

Biosonar adjustments to target range of echolocating bottlenose dolphins (*Tursiops* sp.) in the wild

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SUMMARY

Toothed whales use echolocation to locate and track prey. Most knowledge of toothed whale echolocation stems from studies on trained animals, and little is known about how toothed whales regulate and use their biosonar systems in the wild. Recent research suggests that an automatic gain control mechanism in delphinid biosonars adjusts the biosonar output to the one-way transmission loss to the target, possibly a consequence of pneumatic restrictions in how fast the sound generator can be actuated and still maintain high outputs. This study examines the relationships between target range (R), click intervals, and source levels of wild bottlenose dolphins (*Tursiops* sp.) by recording regular (non-buzz) echolocation clicks with a linear hydrophone array. Dolphins clicked faster with decreasing distance to the array, reflecting a decreasing delay between the outgoing echolocation click and the returning array echo. However, for interclick intervals longer than 30–40 ms, source levels were not limited by the repetition rate. Thus, pneumatic constraints in the sound-production apparatus cannot account for source level adjustments to range as a possible automatic gain control mechanism for target ranges longer than a few body lengths of the dolphin. Source level estimates drop with reducing range between the echolocating dolphins and the target as a function of $17 \log(R)$. This may indicate either (1) an active form of time-varying gain in the biosonar independent of click intervals or (2) a bias in array recordings towards a $20 \log(R)$ relationship for apparent source levels introduced by a threshold on received click levels included in the analysis.

Key words: *Tursiops*, dolphin, echolocation, biosonar, sound production, automatic gain control.

INTRODUCTION

All toothed whale species studied so far use echolocation to navigate and to locate prey by ensonifying their surroundings with powerful ultrasonic clicks of high directionality (Au, 1993). Odontocetes have adapted to foraging niches within a diverse range of habitats where they face the challenge of navigating and finding prey with active sonar under varying noise and clutter conditions. However, despite a dedicated research effort on trained animals over the past 40 years, we still have a limited understanding of how wild odontocetes adjust their biosonar outputs to solve the task of locating prey acoustically in a three-dimensional world with a constantly changing spatial and temporal relationship between the clicking predator and its echo-generating prey (Johnson et al., 2008; Madsen et al., 2005). In particular, little is known about how odontocetes modify the characteristics of the echolocation pulse, such as source level and click interval, with varying range to the target.

For a toothed whale searching for prey, the detection of an ensonified target depends on the echo-to-noise or echo-to-clutter ratios in the hearing system. In a noise-limited echolocation situation that requires a given echo-to-noise ratio for correct detection, the detection range will increase with increasing source level and decreasing noise levels (Au, 1993). The received echo level (EL) generated by the ensonified prey can be evaluated quantitatively with the sonar equation (Urick, 1983) from the source level (SL), the transmission loss (TL) and the target strength of the ensonified

target (TS) (Fig. 1). For a single point target, such as a fish or squid, the returning echo level can be evaluated as:

$$EL = SL - 2 \times TL + TS. \quad (1)$$

Most biosonar systems operate over relatively short ranges (R), allowing for the estimation of transmission loss from simple geometric spreading and frequency-dependent absorption (α):

$$TL = 20 \log(R) + \alpha R. \quad (2)$$

If a toothed whale with a fixed source level approaches a single target with a given target strength, it follows from Eqn 1 and Eqn 2 that the received echo level will increase by 12 dB (four times) for every halving in range to the target. However, if the target is a school of fish or another group of objects with many sound scatterers, a greater number of objects will be ensonified with increasing range. This will lead to a decreased transmission loss compared with the spherical spreading case, such that the echo level will increase with only 6 dB (double the received sound pressure) when target range is halved.

In man-made sonars, changes in received echo level are handled on the receiving side by a time-varying gain (TVG), by which the receiving sensitivity is increased with time from emission of the sonar pulse to compensate for the decreasing echo levels from more and more distant targets. Man-made sonars may either compensate by $40 \log(R)$ or $20 \log(R)$ TVG (MacLennan and Simmonds, 1992).

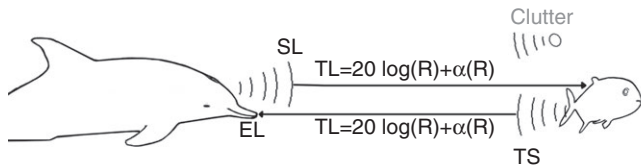


Fig. 1. Toothed whales echolocate prey underwater with broadband, high-intensity clicks. Echolocation clicks are produced pneumatically in the nasal passages and projected forward through the forehead. Clicks of a given source level (SL), measured 1 m in front of the animal on the acoustic axis, propagate through the water and reflect off ensouffled targets. A target at range R receives a sound pressure corresponding to the source level minus the transmission loss (TL), approximated by spherical spreading and frequency-dependent sound absorption. The fraction of sound energy reflected from the target is termed its target strength (TS). The echo level (EL) is the sound pressure of the echo after transmission loss (TL) from target to dolphin. Echoes are received and transmitted through the lower jaw to the auditory system. Ambient noise levels or absolute hearing thresholds will determine the lower limits of how faint echoes can be detected.

