursiops truncatus*) (Kloepper et al., 2014). These adjustments may therefore better be represented as an interaction between hearing and click output level. Since four toothed-whale species have been found to have cognitive control over hearing sensation levels (Nachtigall and Supin, 2017), it is likely that other toothed whales have tight cognitive control over click levels as well. Most studies of time-varying gain also note some variation in adjustments between trials and it is becoming increasingly apparent that toothed whale biosonar adjustment may depend on the context of prey capture (e.g. Ladegaard et al., 2019).

Not all echolocating toothed whales gradually adjust their biosonar output when approaching prey. In contrast to delphinids, Blainville's beaked whales (*Mesoplodon densirostris*) and sperm whales (*Physeter macrocephalus*) searching for prey during deep foraging dives can maintain a stable ICI during the approach phase, thus lacking coupling between the ICI and TWTT as the range towards the target decreases (Fais et al., 2016; Madsen et al., 2005). Moreover, Blainville's beaked whales do not adjust source levels gradually when approaching prey but instead maintain relatively stable apparent output levels up to the foraging buzz (Madsen et al., 2005). They may benefit from stable ICIs and high output levels as this allows them to maintain a long-range acoustic scene, enabling detection and identification of multiple targets (Madsen et al., 2005).

While it is evident that deep-diving beaked and sperm whales have evolved very different biosonar behaviors from shallow-water delphinids, the underlying evolutionary drivers of these differences remain unclear. If such a strategy is an adaptation to foraging in a deep-water habitat, we would expect that deep-diving delphinids would also deviate from the gradual  $\sim 20\log R$  source level adjustments when approaching and capturing prey. Here, we test the hypothesis that deep-diving members of the *Delphinidae* family maintain stable ICI and source levels up to the foraging buzz by investigating *in situ* biosonar adjustment strategies employed by deep-diving Risso's dolphins.

## MATERIALS AND METHODS

### Field effort

We investigated the diving and echolocation behavior of Risso's dolphins [*Grampus griseus* (Cuvier 1812)] off Terceira Island, Azores (Portugal) between May and August of 2013–2017. Risso's dolphins inhabit waters characterized by steep bathymetry and bottom depths reaching up to 1000 m or more (Baird, 2009). Stomach content analyses from Risso's dolphins in the Faroe Islands and the Mediterranean Sea showed a diet primarily composed of cephalopod species inhabiting the deep scattering layer at depths between 400 and 800 m (Blanco et al., 2006; Bloch, 2011). Acoustic and movement data were collected from individuals using version 3 DTAGs (sample rate: 240 kHz sound, 200 Hz accelerometer, magnetometer and depth data), attached with 4 suction cups (Johnson and Tyack, 2003). Individuals were approached and tagged from a small 6 m rigid-hulled inflatable boat using a 7 m carbon-fiber pole. Tag placement varied between deployments, but was aimed between the blowhole

and dorsal fin of the animal. After tags released from animals, they floated to the surface, after which the field crew used the VHF beacon to track and retrieve tags.

Fieldwork was completed under permits 33/2013/DRA, 10/2015/DRA, 8/2016/DRA and 34/2017/DRA, issued by Secretaria Regional da Energia, Ambiente e Turismo of the Direção Regional do Ambiente (Horta, Faial, Açores, Portugal).

### Extraction of echolocation data

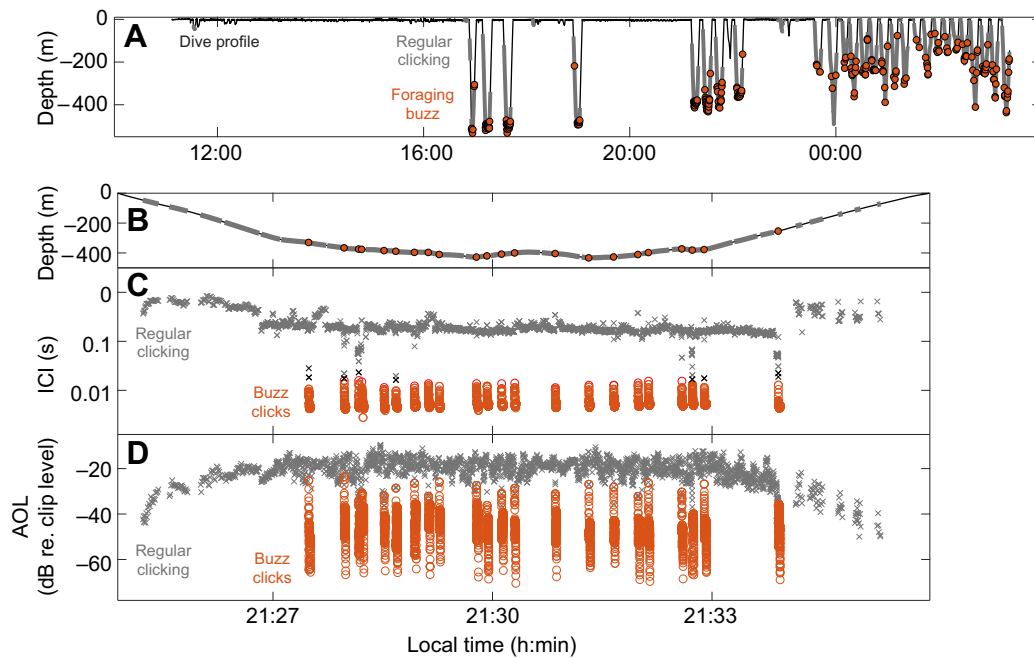
All analyses were performed using MATLAB 2014b (MathWorks, Massachusetts, USA) unless stated otherwise. The acoustic recordings were inspected for echolocation clicks and foraging buzzes using auditing scripts from the DTAG toolbox (<https://www.soundtags.org/>). All echolocation click sequences and foraging buzzes produced by the tagged animal were marked manually. Echolocation clicks produced by the tagged dolphin were distinguished from those produced by non-tagged dolphins by the presence of low-frequency energy (<15 kHz) and a relatively consistent angle of arrival compared with vocalizations from other individuals around the focal whale (Aguilar Soto et al., 2008; Arranz et al., 2016; Johnson et al., 2006; Zimmer et al., 2005).

The exact timing of echolocation clicks was extracted using a modified version of the 'findclicks' function from the DTAG toolbox. To detect clicks, the sound from one channel was first filtered with a 5–80 kHz 4-pole Butterworth filter, after which clicks were detected when the signal envelope exceeded a detection threshold between approximately 106 and 112 dB re. 1  $\mu$ Pa, with the exact detection threshold depending on the background noise level and tag calibration values. To avoid false detection of reflections, peaks within 10 ms and 1 ms of previous peaks were ignored in click series and buzzes, respectively, resulting in maximum repetition rates of 100 Hz (regular clicking) and 1000 Hz (foraging buzz). Since accuracy of click detection was critical, especially at the transition from regular search clicks into a foraging buzz, all automatic click detections were manually verified and corrected for missing or falsely detected clicks through inspection of combined signal envelope and spectrogram plots.

