Acoustic behaviour of echolocating porpoises during prey capture

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SUMMARY

Porpoise echolocation has been studied previously, mainly in target detection experiments using stationed animals and steel sphere targets, but little is known about the acoustic behaviour of free-swimming porpoises echolocating for prey. Here, we used small onboard sound and orientation recording tags to study the echolocation behaviour of free-swimming trained porpoises as they caught dead, freely drifting fish. We analysed porpoise echolocation behaviour leading up to and following prey capture events, including variability in echolocation in response to vision restriction, prey species, and individual porpoise tested. The porpoises produced echolocation clicks as they searched for the fish, followed by fast-repetition-rate clicks (echolocation buzzes) when acquiring prey. During buzzes, which usually began when porpoises were about 1–2 body lengths from prey, tag-recorded click levels decreased by about 10 dB, click rates increased to over 300 clicks per second, and variability in body orientation (roll) increased. Buzzes generally continued beyond the first contact with the fish, and often extended until or after the end of prey handling. This unexplained continuation of buzzes after prey capture raises questions about the function of buzzes, suggesting that in addition to providing detailed information on target location during the capture, they may serve additional purposes such as the relocation of potentially escaping prey. We conclude that porpoises display the same overall acoustic prey capture behaviour seen in larger toothed whales in the wild, albeit at a faster pace, clicking slowly during search and approach phases and buzzing during prey capture.

Key words: echolocation, porpoise, foraging, buzz, biosonar, *Phocoena*.

INTRODUCTION

Echolocating animals can gather information about their environment by emitting sound pulses, then processing echoes returning from ensonified objects in the environment. Echolocation, or biosonar, is used to aid orientation during navigation and foraging, and has been found in various taxa including bats, whales and cave-dwelling birds (Griffin, 1958; Thomas et al., 2004). Detailed studies of the echolocation strategies of various species can provide insight into their foraging ecology and uncover specific features that adapt echolocation to particular niches.

Echolocation by most foraging bats consists of several distinct phases: first, a search phase consisting of regularly spaced echolocation signals; next, an approach phase, in which the bat focuses its attention on one prey target, often with an increasing repetition rate as the bat begins to approach the prey; then, a terminal phase, during which echolocation signals are emitted at an even faster, increasing repetition rate (Schnitzler and Kalko, 2001; Thomas et al., 2004). Often, each phase of echolocation is characterized by specific signal waveforms and patterns of signal repetition rate (Schnitzler and Kalko, 2001). The terminal phase is also termed the buzz (Griffin, 1958); in this phase acoustic characteristics of the echolocation clicks are specialised for precise target localization and range determination, and the more closely spaced clicks provide more frequent updates of prey location (Britton and Jones, 1999). Bat buzz production generally stops at the time of prey capture or slightly before; after a buzz, bats generally

pause echolocation click production for a period of tens to hundreds of milliseconds (Britton and Jones, 1999; Griffin et al., 1960; Hartley, 1992; Hiryu et al., 2007; Kalko, 1995; Kalko and Schnitzler, 1989; Moss and Surlykke, 2001).

A few species of toothed whales have been shown experimentally to use echolocation for navigation or for prey detection and capture, and all other toothed whales recorded to date produce clicks with source properties and signal repetition rates suitable for echolocation, so they are all thought to employ biosonar (Au, 1993; Evans, 1973; Møhl et al., 2003; Reynolds and Rommel, 1999). A sequence of acoustic events analogous to that described for bats has been recorded from echolocating harbour porpoises *Phocoena phocoena* (Verfuss et al., 2009), narwhals *Monodon monoceros* (Miller et al., 1995), sperm whales *Physeter macrocephalus* (Madsen et al., 2002b; Miller et al., 2004), and beaked whales *Mesoplodon densirostris* and *Ziphius cavirostris* (Johnson et al., 2008; Johnson et al., 2004; Madsen et al., 2005). Thus, all toothed whale species studied emit regularly spaced clicks, thought to be functionally analogous to the search phase of bat echolocation, and they also produce buzzes, as bats do (Johnson et al., 2004; Madsen et al., 2002b; Miller et al., 1995; Miller et al., 2004; Thomas et al., 2004). Click rate is not the only feature distinguishing buzzes from regular echolocation clicks; both sperm whale and beaked whale buzz clicks have intensities about 20 dB below the average regular click intensity (Madsen et al., 2005; Madsen et al., 2002b), and the buzz clicks of Blainville's beaked whales are distinguishable from frequency-

modulated search clicks by their shorter duration, higher frequency and lack of frequency modulation (Johnson et al., 2006). Buzz production rate has been proposed as a proxy for toothed whale foraging success rate (Madsen et al., 2002b; Miller et al., 2004; Watwood et al., 2006).

Aside from the statement that trained harbour porpoises end their buzzes 'shortly after the catch' (Verfuss et al., 2009), published data on toothed whales do not indicate whether prey capture occurs during or after the buzz. For beaked whales and sperm whales, capture has been assumed to occur near the end of the buzz, based on two lines of evidence: the timing of impact sounds in tag audio recordings (Johnson et al., 2004) and the observed increase in dynamic acceleration and body movements during buzzes, thought to indicate sudden movement or manoeuvring related to a capture attempt (Johnson et al., 2004; Miller et al., 2004).

