

Echolocation in Blainville's beaked whales (*Mesoplodon densirostris*)

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Abstract Here we use sound and movement recording tags to study how deep-diving Blainville's beaked whales (*Mesoplodon densirostris*) use echolocation to forage in their natural mesopelagic habitat. These whales ensoundify thousands of organisms per dive but select only about 25 prey for capture. They negotiate their cluttered environment by radiating sound in a narrow 20° field of view which they sample with 1.5–3 clicks per metre travelled requiring only some 60 clicks to locate, select and approach each prey. Sampling rates do not appear to be defined by the range to individual targets, but rather by the movement of the predator. Whales sample faster when they encounter patches of prey allowing them to search new water volumes while turning rapidly to stay within a patch. This implies that the Griffin search–approach–capture model of biosonar foraging must be expanded to account for sampling behaviours adapted to the overall prey distribution. Beaked whales can classify prey at more than 15 m range adopting stereotyped motor patterns when approaching some prey. This long detection range relative to swimming speed facilitates a deliberate mode of sensory-motor operation in which prey and capture tactics can be selected to optimize energy returns during long breath-hold dives.

Keywords Echolocation · Biosonar · Beaked whale · Sampling rate · Sensing

Introduction

Aquatic mammals display an array of secondary adaptations to life in water that include dramatic changes to their limbs, insulation, osmoregulation, and sensory systems. Water has very different physical properties than air meaning that the propagation of sensory cues in some cases deteriorate and in other cases improve during the transition from air to water. Sound travels about 4.5 times faster and with much less attenuation in water as compared to air (Urick 1983). Sound is therefore an excellent vehicle for information transfer over long ranges in water, and most marine mammals have evolved acute underwater hearing capabilities (Nummela et al. 2004) for communication, navigation, food finding, and detection of predators. A subset of marine mammals, the toothed whales, have taken the use of sound a step further, evolving the capability to use sound actively for echolocation (Fordyce 2002) to access prey resources in poorly lit waters. Echolocation differs from most other senses in that echolocating animals, like electrolocating animals, must generate energy to probe the environment (Nelson and MacIver 2006). In echolocation, short pulses of sound are projected in a narrow beam ahead of the animal and information is extracted by auditory processing of the returning echoes. Thus, an echolocator obtains a snapshot of information every time it produces a sound, inherently making echolocation a discrete time sensory system with the sound production rate determining the maximum rate at which information can be acquired.

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Using echolocation to find, select and capture prey in darkness requires the close coordination of vocal and locomotor outputs with sensory inputs. This vocal-motor feedback loop uses information extracted from echoes, i.e., the range to and properties of each object ensonified to inform and time body, jaw and head movements, and to adjust the rate and properties of the emitted sonar pulses to gather additional information. Such adjustments are part of an acoustic gaze control wherein the rate, levels, frequencies and beam widths of the emitted clicks all are manipulated in tandem to focus dynamically on regions of interest in the environment ahead of the echolocator (Au and Benoit-Bird 2003; Moore et al. 2008; Wisniewska et al. 2012). Early experiments by Morozov et al. (1972) showed that toothed whales, like bats, determine target range from the two way travel time (TWTT) between the emitted click and the time of the returning echo. Echolocating toothed whales consistently appear to produce clicks with inter-click intervals (ICI) longer than the TWTT to the target of interest, to apparently avoid range ambiguity problems where echoes from a previous click arrive after the emission of a new click. The time difference between the ICI and the TWTT, the so-called lag time, has been proposed to result from the time required to process the received echo information (Au 1993). However, this lag time is highly variable and context dependant, and in some cases so short that the animal cannot possibly process each click–echo pair individually (Wisniewska et al. 2012).

Echolocation involves both detection and classification of targets, and the ranges at which these can happen are defined ultimately by the echo to noise ratio in the auditory system of the whale (Au 1993). Ambient noise and unwanted echoes (termed clutter) within the same integration window of a targeted echo can impede its detection or discrimination. The range, R (m), at which a detectable echo levels (EL) is received from a given target not only hinges on the reflectivity of the object, termed the target strength (TS), but also on the transmission loss (TL) of sound in water, the source level (SL) of the emitted click, and the noise level (NL) at the location of the receiver. For convenience the capitalized parameters are dealt with on a logarithmic scale so that for example the NL in deciBels (dB) is defined as $10\log_{10}(\text{noise power})$. The relationship between the parameters is summarized in the active sonar equation (Urlick 1983; Au 1993) which defines the echo-to-noise ratio [ENR (dB)] as:

$$\text{ENR} = \text{EL} - \text{NL} = \text{SL} - 2 \times \text{TL}(R) + \text{TS} - \text{NL}$$

To achieve efficient backscatter from their prey targets, toothed whales must operate their sonars at wavelengths shorter than the circumference of the ensonified targets (Medwin and Clay 1998), calling for frequencies greater

than 5–10 kHz for typical prey sizes. However, frequencies as high as 150 kHz are used by some species, well beyond what is required for a strong echo from preferred prey, suggesting that other factors, such as crypsis and directionality, have driven the evolution of click frequencies in toothed whales (Morisaka and Connor 2007; Madsen and Surlykke 2013).

Echolocation clicks are generated from a pneumatically driven source in the toothed whale nasal complex and, to produce high source levels, the clicks must be directional. Directionality results from having a large ratio between the dimensions of the sound transmitting aperture of the whale's forehead and the wavelengths of the emitted click. All studied toothed whales are found to have an aperture-to-wavelength ratio of more than 10, providing them with SLs that are 20–30 dB higher than what an equivalent omnidirectional sound source would produce (Au 1993). The second advantage of directionality in sonar beams is the reduction of unwanted echoes (clutter) from targets at similar ranges, but at different angles than the target of interest. Thus, clicks at ultrasonic frequencies serve the multifaceted functions of achieving longer detection ranges via higher directionality and hence SLs, producing efficient backscatter on small prey targets and reducing clutter from unwanted targets. Further, the high frequencies will give rise to interference patterns between reflections from different parts of the ensonified targets providing spectral cues for target discrimination (Au 1993; Ibsen et al. 2009; Kloepper et al. 2010). An important consequence of the high directionality of the toothed whale biosonar is that the whale faces the task of finding small objects in a dark three-dimensional world with a narrow, forward-directed beam.

In toothed whales, echolocation is often the dominant or only sensory modality available for prey location at low light levels, which in turn has led to the evolution of biosonar systems that rival the performance of human sonars at short (<100 m) ranges (Au 1993). Because of this superior performance, toothed whale biosonars have been studied intensively under controlled experimental conditions on captive animals to uncover how information about target range and target properties are extracted from echoes (Au 1993). Trained dolphins can detect small steel spheres at ranges of more than 100 m, and can resolve very small differences in the properties of, and range to, artificial targets on the basis of spectral, temporal and level cues in the returning echoes (Au 1993). Studies on trained animals provide much needed and detailed knowledge on the performance of dolphin biosonars, but most if not all of the experiments have had the animals stationed in a hoop while performing a biosonar task that may have little relation to the situation faced by a toothed whale echolocating for prey items in the wild (Au 1993). Thus, most research on captive toothed whales has taken a biomimetic approach

with the primary goal of reverse-engineering the process of echolocation rather than understanding its biological significance. With that said, carefully controlled studies in captivity have provided a much needed basic and essential understanding of the operation of echolocation in toothed whales and also provided a powerful methodological and conceptual frame work in which to study this sixth sense. However, the biosonar task for a foraging animal not only involves a moving source and target, but also a complex echo pattern arising from many different kinds of ensounded targets, such as non-prey organisms and prey of differing quality, as well as the seafloor and the surface. So, if we wish to understand how echolocation evolved and how it is used by animals in the wild, it is necessary to complement captive studies with investigations of this process in free-ranging animals under circumstances for which their biosonar systems evolved.

A remarkable synergy between field and laboratory studies has been the hallmark of more than 60 years of research on another group of echolocating animals, the bats. Don Griffin, the discoverer of echolocation, quickly realized that much could be learned by using controlled experiments in the lab to understand behaviours observed in the wild and vice versa (Griffin 1958). In these studies, he delineated that prey interception in echolocating bats involves three phases: search, approach and capture, each with distinct acoustic behaviours (Griffin et al. 1960). While searching, bats generally emit powerful, long duration calls at low repetition rates to inspect a large air volume for potential prey. When prey is detected, bats start the approach phase reducing the sensory volume via reductions in the amplitude, duration and interval between calls, while increasing call bandwidth. These adjustments increase the temporal resolution of the sonar at the expense of range and so aid in tracking movements of individual prey while reducing clutter from other targets. A few body lengths away from the prey, bats enter the capture phase indicated by the production of a buzz comprising weak, short echolocation pulses produced at very high repetition rates for fine scale tracking of prey for interception (Griffin et al. 1960; Kalko 1995).

Toothed whales must go through the same process of search, approach and capture when echolocating for prey, but it is only quite recently that corresponding acoustic behaviours have been tested for and found. Miller et al. (1995) to our knowledge published the first paper to apply the term buzz and invoke the Griffin model in describing the sound production patterns of an echolocating toothed whale. Subsequent research in the wild, and more recently with captive animals presented with live prey, have demonstrated that toothed whales produce a buzz consistently when catching prey (Madsen et al. 2002a; Miller et al. 2004; Johnson et al. 2004; Aguilar de Soto et al. 2008;

Verfuss et al. 2009; Deruiter et al. 2009). The Griffin model has thus proven very useful as a conceptual frame work for studying not only echolocating bats, but also toothed whales. The remarkable uniformity of buzzing in both bats and toothed whales speaks to an intriguing functional convergence in these two completely independent biosonar systems (Madsen and Surlykke 2013). However, the convergence is not complete: for some toothed whale species, gaze adjustments in the forms of reducing ICIs and SLs occur prior to the buzz as seen in the approach phase in bats (Au and Benoit-Bird 2003; Akamatsu et al. 2005; Jensen et al. 2009), but other toothed whale species do not appear to do this (Madsen et al. 2005), raising questions about how the process of echolocation is adapted to fit different environments and ecophysiological constraints.