For each click, the ICI was defined as the time between each click and the preceding click. The apparent output level (AOL), defined as the received level on the tag in a fixed, but highly off-axis, position on the body of the whale (Madsen et al., 2005), was calculated as the peak of the Hilbert envelope after applying a 5–80 kHz 4-pole Butterworth bandpass filter. Clipping due to apparent output levels exceeding the maximum recording amplitude of the DTAG was checked, but was not a problem for any of the datasets used here. A three-point median filter was applied to the ICI and AOL datasets to exclude occasional outliers.

### Biosonar behavior segmentation based on ICI

Echolocation clicks were then segmented into regular clicks or buzz clicks based on ICI with the aim of defining the transition phase between regular clicking and the foraging buzz. Inspection of click series supported the observation that Risso's dolphins gradually adjust the ICI over the course of foraging dives, reflecting changes in biosonar inspection range as the diving dolphin approaches prey layers (Arranz et al., 2018; Fig. 1). To accommodate these ICI adjustments, a dynamic threshold was used to define regular clicks based on the ICI at a specific time in a dive. ICI adjustments throughout dives were then tracked by allocating regular clicks into 3 s time bins from which the maximum ICI per bin could be calculated. Next, a robust lowess smoother that performs local regression using weighted linear least squares was used to compute



**Fig. 1. Dive and biosonar behavior of a Risso's dolphin.** (A) Dive profile (black line) showing periods of regular echolocation clicks (thick grey line) and foraging buzzes (orange filled circles) during deep dives. (B) Dive profile and biosonar behavior during a single foraging dive (#6). (C) Adjustment of inter-click interval (ICI) and (D) apparent output level (AOL) of regular and transition clicks (grey crosses) throughout a dive, illustrating the rapid decrease in both AOL and ICI during foraging buzzes (red circles). All data from dataset gg17\_200a.

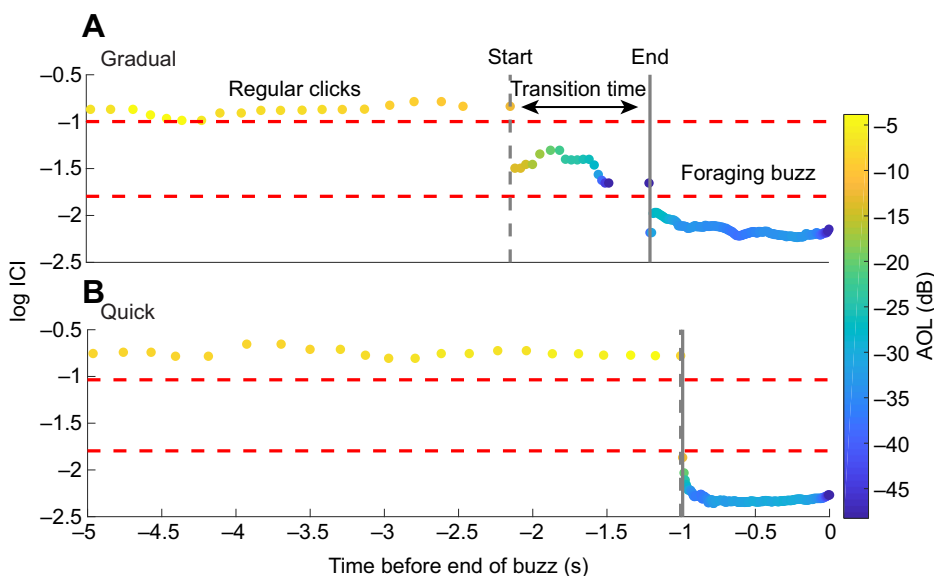
the baseline ICI and estimate how it changed gradually over the course of the dive (Fig. S1).

Only high-quality buzzes were used for subsequent analyses, and these were defined as buzzes that (1) were not preceded by another buzz in a 10 s time frame, (2) had a duration of 5 s or shorter and (3) did not overlap with extensive flow noise or other acoustic interference, making it difficult for clicks to be extracted reliably. For each high-quality buzz, all clicks produced within 10 s prior to the end of the buzz were extracted, their ICIs were used to estimate the transition period between regular clicking and buzz. Regular clicking (search behavior) was initially defined as periods where the ICI was longer than 40% of the baseline ICI, and buzz clicks were defined as clicks with an ICI shorter than 16 ms based on

distribution of click ICIs (Fig. S2). We then identified the last sequence of 5 or more regular clicks before the buzz and selected the last click of this sequence as the end of regular clicking and thus the start of a transition phase, thus ensuring that methods were robust to missing a single click during the transition (Fig. 2). The end of the transition was defined as the first buzz click in a sequence of at least 40 buzz clicks with ICI <16 ms occurring after the transition start time (Fig. 2). Finally, the transition time was computed as the difference between the start and end of the transition of each buzz.

**Apparent output level (AOL) adjustment**

To test when Risso's dolphins start adjusting the AOL of clicks leading up to a buzz, all clicks 10 s prior to the end of a buzz were



**Fig. 2. Parsing biosonar behavior.**

(A) Gradual and (B) quick transition times between regular clicks and buzzes. Horizontal dashed red lines represent the regular click and buzz click ICI threshold, respectively. The vertical grey lines mark the start (dashed line) and end (solid line) of the transition. Each dot represents a click, color coded by AOL; y-axis shows log of ICI measured in seconds.

extracted. The AOL of each click was normalized by subtracting the baseline AOL, defined as the mean AOL of clicks that occurred between 7 and 10 s before the end of the buzz. Buzzes that did not have any clicks within this time frame were excluded. The start of AOL adjustment for each buzz was defined as the time of the first click in a sequence of at least 20 pre-buzz clicks where AOL was more than 3 dB below the baseline AOL (see Fig. S3).

The effect of analyzing individual biosonar adjustments for each buzz separately was compared to the classical approach of pooling multiple adjustments by fitting an exponentially decreasing function (Norum et al., 2012) to individual and pooled data on AOL excluding buzz clicks:

$$\text{AOL}(t) = \text{AOL}_{\text{search}} - \alpha \times e^{(-\beta(t-\tau))}. \quad (1)$$

Here,  $t$  is the time before the end of a buzz,  $\text{AOL}_{\text{search}}$  is the fitted baseline AOL,  $\tau$  is the time point halfway through the adjustment, and  $\alpha$  and  $\beta$  together define the shape of the curve and thus the adjustment intensity.

The pre-transition AOL adjustment was computed from the first click in a 10 s window before the end of a buzz until the click defining the start of AOL adjustment. The transition AOL adjustment was computed from the click defining the start of AOL adjustment until the first buzz click. Rate of adjustment was calculated in decibel per doubling of distance (dB dd<sup>-1</sup>):

$$\text{Rate of adjustment} \left( \frac{\text{dB}}{\text{dd}} \right) = \frac{(\text{AOL}_1 - \text{AOL}_2)}{\log_2(d_1/d_2)}. \quad (2)$$

Here,  $\text{AOL}_1$  and  $\text{AOL}_2$  are the normalized AOLs at the start and end, respectively, and  $d_1$  and  $d_2$  represent the distance towards a target in meters at the start and end, respectively, assuming an approach speed of 2 m s<sup>-1</sup> (Sato et al., 2007).