Thus, toothed whales, like many bats, use echolocation. Although the echolocation signal characteristics and target detection abilities of various toothed whale species have been investigated, there have been relatively few experiments that recorded the acoustic behaviour of free swimming animals as they use echolocation to find prey. Tagging studies in the field and work on trained animals have provided data on sound production and animal movements during foraging behaviour for a variety of species, including sperm whales (Madsen et al., 2002a; Miller et al., 2004; Teloni et al., 2008), beaked whales (Johnson et al., 2006; Madsen et al., 2005; Tyack et al., 2006), pilot whales *Globicephala macrorhynchus* (Aguilar Soto et al., 2008), finless porpoises *Neophocaena phocaenoides* (Akamatsu et al., 2005) and harbour porpoises (Akamatsu et al., 2007; Verfuss et al., 2009). While these studies have provided a wealth of information on echolocation click production rates and characteristics in relation to animal depth and movements, only Verfuss and colleagues were able to collect data on timing of capture or prey capture success rates. Their analysis focused specifically on defining the phases of porpoise echolocation and quantifying regular click rate as a function of range to prey (Verfuss et al., 2009).

Several other papers describe and discuss intriguing evidence of variability in the echolocation strategies of beaked whales (Johnson et al., 2008; Madsen et al., 2005) and sperm whales (Teloni et al., 2008). The studies link different prey capture strategies to variation in prey type pursued, as evidenced by variation in whale movement patterns, buzz characteristics, and prey echo characteristics (Johnson et al., 2008) or capture depth (Teloni et al., 2008). However, none of these studies had the means to collect field data on prey species captured other than echo characteristics. Without such data, it is difficult to interpret variability in echolocation strategies in response to the variable backscattering properties of different prey types, and it is not possible to assess how the timing of echolocation phases relates to the actual capture time.

In the current study, we applied archival tags to trained harbour porpoises (*Phocoena phocoena* Linnaeus 1758) as they captured sinking dead fish. The tags logged acoustic and movement data during the prey captures, allowing us to quantify and analyse the animals' detailed echolocation behaviour leading up to and following prey capture events. In contrast to many previous studies, we were able to analyse echolocation click sequences with respect to the timing of prey capture, and we focused on adjustment of click rate and level over the course of a capture and the detailed timing of the buzz. We addressed hypotheses formulated in light of previous toothed whale tagging studies; specifically, that porpoises: (1) initiate echolocation buzzes just before the time of prey capture, when they are about one body length away from the prey fish; (2) terminate those buzzes at the time of prey capture; (3) reduce their click amplitude significantly during buzzes; and (4) respond to differences in experimental conditions (primarily, availability of visual cues and prey type) by varying the timing of their approach to prey and the level and timing of their echolocation clicks.

MATERIALS AND METHODS
Tag development and tag specifications
To carry out the prey capture experiments, a modified version of the Dtag (Johnson and Tyack, 2003) was developed specifically for use with trained harbour porpoises. The porpoise tag records sound data in stereo with a peak clip level of 191dB re. 1μPa, digitizing the data at sampling frequencies of up to 500kHz per channel (16-bit resolution) and storing it in onboard solid state flash memory. Along with sound, the tag synchronously records data from movement sensors (sampled at 50Hz), including three-axis accelerometers and magnetometers and a pressure sensor, which allow calculation of the animal's acceleration, pitch, roll, heading and depth (Johnson and Tyack, 2003). With lossless data compression, the tag can record about an hour of sound and sensor data in its 3GB memory. The tag attaches noninvasively, with custom-made suction cups (Fig. 1).

Prey capture experiments
Prey capture experiments took place at Fjord & Baelt in Kerteminde, Denmark, which houses four harbour porpoises. Two porpoises participated in the experiments: Eigil [male; at Fjord & Baelt since April 1997; estimated to be 1- to 2-years old at arrival (Lockyer, 2003)] and Sif [female; at Fjord & Baelt since July 2004; estimated to be about 1-year old at arrival (Lockyer, 2003)]. The animals are housed in a 30×10m outdoor facility, connected to the harbour by a series of nets, and with a natural sandy and rocky bottom 2–4m deep. The porpoises were trained to carry the tag using operant conditioning and positive reinforcement (Ramirez, 1999). Addition of the tag did not cause any noticeable alteration in the previously learned prey capture behaviour. The tag was attached dorsally with suction cups, just behind the blowhole, as shown in Fig. 1. At the start of each prey capture trial, a trainer called the tagged porpoise to a station at one end of the experimental pen. On a cue from the trainer, the tagged porpoise was sent across the pen; at the same cue, an assistant at the other end of the pen slapped the water surface with a stick (as an initial orientation cue for the porpoise) and then dropped a fish into the water at the same location. The porpoises' task was to find and eat the fish, then return to the trainer. During each trial, in addition to tag data, we collected underwater video recordings and stopwatch data on the times of key events [trainer cues, fish release, and prey capture (defined as first physical contact between the porpoise's mouth and the fish)]. The tag, video and stopwatch data were all synchronized by simultaneously recording a signal (a short series of gentle taps on the tag housing) on all three records at the start and end of each session. Maximum synchronization error was 0.04s, since the minimum video capture rate was 25 frames per second.