Studies of toothed whale echolocation in the wild have been enabled by the development of new tools to study the sounds and movements of echolocating whales at sea, overcoming one of many stumbling blocks in moving from captive to field studies. Arrays of hydrophones have been used to record sounds and localize sound producing whales in the wild, leading to a better understanding of their repertoire and sound production capabilities (Møhl et al. 1990; Au et al. 2004; Madsen et al. 2004a, b). But particularly the development of acoustic recording tags in the last decade has opened a powerful new window to study free-ranging echolocating whales (Madsen et al. 2002b; Johnson and Tyack 2003; Johnson et al. 2009). These devices combine wide bandwidth sound recording with fine-scale movement sensors enabling the precise synchronization of sound production and movement of the tagged animal. By attaching the recorder to the animal, individual foraging behaviour can be examined in detail for hours at a time providing a fuller picture about when and how echolocating animals sample their environment acoustically.

Acoustic tags (Dtags, Johnson and Tyack 2003) have been highly productive for toothed whale biosonar research in studies of what was previously an almost unknown whale species, the Blainville's beaked whale (*Mesoplodon densirostris*). These relatively small (3–4.5 m, 600–1,000 kg), deep-diving whales are sparsely distributed and usually very difficult to find, making them unlikely candidates for detailed echolocation studies in the wild. But probably as a consequence of their cranial and melon anatomy influencing the direction of the emitted acoustic beam, a tag attached to the dorsal surface of these whales is able to record both the sound produced by the animal and echoes returning from prey. This provides an opportunity to tap into the sensory stream of the animal itself and relate changes in motor and vocal patterns to returning echo information (Johnson et al. 2004; Madsen et al. 2005). Tag recordings from *M. densirostris* have revealed a highly selective foraging behaviour in which many more

organisms are ensounded than are targeted for capture (Arranz et al. 2011). When these whales select a prey item, they tend not to adjust their click rates while approaching it, but, like aerial hunting bats, switch to a high repetition rate buzz when the prey is about a body length ahead of them (Johnson et al. 2004, 2006; Madsen et al. 2005). This behaviour has been interpreted as two operating modes for the beaked whale biosonar: a short range and a long range mode. The long range mode is used to locate, select and approach prey, with the apparent absence of click rate adjustment suggesting that whales maintain a broad auditory scene right up to the buzz (Madsen et al. 2005). Conversely, buzzes represent a short range, fast update biosonar focused on a single target in which the clicking rate adjusts both to the range to the targeted prey and to the type of prey (Johnson et al. 2008). The buzz phase must be preceded by both the search and the approach phases of the Griffin model, but small if any changes in click outputs and rates make these very unreliable to define acoustically for beaked whales (Madsen et al. 2005).

Despite the usefulness of the Griffin model in understanding the process of prey capture by echolocation in toothed whales, it is thought provoking that the only studies to date on a wild echolocator in which prey echoes have been analysed have in fact shown a somewhat different pattern than anticipated by this model. One possible reason for this divergence is that the Griffin model assumes implicitly that prey become available one-by-one allowing the predator to focus on one target at a time without loss of efficiency. The beaked whale studies suggest a very different scenario; one in which the echolocator has to negotiate cluttered echoic scenes containing multiple potential prey items, each perhaps with a different nutritional value and cost of capture. Moreover, this more complex selection task is embedded in the context of a long, deep breath-hold dive (Tyack et al. 2006) in which the time available for prey capture is strictly limited, putting a premium on effective search, approach and capture strategies. Predator avoidance strategies involving silencing near the surface may also influence the sound production patterns of this species (Aguilar de Soto et al. 2011). There is thus more to echolocation in the wild than predicted by the Griffin model, and the tactics employed by individual echolocators to balance foraging opportunities with physiological and behavioural constraints are of great importance in understanding how this active sensory system is used to sample and resolve dynamic perceptual complexities in the wild.

For almost all predators, prey have a patchy distribution both in time and space, and are often segregated by species, size and ontogenetic state. Thus predators face the tasks of (1) locating and selecting a patch in which to concentrate foraging effort, (2) navigating within these patches and, (3)

selecting and intercepting individual prey in the patch. Here we use echolocating Blainville's beaked whales tagged with multi-sensor Dtags to examine how biosonar sampling rates and sensory volumes are adjusted dynamically to the different tasks of finding and navigating prey patches and homing in on individual prey. Our goal is to expand the Griffin model with a conceptual framework that includes the overall search behaviour of echolocating animals. We collate new data with previous findings for Blainville's beaked whales to develop an augmented model for echolocation in the wild. Specifically, we ask what acoustic duty cycles and sampling rates are required to find a patch, navigate within it and intercept individual prey items. Within this augmented framework, we test if sampling rates are influenced by the encounter rates of new water volumes, prey densities or clutter levels.

Materials and methods

Field site and animals

Field work was performed off the island of El Hierro (18°W, 27°40'N) in the Canary Islands during the summers and autumns of 2003–2010 with a total of 8 months of field effort. At this field site, Blainville's beaked whales (*Mesoplodon densirostris*) can be found close to land on the slope of the insular plateau in water depths between 500 and 2,500 m (Arranz et al. 2011). For tagging, groups of 2–5 whales were approached slowly in a small rigid-hulled, inflatable boat with a four stroke engine. Archival Dtags (Johnson and Tyack 2003) were attached dorsally with four suction cups between the dorsal fin and the blowhole using a handheld, 6 m carbon fibre pole. The tags were programmed to record for 18 h after which they released and were recovered using a built-in 150 MHz radio beacon. Nine individual whales were tagged in 14 tag deployments (Table 1).

Tag specifications and recorded data

The Dtag is an archival, multi-sensor tag that records sound, triaxial acceleration, tri-axial magnetic field, and depth of the tagged animal (Johnson and Tyack 2003). Sounds were recorded with 16 bit resolution and 192 kHz sampling rate, providing an overall flat (± 2 dB) frequency response from 0.5–70 kHz including pre-whitening and anti-alias filters. Animal depth and orientation were sampled at 50 Hz (16 bit) but decimated to 5 Hz in post-processing for ease of analysis. Orientation, expressed in the Euler angles pitch, roll, and compass heading, was estimated from the accelerometer and magnetometer data using the methods of Johnson and Tyack (2003). Since the

Table 1 Dive and acoustic parameters

Tag	Individual ID	Tag dur (h)	FD	Duty cycle %	Depth of SOC/EOC (m)	FM click/dive		Meters descent from SOC to first buzz		FM clicks per buzz	Buzz/diver		Inter Buzz interval (IBI, s)	Clicks/buzz		Buzz duration (s)		Buzz duty cycle during vocal interval (%)	
						Mean (std)	Mean (std)	Mean (std)	Mean (std)		Median (IQR)	Mean (std)		Mean (std)	Mean (std)	Mean (std)	Mean (std)	Mean (std)	Mean (std)
md03_284a	MdH1	12.5	5	15.3	414 (198)/710 (119)	3,820 (727)	90.2 (76.9)	70 (154)	26 (12)	32.0 (59.9)	446 (330)	3.6 (2.2)	5.9 (1.7)						
md03_298a	MdH15	3.0	2	23.4	426 (13)/759 (60)	3,626 (420)	171.1 (109.6)	63 (101)	23 (5)	26 (28.2)	401(274)	3.1 (2.6)	4.3 (0.8)						
md04_287a	MdH22	18.3	4	21.6	473 (23)/818 (88)	3,711 (148)	139.1 (34.4)	67 (123)	32 (5)	26.8 (49.6)	490 (262)	2.9 (1.2)	5.5 (0.8)						
md05_277a	MdH6	7.3	3	13.9	518 (6)/797 (79)	3,374 (233)	38.0 (7.2)	78 (161)	29 (7)	31.1 (68.7)	289 (239)	2.5 (1.4)	5.5 (0.3)						
md05_285a	MdH43	17.4	3	17.2	505 (31)/732 (77)	4,111 (1,044)	69.7 (19.6)	47 (875)	42 (8)	19.05 (31)	402 (265)	2.7 (1.6)	6.9 (3.0)						
md05_294a	MdH22	2.9	1	–	488 (0)/571 (0)	5,842 (0)	72.1(0)	82 (166)	18 (0)	36.8 (89.7)	334 (214)	2.6 (1.6)	4.7 (0)						
md05_294b	MdH1	5.7	3	17.9	489 (31)/601 (46)	3,217 (590)	125.7 (98.1)	65 (134)	22 (5)	30.6 (49.0)	401 (297)	3.3 (2.1)	6.3 (1.6)						
md08_136a	MdH6	2.9	2	18.6	390 (91)/698 (59)	3,453 (619)	61.6 (82.06)	62 (160)	25 (7)	28.2 (64.5)	399 (236)	3.2 (1.6)	5.8 (3.0)						
md08_137a	MdH1	18.4	7	18.4	448 (258)/663 (229)	3,694 (465)	108.7 (108.1)	56 (85)	35 (13)	28.1 (38.5)	309 (191)	2.7 (1.6)	5.6 (2.2)						
md08_142a	MdH74	1.8	1	–	419 (0)/710 (0)	3,047 (0)	187.5 (0)	53 (72)	12 (0)	38.2 (74)	364 (232)	3.2 (1.6)	3.2 (0)						
md08_148a	MdHC1	6.2	2	12.1	461 (36)/789 (3)	3,475 (1,180)	126.4 (12)	61 (126)	34 (3)	24.8 (46.1)	428 (281)	3.0 (1.6)	6.3 (1.1)						
md08_289a	MdH22	19.5	7	16.9	366 (169)/634 (199)	3,584 (1,321)	180.8 (22.8)	65 (213)	24 (13)	43.6 (62.1)	307 (293)	3.1 (1.1)	5.1 (1.3)						
md10_146a	MdHX33	2.9	1	–	503 (0)/840 (0)	3,038 (0)	199.5 (0)	29 (223)	34 (0)	29.3 (27.7)	619 (582)	4.2 (3.6)	10.8 (0)						
md10_163a	MdH86	15.3	8	17.0	353 (129)/732 (120)	2,878 (721)	126.7 (61.1)	97 (222)	18 (6)	38.3 (66.5)	406 (247)	3.0 (1.3)	5.3 (2.0)						
Median				17.2	462/728	3,529	126.1	64	22	30.0	401	3.0	5.6						

FD Number of foraging dives, SOC start of clicking, EOC end of clicking, FM frequency modulated

tag was seldom perfectly aligned with the body axes of the animal, sensor data were first rotated to correct for this misalignment (Johnson and Tyack 2003) using the surfacing orientation as the reference (Zimmer et al. 2005). The tags contained 16 GByte of memory and used a 3x loss-less audio compression algorithm (Johnson et al. 2013) to achieve a continuous recording duration of 18 h.