### Movement parameters

All inertial data used for movement analysis (accelerometer, magnetometer and depth data) were down-sampled to 10 Hz during initial sensor data processing. In order to perform a tag-to-whale frame rotation, the tag position was estimated at the start and end of each dive (>50 m) using the 'prhpredictor' function within the DTAG toolbox. Times when the tag slid on the body of the dolphin were identified when the predicted position changed by more than 10 deg in any axis. From the whale frame data, we calculated animal pitch, roll and heading following methods in Johnson and Tyack (2003) and the DTAG toolbox.

To test how different biosonar strategies relate to movement of the predator, we calculated two movement metrics. As a relatively direct measure of speed, the orientation-corrected depth rate (OCDR, m s<sup>-1</sup>) (Miller, 2004) was calculated after applying a low-pass filter with a cutoff frequency of 0.63 Hz (0.7×dominant stroke frequency) to track body orientation. For each buzz, we calculated the mean

speed from a 5 s window preceding the end of the buzz. This method for estimating forward speed is less accurate at low pitch angles and therefore speed was computed only when pitch angle of the whale was higher than 20 deg for at least half the time during this window. As an indirect proxy for movement effort valid for low pitch angles, we calculated the mean minimum specific acceleration (MSA; m s<sup>-2</sup>) (Simon et al., 2012), from the 5 s window preceding the end of each buzz. MSA is a proxy for movement-related energy expenditure, used as a relative measure because it depends on the position of the tag on the body of the animal. Both speed and MSA were computed from functions in the DTAG toolbox.

### Statistical analyses

To test for different biosonar adjustment strategies within the overall population, we fitted a Gaussian mixture model to the transition times from regular clicks to buzzes using MATLAB. All other statistical analyses were performed using R version 3.4.3 (<https://www.r-project.org/>). To assess whether animals preferred one strategy over the other, we performed a Wilcoxon signed rank test. The effect of biosonar adjustment strategy on start of AOL adjustment (seconds before end of buzz), rate of AOL adjustment (dB dd<sup>-1</sup>) and forward speed was analyzed using a generalized linear mixed model (GLMM) with animal ID as random effect. To test for differences in MSA between biosonar strategies, we included tag position as a random effect nested within ID in the GLMM to include the effect of tag slides. GLMMs were performed with the lme4 package (Bates et al., 2015).

## RESULTS

### Data collection

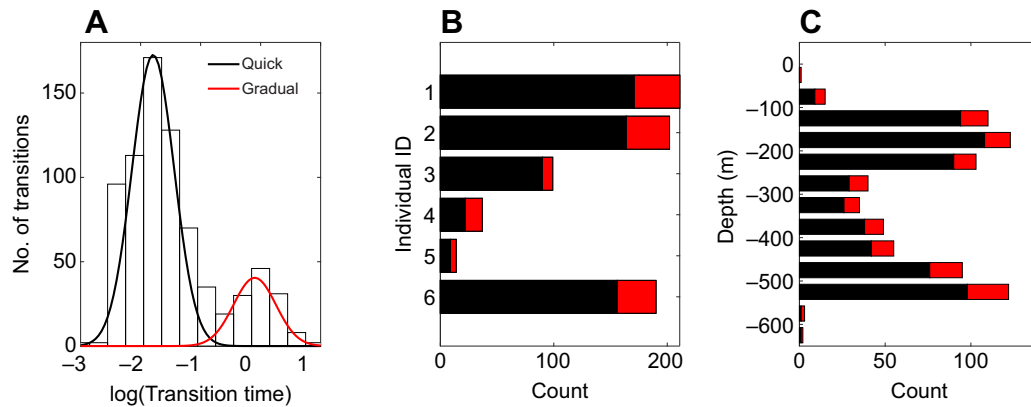
We analyzed dive and echolocation behavior of 7 tag deployments across 6 individuals, including 596,654 echolocation clicks and 1059 foraging buzzes. In total, 781 buzzes qualified as high quality. The majority of buzzes omitted were preceded by another buzz in a 10 s time frame, and thus measuring pre-buzz sonar adjustments was impossible. For 28 high quality buzzes, the transition phase between regular clicks and buzz clicks could not be extracted successfully because either the last regular click or first buzz click could not be automatically identified. Therefore, 753 (71%) high quality buzzes were included in the analysis (Table 1).

### Dive and echolocation behavior

Risso's dolphins typically started foraging in the afternoon and continued foraging during the night at depths ranging from 50 to 600 m (Fig. 1A,B). A dive consisted of a descent phase, a bottom phase and an ascent phase where prey capture effort (measured by number of buzzes) typically concentrated during the bottom phase (Fig. 1B). Risso's dolphins adjusted their ICI throughout a foraging dive. The ICI typically decreased during the descent phase, remained relatively stable during the bottom phase and increased

**Table 1. Summary of tag deployments**

Individual	Tag ID	Date of tagging (day-month-year)	Duration of deployment (h:min:s)	No. of clicks	No. of buzzes	No. of buzzes analyzed (%)
1	gg13_238a	26-8-2013	5:40:42	33,288	21	15 (71%)
1	gg17_203a	22-7-2017	9:21:04	99,575	274	196 (72%)
2	gg15_229a	17-8-2015	16:40:00	162,457	263	202 (77%)
3	gg15_229c	17-8-2015	10:59:00	77,719	138	99 (72%)
4	gg16_169a	17-6-2016	4:51:46	54,224	65	37 (57%)
5	gg16_171a	19-6-2016	11:47:19	28,655	20	14 (70%)
6	gg17_200a	19-7-2017	15:53:46	140,736	278	190 (68%)
Total				596,654	1059	753 (71%)



**Fig. 3. Quick and gradual biosonar adjustment strategies in Risso's dolphins.** (A) Distribution of transition times overlaid with best-fitting two-component Gaussian mixed model distributions for quick and gradual transition times between regular clicks and buzzes. x-axis shows log of transition time in seconds. (B) Distribution of biosonar adjustment strategies within individuals. (C) Distribution of biosonar adjustment strategies as a function of depth.

during the ascent phase (Fig. 1C). Animals also adjusted the AOL of echolocation clicks throughout foraging dives, reaching the highest values during the bottom phase (Fig. 1D). Buzzes were characterized by a steep drop in both ICI and AOL (Fig. 1C,D).

#### Identification of different biosonar adjustment strategies

To investigate biosonar adjustment strategies during prey captures, we tested for variation in the transition time from regular clicks to buzzes (Fig. 2). The Gaussian mixture model identified two biosonar adjustment strategies during the transition phase from regular clicking to buzz: quick and gradual transitions separated by a transition time of roughly 0.15 s (Fig. 2 and Fig. 3A). Throughout the results, we report mean values ( $\pm$ s.d.) unless stated otherwise. 'Quick' transitions showed a mean transition time of  $0.026 \pm 0.03$  s, while 'gradual' transitions were considerably longer ( $1.20 \pm 1.09$  s). All 6 individuals used quick transitions ( $N=612$ ) significantly more often than gradual transitions ( $N=141$ ; Wilcoxon signed rank test:  $V=21$ ,  $P=0.016$ ; Fig. 3B).