Evidence of TVG in the receiver has been found in some bat species who tighten muscles attached to their middle ear bones just prior to emission of a sonar cry (Henson, 1965; Suga and Jen, 1975), followed by a gradual relaxation and consequent increase in hearing sensitivity over the next 6.4 ms (Kick and Simmons, 1984). Along with neural attenuation in the midbrain, this gain-control mechanism provides 6–11 dB attenuation for a time delay between emitted sound and echo that corresponds to halving the distance between the bat and target (Hartley, 1992; Kick and Simmons, 1984; Simmons et al., 1992). Similar mechanisms have recently been found in the false killer whale (*Pseudorca crassidens*), possibly as a consequence of the small time separation between the powerful outgoing click and the weak returning echo (Nachtigall and Supin, 2008; Supin et al., 2004; Supin et al., 2008). By contrast, the harbour porpoise (*Phocoena phocoena*) shows no evidence of adjusting hearing sensitivity during echolocation (Beedholm et al., 2006). Thus, it seems that some, but not all, terrestrial and aquatic biosonar systems incorporate TVG in their auditory systems.

While man-made sonars normally do not adjust the source level to the time delay between pulse emission and echo reception, some bats have been shown to use such a form of dynamic TVG on the transmission side (Hiryu et al., 2007; Kobler et al., 1985). Au and Benoit-Bird (Au and Benoit-Bird, 2003) and Au (Au, 2004) reported that four species of free-ranging delphinids also use TVG control on the transmission side of their biosonar systems. They found that back-calculated source levels from dolphins echolocating on a star-shaped hydrophone array exhibited a $20 \log(R)$ relationship with target range and proposed that this is an adaptation to stabilize the returning echo levels from fish schools with volume reverberative properties in which the echo level for a constant source level biosonar would increase with $20 \log(R)$. Au and Benoit-Bird further inferred that this dynamic TVG of lower source level at short target ranges is a passive biophysical consequence of reducing the interclick interval (ICI) to decreasing two-way travel time (TWT) as the source approaches a target (Au and Benoit-Bird, 2003).

Toothed whales generally use ICI that are longer than the TWT to the target (Au, 1993; Teilmann et al., 2002). All available evidence suggests that the toothed whale sound production system operates as a pneumatic capacitor that relaxes partially during each click emission (Cranford and Amundin, 2004; Cranford et al., 1996;

Ridgway, 1980). This means that below a certain ICI, the source level is expected to decrease with increasing repetition rate (Madsen et al., 2002). Thus, if a delphinid decreases the ICIs when approaching a target, and thus consequently reduces the source level, the result is an adjustment of source level to target range produced by the physical limitations of the sound production system. This form of TVG is thus not seen as an active cognitive process but rather a passive consequence of the ICI to TWT adjustment that is termed automatic gain control (AGC) (Au and Benoit-Bird, 2003). However, recordings on foraging toothed whales using acoustic tags do not support the presence of a simple AGC that reduces source level with reducing range to a prey target (Johnson et al., 2008; Madsen et al., 2005). Rather, available data suggest that foraging beaked whales employ a bimodal output mode in which the ICIs and click amplitudes are not adjusted to target range during search and approach phases (first mode) but where the ICIs and click amplitudes are reduced dramatically when the whale switches to the buzz phase (second mode) when the prey is about one body length from the whale (Johnson et al., 2008; Madsen et al., 2005).

These conflicting findings show that we do not fully understand how and why toothed whales adjust their acoustic output as a function of target range. The AGC hypothesis for the biosonar of free-ranging delphinids echolocating on hydrophone arrays is based on the work of Au (Au, 1993) that the ICIs are linked to the TWT in trained bottlenose dolphins (*Tursiops truncatus*). However, it remains unknown whether reduced ICIs actually entail lower source levels from these animals, and no studies have tested whether bottlenose dolphins actually do reduce ICI with TWT in the wild. Finally, it needs to be tested if such effects always lead to a $20 \log(R)$ AGC, as reported for four delphinid species (Au and Benoit-Bird, 2003).

Here, we use a vertical array of four calibrated hydrophones to test the hypotheses that (1) wild bottlenose dolphins (*Tursiops* sp.) adjust their ICI to the range between dolphin and array, (2) decreasing click intervals reduce the source level and (3) the click interval reduction gives rise to a $20 \log(R)$ AGC mechanism.

MATERIALS AND METHODS

Recording site

The measurements were conducted in a shallow-water area within Koombana Bay, Bunbury, Western Australia ($33^{\circ}17'S$, $115^{\circ}39'E$) during daylight hours in February 2007. Snapping shrimps contribute to high background noise levels that are comparable to other subtropical habitats (Au et al., 1985). A coastal bottlenose dolphin (*Tursiops* sp.) population of a few hundred individuals inhabits the nearby coastline and frequently forages in the recording area.

Recording equipment

A small 6 m aluminium-hulled dinghy was anchored with the engine off and used as a recording platform. A vertical array of four Reson TC4034 hydrophones (RESON, Slangerup, Denmark), separated by 1.0 m, was suspended between a surface buoy and a 0.5 kg lead weight. The array support was made of PVC with an acoustic impedance close to seawater in order to minimize shadowing and reflections. The hydrophones were connected to a custom-built four-channel amplifier with 40 dB gain, 1 kHz high-pass filter (2-pole) and 200 kHz low-pass filter (3-pole). The amplified and filtered signals were digitized with a four-channel, 12-bit analogue-to-digital converter (ADlink Technology, Chungo City, Taiwan) writing data to a laptop computer via a PCMCIA interface (Magma, San Diego, CA, USA) sampling each channel at 800 kHz. The nominal