Analysis

Analysis was performed with custom scripts in Matlab 6.0 and 7.5 (Mathworks, Natick MA, USA). An interactive spectrogram (512 sample Hann window, 1,024 sample FFT, 50 % overlap) and dive profile display of each 20 s of the recording was used to identify the start and stop time of clicking, and of buzzes using the definitions of Johnson et al. (2006). The emission time of each click produced by the whales was determined using a supervised click-detector. Clicks from the tagged whale were separated from those of other nearby clicking whales based on the spectra and on the time of arrival differences at the two hydrophones (Johnson et al. 2009). Buzzes were taken as starting and ending at the first/last click with ICI <0.05 s. The inter-buzz interval (IBI) was defined as the time from the end of one buzz to the start of the next.

Echo streams from ensonified objects before and during buzzes were detected manually in 10 s segments of sound by producing echograms from the high-pass filtered (2 pole, 25 kHz cutoff) sound for the eight whales where tag placement allowed for echo extraction. Echograms are stack-plots that display the sound energy received at the tag as a function of time synchronized to each emitted click (Fig. 3, Johnson et al. 2009). Echograms were displayed with a time ordinate by representing the energy of each click as a coloured bar with a width determined by the instantaneous ICI (Johnson et al. 2009). To quantify the clutter level, an automatic echo counting method was used following Arranz et al. (2011). In this method, the root-mean-square (RMS) received level is computed for ten 1 ms samples of filtered sound (6-pole Butterworth band-pass filter with 25–50 kHz cut-off frequencies) taken from the 5th to the 15th ms (i.e., one way travel of 3.75–11.5 m) after each click produced by the whales. The RMS level in each 1 ms sound sample was compared against the RMS level of a 10 ms sound sample taken just before the same click, with the same filter settings, providing a measure of the noise level on the tag around each click. Post-click samples that were 6 dB or more above the pre-click noise levels were considered to include an echo.

To quantify the rate at which the whale encounters new water volumes, a residence index (RI) of the whale was computed following the approach of Johnson et al. (2008). The RI is calculated by first estimating the 3-dimensional

track of the whale and then, for each point on the track, counting the number of track samples lying within a sphere of radius 20 m centred on the current point. This number is then divided by the track sampling rate (5 Hz) and $2r$ (i.e., 40 m) to produce a RI with units of seconds per metre. The track of the whale was determined by dead-reckoning (Wilson and Wilson 1988; Johnson et al. 2009) based on the orientation recorded by the tag and a speed estimate derived from a 2-state Kalman filter matching the pitch angle and depth (Zimmer et al. 2005). This localization method is far from accurate (Wilson et al. 2007) but is suitable for distinguishing rapid turning movements from straight-line swimming over short intervals (Schmidt et al. 2010) as required to estimate the RI. The turning rate following buzzes was computed by first estimating the orientation of the time varying longitudinal body vector of the whale, X_t , in the navigation frame (i.e., the axes north, east, down). This vector was derived from the pitch and heading of the whale (Miller et al. 2004) using:

$$X_t = [\cos(p_t) \cdot \cos(h_t), \cos(p_t) \cdot \sin(h_t), \sin(p_t)]$$

where the pitch (p_t) and heading (h_t) were estimated using 1 s averages of the triaxial accelerometer and magnetometer measurements to reduce noise from specific acceleration. The turning rate was then calculated from the angular change in X_t over a 5 s interval starting 1 s after the end of each buzz, i.e., turning rate = $\arccos(X_{t+5} X_t^T) / 5$.

To visualize the biosonar beamwidth during regular clicking, we computed the angles of arrival, θ , of emitted clicks and the corresponding echoes identified in echograms. The angles were derived from time of arrival differences at the stereo hydrophones using $\theta = \arcsin(c/d)$, where c is the speed of sound in seawater, d is the hydrophone separation (25 mm), and τ is the time delay between the two hydrophones, estimated by cross-correlation (Johnson et al. 2006). Echoes were excluded from this analysis if the correlation coefficient between the two hydrophones was <0.8 or if the echo range was <3 m or >20 m. As the hydrophones in the tag are separated laterally and the tags were generally placed horizontally on the dorsal surface, θ is approximately equal to the arrival angle of the sound in the frontal body plane of the animal, i.e., the angle to the left or right of the mid-line of the animal. Beaked whales appear to turn their heads from side-to-side while echolocating, presumably to scan larger water volumes (Shaffer et al. 2013). To estimate the arrival angle of each echo with respect to the launch angle of the click, the echo angles were regressed against the outgoing click angle as measured by the tag. The regression line was then removed from the echo angles to give the echo angle with respect to the beam centre. This method results in a histogram of detected echoes as a function of off-beam angle, i.e., an angular detection function. This function

cannot be converted directly into a beampattern because neither the target strength of the echoing objects nor the whale's source level is known. Instead, we computed a sequence of candidate beampatterns based on a circular piston aperture of varying dimension and used these to predict the angular detection function. The beampattern corresponding to the best-fitting detection function was then taken as representing the whale's transmitting beampattern. The candidate beampatterns were computed by integrating the circular piston radiation function over the frequency range of a Blainville's beaked whale click (Zimmer et al. 2005). The beampatterns were then combined with the measured echo levels at small off-beam angles (-2 to 2°) to simulate the attenuation at larger angles. Finally, a detection function was formed for each candidate beampattern by counting the number of echoes in each degree-wide bin that exceeded a predetermined detection threshold.

Results

Overall foraging and acoustic behaviour

Blainville's beaked whales perform an average of 10 (4) foraging dives per day (Fig. 1a) of duration 48 (6) min [all results are reported as mean (std) over the ten tagged animals, unless stated otherwise]. Echolocation clicks are produced for 24.1 (5.2) min during each dive starting at 417 (118) m on the descent and ending at 728 (152) m depth at the start of the ascent (Table 1; Fig. 1b). Thus the echolocation duty cycle of a Blainville's beaked whale is only 17 (3) % (Table 1) with almost all clicks produced deeper than 200 m, i.e., in the mesopelagic zone (Arranz et al. 2011; Aguilar de Soto et al. 2011). The first prey capture attempt, as signified by the production of a buzz (Johnson et al. 2004), is made after 134 (73) s of clicking (Arranz et al. 2011), and occurs 126 (80) m deeper than the depth of the first emitted click (Fig. 1), corresponding to the emission of 304 (232) frequency modulated (FM) clicks to locate and approach this first prey item. The whales continue to produce FM clicks throughout the vocal phase of the dive interspersed with either buzzes or with occasional short pauses in which air-recycling sounds from the nasal system can be heard. On average a total of 3,529 (779) FM clicks are produced in each dive to search for and approach an average of 27 (11) prey items with a median IBI of 30 s (Table 1). The IBI is roughly log-normal with log mean and std of 3.4 and 1.05 (log-seconds), respectively. The whales use a median of 62 FM clicks to search for and approach each prey item with mean ICIs around 0.4 s (Fig. 1c). At swimming speeds of 1–2 m/s (Johnson et al. 2008) these 4.5 m long whales thus produce

a click for every 0.4–0.7 m or 0.09–0.15 body lengths of forward motion outside buzzes.

Width of acoustic gaze

The beam pattern of toothed whale echolocation clicks is normally quantified with a hydrophone array in the far-field of the whale that records the level of clicks as a function of the whale's aspect (Au 1993). The unique capability here to record returning echoes from backscattering objects ahead of Blainville's beaked whales offers an alternative and more direct way to visualize the field of view. Figure 2 shows the angle of arrival of echoes from 5,600 clicks from one whale with the launch angle of the clicks removed. While the whale may well detect weak echoes that are not detected by the tag, Fig. 2a provides an indication of the effective search volume of the whale in terms of angle and range. Some 91 % of echoes recorded by the tag are within $\pm 10^\circ$ of the acoustic beam centre, suggesting a functional beamwidth of some 20° . The detection vs. angle histogram shown in Fig. 2c is closely approximated by the beam pattern of a beaked whale FM click radiated from a 0.25 m circular piston, implying a half-power beamwidth of about 9° .