#### Adjustment of the apparent output level

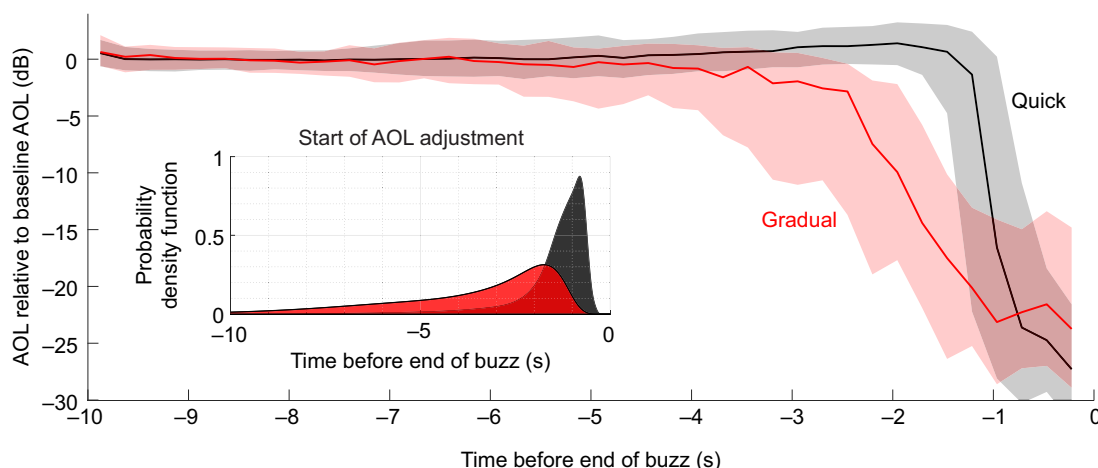
Start of AOL adjustment was computed successfully for 748 buzzes (see Fig. S3). The mean start of the AOL adjustment was significantly earlier for buzzes with gradual biosonar adjustment

compared with buzzes with quick biosonar adjustment (GLMM:  $t=-16.57$ , d.f.=746.3,  $P<0.001$ ; Fig. 4). During gradual biosonar adjustments, the mean start of AOL adjustment was  $3.54 \pm 2.0$  s before the end of a buzz compared with  $1.49 \pm 1.1$  s for quick biosonar adjustments.

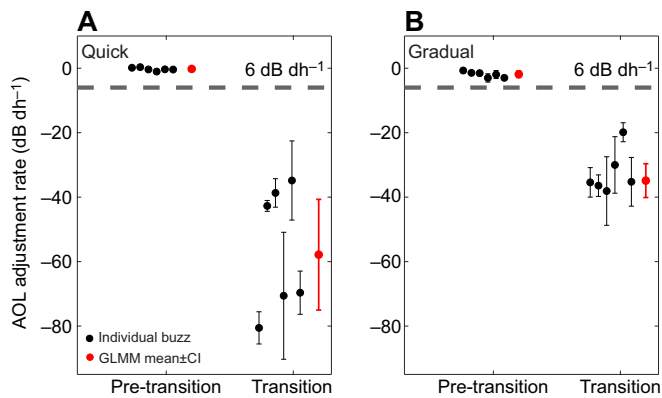
Pre-transition and transition AOL adjustments ( $\text{dB dd}^{-1}$ ) were calculated for 726 buzzes. Biosonar AOL adjustment rates during individual prey approaches are highly variable, which is not clear when pooling data (Fig. S4). The mean pre-transition AOL adjustment rate across individuals was  $0.06 \pm 1.64$   $\text{dB dd}^{-1}$  for quick and  $1.77 \pm 3.94$   $\text{dB dd}^{-1}$  for gradual biosonar adjustments, indicating that for the latter, some minor AOL adjustment may have occurred before the  $-3$  dB AOL adjustment criterion (Fig. 5). The transition AOL adjustment rate was higher for quick biosonar adjustment strategies compared with gradual biosonar adjustments (GLMM:  $t=5.1$ , d.f.=725.1,  $P=0.001$ ). The mean AOL adjustment rate for gradual biosonar adjustments was  $34.87 \pm 31.1$   $\text{dB dd}^{-1}$ , approximately half the rate observed for quick biosonar adjustments ( $57.85 \pm 61.57$   $\text{dB dd}^{-1}$ ).

#### Movement

Mean speed estimates for the 5 s window preceding the end of buzzes were obtained for 398 buzzes that occurred at pitch angles high



**Fig. 4. Adjustment of apparent output level preceding foraging buzzes.** The median AOL value was calculated in 0.25 s time bins for each buzz. For quick and gradual biosonar adjustments, the median, 25th and 75th percentile AOL was calculated across buzzes. The inset shows the timing of the start of AOL adjustment (defined as the point at which AOL is 3 dB below baseline AOL) for quick (black) and gradual (red) biosonar adjustments.



**Fig. 5. Apparent output level adjustment rates (dB per halving of distance).** (A) Quick and (B) gradual biosonar adjustment strategies. Mean AOL adjustment rate ( $\pm$ s.e.m.) per individual (black circles) before and during transitions and corresponding generalized linear mixed model (GLMM) mean ( $\pm$ 95% CI) ignoring random effects of individual (red circles). The horizontal dashed lines represent the AOL adjustment rate of 6 dB  $dh^{-1}$ , typically found in cetaceans applying gain control (from pooled approach).

enough to reliably estimate speed. These included 312 quick and 86 gradual adjustments. Mean speed was significantly higher during gradual than during quick adjustments,  $2.7 \pm 0.7$  vs  $2.3 \pm 0.6$   $m s^{-1}$ , respectively (GLMM:  $t = -4.9$ , d.f. = 398,  $P < 0.001$ ; Fig. 6). MSA was computed for all 753 buzzes. For gradual adjustments, mean MSA was significantly higher than for quick adjustments,  $0.89 \pm 0.6$  vs  $0.55 \pm 0.4$   $m s^{-2}$ , respectively (GLMM:  $t = -8.1$ , d.f. = 749.3,  $P < 0.001$ ; Fig. 6).