Trials were conducted with and without eyecups (suction cups that covered the porpoises' eyes like blindfolds and forced them to locate the fish without the aid of vision). We ran 71 prey capture trials between January 9 and January 13, 2008. They were carried out in 12 sessions of four to eight trials per session; all sessions contained trials with and without eyecups and trials with different fish types, as detailed elsewhere (DeRuiter, 2008). Fish used in the trials were dead, frozen then thawed from the same stock that constituted the porpoises' normal diet at Fjord & Baelt. They included herring (*Clupea harengus*, 28 trials, mean fork length
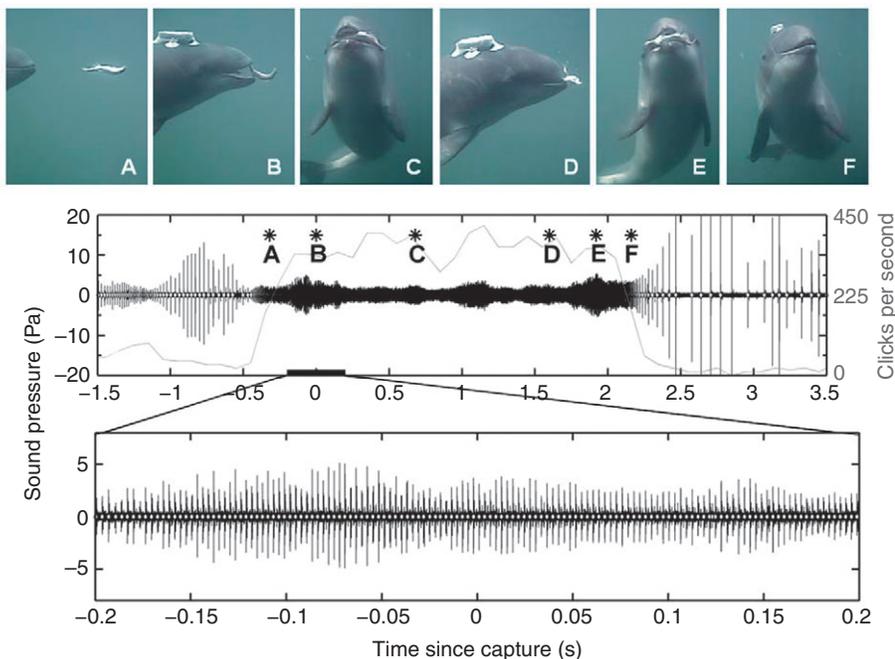
Fig. 1. Images (from underwater video footage) and waveforms (from tag audio recording) during a prey capture event. Time 0 (B) is defined as the moment of prey capture. Asterisks on the upper waveform plot indicate the times at which the photos were taken. The *y*-axis scales are set for optimal viewing of the echolocation buzz (clicks are not clipped in the recording). Clicks detected by the click detector are indicated on the waveform plots as white diamonds at amplitude zero (they are not visible during the buzz in the middle panel because they are too closely spaced in time). The lower waveform is an expanded view of the time of capture to illustrate click level and signal-to-noise ratio during the buzz. In the middle panel, the grey line plots click rate in clicks per second (scale on right *y*-axis).

21.0 cm), capelin (*Mallotus villosus*, 37 trials, mean fork length 15.1 cm), and sprat (*Sprattus sprattus*, six trials, mean fork length 12.6 cm).

Data analysis

For each trial, we used stopwatch data to calculate the time it took the porpoises to catch each fish, defined as the time from the trainer sending the cue until the fish (or part of the fish) was in the porpoise's mouth. Comparison with video data confirmed the accuracy of the stopwatch-measured capture times (stopwatch error had a mean of +0.012 s, and a median absolute value of 0 s, for 40 trials with clear video of the time of capture). Porpoises were never observed to lose fish after having them in their mouths, although they did sometimes manipulate or carry the fish before swallowing them. We applied a two-sample *t*-test to test whether the mean capture duration was different for trials with and without eyecups.

For each trial, a 30-s segment of the tag audio recording was analyzed: 15 s before and 15 s after the stopwatch time of prey capture. Tag audio data were filtered in Matlab (The Mathworks, Natick, MA, USA) with an eight-pole Butterworth bandpass filter between 100 and 200 kHz. Porpoise clicks were detected in the filtered audio recordings using a custom-written envelope-based click detector in Matlab. The click detection algorithm was designed to detect clicks despite high variability in click levels and inter-click intervals in the tag data, as described in detail elsewhere (DeRuiter, 2008). Briefly, the algorithm worked as follows. (1) Calculate the envelope of the audio signal; detect candidate clicks according to an envelope-level detection threshold. (2) After a candidate click is detected, do not detect any additional clicks within 1.3 ms following the initial detection. (This blanking time was selected after manual inspection of prey capture buzzes in the dataset, none of which contained inter-click intervals of less than 1.3 ms.) (3) Compare the maximum envelope level (MEL) of the detected click to L, the mean of the maximum envelope levels of the preceding three clicks. Compare the inter-click interval (ICI) preceding the detected click to I, the mean ICI of the preceding three clicks. Accept the click if MEL≥0.5L and ICI≥0.2I. Also accept clicks for which ICI<0.2I but MEL≥3L. These criteria help reduce

detections of surface and bottom reflections. (4) Accept clicks for which MEL<0.5L but ICI>3I. In this case, reset I to 100 ms. This rule allows detection of trains of low amplitude clicks after long inter-click intervals or sudden drops in click level, without promoting detection of quiet reflections and/or echoes between higher amplitude clicks. Click detector performance was checked visually by examining plots of the data waveforms overlaid with click detections. The time (in seconds until prey capture) and received peak-to-peak (pp) level of each detected click was recorded. Animal movement data (specifically roll angle) were filtered and resampled to obtain an effective sampling rate of 5 Hz.