Acoustic gaze adjustments

While the solid angle encompassed by a biosonar is determined by the spectra of the emitted sounds and the size and morphology of the sound producing nasal structures, the sensing range is in part determined by the production rate and intensity of clicks, both of which can be controlled dynamically to manipulate the acoustic gaze or field of view. The most dramatic change in acoustic gaze occurs when beaked whales switch from FM clicks to buzzes about one whale body length from a prey item (Fig. 3, Johnson et al. 2006). The switch is abrupt and involves a step change in the type, level and rate of clicks. Buzzes last an average of 3.0 (1.8) s (Table 1) and contain 375 (240) buzz clicks with ICIs as low as 3 ms and output levels about 20 dB lower than for FM clicks (Fig. 3). This means that whales with a forward speed of 1–2 m/s produce a click for every 3–6 mm of forward motion during buzzing compared to about 0.5 m for FM clicks. The rapid reduction in ICIs also means that the whales switch from a long lag time (200–400 ms) between receiving an echo and emitting the following click during the approach phase to a very short lag time during the buzz with only a few milliseconds between the ICI and the TWTT (Fig. 3b, c). Thus, when switching from FM to buzz clicks, the ICIs and energy outputs both drop by up to two orders of magnitude (Figs. 1b, 3a, c), drastically reducing the sensory volume and hence the complexity of the perceived auditory scene

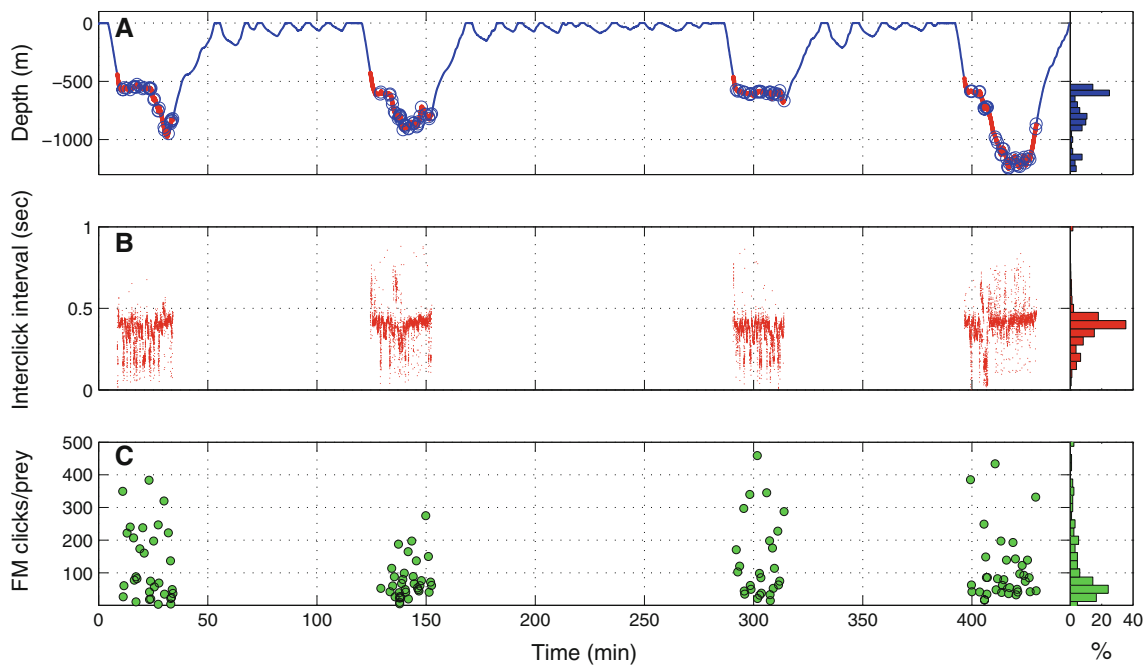


Fig. 1 **a** Dive profile of Blainville's beaked whale, showing four deep foraging dives interspersed with long periods of recovery dives with no echolocation or foraging. *Red lines* indicate production of FM clicks and *blue circles* show occurrence of buzzes. The *blue histogram* on the *right* shows the depth distribution of buzzes. **b** Inter-click intervals (ICIs) of FM clicks during foraging dives. The

histogram on the *right* shows the ICI distribution centred around a mean ICI of 0.4 s. **c** Number of FM clicks preceding each prey capture attempt in the form of a buzz. The *histogram* on the *right* shows distribution of FM clicks preceding each buzz. More than 70 % of the displayed prey capture attempts required <100 FM clicks during the search and approach phases

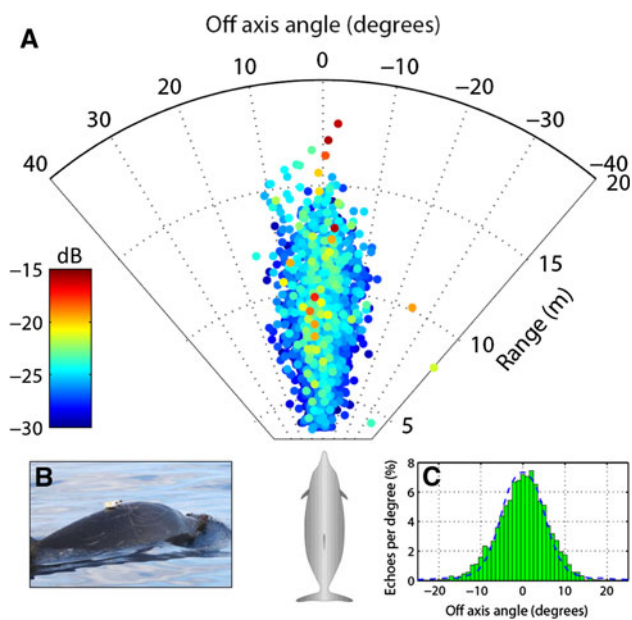


Fig. 2 **a** 2D projection of targets ensounded by a tagged Blainville's beaked whale **b** as a function of range in metres and angles in degrees. *Colour* indicates the received level of echoes corrected for the two way transmission loss. Note how only targets within a narrow cone ahead of the tagged animal give rise to detectable echoes. This transmitting directionality provides, along with a matching receiving directionality, a narrow acoustic field of view ahead of the whale **c**

(Johnson et al. 2006). Thus, a buzz leads to a dramatic change in acoustic gaze by providing much faster updates on prey location using much shorter ICIs (Fig. 3c) while the complexity of the actively generated auditory scene is also reduced dramatically to focus on the selected prey target via reductions in SL that give rise to fewer echoes from distant objects (Fig. 3b). A total of some 8,000 buzz clicks are produced per dive, meaning that more than 70 % of all clicks are produced in buzzes during intense bouts of fast sampling only lasting some 6 % of the total vocal time in foraging dives (Table 1).

Although less dramatic than the difference between FM and buzz clicks, there are also substantial adjustments in the rate and output levels of FM clicks. Click levels appear to vary by about 10 dB, at least in terms of the levels arriving at the tag, while the ICI generally varies from 0.2 to 0.4 s (Figs. 1b, 4). However, these changes are typically gradual: the ICI variation from click-to-click has an interquartile range (IQR) of 14 ms or about a 4 % change compared to the previous ICI. In other animals echolocating in the wild, ICI adjustments have been related to several factors. Sperm whales and pilot whales have been reported to adjust the ICI during the descent (i.e., between the start of clicking and the first buzz) in deep dives so as to track the sea-floor or a prey layer (Thode et al. 2002;

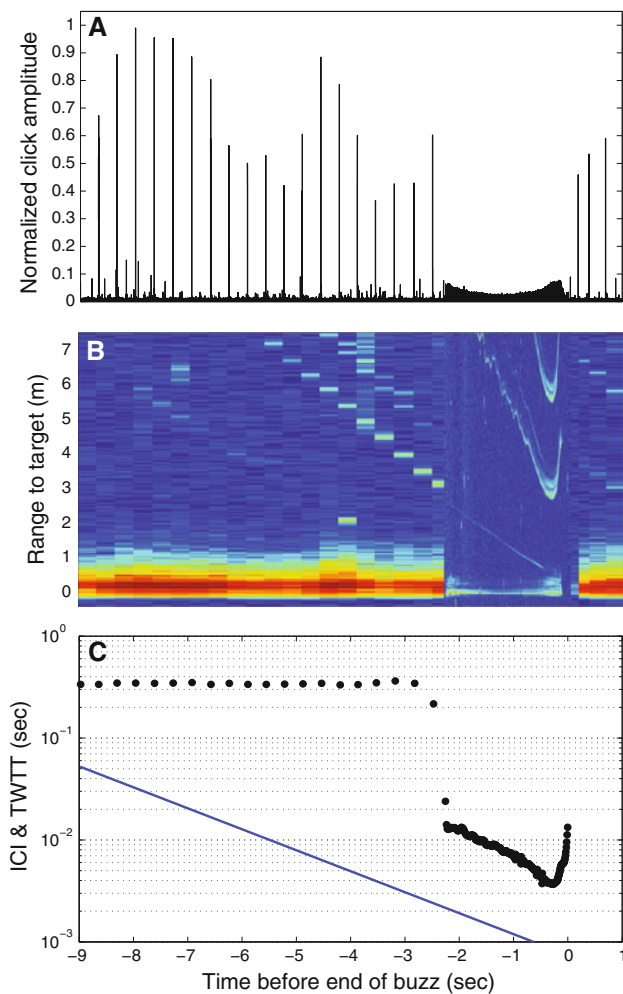


Fig. 3 **a** The envelope of the FM and buzz clicks during the approach and capture phase as a function of time from the end of the buzz. Note the dramatic change in acoustic gaze via a reduction in amplitude (two orders of magnitude) and increase in sampling rate (two orders of magnitude) that effectively reduce the auditory scene to a single target during the buzz. **b** Echogram of the approach to and capture of a prey using the clicks displayed in **a**. All clicks are time aligned at range 0 m, and energy is then colour coded as a function of the TWTT and hence range from each click. Note how several targets can be seen in the approach phase, but that the transition to a buzz leaves only a single target for fine scale tracking. The spurious v-shaped structures at range 3 and 5.5 m in the buzz are generated by the next clicks. **c** Inter click intervals (ICIs) of FM and buzz clicks showing the lack of TWTT adjustment in the approach phase, but close tracking in the buzz phase. The *blue line* is the TWTT derived from the echo delays in **b**