## DISCUSSION

### Shared biosonar strategy among deep-diving toothed whales

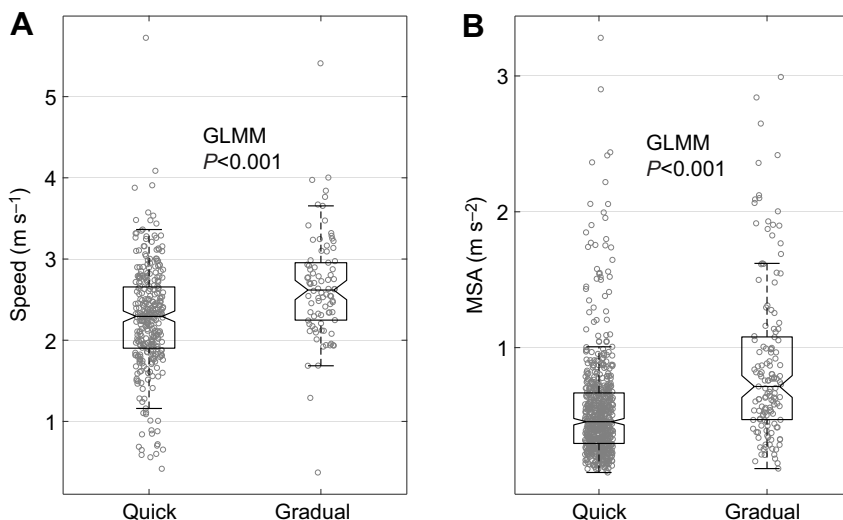
Echolocating animals are able to manipulate their auditory scene through adjustments to their biosonar behavior, the characteristics of individual biosonar signals, and auditory processing. To date, studies quantifying biosonar adjustments have shown that many wild species of small, toothed whales gradually decrease ICI and decrease source levels by approximately 20logR with decreasing target range (Atem et al., 2009; Au and Benoit-Bird, 2003; Au and Würsig, 2004; Beedholm and Miller, 2007; Ladegaard et al., 2017; Linnenschmidt et al., 2012; Rasmussen et al., 2002). Here, we show that deep-diving

Risso's dolphins do not follow typical 20logR source level adjustments seen in shallow-water species. Instead, Risso's dolphins predominantly (in 81% of foraging buzzes) maintained a high and relatively stable ICI and apparent output level (mean = 0.06 dB  $dd^{-1}$ ) up to the point at which they rapidly adjusted both parameters (Fig. 4), resulting in a mean adjustment of 60.57 dB  $dd^{-1}$  when transitioning into the foraging buzz (Fig. 5). Whilst the remaining 19% of buzzes analyzed were more gradual, adjustment rates were still much steeper (34.87 dB  $dd^{-1}$  on average) than the roughly 6 dB  $dd^{-1}$  adjustment adopted by shallow-water toothed whales. While toothed whales may adjust directivity during approach (Jensen et al., 2015) and buzz phase (Wisniewska et al., 2015), these small variations are unlikely to explain constant source levels, nor are they sufficient to explain the rapid changes during the transition. The biosonar adjustment strategies observed in Risso's dolphins resemble the biosonar behavior of deep-diving beaked whales and sperm whales that switch rapidly into a buzz when prey is within a distance of around one body length (Fais et al., 2016; Madsen et al., 2005) and these strategies therefore demonstrate convergent biosonar behavior for animals that have independently transitioned to a deep-water foraging niche.

### Biosonar adjustment strategies may reflect ecological adaptations

Deep-diving toothed whales, including at least sperm whales, two species of beaked whales and Risso's dolphins, all seem to employ a shared biosonar strategy that has thus far not been recorded in shallow-diving toothed whales. The contrast in biosonar strategy between deep- and shallow-diving toothed whales may indicate that ecological context is important in determining how toothed whales dynamically adjust their acoustic scene when approaching and capturing prey. By continuing to emit high source levels with a long inspection range after identifying and approaching prey, deep-diving beaked whales maintain a long-range acoustic scene that may increase foraging efficiency in a multi-target environment (Madsen et al., 2005, 2013). Our findings suggest that not only beaked whales and sperm whales (Fais et al., 2016; Madsen et al., 2005), but also at least some deep-diving delphinid species, seem to use biosonar behaviors that may facilitate perceptual organization of more complex multi-target acoustic scenes.

One major difference between deep-diving and shallow-diving species is the environment in which they operate their sonar. Species



**Fig. 6. Adjustment strategy shaped by context.**

Boxplots of (A) speed ( $m s^{-1}$ ) and (B) minimum specific acceleration (MSA;  $m s^{-2}$ ) grouped by biosonar adjustment strategy. Raw datapoints (grey) for each strategy are plotted in the background.

foraging in shallow water may seldom benefit from enabling long-range echolocation if their prey are close and located near clutter or reverberation. Shallow-diving species mostly echolocate and find prey near the surface, on the bottom, or even prey buried under ground. These extended surfaces act as acoustic reflectors to generate reverberation following each echolocation click that could potentially mask returning echoes. Porpoises solving target-approach experiments respond to an increase in reverberation from the environment by lowering source levels (Ladegaard and Madsen, 2019). River dolphins inhabiting complex shallow water habitats characterized by high levels of clutter and reverberation produce clicks at lower source levels and ICIs compared with species of the same size, effectively simplifying the acoustic scene and enhancing prey tracking abilities (Jensen et al., 2013; Ladegaard et al., 2015). These biosonar strategies are mirrored in terrestrial echolocating species, where bats hunting in uncluttered environments emit louder calls (Surlykke and Kalko, 2008) at lower rates (Petrites et al., 2009) than bats hunting in cluttered environments (Brinkløv et al., 2010), although surrounding conspecifics tend to pose additional demands to biosonar behavior (Warnecke et al., 2015). Instead of maintaining a long-range acoustic scene, toothed whales foraging in shallow habitats may benefit from simplifying the acoustic scene and enhancing their ability to track and capture single prey by lowering source levels very gradually, resulting in a  $\sim 20\log R$  adjustment. However, biosonar decision-making during a single foraging event probably depends on the interaction of additional factors (e.g. prey behavior) that collectively determine the challenges faced by foraging toothed whales.

#### Adapting biosonar to evasive prey

The predominant biosonar mode adopted by all foraging Risso's dolphins sampled in this study was a rapid adjustment from regular clicking to buzzing. However, echolocation is an active sense, allowing for dynamic sensory adjustments to suit the needs of local conditions (Moss and Surlykke, 2010). Our results highlight the importance of context and local conditions since 19% of the prey interceptions involved a gradual biosonar adjustment that started approximately 2.5 times further ahead of intercepting prey (the end of a buzz) compared with quick adjustments. These gradual adjustments were markedly steeper than and thus different from the  $20\log R$  found in shallow-diving toothed whales. Anecdotal evidence from sperm whales further suggests that biosonar adjustment strategies are dynamic, driven by context and not species specific (see fig. 4 in Fais et al., 2016). In our data, early click-to-buzz transitions with a more gradual change in both ICI and AOL as the predator approaches prey are found across individuals and at all depths (Fig. 3), highlighting that other factors are driving biosonar strategies.

Several studies have shown that toothed whales adjust biosonar behavior and movement according to prey characteristics, although studies relating biosonar adjustment strategies in wild toothed whales to prey characteristics remain scarce (DeRuiter et al., 2009; Isojunno and Miller, 2018; Johnson et al., 2008; Madsen et al., 2013). We hypothesize that when toothed whales approach and chase evasive prey, they choose to adjust their sonar more gradually, thereby trading a deep acoustic scene for increased sampling rates and reduced complexity of the acoustic scene. Echograms have proven useful to study the size and behavior of targeted prey and can therefore be a good tool to study biosonar and movement behavior in more detail in relation to prey characteristics (Johnson et al., 2004; Wisniewska et al., 2016). However, echoes of clicks from Risso's dolphins are not recorded well enough on the tag for reliable calculation of echograms. We therefore used movement effort as a proxy for evasiveness of

prey. Our results indicate that Risso's dolphins changed their locomotor patterns by adopting a higher mean speed and MSA, thus increasing the effort to capture prey that is most likely trying to escape which supports our hypothesis. A correlation between biosonar and movement behavior was also observed in foraging sperm whales, which produce longer buzzes with higher click rates during more active pursuits (Isojunno and Miller, 2018).