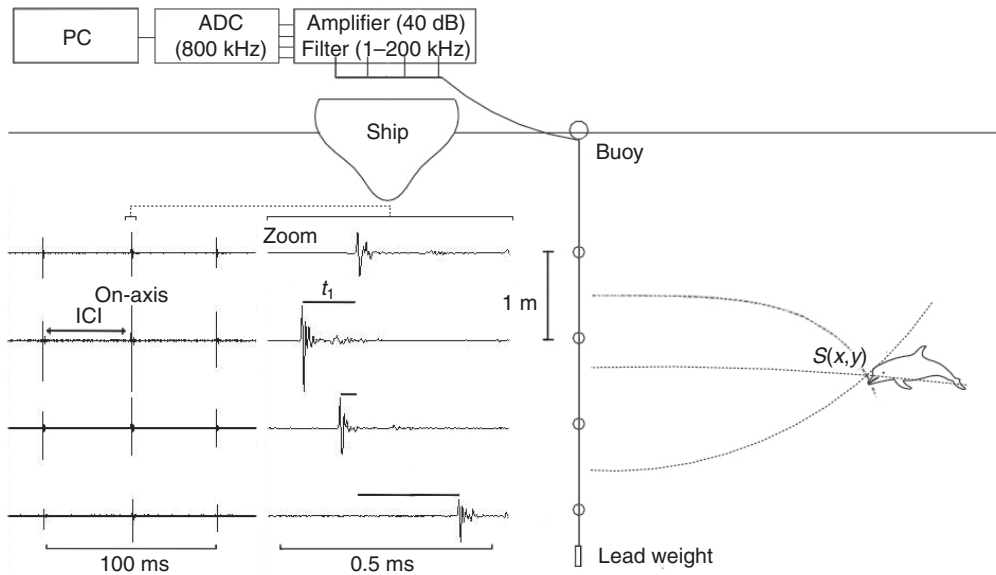


Fig. 2. The experimental setup consisted of a linear array of four vertical hydrophones connected through an amplification and filtering box to an analogue-to-digital converter (ADC) sampling to a PC laptop. Clicks were detected if they exceeded 160 dB re. 1 μ Pa (peak–peak). Clicks fulfilling on-axis criteria (see text) were localized acoustically by triangulating the source position $S(x,y)$ from time-of-arrival differences (t_1-t_2) of the same signal at the four receivers.

hydrophone sensitivity (calibrated before and after field experiments to ± 1 dB) was -220 dB re. $1 \text{ V}/\mu\text{Pa}$, with an omni-directional receiving characteristic (spherical element) in the relevant frequency range from 10 kHz to 200 kHz (± 2 dB). The frequency response of the amplification box was corrected for post-processing, giving an overall flat frequency response of the recording chain (± 2 dB) between 1 kHz and 200 kHz, with a clipping level of 194 dB re. $1 \mu\text{Pa}$ peak received level as limited by the peak voltage that can be handled by the ADC.

Data collection

Small groups and individual dolphins frequently approached the recording platform. Data acquisition was manually initiated whenever approaching dolphins were observed surfacing within 100 m of the array to optimize the chance of recording dolphins within the accurate localization range of 40 m (see below). Acquisition lasted until the dolphins had passed the array, interrupted only briefly (~ 5 s) for data storage approximately every minute.

Signal analysis

All signal analyses were made with custom-written routines in Matlab 6.5 (The Mathworks, Inc., Natick, MA, USA). Because of the highly directional nature of toothed whale echolocation clicks (Au, 1993), most recordings did not yield clicks suitable for analysis. To prevent ambiguities in ICI measurements, each click series was examined visually and discarded if the click intervals were very irregular or alternating between being short and long, indicating that several dolphins might have been clicking simultaneously. Echolocation clicks in each approach were then located for further analysis with an automated click-detector set to a minimum detectable received level (threshold) of 154 dB re. $1 \mu\text{Pa}$ (peak) on the top hydrophone. If the click could not be located on all channels, the click was not analyzed further.

Localization

To quantify source parameters, an estimate of the source position relative to the receivers was found using acoustic localization techniques based on time-of-arrival differences of the same click on the four receivers (Wahlberg et al., 2001). The time-of-arrival differences were determined by cross-correlating the signal recorded

on the top hydrophone with the signals recorded at the other hydrophones, excluding surface reflections. We calculated a sound propagation speed of 1520 m s^{-1} from the Leroy equation (Urlick, 1983) based on an average measured temperature of 23.5°C and a salinity value of 35 p.p.m. For each pair of hydrophones, the time-of-arrival difference renders a single hyperbola as a function of a two-dimensional coordinate set by depth and range (Fig. 2). Three independent hyperbolas are generated from four receivers, and the unknown source coordinates were estimated by solving the three equations with a method of least-squares (Madsen and Wahlberg, 2007; Spiesberger and Fristrup, 1990).

The localization precision for an array of this aperture was tested in shallow water by transmitting artificial dolphin clicks (two cycles, centroid frequency 70 kHz) at a depth of 3 m using an omnidirectional HS70 hydrophone (Sonar Products) at measured ranges from the array (Fig. 3). The RMS error, or standard error, defined as the root-mean-squared range deviations from the true range (Villadsgaard et al., 2007), was below 9% for range estimates within 40 m but increased significantly beyond this range. Transmission loss [estimated as $20 \log(R) + \alpha R$] for dolphins localized within 40 m would consequently be estimated with an RMS error of < 0.8 dB from the ranging procedure. Given the combined uncertainty of localization and the calibrated recording system, the back-calculated sound pressure 1 m from the clicking animals could therefore be estimated with an uncertainty of < 2 dB for source ranges within 40 m. Accordingly, we only included clicks from dolphins localized at ranges closer than 40 m in the analysis.