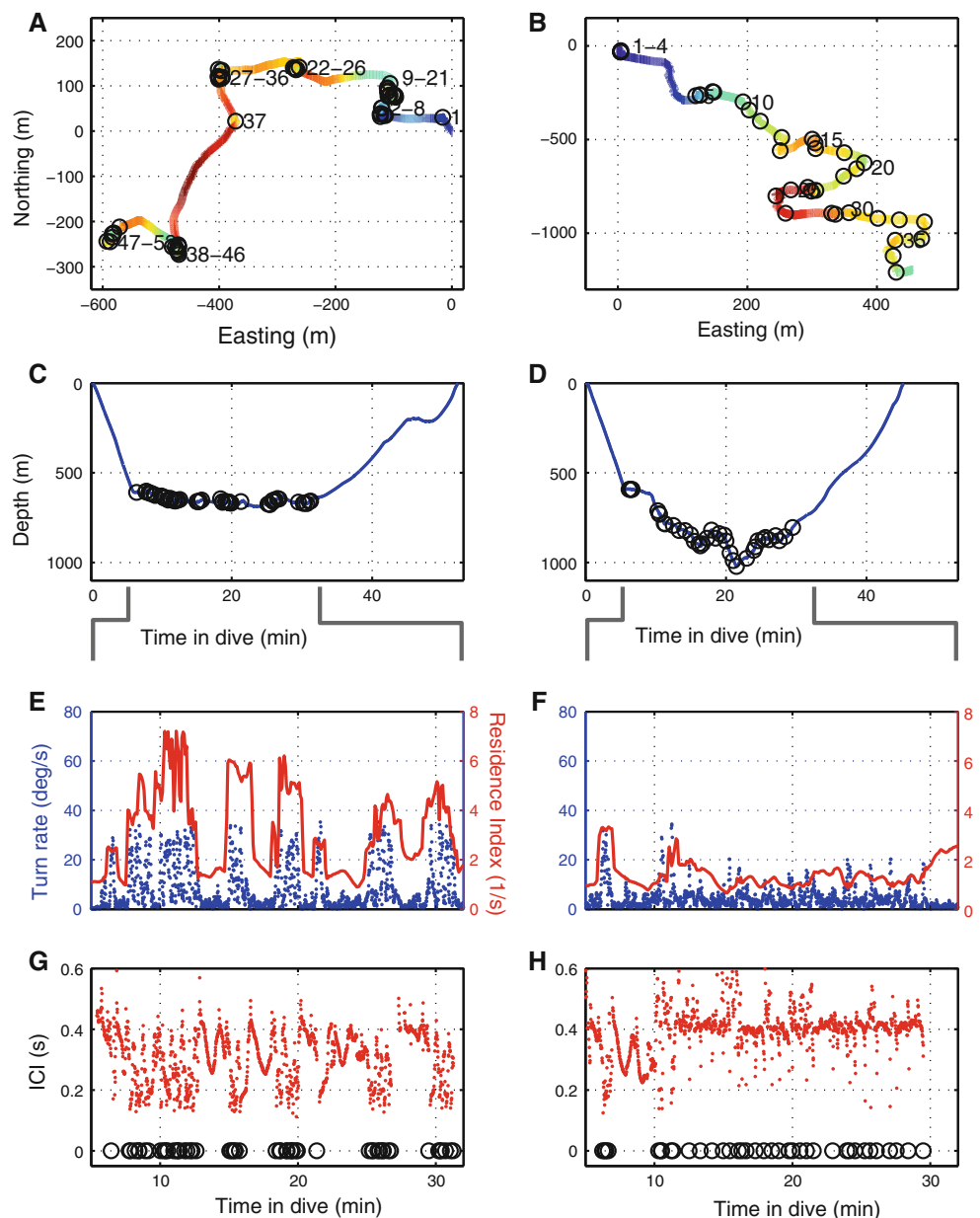
Madsen et al. 2002b; Aguilar de Soto et al. 2008). Although a few dives in this data set show a similar downward ICI adjustment (Fig. 1), there is no consistent pattern for Blainville’s beaked whales as the mean change in ICI during descent is not different from 0 (*t* test, *p* = 0.2). Adjustment of ICI to track target proximity has been observed in a number of bats and captive toothed whales, and this has been used to separate search and

approach phases in the Griffin model (Griffin 1958). Assuming that Blainville’s beaked whales detect prey several seconds before they begin a capture attempt, Madsen et al. (2005) tested for ICI and click level variations prior to buzzes in two animals and found no consistent adjustment. That result is confirmed here with a larger data set of 14 tag deployments on nine individuals (Fig. 3c).

Another factor that might be expected to influence ICI is the degree of clutter of the acoustic scene (Madsen et al. 2005). Blainville’s beaked whales dive to exploit dense and stable meso and benthopelagic prey layers (Arranz et al. 2011), where they appear to target less than 1 % of the organisms they ensonify. The whales therefore face both a detection and a discrimination problem in which preferred prey must be identified in a dynamic and often highly cluttered acoustic scene. Clutter is partly mitigated by having a highly directional beam (Fig. 2), but in a dense patch of organisms, there may be many echoic targets along the acoustic axis causing range ambiguity problems if echoes from distant targets arrive after the emission of the next click. In this milieu, echolocating whales must click slow enough to encompass all strong echoic targets in the ensonified volume, while still clicking fast enough to search for and track prey effectively (Madsen and Wahlberg 2007). This suggests that ICIs should relate to clutter levels, increasing at high clutter levels to avoid range ambiguity. To test this hypothesis, we compared ICI to a proxy for clutter; an echo index computed from echo counts in a 5–15 ms time window after click emission. A non-parametric Spearman test for individual whales showed no correlation between ICI and echo index (median Spearman’s rank correlation coefficient of 0.014) showing that clicking rates are not adjusted to the density of the echoic scene.

If the ICI is not adjusted to track prey layers, individual prey or clutter, what then causes the substantial observed variations in ICI (Fig. 1c)? A clue may be contained in the temporal sequence of buzzes and the movement patterns of whales between buzzes. Buzzes often occur in bouts with several buzzes within 30 s of each other followed by a much longer interval before the next buzz (Fig. 4a, b). Buzz bouts typically coincide with high residence indices (RI) and variable but high turning rates (Fig. 4c) of up to 50°/s, suggesting that the whales remain in a small water volume to exploit a prey patch. To test this interpretation, we compared the RI at the midpoint between each buzz pair to the corresponding IBI. The midpoint RI shows two distinct distributions with the changeover occurring at an IBI of about 30 s (*p* < 0.001, Kolmogorov–Smirnov test on $RI_{IBI < 30}$ vs $RI_{IBI > 30}$, *n* = 726 and 580 IBIs, respectively): in long IBIs, the RI is rarely greater than 2 (mean $RI_{IBI > 30}$ = 1.6 s) implying largely straight-line swimming,

Fig. 4 **a, e** Horizontal projections of a whale's movements during two consecutive dives colour coded by depth. Occurrence of buzzes is indicated by *dark circles*. **a** and **b** display a dive with a patchy distribution of prey while **e** and **f** are an example of a dive with more evenly distributed and scattered prey. **c** and **g** show the corresponding residence index (in *red*) and the turning rate (*blue dots*) during the vocal interval as a function of time. **d** and **h** display the inter-click intervals (ICI) as a function of time, with occurrence of buzzes shown as *black circles*. Note how patchy prey distributions give rise to high turning rates, high residence indices and lower ICI



while in short IBIs, it is highly variable with mean $RI_{IBI < 30} = 2.4$. This implies that whales encounter some prey types in patches (Johnson et al. 2008) and manoeuvre to remain within patches for a while attempting to capture several prey. Comparing Fig. 4c and d it appears that the ICI changes with the residence index (RI): during intervals with low RI (e.g., < 2) the ICI is long and slowly varying, while in intervals with high RI, the ICI is shorter and variable.

Interpreting high RIs as indicative of a prey patch, the short and variable ICI when whales are in patches could be a tracking adjustment to the general proximity of the next prey or an increase in sampling rate to accommodate the rapid turning needed to stay within the patch after a buzz.

These explanations are not mutually exclusive and cannot be tested separately with the data available but it is possible to test if ICI correlates with turning rate which would indicate that these two parameters are either causally related or co-vary as whales enter and leave patches. For this test, we regressed clicking rate ($1/ICI$) against turning rate using average values in 5 s time bins to reduce outliers. Clicking rate was used instead of ICI to improve homoscedasticity. To decouple the test from possible movement dynamics associated with prey approach, we took 5 s samples starting 1 s after each buzz, eliminating buzzes with $IBI < 10$ s. Whether or not whales are in a patch, there should be an interval after each buzz in which they are searching for a new prey item and this is the

interval that we are attempting to sample. The relationship between turning rate and clicking rate after buzzes is highly significant (slope = 0.77 Hz per $10^\circ/\text{s}$, $r^2 = 0.51$, $p \ll 0.001$, $n = 1,014$ 5 s samples from all individuals) although, given the r^2 value of 0.51, other factors clearly contribute to the ICI variation. Nonetheless, this correlation accounts for the two distinct ICI modes apparent in Fig. 4c: for turning rates below $15^\circ/\text{s}$, the mean ICI is 0.36 s, averaging over all animals, while for turning rates $>15^\circ/\text{s}$, the mean ICI is 0.24 s. Thus, whales click faster when they are turning rapidly and this occurs when they are exploring a prey patch. Prey are not always found in patches as exemplified by the right-hand panel of Fig. 4. In this dive, performed by the same whale as in the left-hand panel, few dense prey patches are found and the median IBI is 30 s compared to 10 s in the left-hand panel. During these longer inter-buzz-intervals, the ICI is uniformly high around 0.3–0.4 s as it is also between patches in Fig. 4c.