The variation observed in both speed and MSA suggests that additional characteristics of the acoustic scene may also influence biosonar decision making. While none of the foraging attempts here were near the surface, it is possible that some prey captures may take place close to the seafloor. Risso's dolphins feed mostly on squid, but occasionally feed on fish and benthic octopods, at least near the Faroe Islands and in the Mediterranean Sea (Blanco et al., 2006; Cockcroft et al., 1993). The ocean floor acts as an acoustic reflector, making it a source of more reverberation than is present in pelagic waters. This might necessitate a gradual reduction in source levels to minimize reverberation as observed in captive porpoises solving target detection tasks in environments with variable degrees of reverberation (Ladegaard and Madsen, 2019). Captive harbor porpoises reduce their ICIs when tasked with capturing fish positioned in front of an acoustic reflector screen; however, source levels were not reported (Miller, 2010). On the other hand, when Blainville's beaked whales are foraging at distances of 5 m to the sea floor, no gradual reduction in source levels nor ICIs have been reported (Arranz et al., 2011). Whether proximity to acoustic reflectors such as the ocean floor or seamounts influences biosonar adjustments is impossible to answer here, but could be tested by experimentally manipulating position of prey (as in Miller, 2010) or comparing *in-situ* biosonar adjustment strategies for deep-diving animals foraging in pelagic water versus near the sea floor.

#### Conclusion

By analyzing biosonar adjustments during prey approaches, we demonstrated that Risso's dolphins adopt several biosonar adjustment strategies to capture prey. We show that when Risso's dolphins are foraging during deep dives, they do not use  $20\log(\text{range})$  source level adjustments observed in shallow-diving delphinids. Instead, Risso's dolphins maintain stable interclick intervals and apparent output levels during the approach to maintain a long-range acoustic scene until the onset of the foraging buzz. This strategy closely resembles that of deep-diving beaked and sperm whales and hence may reflect shared acoustic challenges for foraging in the mesopelagic zone. Furthermore, Risso's dolphins occasionally adopt a more gradual biosonar adjustment strategy that is characterized by a higher effort to capture prey. We hypothesize that deep-diving toothed whales increase click rates earlier to simplify the acoustic scene and to increase the odds of successfully capturing evasive prey.

#### Acknowledgements

The authors would like to acknowledge all members of Kelp Marine Research, CEREMA and Leiden University that have assisted during fieldwork efforts, in particular Machiel Oudejans and Annabelle Kok. We are grateful to the Bioscience Department at Aarhus University for providing office space during a research visit to Aarhus University, and to Peter T. Madsen, Michael Ladegaard and the Marine Bioacoustics Lab for support and for comments and feedback on the study. Finally, we would like to thank three anonymous reviewers for their helpful and constructive feedback.

#### Competing interests

The authors declare no competing or financial interests.

#### Author contributions

Conceptualization: F.H.J.; Methodology: F.H.J., O.A.K.; Software: F.H.J., O.A.K.; Validation: O.A.K.; Formal analysis: O.A.K.; Investigation: F.H.J., O.A.K., P.L.T.;

Resources: O.A.K., P.L.T., F.V.; Data curation: O.A.K., F.V.; Writing - original draft: O.A.K.; Writing - review & editing: F.H.J., O.A.K., P.L.T., F.V.; Visualization: F.H.J., O.A.K.; Supervision: F.H.J., F.V.; Project administration: F.H.J., O.A.K.; Funding acquisition: F.H.J., O.A.K., P.L.T., F.V.

### Funding

F.H.J. was supported by an AIAS-COFUND fellowship from Aarhus Institute of Advanced Studies under the FP7 program of the EU Seventh Framework Programme (agreement no. 609033). F.V. was supported by the Office of Naval Research (ONR) (grants N00014-15-1-2341 and N00014-17-1-2715) and the Dutch Research Council (award number 016.Veni.181.086). P.L.T. was supported by ONR (grants N00014-15-1-2553 and N00014-18-1-2062) and acknowledges the support of the MASTS pooling initiative (The Marine Alliance for Science and Technology for Scotland) in the completion of this study. MASTS is funded by the Scottish Funding Council (grant reference HR09011) and contributing institutions.

### Data availability

Analysis code and example datasets for estimation of biosonar adjustments for individual foraging events, as well as code and data used for this paper, can be found at <https://osf.io/2f86h/>.

### Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.216283.supplemental>

### References

- Aguilar Soto, N., Johnson, M. P., Madsen, P. T., Díaz, F., Domínguez, I., Brito, A. and Tyack, P. (2008). Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *J. Anim. Ecol.* **77**, 936-947. doi:10.1111/j.1365-2656.2008.01393.x
- Arranz, P., de Soto, N. A., Madsen, P. T., Brito, A., Bordes, F. and Johnson, M. P. (2011). Following a foraging fish-finder: diel habitat use of Blainville's beaked whales revealed by echolocation. *PLoS ONE* **6**, e28353. doi:10.1371/journal.pone.0028353
- Arranz, P., DeRuiter, S. L., Stimpert, A. K., Neves, S., Friedlaender, A. S., Goldbogen, J. A., Visser, F., Calambokidis, J., Southall, B. L. and Tyack, P. L. (2016). Discrimination of fast click-series produced by tagged Risso's dolphins (*Grampus griseus*) for echolocation or communication. *J. Exp. Biol.* **219**, 2898-2907. doi:10.1242/jeb.144295
- Arranz, P., Benoit-Bird, K. J., Southall, B. L., Calambokidis, J., Friedlaender, A. S. and Tyack, P. L. (2018). Risso's dolphins plan foraging dives. *J. Exp. Biol.* **221**, jeb165209. doi:10.1242/jeb.165209
- Atem, A. C. G., Rasmussen, M. H., Wahlberg, M., Petersen, H. C. and Miller, L. A. (2009). Changes in click source levels with distance to targets: studies of free-ranging white-beaked dolphins, *Lagenorhynchus albirostris* and captive harbour porpoises, *Phocoena phocoena*. *Bioacoustics* **19**, 49-65. doi:10.1080/09524622.2009.9753614
- Au, W. W. L. (1993). *The Sonar of Dolphins*. New York, NY: Springer New York.
- Au, W. W. L. and Benoit-Bird, K. J. (2003). Automatic gain control in the echolocation system of dolphins. *Nature* **423**, 861-863. doi:10.1038/nature01727
- Au, W. W. L. and Würsig, B. (2004). Echolocation signals of dusky dolphins (*Lagenorhynchus obscurus*) in Kaikoura, New Zealand. *J. Acoust. Soc. Am.* **115**, 2307-2313. doi:10.1121/1.1690082
- Baird, R. W. (2009). Risso's dolphin: *Grampus griseus*. In *Encyclopedia of Marine Mammals*, 2nd edn. (ed. W. F. Perrin, B. Würsig and J. G. M. Thewissen), pp. 975-976. London: Academic Press.
- Bates, D., Mächler, M., Bolker, B. and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**, 1-47. doi:10.18637/jss.v067.i01
- Beedholm, K. and Miller, L. A. (2007). Automatic gain control in Harbor porpoises (*Phocoena phocoena*): Central versus peripheral mechanisms. *Aquat. Mamm.* **33**, 69-75. doi:10.1578/AM.33.1.2007.69
- Blanco, C., Raduán, M. Á. and Raga, J. A. (2006). Diet of Risso's dolphin (*Grampus griseus*) in the western Mediterranean Sea. *Sci. Mar.* **70**, 407-411. doi:10.3989/scimar.2006.70n3407
- Bloch, D. (2011). Life history of Risso's dolphin (*Grampus griseus*) (G. Cuvier, 1812) in the Faroe Islands. *Aquat. Mamm.* **38**, 250-266. doi:10.1578/AM.38.3.2012.250
- Brinkløv, S., Kalko, E. K. V. and Surlykke, A. (2010). Dynamic adjustment of biosonar intensity to habitat clutter in the bat *Macrophyllum macrophyllum* (Phyllostomidae). *Behav. Ecol. Sociobiol.* **64**, 1867-1874. doi:10.1007/s00265-010-0998-9
- Cockroft, V. G., Haschick, S. L. and Klages, N. T. W. (1993). The diet of Risso's dolphin, *Grampus griseus* (Cuvier, 1812), from the east coast of South Africa. *Z. Säugetierkd* **58**, 286-293.
- Denzinger, A., Kalko, E. K. V., Tschapka, M., Grinnell, A. D. and Schnitzler, H.-U. (2016). Guild structure and niche differentiation in echolocating bats. In *Bat Bioacoustics* (ed. B. M. Fenton, D. A. Grinnell, N. A. Popper and R. R. Fay), pp. 141-166. New York, NY: Springer.
- DeRuiter, S. L., Bahr, A., Blanchet, M.-A., Hansen, S. F., Kristensen, J. H., Madsen, P. T., Tyack, P. L. and Wahlberg, M. (2009). Acoustic behaviour of echolocating porpoises during prey capture. *J. Exp. Biol.* **212**, 3100-3107. doi:10.1242/jeb.030825
- Fais, A., Johnson, M., Wilson, M., Aguilar Soto, N. and Madsen, P. T. (2016). Sperm whale predator-prey interactions involve chasing and buzzing, but no acoustic stunning. *Sci. Rep.* **6**, 28562. doi:10.1038/srep28562
- Fenton, B. M., Jensen, F. H., Kalko, E. K. V. and Tyack, P. L. (2014). Sonar signals of bats and toothed whales. In *Biosonar* (ed. A. Surlykke, P. E. Nachtigall, R. R. Fay and A. N. Popper), pp. 11-59. New York, NY: Springer.
- Griffin, D. R., Webster, F. A. and Michael, C. R. (1960). The echolocation of flying insects by bats. *Anim. Behav.* **8**, 141-154. doi:10.1016/0003-3472(60)90022-1
- Hartley, D. J. (1992). Stabilization of perceived echo amplitudes in echolocating bats. II. The acoustic behavior of the big brown bat, *Eptesicus fuscus*, when tracking moving prey. *J. Acoust. Soc. Am.* **91**, 1133-1149. doi:10.1121/1.402640
- Isojunno, S. and Miller, P. J. O. (2018). Movement and biosonar behavior during prey encounters indicate that male sperm whales switch foraging strategy with depth. *Front. Ecol. Evol.* **6**, 200. doi:10.3389/fevo.2018.00200
- Jensen, F. H., Bejder, L., Wahlberg, M. and Madsen, P. T. (2009). Biosonar adjustments to target range of echolocating bottlenose dolphins (*Tursiops sp.*) in the wild. *J. Exp. Biol.* **212**, 1078-1086. doi:10.1242/jeb.025619
- Jensen, F. H., Rocco, A., Mansur, R. M., Smith, B. D., Janik, V. M. and Madsen, P. T. (2013). Clicking in shallow rivers: Short-range echolocation of Irrawaddy and Ganges river dolphins in a shallow, acoustically complex habitat. *PLoS ONE* **8**, e59284. doi:10.1371/journal.pone.0059284
- Jensen, F. H., Wahlberg, M., Beedholm, K., Johnson, M., de Soto, N. A. and Madsen, P. T. (2015). Single-click beam patterns suggest dynamic changes to the field of view of echolocating Atlantic spotted dolphins (*Stenella frontalis*) in the wild. *J. Exp. Biol.* **218**, 1314-1324. doi:10.1242/jeb.116285
- Jensen, F. H., Johnson, M., Ladegaard, M., Wisniewska, D. M. and Madsen, P. T. (2018). Narrow acoustic field of view drives frequency scaling in toothed whale biosonar. *Curr. Biol.* **28**, 3878-3885.e3. doi:10.1016/j.cub.2018.10.037
- 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/JOE.2002.808212
- Johnson, M., Madsen, P. T., Zimmer, W. M. X., Aguilar de Soto, N. and Tyack, P. L. (2004). Beaked whales echolocate on prey. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* **271**, S383-S386. doi:10.1098/rsbl.2004.0208
- Johnson, M., Madsen, P. T., Zimmer, W. M. X., de Soto, N. A. and Tyack, P. L. (2006). Foraging Blainville's beaked whales (*Mesoplodon densirostris*) produce distinct click types matched to different phases of echolocation. *J. Exp. Biol.* **209**, 5038-5050. doi:10.1242/jeb.02596
- Johnson, M., Hickmott, L. S., Aguilar Soto, N. and Madsen, P. T. (2008). Echolocation behaviour adapted to prey in foraging Blainville's beaked whale (*Mesoplodon densirostris*). *Proc. R. Soc. B Biol. Sci.* **275**, 133-139. doi:10.1098/rspb.2007.1190
- Kalko, E. K. V. (1995). Insect pursuit, prey capture and echolocation in pipistrelle bats (*Microchiroptera*). *Anim. Behav.* **50**, 861-880. doi:10.1016/0003-3472(95)80090-5
- Klopper, L. N., Smith, A. B., Nachtigall, P. E., Buck, J. R., Simmons, J. A. and Pacini, A. F. (2014). Cognitive adaptation of sonar gain control in the Bottlenose dolphin. *PLoS ONE* **9**, e105938. doi:10.1371/journal.pone.0105938
- Kothari, N. B., Wohlgenuth, M. J., Hulgard, K., Surlykke, A. and Moss, C. F. (2014). Timing matters: sonar call groups facilitate target localization in bats. *Front. Physiol.* **5**, 168. doi:10.3389/fphys.2014.00168
- Ladegaard, M. and Madsen, P. T. (2019). Context-dependent biosonar adjustments during active target approaches in echolocating harbour porpoises. *J. Exp. Biol.* **222**, jeb206169. doi:10.1242/jeb.206169
- Ladegaard, M., Jensen, F. H., de Freitas, M., Ferreira da Silva, V. M. and Madsen, P. T. (2015). Amazon river dolphins (*Inia geoffrensis*) use a high-frequency short-range biosonar. *J. Exp. Biol.* **218**, 3091-3101. doi:10.1242/jeb.120501
- Ladegaard, M., Jensen, F. H., Beedholm, K., da Silva, V. M. F. and Madsen, P. T. (2017). Amazon river dolphins (*Inia geoffrensis*) modify biosonar output level and directivity during prey interception in the wild. *J. Exp. Biol.* **220**, 2654-2665. doi:10.1242/jeb.159913
- Ladegaard, M., Mulsow, J., Houser, D. S., Jensen, F. H., Johnson, M., Madsen, P. T. and Finneran, J. J. (2019). Dolphin echolocation behaviour during active long-range target approaches. *J. Exp. Biol.* **222**, jeb189217. doi:10.1242/jeb.189217
- Linnenschmidt, M., Beedholm, K., Wahlberg, M., Højer-Kristensen, J. and Nachtigall, P. E. (2012). Keeping returns optimal: gain control exerted through sensitivity adjustments in the harbour porpoise auditory system. *Proc. R. Soc. B Biol. Sci.* **279**, 2237-2245. doi:10.1098/rspb.2011.2465
- Madsen, P. T., Johnson, M., Aguilar de Soto, N., 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
- Madsen, P. T., de Soto, N. A., Arranz, P. and Johnson, M. (2013). Echolocation in Blainville's beaked whales (*Mesoplodon densirostris*). *J. Comp. Physiol. A* **199**, 451-469. doi:10.1007/s00359-013-0824-8