Source parameter estimation

The time between each click and the previous click was defined as the ICI (Au, 1993), and it was manually verified that ICIs were not calculated incorrectly due to recording several dolphins at the same time. The range from source to each hydrophone was calculated from source coordinates with the Pythagorean equation. Received levels at the hydrophones were calculated as peak–peak (pp) sound pressure given by the pp amplitude of the click (Au, 1993). Apparent source levels (ASL_{pp}) were defined as the back-calculated sound pressure level 1 m from the source at an unknown angle from the acoustic axis (Madsen and Wahlberg, 2007; Møhl et al., 2000)

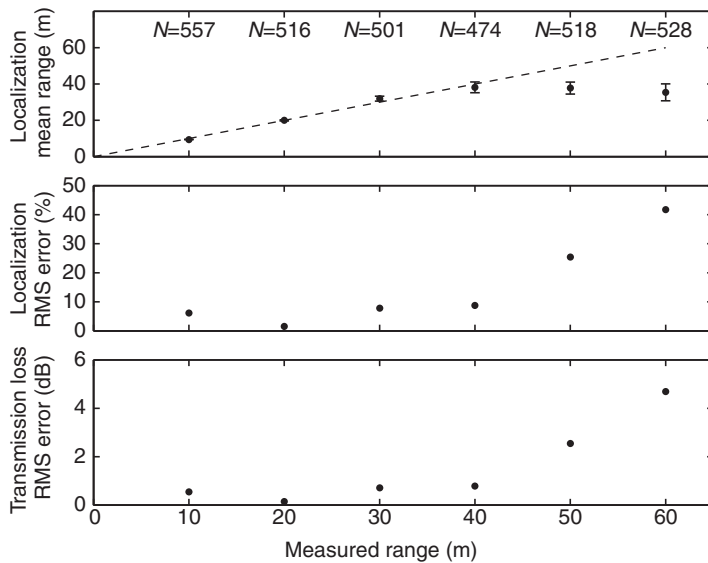


Fig. 3. Source localization accuracy and transmission loss error. (A) Localization mean range and standard deviations from a number of trials (N) for each distance. The broken line indicates the true range. (B) Localization RMS error calculated as the root-mean-squared differences between estimated range and known range. (C) Transmission loss RMS error associated with the localization as a function of range. Only clicks from dolphins within a range of 40 m were used in this study.

and calculated according to Eqn3, in accordance with previous studies (e.g. Madsen et al., 2004):

$$ASL = RL + TL = RL + 20 \log(R) + \alpha R. \quad (3)$$

The transmission loss (dB) was estimated from spherical spreading and frequency-dependent absorption over the range R (m), using an absorption coefficient α of 0.025 dB m^{-1} at 90 kHz (close to the centre frequency of on-axis *Tursiops* clicks).

On-axis criteria

When investigating source properties of directional biosonar signals, it is essential to quantify the signal on or as close to the acoustic axis as possible (Madsen and Wahlberg, 2007) due to strong off-axis distortion (Au, 1993; Madsen et al., 2004). Insufficient on-axis criteria will include off-axis clicks in the analysis, leading to underestimated source levels and a lowered frequency emphasis of the reported on-axis clicks (Madsen and Wahlberg, 2007). With a one-dimensional array, it is difficult to ensure that a given click is on-axis, and most recorded clicks will be recorded at various degrees off the acoustic axis. To maximize the chance of analysing clicks recorded on or close to the acoustic axis in the horizontal plane, we identified longer click sequences, here called scans, most likely associated with the acoustic beam of the animal passing across the axis of the hydrophone array. Provided that the animal maintains the same source level and directionality, the click with highest amplitude has the highest likelihood of being on-axis. In this study, we defined a scan as any sequence of 10 or more clicks with ICIs less than 1 s. For each scan, we then classified a click as on-axis and analysed it if it fulfilled the following criteria: (1) the click could be localized, (2) the click had the highest received level in a scan, (3) the highest received level was recorded on one of the two central hydrophones and (4) the received level was higher than the received level of both the preceding and following click from the same hydrophone. These criteria will maximize the chance of recording signals that are on-axis in both vertical and horizontal planes.

RESULTS

Data collection

Five hours of recordings (17 Gb) were made over two days of field effort in sea state 2 or lower. Animals often passed by the array and

were sometimes visually observed pointing directly towards the array before passing the research vessel. 3868 regular (non-buzz) clicks were detected in the recordings and successfully analyzed for source location and source level. Of these, 85 clicks (~2%) were classified as on-axis from a total of 26 different approaches. Seven well-known individuals from the population were identified and represented in this sample. None of these animals continuously visited the recording station throughout the recording sessions, making it unlikely that a few animals contributed to the bulk of the dataset.

Interclick interval adjustment

Clicks designated as on-axis had a median ICI of 52 ms. A lower limit on ICIs was imposed by the click detector with a blanking time of 1.9 ms after each detection, and an upper limit was caused by our definition of a scan as a series of clicks separated by <1000 ms. The ICI variance was high, with a standard deviation of 58 ms and values ranging between 17 and 462 ms for on-axis clicks. The ICI was significantly correlated with range (Fig. 4B) (linear regression: $ICI = 2.2R + 30 \text{ ms}$, $P < 0.05$) but with a very large scatter ($r^2 = 0.12$). All ICIs for on-axis clicks exceeded the TWT from the dolphin to the array (1.33 ms m^{-1}) by a median lag time of 31 ms.