Detection, discrimination and prey-specific motor patterns

The lack of apparent ICI adjustment when whales approach individual prey makes it challenging to determine at what ranges the whales actually detect and classify prey. Although the hand-off distance at the start of buzzes, about 3.5 m, provides a definitive lower bound for this range, it is likely that whales have detected and selected the prey well before the buzz as indicated by the recorded echo streams (Fig. 3b). One way to explore this is to look for stereotyped movements preceding buzzes that may indicate when the whale has decided to attempt a capture and is preparing for this. Movement patterns are affected both by prey behaviour and by the individual tactics of the predator when capturing different prey types making them complicated to analyse. But several tagged Blainville's beaked whales display highly stereotyped motor patterns prior to some prey capture attempts, providing an opportunity to estimate prey detection and classification distances for these individuals and prey. Although all tagged whales approach prey from a variety of pointing angles, they seldom roll (i.e., rotate around the longitudinal body axis) substantially while foraging. However, when approaching certain prey, some individuals perform a roll of more than 60° beginning several seconds before the buzz and culminating at about the start of the buzz. This behaviour is readily distinguished from non-rolling approaches by measuring the roll angle at the start of the buzz. Figure 5 shows the average roll angle during 116 rolling approaches and 110 non-rolling approaches performed by one whale in two tag deployments excluding buzzes that are closer than 12 s apart to avoid including movements from a previous capture. In the high roll group, the rolling starts at least 10 s

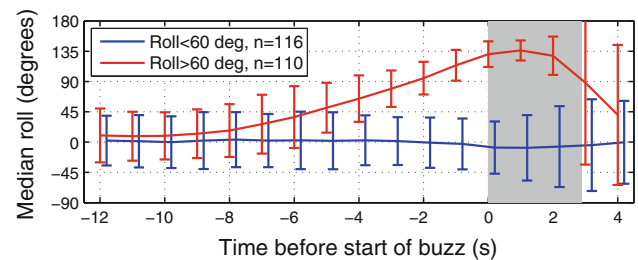


Fig. 5 Example of roll behaviour of a tagged whale as a function of time around the start of buzzing. Two distinct behaviours of high rolling and low rolling can be identified. The high rolls start on average 11 s before the buzz indicating that the prey has not only been detected, but also classified at some 15 m range, and that prey-specific motor patterns are initiated to facilitate capture

before the start of the buzz (the first 1 s time bin with a significant difference in mean roll between the two groups is at 11 s before the buzz, two-sided T test, $p < 0.02$). This implies that the target has not only been detected at that range, but also classified as a prey type that requires a particular motor pattern for capture. This stereotyped rolling behaviour appears to be an individual tactic of some whales when exploiting certain prey at 550–650 m depth, but it offers an indication of the ranges over which whales can not only select, but also classify prey.

Discussion

Studies of the functional implementation of sensory systems in marine mammals often suffer from either a lack of ecological validity in the case of lab studies, or a complete lack of control and limited power to see in field studies. Echolocating toothed whales offer a way, at least in part, to bridge that gap, because they must emit clicks to use their sonars that can be recorded. This enables field studies in which the precise time of each sensory sample can be determined and analysed in the context of their behaviour. For Blainville's beaked whales, the fortuitous cranial anatomy of this species and the very quiet waters off El Hierro, in the Canary Islands, also allow for recording the returning echoes along with the movements of the tagged whale using a multisensor, archival tag. The resulting capability to record every emitted echolocation click and resulting echoes over time periods of hours offers a more complete view of how animals use echolocation to make a living compared to studies with recording arrays in the wild in which an individual whale or bat can only be studied for a few seconds or minutes in a particular context. Here we use tag data from Blainville's beaked whales foraging at depth in their natural habitat to study how animals echolocating in the wild adjust their sensory volumes and acoustic gaze to find and select prey in a complex dynamic

multi-target environment. While the Blainville's beaked whale is only one among more than 80 species of echolocating toothed whales, adapted to a wide range of foraging niches, many of the basic challenges in echolocation must be faced by animals of any body size or habitat. Thus, we argue that observations of this species provide insight into some of the basic principles that guide biosonar operation in all toothed whales and bats.

Overall foraging and acoustic behaviour

Most sensory systems remain to some extent operational both when animals are awake and asleep so that relevant information can be acquired and reacted upon in a fashion that improves fitness. Toothed whales in particular have been shown to remain vigilant in terms of receiving and responding to sensory cues with no signs of fatigue over long (up to 72 h) time periods (Ridgway 2011). It is therefore surprising that Blainville's beaked whales only use one of their primary modalities, echolocation, in short 24 min bouts amounting to less than 20 % of their life (Table 1, Aguilar de Soto et al. 2011; Arranz et al. 2011). Clearly other sensory modalities such as vision and hearing must be used to form and update the sensory Umwelt outside the short periods of intense acoustic sampling during deep dives to between 400 and 1,300 m (Tyack et al. 2006) (Fig. 1). The lack of continuous acoustic sampling of these whales suggests that it is costly. The direct costs of sound production are likely small (Elsberry 2003; Jensen et al. 2012), but the indirect costs from eavesdropping from predators such as killer whales seem to be high enough to shape the acoustic behaviour of beaked whales significantly so that they only produce echolocation clicks and communication sounds at great depths (Aguilar de Soto et al. 2011).

Blainville's beaked whales target prey in and below the deep scattering layer at meso and benthopelagic depths (Arranz et al. 2011) performing 48 min long foraging dives that are well in excess of the estimated aerobic dive limit for these animals (Tyack et al. 2006). Foraging dives are interspersed with long periods of silent shallow dives (Fig. 1) that may serve to deal with lactate build up during long foraging dives (Tyack et al. 2006). As a result, these whales perform only some ten foraging dives per 24 h with about 50 % of each dive devoted solely to transport between the surface and foraging layers. Thus, Blainville's beaked whales acquire all their food during 24 min bouts of echolocation that total about 4 h per day (Arranz et al. 2012).

Like most beaked whales, Blainville's beaked whales are functionally edentulous with a limited gape and so can only target small (e.g., <30 cm body length) prey (Santos et al. 2007). This necessitates the capture of many prey

items in the limited time spent at depth, requiring a stable, readily located food resource, and foraging decisions that ensure high net energy returns. The stability of this meso and benthopelagic food source is evidenced by the more than 25 prey capture attempts per foraging dive (Arranz et al. 2011), with a median of 30 s between attempts (Table 1; Fig. 1). Also, the depths of prey layers seem to be quite predictable, offsetting the transport costs of deep diving. Whales start clicking in a narrow depth interval from 350 to 500 m in the descent and typically find the first prey within 3 min of active acoustic search, during which they have descended some further 100–150 m deeper. Although apparently abundant, prey have a patchy distribution: the time between prey capture attempts (the IBI) is close to log-normal, with many prey taken just a few seconds apart when the whale is within a patch, but then long dry intervals in which the whale searches for the next patch. Thus, the location of discrete prey patches and the rapid exploitation of prey within them seem to be critical components of successful foraging for Blainville's beaked whales.

Beaked whales need to locate and identify prey patches using echolocation in a three-dimensional environment which can also contain large aggregations of non-targeted organisms in the deep scattering layer that form a complex and often cluttered acoustic scene (Madsen et al. 2005; Arranz et al. 2011). In terms of biosonar sampling, finding the first prey requires the emission of some 300 FM clicks, and the whales go on to produce a total of about 3,500 FM clicks and some 8,000 buzz clicks per dive. The processes of locating a prey patch, and then selecting and approaching individual prey within it happen at consistently long ICIs of between 0.2 and 0.4 s. Given the short median IBIs, this means that 50 % of all prey items are located and approached for capture using less than 64 FM clicks (Table 1; Fig. 1) while swimming less than 50 m on average. In comparison, about 400 buzz clicks are produced during the final approach and capture attempt of each prey with whales swimming some 3–4 m in this phase. The overall sampling investment of Blainville's beaked whales is then about 120,000 clicks per day which are used to locate and attempt to capture around 300 prey items.

The 64 clicks produced by Blainville's beaked whales on average to detect, select and approach individual prey is comparable to the 30–100 clicks typically used by trained, stationed delphinids and porpoises to detect a target in a noise or clutter limited setting in captivity (Au and Turl 1984; Turl 1991; Kastelein et al. 2008). But, whereas the trained animals need only decide if the target is present or absent with little classification needed, echolocation in the wild also involves classification and selection of a suitable prey also amidst noise and clutter, followed by echo-guided

changes to motor outputs as the prey is approached. This apparent increase in sampling efficiency (i.e., tasks solved per click emitted) for echolocation in the wild may relate to species differences, but likely also results from a fundamental difference in the pay-off matrices between the two situations. For a deep-diving whale pursuing moving prey under behavioural and physiological constraints, the time to acquire prey is severely limited, placing an evolutionary premium on rapid evaluation of acoustic scenes and accurate echo-based decision-making. The low number of clicks required for detection, classification and target tracking in echolocating beaked whales suggests that they can extract echo information from a sensory volume formed by emission of very few or single clicks. In addition, as we shall see below, this sensory volume is spatially very limited to a narrow field or view ahead of the whale.

Width and use of the field of view

The functional beam width of a Blainville's beaked whale biosonar is depicted in a qualitative fashion in Fig. 2a where the 2D arrival angle of echoes detected on the tag are displayed as a function of range. Although the whale will likely detect echoes that the tag cannot, this figure suggests a functional beamwidth of about $\pm 10^\circ$ and demonstrates that the echolocation beam forms a narrow acoustic gaze ahead of the animal. A circular piston approximation is used widely to quantify the beampattern of toothed whale echolocation clicks (Au 1993) and fitting this function to the echo angles here indicates a half-power beamwidth of 9° . This is remarkably close to the only other beamwidth estimate for this species: Shaffer et al. (2013) used far-field recordings of tagged Blainville's beaked whales in the Bahamas to estimate a beamwidth of around 13° , although this may be an overestimate as it does not include the effect of head-turning. This is considerably narrower than the beamwidth inferred from Fig. 2 suggesting that the functional beam width of some 20° in which more than 90 % of the echoes are generated is approximately twice the size of the half power beam width of around 10° .