For acoustic time-series analysis, click rate data were binned into 0.1 s bins. To calculate echolocation buzz start times, end times and durations, we defined the buzz as the time period during which click rate exceeded 125 clicks per second [about three to four times the mean pre-buzz click rate, and slightly higher than the upper values observed in transient variations about that mean (Fig. 2)]. For the purposes of these calculations, a buzz started when the threshold click rate of 125 clicks per second was first exceeded, and ended when the click rate fell below threshold for the last time. Using the above criteria, we calculated the start time, end time and duration of each prey capture buzz, as well as the mean start time, end time and buzz duration for the set of all 67 successful captures. We excluded buzzes that ended more than 5 s before prey capture or began more than 5 s after prey capture in our analysis. As seen in Fig. 2, buzzes outside those time limits did not seem to be associated with prey capture. Rather, the rare buzzes that occurred more than 5 s before capture were probably related to non-prey objects (including landmarks or other porpoises) in the pool, and the buzzes that occurred more than 5 s after capture were probably related to the porpoises' returning to station with the trainers. To assess the effects of eyecups, prey type, and individual porpoise on buzz duration, we log-transformed the buzz duration data to meet normality and homoscedasticity assumptions and then carried out a three-way ANOVA.

Bats and toothed whales often fall silent for a short period following an echolocation buzz; this pause duration (if any) was calculated for each of the 67 successful prey captures by determining the longest inter-click interval in the 5 s following prey capture.
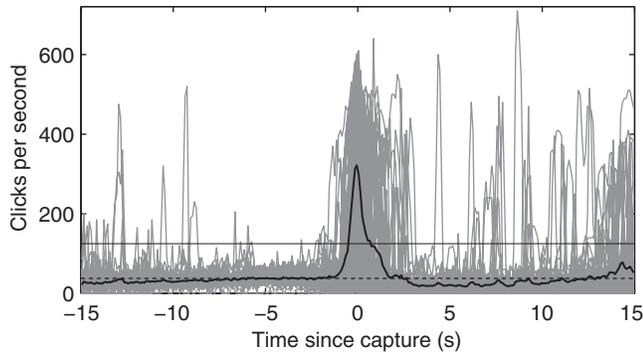
Fig. 2. Click rate as a function of time since prey capture. Each trace is data from one prey capture trial; the thick black line is the mean click rate over all 67 trials. Data are in 0.1 s bins. The dotted black horizontal line indicates the overall mean click rate outside buzzes (37.6 clicks per second), and the thin black horizontal line indicates the threshold used to determine buzz start and end times (125 clicks per second).

RESULTS
Timing of prey capture

It took the porpoises an average of 19.6 s to find and collect a fish while wearing eyecups, longer than the 15.9 s average time without eyecups; the difference was significant at the P=0.05 level (t-test, d.f.=32, P=0.000027).

Porpoise movements during prey capture

Fig. 3 summarizes the porpoise orientation data. Variability in porpoise roll angle increased around the time of prey capture, indicating that the porpoises turned their bodies more, or more frequently, as they neared the fish and captured it. However, average roll remained relatively constant throughout the trials, indicating that the porpoises did not have a preferred roll angle during their final approach to their prey. They never rolled completely upside down during the prey capture experiments.

Porpoise acoustic behaviour during prey capture

The porpoises produced echolocation buzzes in 66 of the 67 successful prey capture trials. Figs 2 and 4 show the data on click rate as a function of time for all 67 prey capture trials; they clearly indicate that, on average, the porpoises began buzzing before they captured the fish, and continued to buzz after the capture event. The click rate within the buzz generally increased rapidly and peaked around the time of prey capture, with maximum observed buzz click rates averaging 321 clicks per second (3.1 ms ICI) and as high as 640 clicks per second (1.6 ms ICI).

For the 66 captures in which buzzes were detected, the mean buzz start time was 0.53 s before prey capture, end time was 0.83 s after prey capture, and mean buzz duration was 1.37 s. After buzzes, porpoises sometimes paused their production of echolocation clicks, but few post-buzz pauses were long enough to clearly distinguish them from longer ICIs that regularly occurred before the buzz (mean maximum post-buzz ICI 481 ms; pause duration ≥1 s in 9 of 67 trials).

During buzzes, porpoises not only increased their click rate, but also apparently decreased the level of their emitted clicks by about 10 dB compared with the average level outside buzzes. Fig. 5 shows the data on tag-recorded click level as a function of time for all 67 successful prey captures. Because the tag was physically attached to the animal and positioned off-axis, behind the sound generator, these levels are not source levels. They are probably at least 40 dB lower than on-axis source levels (Hansen, 2007). However, the tag-
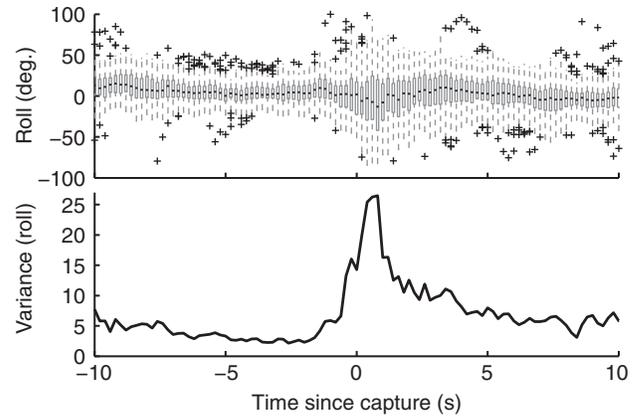

Fig. 3. Roll as a function of time since prey capture. Top panel: box-and-whiskers plot of roll as a function of time for the 67 successful prey captures (data in 0.2 s bins). The black horizontal lines show the median value in each time bin; the top and bottom of the grey rectangles are the upper and lower quartiles within the bin. The dotted grey lines extend to the largest and smallest observed values in the time bin, up to 1.5 times the interquartile range beyond the grey box. Larger and smaller observed values are plotted as black crosses. Bottom panel: variance in roll, calculated for all 67 roll measurements at each sampled time point (sampling rate 5 Hz).

received levels are probably correlated with the source levels (Madsen et al., 2005; Madsen et al., 2002a).