Effect of interclick interval on acoustic output

Interclick intervals for on-axis clicks significantly correlated with the ASLs (Fig. 5B) [regression: $ASL_{pp} = 193 \text{ dB} + 6.46 \times \log(ICI)$, $P < 0.05$] but with a very large scatter ($r^2 = 0.06$). If range to the target has an effect on the source level of dolphins as reported in previous studies, any interaction between ICIs and range (such as a decrease in ICI with decreasing range) would complicate the interpretation of a regular regression of ICI *versus* source level. To overcome this interaction, a mixed-model analysis was completed with effects of the two variables $\log(ICI)$ and $\log(R)$ on the dependent variable ASL. Once the ASL variability explained by range was taken into account, the remaining ASL residuals were not significantly correlated with the ICI ($P = 0.24$), implying that, for a given range, clicks with lower ICIs did not have significantly lower ASLs.

Time-varying gain control

Back-calculated source levels for on-axis clicks were significantly lower when the dolphins were closer to the array (Fig. 6) [linear

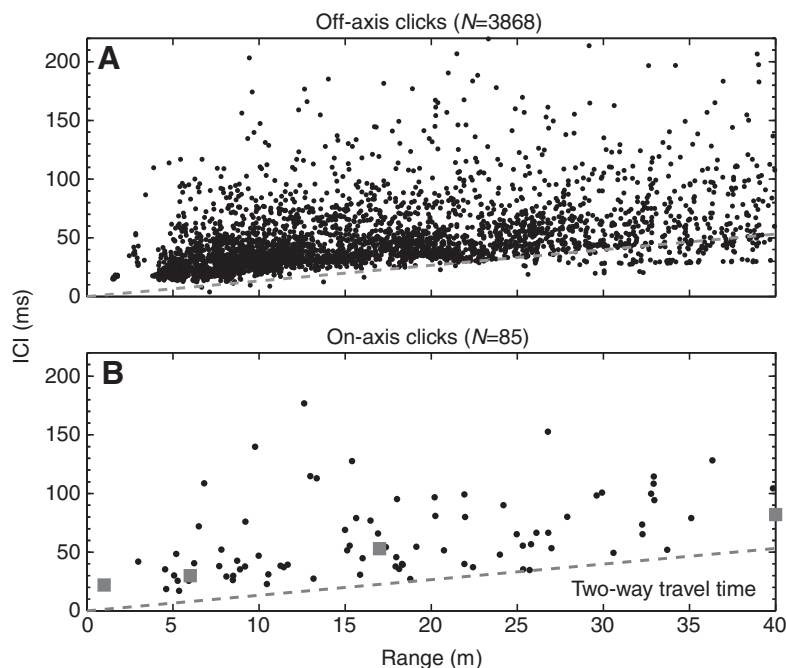


Fig. 4. Interclick intervals (ICI) as a function of range to the recording array from bottlenose dolphins within 40 m. (A) All clicks that could be localized (dots), along with the two-way travel time (grey line) that a click would take to travel to the array and back to the dolphin. (B) On-axis clicks (dots), along with the two-way travel time (grey line) and averaged data from captive dolphins doing target detection experiments [squares, from Au (Au, 1993)].

regression: $ASL_{pp}=184\text{ dB}+16.7\times\log(R)\text{ dB}$, $P<0.0001$, $r^2=0.44$]. The slope of this relationship was not significantly different from a $20\log(R)$ TVG [slope 95% confidence interval: $12.5:20.8\times\log(R)$] that explained nearly the same variation ($r^2=0.42$). If all recorded clicks were investigated irrespective of the source-to-array aspect, the correlation is closer to a $20\log(R)$ relationship [linear regression: $ASL_{pp}=173\text{ dB}+19.2\log(R)\text{ dB}$, $P<0.0001$, $r^2=0.33$].

DISCUSSION

It is still poorly understood how free-ranging toothed whales adjust their echolocation signals when locating, approaching and catching prey. The use of echolocation by toothed whales is governed by a complex mixture of the sonar requirements to handle a changing, actively generated auditory scene and the biophysical constraints of generating ultrasonic transients pneumatically with a finite amount of air. The present study explored the relationships between target range, click intervals and source levels of free-ranging bottlenose dolphins echolocating on a vertical hydrophone array. We investigated whether free-ranging bottlenose dolphins adjust their ICIs according to the TWT from source to target and whether lowered ICIs limited the source level. Based on these findings, we address the question of a possible TVG control in the bottlenose dolphin biosonar and whether decreasing ICIs when approaching prey might offer a biophysical explanation for a possible $20\log(R)$ AGC (Au and Benoit-Bird, 2003).

Sample size and scatter

Because of the highly directional nature of high-frequency clicks used for echolocation, most of our recordings did not contain suitable on-axis clicks, and only 85 clicks conformed to our on-axis criteria. Previous studies often accept a large proportion of the dataset (upwards of two-thirds of the recorded clicks) as on-axis (Au and Herzing, 2003; Rasmussen et al., 2002). This provides a large sample size but at the risk of underestimating the actual source levels by including clicks recorded further from the acoustic axis of the dolphin (Madsen and Wahlberg, 2007). In the present study, we implemented strict on-axis criteria in order to prioritize accurate source level estimates over sample size.

Both this and previous studies of free-ranging delphinids (Au, 2004; Au and Benoit-Bird, 2003) are based on data with a high scatter. For these studies, the individual identity, movement pattern and behaviour of a given clicking dolphin is seldom known, and data will inevitably be based on clicks from many different dolphins engaged in various activities and recorded at various degrees off the acoustic axis. Moreover, individual toothed whales are known to adjust source levels of their biosonar to background noise levels (Au et al., 1985) and it is still undetermined whether they adjust signal parameters to the amount of clutter in their environment, as bats do (Moss et al., 2006; Surlykke and Moss, 2000). Hence, any studies in the wild will tend to exhibit some degree of variation in the estimated ASLs caused by intraindividual differences and differences in behaviour.