Such high directionality is advantageous in terms of reducing clutter and producing a higher source level within the beam, but results in a limited sensory volume. Shaffer et al. (2013) have shown that beaked whales scan their heads continuously while foraging with a maximum angular extent of about $\pm 10^\circ$ and a rate of some $4^\circ/\text{s}$. Thus beaked whales extend the limited beamwidth of their biosonar by exploring larger volumes of water sequentially, moving their beam as they click to ensonify new swaths as also found for both dolphins (Bullock et al. 1968) and porpoises (Wisniewska et al. 2012). This implies a spatial memory in which echoes from each click are combined

with proprioceptive information about the acoustic pointing direction to update an active auditory scene that spans several beamwidths.

The narrow acoustic gaze may also help interpret the prey range at which whales switch from FM clicks to a buzz. Johnson et al. (2006) reported a mean prey range of some 3.5 m at the start of buzzes for this species, the only toothed whale for which it has been measured in the wild. This range is likely determined, at least in part, by the range at which the solid ensonification angle is too small to provide effective tracking of a small moving prey target with 0.2–0.4 s sampling intervals. At a range of 3.5 m, a beamwidth of 20° ensonifies a circle with radius 0.6 m. With an ICI of 0.4 s, prey in the centre of the beam at this range would have to move perpendicularly to the acoustic axis at 1.5 m/s (i.e., 0.6 m/0.4 s) to escape the beam between two clicks. That corresponds to a speed of some 5–8 body lengths/s for the prey sizes that beaked whales are assumed to target (Santos et al. 2007). If the whale has a narrower beam or switches to a buzz later, the required escape speed reduces. For example, if the whale has a 10° beam and switches to a buzz at a range of 2 m, prey would only need to move at some 0.6 m/s to escape the beam before the buzz. Little is known about the sensory and locomotory capabilities of deep-water fish and squid, making it difficult to judge if this speed and escape tactic are feasible. But, it is clear that the combination of slow clicking and a narrow beam are incompatible with tracking close mobile prey suggesting that the stereotyped switching distance from FM to buzz clicks are adapted to the field of view of the predator and the sensory and locomotory means of the targeted prey.

Acoustic gaze adjustments

The acoustic gaze of an echolocating animal is not only defined by the width of the emitted sound beam and its pointing angle, but also by the output levels and the rate at which clicks are emitted. Toothed whales and bats appear to be able to adjust these parameters gradually, from pulse to pulse, to implement dynamic gaze control (Griffin et al. 1960; Moss and Surlykke 2001; Linnenschmidt et al. 2012; Wisniewska et al. 2012). A dramatic example of gaze adjustment is the sudden change from FM clicking to buzzing in Blainville's beaked whales, involving a simultaneous two order of magnitude drop in SL and ICI in a process that trades detection range for temporal resolution (Fig. 3). The high click rates in buzzes provide fast updates on the location of a targeted prey item while the low SLs reduce the complexity of the auditory scene (Fig. 3). The reduction in SL also reduces range ambiguity problems despite ICIs as short as 3 ms, corresponding to maximum unambiguous target ranges of some 2 m. In keeping with

the Griffin model for bats, Madsen et al. (2005) suggested that toothed whale buzzes represent an interval in which the animal is focused on capturing a single prey target. Exemplifying the synergy possible between field observations and laboratory experiments, recent results for porpoises performing a target selection and approach task have confirmed that these animals focus on a single target in buzzes, and consistently abandon a buzz and resume regular clicking when they change their target during a buzz (Wisniewska et al. 2012).

Outside of buzzes, the current view on gaze adjustments in echolocating toothed whales is heavily inspired by the Griffin model (Griffin 1958), which assumes that animals encounter one target at a time and track it by adjusting their acoustic gaze as they approach it. Research on smaller stationed toothed whales in target detection experiments supports that notion with both SL and ICI decreasing with decreasing target range (Au 1993; Au and Benoit-Bird 2003; Linnenschmidt et al. 2012). Similar gaze adjustments are also seen during active swimming towards a target in porpoises (Wisniewska et al. 2012) and delphinids (Jensen et al. 2009; Au et al. 2004). In general, gaze adjustment in the approach phase for toothed whales seems to involve automatic gain control with a rough halving of the SL for every halving of range (Au and Benoit-Bird 2003), and an ICI given by the TWTT plus a fixed short lag time of some 20 ms (Au 1993). However, taking a closer look at studies with known ranges between the echolocator and the target, there are often large ICI variations that do not fit a fixed lag time plus TWTT model (Turl et al. 1987; Au 1993; Jensen et al. 2009). Kadane and Penner (1983) proposed that such ICI variations could be involuntary jitter evolved to reduce range ambiguity problems, but recent studies have shown that toothed whales have acute control over their sound production system and can adjust ICI rapidly to different target ranges (Linnenschmidt et al. 2012; Wisniewska et al. 2012) and target types (Johnson et al. 2008). So toothed whales can adjust their gaze to the changing spatial relationship with a target, but do not always choose to do so. In this context, Blainville's beaked whales are particularly interesting as they rarely seem to adjust ICI and SL when approaching targets prior to buzzes. This has been interpreted to serve the function of keeping a wide auditory scene while foraging (Madsen et al. 2005). Nevertheless, there are distinct patterns of ICI changes in Blainville's beaked whales that seem to represent purposeful sampling adjustments (Figs. 1, 4). In the following we examine the relationship between these adjustments and the complex cluttered and patchy environments in which beaked whales forage.

Although the ICI of beaked whales is broadly comparable to that of other deep-diving toothed whales (Aguilar de Soto et al. 2008; Madsen et al. 2002b), there are several

reasons to suspect that Blainville's beaked whales do not rely on long range prey echolocation in the way that sperm whales and probably pilot whales seem to do. Both of these latter species begin echolocating relatively soon after leaving the surface in a deep dive and appear to adjust the ICI as they descend to track the sea-floor or a deep foraging layer (Thode et al. 2002; Aguilar de Soto et al. 2008). In comparison, Blainville's beaked whales start clicking late in the descent, some 125 m above the depth layer where they will begin foraging, and typically make little ICI adjustment as they descend. The source level of beaked whales' clicks is also more than 20 dB lower (Johnson et al. 2004; Shaffer et al. 2013) than that of sperm whales (Møhl et al. 2000) making them much less suitable for long-range echolocation. Once beaked whales reach a foraging layer, the median time between prey capture attempts of 30 s implies that prey detection usually occurs over ranges of less than some 50 m. This implies that prey targeted at these depths are fairly abundant (Fig. 1) and that their detection may be more limited by clutter from other prey and non-prey targets (Madsen et al. 2005) than by noise (and hence range).

Although beaked whales often forage below the densest parts of the deep scattering layer (Arranz et al. 2011), echoic targets are nonetheless abundant in echograms such as Fig. 3, showing that beaked whales cope routinely with multi-target auditory scenes. Range ambiguity will occur in this environment if the ICI is shorter than the TWTT to strong echoic targets, leading us to hypothesize that whales will increase ICI (or reduce SL) when there is more clutter. However, there is no correlation between ICI and clutter levels for the animals tested here, and beaked whales in general maintain long and relatively stable ICIs of around 0.36 s irrespective of the clutter density. At this ICI, range ambiguity will occur for targets at ranges of more than some 250 m (i.e., $0.36 \text{ s} \times 1,500 \text{ m/s}$ divided by 2) from the whale. But the echo level from individual targets attenuates as $40 \log_{10}(\text{range})$ meaning that an organism at 250 m would need to have an extremely high target strength for its aliased echo to interfere substantially with echoes from objects closer to the whale. Thus, there seems to be little need for whales to increase ICIs over their already large values when negotiating cluttered scenes, and this slow clicking can evidently provide enough information to search for and approach prey.

Another situation in which ICI adjustment can be expected is during approaches to prey. In the bat and toothed whale species in which it has been studied, animals generally decrease their ICI to match the decreasing TWTT as they approach a target (Griffin et al. 1960; Verfuss et al. 2009; Jensen et al. 2009), presumably to maximize the temporal resolution of echo information. Using the larger data set available here, we confirm the findings of Madsen

et al. (2005) that Blainville's beaked whales produce ICIs during approaches to prey that are many times longer than the TWTT (Fig. 3) and that they make no consistent adjustments in the ICI (Fig. 3). In fact, the very long ICIs prior to buzzes may make such adjustments meaningless. A mean prey range of 3.5 m at the hand-off to the buzz (Johnson et al. 2006) implies a TWTT of some 5 ms. But, averaging over all tagged whales, the mean ICI in the 2 s preceding buzzes is 0.35 s or some 70 times the TWTT at this point in the approach. An ICI adjustment of 3–5 ms would be needed to track the reducing TWTT over these 2 s, but this adjustment is only about 1 % of the ICI and would as so serve little purpose. Thus there is no evidence that these whales attempt to maximise sampling rate in the approach phase as predicted by the Griffin model and, compared to the ICIs, the required tracking adjustments are so small as to have no practical benefit. This lack of adjustment does not imply that whales are unaware of the proximity of prey prior to buzzes: the stable hand-off distance between FM clicking and buzzes (Johnson et al. 2006) shows that whales must be acutely aware of their spatial relationship to the prey but choose to continue sampling the entire auditory scene ahead of them while approaching it. This shows that Blainville's beaked whales can track individual targets in time and space without any detectable acoustic gaze adjustments. We propose that long ICI's not only serve to avoid range ambiguity in clutter, but also to maintain a broad auditory scene that involves tracking of several targets for sequential capture to facilitate efficient foraging and so improve net energy returns in foraging dives. Simultaneous tracking of multiple targets at different ranges would involve active auditory stream segregation as has been demonstrated for bats (Moss and Surlykke 2001; Barber et al. 2003).