Figs 6–8 compare click rates and levels between varying sets of conditions: with and without eyecups (Fig. 6); Eigil *versus* Sif (Fig. 7); and herring *versus* capelin (Fig. 8). As shown in Fig. 6, the presence or absence of eyecups had no obvious effect on maximum buzz click rate; buzzes appeared to begin slightly earlier in trials with eyecups and to include a second peak in click rate after capture in trials with eyecups, but there was no significant effect of eyecups on buzz duration [three-way ANOVA, F(1 d.f.)=0.43, P=0.50]. Compared with trials without eyecups, click levels during trials with eyecups tended to be a bit lower before capture and a bit higher after. Fig. 7 shows that Sif tended to use click levels about 5–10 dB higher than Eigil in all trials; in addition, her buzz click rate was much faster than his. Sif's buzzes were longer than Eigil's [three-way ANOVA, F(1 d.f.)=11.54, P=0.0012]. Fig. 8 compares click rates and sound levels during trials with herring and capelin.
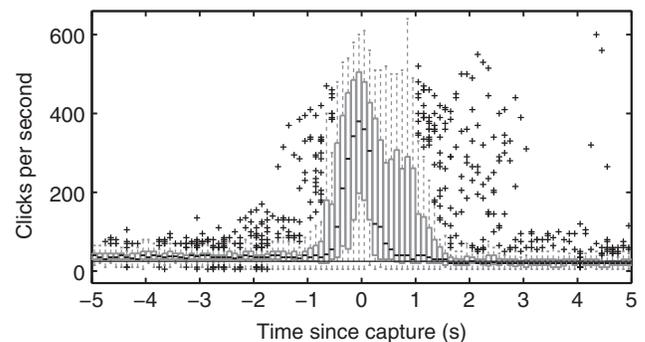

Fig. 4. Box-and-whiskers plot of click rate as a function of time for 67 prey captures by harbour porpoises (data in 0.1 s bins). Symbols and notation are the same as in Fig. 3 (top panel). The black horizontal line indicates median click rate outside buzzes (25 clicks per second). Mean buzz start time was 0.53 s before prey capture, end time was 0.83 s after prey capture, and mean buzz duration was 1.37 s.
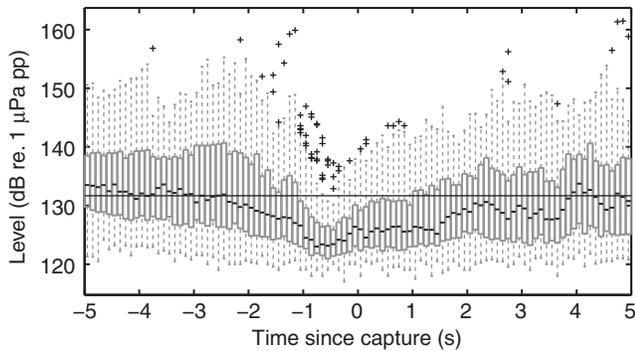
Fig. 5. Box-and-whiskers plot of click level as a function of time for 67 prey captures by harbour porpoises (data in 0.1 s bins). Levels are the off-axis, on-animal levels from the tag recordings, not click source levels. Symbols and notation are the same as in Fig. 3 (top panel). The black horizontal line indicates the median click level outside buzzes (132 dB). Mean buzz start time was 0.53 s before prey capture, end time was 0.83 s after prey capture, and mean buzz duration was 1.37 s.

Fig. 7. Porpoise click rates (top panel) and levels (bottom panel) as a function of time. Solid traces show data from trials with Eigil (N=33); dotted traces show data from trials with Sif (N=34). Data are in 0.1 s bins. Grey horizontal lines indicate the overall mean click rate (37.6 clicks per second) and level (136 dB) outside buzzes.

Although click rates were very similar for the two prey types, the mean click levels were about 3 dB higher for capelin captures, except immediately preceding prey capture, when they were equal. Buzzes were longer during trials with herring than during trials with capelin and sprat [three-way ANOVA, F(1 d.f.)=5.06, P=0.028].

In addition to considering variations in click rate and level as functions of time since prey capture, we also investigated recorded click level as a function of inter-click interval, or ICI (Fig. 9). Click levels were relatively constant for ICIs greater than about 40 ms, but they decreased with decreasing ICI for ICIs less than about 40 ms. Fig. 9B shows the click level *versus* ICI data as a scatter plot. The figure does not provide evidence for a clear distinction between buzz clicks and regular clicks on the basis of either ICI or click level. It is important to note that we cannot be completely certain that none of the detected clicks were produced by other animals; some of the clicks in Fig. 9 (perhaps especially the highest-amplitude clicks) may have been produced by animals other than the tagged porpoise.