Interclick interval adjustment

When an echolocating animal approaches a target, the TWT between emission of the outgoing click and return of the target echo decreases as the animal approaches the ensonified target. Experiments with trained bottlenose dolphins in captive settings have shown that ICIs in target detection tasks are given by the TWT plus a short lag time of 19–45 ms (Au, 1993). By contrast, a fundamental problem of studies using hydrophone arrays to study free-ranging dolphins is that the range between the dolphin and the actual target of interest is unknown, and instead the calculated range from the dolphin to the recording array is taken as a proxy by assuming that the array is the target. However, if dolphins are not echolocating on the recording array but on prey items or other objects, there should be no evident relationship between ICIs and dolphin-array range, even if the dolphins do adjust their ICIs according to the TWT to their chosen target. To address this problem, experimental designs should preferably include a mechanism to test if dolphins are actually ensonifying the array as their target of interest. In the present study, we found no on-axis clicks with ICIs shorter than the TWT (Fig. 4), which might indicate that dolphins were attending to either the array or to targets further away. Since it is difficult to test the second possibility, the following discussion assumes, as in previous studies (Au and

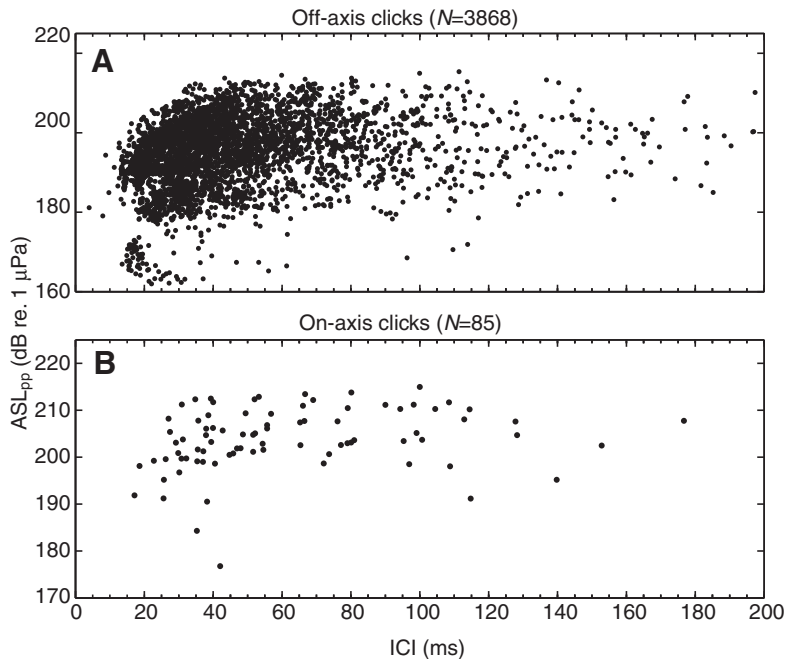


Fig. 5. Back-calculated apparent source levels (ASLs) as a function of click intervals (ICIs) for either all the received and localized clicks (A) or for those clicks fulfilling on-axis criteria (B). The logarithmic relationship for on-axis clicks is weak, with the best-fitting relationship described by: $ASL_{pp} = 193 \text{ dB} + 6.46 \times \log(\text{ICI})$ ($r^2 = 0.06$). Two on-axis clicks lie outside the depicted ICI range, with the most extreme at an ICI of 462 ms and an ASL of 196 dB.

Benoit-Bird, 2003), that dolphins were ensonifying the array (referred to hereafter as a target).

We observed a reduction in ICI with decreasing target range in a $2.2 \times (R) + 30.2 \text{ ms}$ fashion in line with earlier studies on trained bottlenose dolphins (Au, 1993) where the mean ICI increases with the TWT (Fig. 4B, filled squares). The relationship between ICIs and TWT displays similar levels of variation to raw data from target detection experiments with trained bottlenose dolphins (Turl and Penner, 1989).

Wild porpoises occasionally decrease their ICIs systematically over time during events that have been interpreted as prey approaches (Akamatsu et al., 2007). However, in contrast to bottlenose dolphins, captive porpoises in target detection tasks appear to use a much more constant ICI (between 50 and 80 ms) with no apparent range adjustment (Teilmann et al., 2002). Similar steady ICIs during search phases are observed for two species of beaked whales and in sperm whales, which exhibit search or approach phases with a very long lag time (>300 ms) leading up to the buzz phases (Madsen et al., 2005). On the other hand, beaked whale ICIs measured at the start of a buzz are sometimes correlated with the TWT (Johnson et al., 2008). Belugas trained for target detection tasks have even been shown to exhibit a unique type of echolocation in which clicks are sent out in packets with a high click repetition rate that does not allow the echoes to return before the next click is emitted (Turl and Penner, 1989). Thus, it seems that while the odontocete auditory and neural system may be flexible enough to handle biosonar range ambiguities that may arise when ICIs are lower than the TWT (Turl and Penner, 1989), the general approach phase for toothed whales in the wild involves processing the returning echoes before a new click is emitted.