- Miller, P. J. O. (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J. Exp. Biol.* **207**, 1953-1967. doi:10.1242/jeb.00993
- Miller, L. A. (2010). Prey capture by harbor porpoises (*Phocoena phocoena*): a comparison between echolocators in the field and in captivity. *J. Mar. Acoust. Soc. Japan* **37**, 156-168.
- Moss, C. F. and Surlykke, A. (2010). Probing the natural scene by echolocation in bats. *Front. Behav. Neurosci.* **4**, 33. doi:10.3389/fnbeh.2010.00033
- Moss, C. F., Chiu, C. and Surlykke, A. (2011). Adaptive vocal behavior drives perception by echolocation in bats. *Curr. Opin. Neurobiol.* **21**, 645-652. doi:10.1016/j.conb.2011.05.028
- Nachtigall, P. E. and Supin, A. Y. (2008). A false killer whale adjusts its hearing when it echolocates. *J. Exp. Biol.* **211**, 1714-1718. doi:10.1242/jeb.013862
- Nachtigall, P. E. and Supin, A. (2017). Biosonar gain control in odontocetes: Evoked-potential studies. *J. Acoust. Soc. Am.* **142**, 2690-2690. doi:10.1121/1.5014813
- Norum, U., Brinklov, S. and Surlykke, A. (2012). New model for gain control of signal intensity to object distance in echolocating bats. *J. Exp. Biol.* **215**, 3045-3054. doi:10.1242/jeb.069427
- Petrites, A. E., Eng, O. S., Mowlds, D. S., Simmons, J. A. and DeLong, C. M. (2009). Interpulse interval modulation by echolocating big brown bats (*Eptesicus fuscus*) in different densities of obstacle clutter. *J. Comp. Physiol. A* **195**, 603-617. doi:10.1007/s00359-009-0435-6
- Rasmussen, M. H., Miller, L. A. and Au, W. W. L. (2002). Source levels of clicks from free-ranging white-beaked dolphins (*Lagenorhynchus albirostris* Gray 1846) recorded in Icelandic waters. *J. Acoust. Soc. Am.* **111**, 1122-1125. doi:10.1121/1.1433814
- Sato, K., Watanuki, Y., Takahashi, A., Miller, P. J. O., Tanaka, H., Kawabe, R., Ponganis, P. J., Handrich, Y., Akamatsu, T., Watanabe, Y. et al. (2007). Stroke frequency, but not swimming speed, is related to body size in free-ranging seabirds, pinnipeds and cetaceans. *Proc. R. Soc. B Biol. Sci.* **274**, 471-477. doi:10.1098/rspb.2006.0005
- Simmons, J. A., Eastman, K. M., Horowitz, S. S., O'Farrell, M. J. Lee, D. N. (2001). Versatility of biosonar in the big brown bat, *Eptesicus fuscus*. *Acoust. Res. Lett. Online* **2**, 43-48. doi:10.1121/1.1352717
- Simon, M., Johnson, M. and Madsen, P. T. (2012). Keeping momentum with a mouthful of water: behavior and kinematics of humpback whale lunge feeding. *J. Exp. Biol.* **215**, 3786-3798. doi:10.1242/jeb.071092
- Sørensen, 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**, 9702. doi:10.1038/s41598-018-28022-8
- Surlykke, A. and Kalko, E. K. V. (2008). Echolocating bats cry out loud to detect their prey. *PLoS ONE* **3**, e2036. doi:10.1371/journal.pone.0002036
- Warnecke, M., Chiu, C., Engelberg, J. and Moss, C. F. (2015). Active listening in a bat cocktail party: Adaptive echolocation and flight behaviors of big brown bats, *Eptesicus fuscus*, foraging in a cluttered acoustic environment. *Brain. Behav. Evol.* **86**, 6-16. doi:10.1159/000437346
- Wisniewska, D. M., Johnson, M., Nachtigall, P. E. and Madsen, P. T. (2014). Buzzing during biosonar-based interception of prey in the delphinids *Tursiops truncatus* and *Pseudorca crassidens*. *J. Exp. Biol.* **217**, 4279-4282. doi:10.1242/jeb.113415
- Wisniewska, D. M., Ratcliffe, J. M., Beedholm, K., Christensen, C. B., Johnson, M., Koblitz, J. C., Wahlberg, M. and Madsen, P. T. (2015). Range-dependent flexibility in the acoustic field of view of echolocating porpoises (*Phocoena phocoena*). *eLife* **4**, e05651. doi:10.7554/eLife.05651
- Wisniewska, D. M., Johnson, M., Teilmann, J., Rojano-Doñate, L., Shearer, J., Sveegaard, S., Miller, L. A., Siebert, U. and Madsen, P. T. (2016). Ultra-high foraging rates of harbor porpoises make them vulnerable to anthropogenic disturbance. *Curr. Biol.* **26**, 1441-1446. doi:10.1016/j.cub.2016.03.069
- Zimmer, W. M. X., Johnson, M. P., Madsen, P. T. and Tyack, P. L. (2005). Echolocation clicks of free-ranging Cuvier's beaked whales (*Ziphius cavirostris*). *J. Acoust. Soc. Am.* **117**, 3919-3927. doi:10.1121/1.1910225