DISCUSSION
Buzzes
In all 67 of the successful prey capture trials, porpoises produced echolocation clicks throughout the prey capture trial regardless of whether or not they were wearing eyecups; in only one of the 67
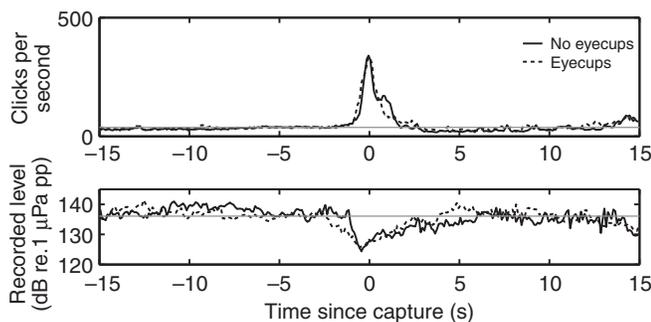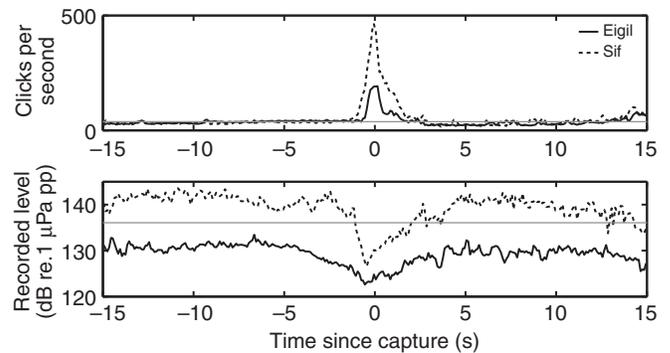
trials did the porpoise capture the fish without producing an echolocation buzz [in one trial, Eigil (with eyecups) caught a herring without producing a discernible buzz]. These data and data from the field (Akamatsu et al., 2007) support the notion that porpoises emit echolocation clicks most of the time, and that echolocation is a primary sensory modality for prey localization. The consistent use of buzzes in the present study also indicates that they are an integral part of the capture phase of biosonar-based foraging, for porpoises as for many bats (Schnitzler and Kalko, 2001; Thomas et al., 2004) and larger toothed whales (Johnson et al., 2004; Madsen et al., 2002b; Miller et al., 1995; Miller et al., 2004; Thomas et al., 2004).

On average, the porpoises initiated echolocation buzzes less than a second before prey capture, when they were within about a porpoise body length of the prey fish. Maximum buzz rates exceeded 300 clicks per second on average, and ranged up to 640 clicks per second; highest rates often coincided with the time of prey capture. These buzz click rates are similar to those previously reported for harbour porpoises (several hundred to about 700 clicks per second) (Akamatsu et al., 2007; Verboom and Kastelein, 2004; Verfuss et al., 2009). However, we consider them to be minimum estimates of the actual observed click rates, since we may have failed to detect very low-level buzz clicks (see Click levels section). The minimum ICI during buzzes (on
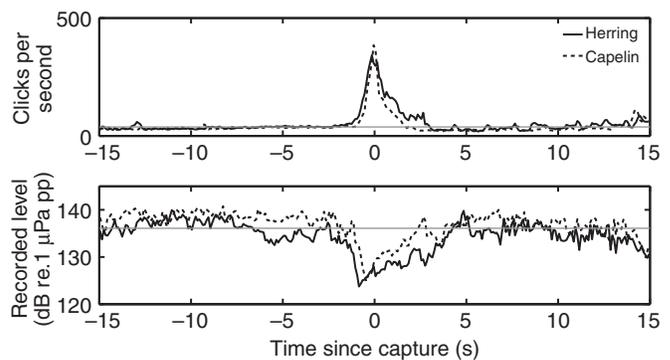

Fig. 6. Porpoise click rates (top panel) and levels (bottom panel) as a function of time. Solid traces show data from trials without eyecups (N=34); dotted traces show data from trials with eyecups (N=33). Data are in 0.1 s bins. Grey horizontal lines indicate the overall mean click rate (37.6 clicks per second) and level (136 dB) outside buzzes.

Fig. 8. Porpoise click rates (top panel) and levels (bottom panel) as a function of time. Solid traces show data from trials with herring (N=27); dotted traces show data from trials with capelin (N=35). Data are in 0.1 s bins. Grey horizontal lines indicate the overall mean click rate (37.6 clicks per second) and level (136 dB) outside buzzes.
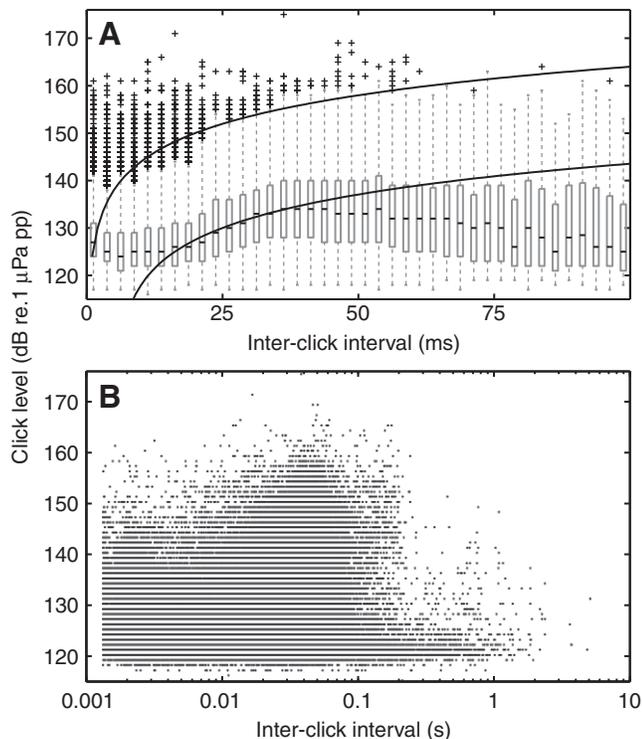
Fig. 9. (A) Box-and-whiskers plot of click level as a function of inter-click interval (ICI). Data are in 2.5 ms bins. Symbols and notation are the same as in Fig. 3 (top panel). The solid black lines show sample $20\log_{10}$(ICI) relationships for comparison with the data. (B) Scatter plot of click levels as a function of ICI.

average 3.1 ms) was much shorter than the auditory processing time estimated for single echoes [20–35 ms (Au et al., 1999)]. Assuming the accuracy of that estimate, our data confirm that although porpoises may adjust their ICI to allow for echo processing time during search and approach phases, they switch to another mode in the terminal phase, termed a 'pitch processing mode' (Verfuss et al., 2009), in which they either process buzz clicks more rapidly or integrate echo information from multiple clicks.