Effect of interclick interval on acoustic output

Toothed whales generate echolocation clicks by pneumatically accelerating a pair of connective tissue lips that allow a small volume of pressurized air to pass from the bony nares to the vestibular air sacs (Cranford et al., 1996; Ridgway, 1980; Ridgway and Carter, 1988). The current model of toothed whale sound production suggests that this system operates as a pneumatic capacitor that

requires a certain air pressure in the nasal passage before the muscularly controlled tension in the connective tissue of the phonic lips is overcome and a click is generated (Ridgway, 1980; Ridgway and Carter, 1988). If the repetition rate of echolocation clicks exceeds a critical rate, the nasal air pressure may not have time to build up fully before the next click generation event. This would cause the acoustic output to drop with increasing clicking rate, a phenomenon that would explain the drop in source level seen in buzzes with fast repetition rates (Madsen et al., 2005). This is the proposed cause of an AGC in delphinid biosonar (Au and Benoit-Bird, 2003). Such a correlation between ICIs and source level is evident in harbour porpoise biosonar operating at high repetition rates with ICIs below 20 ms (Beedholm and Miller, 2007). Although we should be careful about addressing causality in our study, the observed drop in ASL for ICIs below 30 ms supports the contention that the pneumatic sound generator will start to limit the acoustic output below a certain ICI (Fig. 5), as found by Au and Benoit-Bird (Au and Benoit-Bird, 2003). Although more data are needed to address this matter fully, the present data imply that the highest source levels recorded here can be generated when the ICIs exceed 30–40 ms.

The source levels reported here are lower than the maximum values of 227 dB re. 1 μPa (pp) reported for trained bottlenose dolphins rewarded for long-range target detection (Au et al., 1974). Hence, the ASLs found in this study may not reflect the highest source level potential of bottlenose dolphins, but rather the typical source levels utilized in this specific habitat. It is possible that maximum source level values would require longer ICIs than the 30 ms we tentatively propose here, but the source levels in the present study are still comparable to the source levels of other free-ranging delphinids where apparent effects of AGC have been observed (Au and Benoit-Bird, 2003).

If we assume an average lag time of 19–45 ms from detecting the incoming click echo to emitting the next click (Au, 1993), a 30 ms ICI would correspond to a target range of less than 8 m. Blainville's beaked whales switch from regular clicking (ICI 200–600 ms) to a buzz phase (ICIs below 20 ms) when they approach within a body length of the prey (Madsen et al., 2005). The decrease in source level for ICIs less than 30 ms in bottlenose

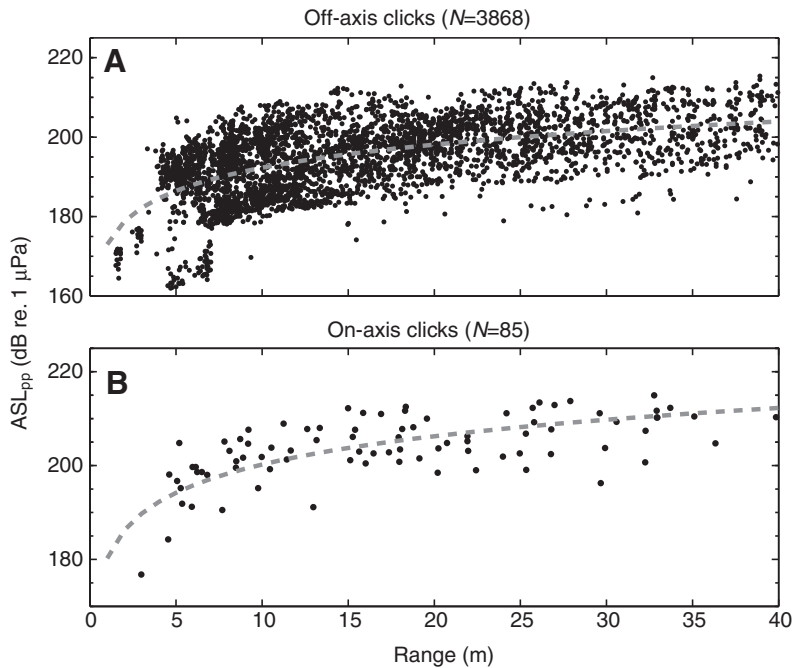


Fig. 6. Back-calculated apparent source levels (ASLs) as a function of range to the array for all clicks (A) or those fulfilling on-axis criteria (B). The best-fitting logarithmic relationship (grey lines in both plots) for all clicks are given as $ASL_{pp}=19.2 \log(R)+173 \text{ dB}$ ($r^2=0.33$) and for on-axis clicks as $ASL_{pp}=16.7 \log(R)+184 \text{ dB}$ ($r^2=0.44$). On-axis methodology requires 10 or more consecutive clicks to exceed the click detector threshold of $160 \text{ dB}+20 \log(R)$ before looking for an on-axis click, and so both plots are based on data filtered with a constant-threshold detection level.

dolphins might therefore signify the proximity to this border region between regular clicking and buzz clicks.

Time-varying gain control

So far we have shown that the recorded bottlenose dolphins decrease their ICIs when they close in on the recording array and that the ICIs for on-axis clicks always allow enough time for the array echo to return before sending out the next click. We have shown that the acoustic output may be limited biophysically when ICIs decrease below around 30–40 ms. While there is little evidence for the contention that a link between target range and source level is dictated by a simple biophysical coupling between output and ICIs longer than 30 ms, the next question to ask is whether echolocating bottlenose dolphins may still display a form of TVG control governed by a different mechanism.