The porpoises studied here manoeuvred more during prey capture than at other times, as indicated by increased variability in roll angle (Fig. 3). Increased variability in body orientation simultaneous with an echolocation buzz may thus be an indicator of prey capture attempts in toothed whales, as suggested by Miller and colleagues for sperm whales (Miller et al., 2004). However, in contrast to sperm whales (Miller et al., 2004) and to porpoises in a previous study conducted at the same facility (Verfuss et al., 2009), the porpoises never rolled upside down during our trials (Fig. 3). These differences could be explained by the fact that we used dead fish rather than live prey, or could signify a change in the animals' behaviour over years in captivity.

Unlike bats, for which the end of the echolocation buzz occurs before or coincides with prey capture (Griffin et al., 1960; Hartley, 1992; Hiryu et al., 2007; Kalko, 1995; Kalko and Schnitzler, 1989; Melcón et al., 2007; Moss and Surlykke, 2001), the harbour porpoises in this study continued their buzzes after prey capture (that is, beyond the start of prey handling). Although porpoises and odontocetes in general are thought to be suction feeders (Kastelein et al., 1997; Werth, 2006), and the porpoises we studied did appear to use suction to get prey into their mouths, we also observed them

to manipulate or carry the prey in their mouths for periods of up to a few seconds, generally buzzing throughout this handling time (Fig. 1). A similar extension of the buzz phase may be more difficult for bats that emit sounds through the mouth once they have actually begun to consume prey, since eating prey could interfere with vocalizing. By contrast, the toothed whale sound production system is completely separated from the digestive tract, so prey in the mouth should not interfere with the sound generator. In porpoises, the continuation of the buzz post-capture might also stem from some physiological limitation, but that explanation seems somewhat less likely, considering the extent to which toothed whales can control the timing and spectra of their clicks (Au, 1993). Alternatively, continuing to buzz after capture may allow immediate re-localization of prey items that escape after nearly successful capture attempts or facilitate post-capture pursuit of other, nearby prey items (especially for schooling prey like herring). Finally, we cannot fully exclude the possibility that the extended buzzes we observed have developed over years in captivity, being fed dead fish.

Almost all of the porpoises' prey capture attempts were successful during our experimental trials, which is not surprising considering that we used dead prey items. Consequently, the dataset is not suitable for comparing the post-buzz pause durations and click characteristics of successful and unsuccessful capture attempts.

Click rates
During the approach phase, the average click rate of the porpoises in this study was about 35 clicks per second, corresponding to an ICI of about 29 ms (Figs 2 and 4), which is similar to the minimum ICI (30 ms) observed in a study of free-ranging harbour porpoises in Danish waters (Villadsgaard et al., 2007). The observed ICIs were somewhat less than those observed in a study of the same animals by Verfuss et al. (Verfuss et al., 2009), which might be explained by the fact that the experimental pool was larger at the time of Verfuss' experiments. The mean ICI was relatively constant over time, decreasing slightly from about 39 ms 15 s before capture to about 26 ms just before initiation of the echolocation buzz (Fig. 2), which could be interpreted as a response to reduction in porpoise–prey range. However, the trend is weaker in the median data (Fig. 4). Figs 1, 2 and 4 also show that there was some variability in ICI over the course of individual captures, which often showed bursts of fast clicks followed by resumption of a slower click rate, rather than a consistent reduction in ICI as range decreased leading up to the time of prey capture. It is possible that the porpoises investigated multiple targets during each trial, and were not focusing on detecting the fish the entire time. Previous studies with porpoises provide conflicting findings on this topic, with some results suggesting no significant ICI/range adjustment during foraging (Verfuss et al., 2009) and target detection (Teilmann et al., 2002) tasks and others finding such a relationship during navigation (Verfuss et al., 2005) or presumed foraging activity (Akamatsu et al., 2007; Akamatsu et al., 2005). Although not conclusive, our results are consistent with the idea that porpoise inter-click intervals remain relatively constant as porpoise–prey range declines, then decrease rapidly following buzz initiation. This pattern would match more closely with observations from free-ranging echolocating beaked whales and sperm whales (Madsen et al., 2005). Overall, it seems that the non-buzz ICIs of echolocating toothed whales in general, and also porpoises, are longer than the two-way travel time, but that adjustments in the ICIs are not only, or not necessarily, dictated by the changing two-way travel time to the prey during the initial approach phase.