We found a significant decrease in on-axis click source level as a function of $17 \log(R)$ (Fig. 6), and this may partly compensate for the increasing echo level when dolphins are approaching a target. This compensation matches well with previous studies of AGC in free-ranging delphinids (Au and Benoit-Bird, 2003). The findings also suggest a likely pneumatic reduction in source level for ICIs below 30–40 ms, which could give rise to an AGC mechanism for short ICIs and short target ranges. However, 88% of our recorded on-axis clicks had ICIs longer than 30 ms but still display a correlation between range and source level, even though the sound generator should be able to maintain high outputs biophysically.

One explanation might be that the dolphins actively decrease their source level during target approach, giving rise to a form of TVG that is not a passive consequence of pneumatic restrictions in the sound generator for longer ICIs. Dolphins are well known to adjust their acoustic output to their surroundings. For example, source levels of free-ranging dolphins are much higher than those of dolphins held in tanks (Au et al., 1974; Madsen et al., 2004) and may vary depending on ambient noise levels (Au, 1993). An active TVG control mechanism would still allow the animals to compensate for the decreased two-way transmission loss when approaching a

target and could act to reduce echo level fluctuations from different types of targets and under different clutter conditions.

How different species of toothed whales stabilize the returning prey echoes when approaching prey is still an unsolved issue and seems to differ between species. A trained false killer whale seems to adjust its hearing sensitivity to fully compensate for the two-way transmission loss while keeping their source levels constant (Nachtigall and Supin, 2008). By contrast, harbour porpoises do not seem to decrease their hearing sensitivity (Beedholm et al., 2006), and whether they exhibit TVG in their biosonar output (Li et al., 2006) remains unresolved (Beedholm and Miller, 2007).

Another possible explanation is that the apparent AGC at long ranges does not actually reflect adjustments in the dolphin biosonar but instead arises as an artefact in the data collection or processing methods. All studies reporting AGC in free-ranging delphinids have been conducted with either a single hydrophone and reflections from surface and bottom (Li et al., 2006) with a short, star-shaped array (Au and Benoit-Bird, 2003) or with a linear vertical array (present study) used to record and localize the clicking dolphins. A limitation of these setups is that, in order to detect clicks for analysis, the received sound levels must exceed a certain absolute threshold independent of the localization range. Subsequently, the received levels are back-calculated to ASLs by compensating for the one-way transmission loss of $20 \log(R)+\alpha R$ between the dolphin and the recording array. The actual received SPL at the array may vary because of several factors, including the acoustic output or source level, the aspect from the delphinid to the recording array, and the range between the dolphin and the receiver. On-axis criteria are designed to maximize the probability of analysing clicks recorded close to the acoustic axis, so that back-calculated source levels reflect the true source levels. Having insufficient on-axis criteria will increase the amount of off-axis clicks that are included in the analysis.

To illustrate the effect of insufficient on-axis criteria, we can temporarily relax our on-axis criteria and include all (i.e. both on- and off-axis) clicks received by one hydrophone in the analysis (Fig. 6A). This leads to an underestimate of the true source level,

and the data fit closer to a $20 \log(R)$ function. This would imply that dolphins echolocating at targets other than the array still adjust their biosonar to the array in a $20 \log(R)$ fashion. However, the main reason for these perplexing results is that clicks with low source levels recorded from afar will fall below the detection threshold because of a large transmission loss whereas clicks with equally low source levels recorded close to the array are more likely to exceed the received level detection threshold and be included in the analysis. Regardless of the detector type, click detection will always ultimately be limited by a set threshold or by a background or system noise floor in the recordings. The geometric spreading loss model of $20 \log(R)$ used will therefore effectively filter clicks in a fashion that excludes clicks with low SLs at longer ranges and hence bias the data towards a $20 \log(R)$ relationship, irrespective of whether dolphins actually adjust their source levels at all.

In conclusion, we have shown that free-ranging bottlenose dolphins emit echolocation clicks at ICIs that exceed the roundtrip travel time to the target, and with some adjustment to the decreasing TWT as they approach a target. At the regular (non-buzz) echolocation click rates studied here, the acoustic output generated by the pneumatic sound generator is only limited by the repetition rate when the ICI drops below 30–40 ms. This supports the idea of a pneumatic constraint in the sound production system that may account for the large reductions in source level of fast repetition rate buzzes. We observe an apparent AGC of $17 \log(R)$ that is close to the $20 \log(R)$ relationship reported in previous studies. For targets within a few body lengths (when ICIs decrease below 30–40 ms), the adjustment of source levels to target range may be a passive consequence of adjusting ICIs to target range to a degree where the nasal pressure does not have time to build up fully. By contrast, this study suggests that the adjustment of source level to target ranges beyond a few body lengths cannot be explained by pneumatic restrictions in the sound generator. Instead, they may stem from (1) an active, cognitive adjustment of source level to target range to reduce fluctuations in received echo levels or (2) an inherent observer bias caused by using click detectors with fixed received level thresholds and back-calculating source levels with a geometric spreading loss model of $20 \log(R)$. Thus, bottlenose dolphins do adjust their sound production to target range in terms of ICIs, and to some degree also in terms of the biosonar output, but the question of overall TVG in the bottlenose dolphin biosonar remains unclear. This matter should be addressed experimentally in studies with variable target location and constant source-to-array geometry (for example, experiments with phantom echoes) or with onboard acoustic tags on animals that use their biosonars to echolocate on prey rather than recording arrays.

LIST OF ABBREVIATIONS

AGC	automatic gain control
ASL	apparent source level
EL	echo level
ICI	interclick interval
R	range
RL	received level
SL	source level
TL	transmission loss
TS	target strength
TVG	time-varying gain
TWT	two-way travel time

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