Click levels

Our results show that porpoises reduce the apparent output of their clicks by about 10 dB during buzzes. Although this observation matches the general trend observed in other toothed whales when they are foraging in the wild, other species display even greater reductions in click levels during buzzes: 15–20 dB for Blainville's beaked whales (Madsen et al., 2005) and about 20 dB for sperm whales (Madsen et al., 2002b). Porpoise average click levels decreased leading up to buzz initiation (Fig. 5), but such a steady decline was not consistently apparent in individual-trial data (Fig. 1). Our data also indicate that apparent click levels decrease as click rates increase; unlike beaked whales (Madsen et al., 2005), for porpoises there is no clear separation between regular and buzz clicks in the level/ICI plane (Fig. 9), at least when recorded off the acoustic axis. This result may indicate that porpoises purposefully reduce the source level of faster clicks, perhaps to reduce clutter echoes and focus on a single target, or to maximize their ability to detect returning echoes at close ranges (Supin et al., 2005; Supin et al., 2007; Supin et al., 2008). It is also possible that the porpoise click generator is restricted in the acoustic energy it can produce per unit time, resulting in lower click levels at higher click rates, as observed by Beedholm and Miller (Beedholm and Miller, 2007). Transmit-side automatic gain control (AGC), in which transmission power varies as a function of source–target range to adjust for transmission loss and to stabilise echo levels (Au and Benoit-Bird, 2003), could also result in an ICI/level relationship if ICI is proportional to range (r). In previous work with some of the same animals we studied, click level varied according to $14–17\log_{10}(r)$ or $\log_{10}(ICI)$ (Beedholm and Miller, 2007) or $20\log_{10}(r)$ (Atem et al., 2009) as porpoises approached real or simulated targets in a limited number of trials. An apparent level increase of about 6 dB per doubling of ICI [$20\log_{10}(ICI)$] does not provide a clear fit to our data (Fig. 9), as click levels were highly variable both within and between trials (Figs 1 and 5). Our data thus suggest that any range/time varying output adjustments are not mechanically hardwired to target range through a strong ICI to two-way travel time adjustment, as also demonstrated recently for bottlenose dolphins (Jensen et al., 2009).

The lowest click level detectable in the tag recordings was 117 dB re. 1 µPa (peak-to-peak; pp). Because of the position of the tag on the animal, on-tag click levels are probably ~40 dB lower than on-axis source levels (Hansen, 2007). Although our tag threshold was much lower than the detection threshold (136 dB re. 1 µPa pp) of tags previously deployed on porpoises in a similar position (Akamatsu et al., 2007), we were still not able to detect every click, especially low-level buzz clicks. Since lower-level clicks tended to occur near the start or end of buzzes, these detection limitations could have led us to underestimate level reductions during buzzes or introduced some error into our estimates of buzz start and/or end times.

Effects of eyecups, individual, and prey type

There were no major differences in echolocation phases or click rates and levels between our trials with and without eyecups. However, porpoises took longer to capture prey with eyecups, so visual input, when available, seems to facilitate prey capture in some way.

We observed a striking difference in click levels between the two animals that participated in the study; Sif's clicks had about 5–10 dB higher amplitude on the tag than Eigil's, and her buzz click rates were faster than Eigil's (possibly because of level and/or detectability

differences). Small but statistically significant differences in average click source levels have previously been reported for these animals (Atem et al., 2009). Sif is thought to have sustained minor hearing damage in the past that has caused her to increase her outgoing echolocation click levels (M.W., unpublished observation), so the differences between Sif and Eigil may exceed the normal range of intraspecific variation. Nevertheless, they provide a benchmark for the click level variations that may result from differences in hearing sensitivity, and emphasize the need to include more animals in audiology and biosonar experiments.

Interestingly, we also observed differences in click levels between trials with herring and capelin; apparent click amplitudes were about 3 dB higher for capelin than for herring (Fig. 7). Many bats employ AGC to compensate for transmission loss (Hartley, 1992; Surlykke and Kalko, 2008), but changes in source level to compensate for variations in prey target strength have not previously been reported [but see Au (Au, 1993) for a brief discussion of the topic for dolphins]. The average acoustic target strength of the capelin used in our experiments was measured to be –55 dB, about 18 dB less than that of the herring (–37 dB; S.D., unpublished observation). Since the difference in target strengths so exceeds the apparent increase in click amplitude, it seems clear that the porpoises were not using source-level adjustment alone to keep echo levels from the two prey types constant. Our findings are consistent with data on bats collected by Boonman and Jones (Boonman and Jones, 2002), who observed a 4 dB increase in source level when target strength was reduced by 17–18 dB, a change they judged insignificant. However, the mismatch between target strength and level increase does not automatically imply this conclusion. It is possible that acoustic clutter could have limited maximum source levels used by the animals in their pen. Alternately, animals may adjust their source levels to maintain target detectability rather than to stabilize echo levels (Au, 1993), for which a modest 3 dB increase in outgoing click level could have been sufficient. Finally, perceived echo intensity is determined not only by click levels and target strength, but also by transmission loss and auditory sensitivity (which may vary by situation, including possible forward masking by the outgoing click) (Supin et al., 2005; Supin et al., 2007; Supin et al., 2008).

Conclusions

Echolocating harbour porpoises used relatively stable mean click intervals (mean 29 ms) during search and initial approach phases. A decrease in ICI from about 39 to 26 ms over the course of approach was evident in the data average but less so in individual trial data, which showed significant click-to-click variability and few linear trends. When ~1–2 porpoise body lengths away from the fish, the porpoises initiated an echolocation buzz, during which inter-click intervals decreased by an order of magnitude, and apparent source levels decreased by about 10 dB. The most striking finding of this study is that the porpoises continued to buzz after they had reached prey and begun to handle it in their mouths. They generally intercepted prey about halfway into the buzz during increased manoeuvring, which illustrates that buzz termination does not necessarily correspond to the moment of prey capture, and suggests that buzzes may have functions other than providing detailed information on target location leading up to capture. These functions remain unknown, and could include re-capturing escaping prey, or closely monitoring the acoustic scene immediately surrounding the porpoise for other prey, landmarks or objects of interest. The echolocation behaviour of the porpoises in this study – slow clicking during search and approach and buzzing during prey capture

– is akin to that of other much larger toothed whales, but the porpoises seem to operate a shorter range biosonar system, with faster overall click rates during search, approach and interception of prey.

LIST OF ABBREVIATIONS

AGC	automatic gain control
dB	decibels (dB)
ICI	inter-click interval
pp	peak-to-peak
r	range

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