Despite the lack of ICI adjustment to clutter or prey distance, there are, nevertheless, periods during deep foraging dives where the ICIs do deviate from their normal value of around 0.4 s (Figs. 1, 4), with whales often switching to an ICI of about half of this. The bimodality in ICIs (Madsen et al. 2005) appears to be linked to a bimodality in residence indices. High residence indices (RIs, i.e., the amount of time spent in a volume of water relative to the swim speed) occur when whales encounter prey in patches, as evidenced by the short intervals between prey capture attempts. To stay within patches, whales must turn rapidly after each capture attempt leading to high RIs. The shorter ICIs when whales are within patches could imply that whales require higher update rates to track multiple prey or could relate more to the increased manoeuvring of the whale to stay within the patch. While we know little about the sampling needs for multiple target tracking, a case can certainly be made for a link between ICI and turning rate. When turning rapidly, whales encounter more

new water volume per unit of time compared to straight line swimming. Higher sampling rates are therefore needed to inspect the entire water volume ahead of the whale and so not miss prey during turns. For uninterrupted coverage, the turn-rate in degrees per second must be less than the beamwidth divided by the ICI so for a 20° beamwidth and an ICI of 0.4 s, turn-rates of less than 50°/s are needed while the 0.2 s ICI mode supports turn-rates of 100°/s. The turn-rate limits will be proportionally lower if the beamwidth is narrower or if whales require multiple clicks to sample a water volume. The animals studied here produced time-averaged turn-rates of up to 50°/s in the 3 s following buzzes and so routinely turn fast enough to suffer near incomplete sampling with a 0.4 s ICI.

The notion that ICI is linked to turn-rate is supported by Fig. 4, where the same whale forages primarily in patches in one dive (Fig. 4a–d) and then finds more scattered prey in a second dive (Fig. 4e–h). High turn rates in the first dive (Fig. 4a) give rise to periods of high residence index (Fig. 4c) which are associated with bouts of buzzes and with a high occurrence of the 0.2 s ICI mode (Fig. 4d). The more scattered prey distribution in the second dive leads to low turning rates and residence indices (Fig. 4g), and little use of the 0.2 s ICI mode (Fig. 4h). That pattern holds true when testing this hypothesis on the entire data set: there is a significant negative correlation between turning rates and ICIs with about 50 % of the ICI variation across whales explained by the turning rates. This correlation could of course mean that ICI and turning rate co-vary due to some other causal factor when whales are in patches, but the model that we propose for the link between ICI and turning-rate provides a simple causal explanation for this result. Efficient exploitation of prey in a patch must be critical in time-limited foraging and it seems likely that whales have developed sensory capabilities to support continuous sampling during fast turns to facilitate re-acquisition of prey within a patch following a prey-capture. Range ambiguity at 0.2 s is less of a problem at high turning rates, because the directional hearing of the whale is partly directed towards a volume of new water from which no unwanted echoes from previous clicks arrive.

Thus, the change in ICI and therefore acoustic gaze when whales are in patches is seemingly not an adjustment to the range or behaviour of individual prey, but rather to the movements of the echolocating whale in exploiting the patch. If this interpretation is correct, it involves a level of gaze adjustment that is missing from the Griffin model. To date, most workers have assumed that ICI relates to the range to a single target (Au 1993) and have used this to interpret sensing volumes. The evidence presented here that ICIs may also relate to the movements of the echolocator and to the distribution of prey leads us to propose a modified version of the Griffin model that attempts to

predict the sequence of echolocation behaviour when prey is found in patches (Fig. 6). In this model, we identify a sequence of operations that animals must perform repetitively while exploiting a patch, namely: prey selection, capture, and re-orientation (Fig. 6). While selecting prey and re-orienting, we expect an echolocator to choose sampling rates that are fast enough to ensure full coverage of the volume around the predator but slow enough to keep track of, and evaluate, multiple potential prey targets. During the brief capture phase, we expect the predator to focus entirely on a single selected prey and adjust the sampling rate to track the rapidly changing spatial relationship between predator and prey. Outside of patches, animals are expected to search for new prey or prey patches with a constant ICI as in the conventional model (Fig. 6).

Detection, discrimination and prey-specific motor patterns

Beaked whales pass through dense layers of organisms without capture attempts, ignoring up to 99 % of the targets they ensonify (Madsen et al. 2005; Arranz et al. 2011). This implies that beaked whales carefully extract information from echoes (Au et al. 2009) to classify ensonified organisms as prey or non-prey (Jones et al. 2008) in a highly selective foraging scheme. This process must happen before the buzz, i.e., at 3.5 m or more from the target, to avoid capture attempts on unrewarding targets. The absence of ICI adjustment in the approach phase makes it difficult to judge at what distance this decision-making

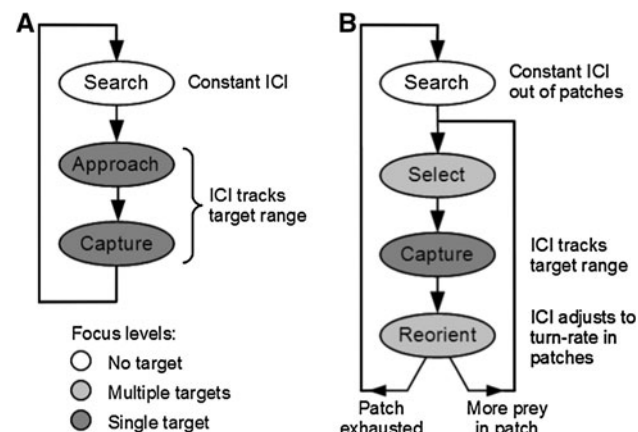


Fig. 6 **a** The Griffin model for echolocation comprising a search phase with constant ICIs, followed by approach and buzz phases in which the acoustic gaze tracks a single target. **b** An augmented model accounting for patchy prey distribution. In this model, the search phase still involves stable, long ICIs, but the approach phase in a patch involves tracking without ICI and SL adjustments to keep a wide auditory scene. Gaze adjustments take place both in the buzz phase (to track mobile prey) and when the whale reorients to return to the patch (to handle high encounter rates of new water volume)

takes place. But the stereotyped rolling capture attempts by some whales provide an indication that prey may be classified as early as 11 s before the start of the buzz, implying a classification distance of some 15–20 m for these prey. We interpret the stereotyped rolling manoeuvre (Fig. 5) as an echo-guided prey capture technique to facilitate capture of a particular prey type, perhaps related to the typical orientation or response to predation of this prey type. The implication is that beaked whales can differentiate between different prey types well before buzzes, allowing them time to adopt appropriate motor plans for efficient capture.

That situation is very different for echolocating bats: due to the physics of ultrasound propagation in air, bats cannot normally detect their insect prey at ranges of more than 2–5 m (Kick 1982; Kalko 1995), which means that, at normal flight speeds of 3–5 m/s, they have some 0.5 s between detection and possible capture of aerial prey in the wild (Kalko 1995). This short time span may explain why aerial hunting bats seem to discriminate little between different similar-sized prey targets when foraging in the wild (Barclay and Brigham 1994). The detection and classification of prey more than 10 s prior to capture, provides beaked whales with more than an order of magnitude more time than bats to initiate prey-specific capture tactics. This larger time span is a consequence of whales moving at less than half the speed of echolocating bats, and because the detection range of a toothed whale biosonar system in water is one to two orders of magnitude greater than for bats echolocating in air (Au et al. 2007; Madsen et al. 2004a, b, 2007). That means that beaked whales can employ a deliberate mode of sensorimotor operation (Snyder et al. 2007) in which the sensory volume is large compared to the stopping volume, so that careful selection of prey can precede initiation of specific motor patterns to maximize energy returns. In comparison, bats must operate in a reactive mode even during search, and hence have very little time for discrimination and initiation of prey-specific motor patterns. This may not have big consequences in air, as most small targets at night are edible insects. For deep-diving beaked whales the situation is very different: in long deep foraging dives whales will find many organisms that are either of low nutritional value or simply too costly in terms of oxygen and energy to be worth a capture attempt.

Conclusion

Blainville's beaked whales foraging in the wild are confronted with several tasks when aiming to capture some 25 prey per dive during a strictly limited time period at depth. Clicks are produced with a narrow 20° functional beam-width and at a relatively low rate of some 2.5 clicks/s, but still whales manage to detect, select and approach suitable

prey with only 60 echolocation clicks on average. The results here unveil some of the echolocation tactics that enable this foraging efficiency. Blainville's beaked whales are able to select individual prey well before the prey capture attempt, but they continue to sample food patches at relatively long stable ICIs rather than focussing their acoustic gaze on the prey item targeted for capture. However, higher sampling rates are employed by the whales when turning rapidly to stay within a prey patch, enabling continuous sampling of the surrounding water volumes. Thus, when there is a large size difference between predator and prey, the movements of the echolocating predator during the search and approach phases may be more important than those of the prey in determining the appropriate sampling rate. These results suggest that the Griffin search–approach–capture model of echolocation foraging must be expanded to account for sampling behaviours adapted to the distribution of prey. At short ranges the need to handle evasive prey manoeuvres likely determines the hand-off distance between the approach and buzz phases, and during capture attempts, individual prey are tracked carefully via acute gaze control in the buzz. We demonstrate that echolocating Blainville's beaked whales can classify and track prey at ranges of more than 10 m using echo information to inform prey-specific changes to motor patterns. These long detection and classification ranges with respect to the swimming speed enable a deliberative mode of sensory-motor operation when searching for and approaching both patches and prey. This is probably a key factor enabling these air-breathing mammals to optimize energy returns in the challenging task of foraging at great depths during short 24 min foraging bouts. That echolocation behaviours are matched to prey distribution and to the movements needed to exploit prey patches, as demonstrated here, has not been noticed previously. However, this is likely a common phenomenon for all echolocating animals, and we expect that, as it becomes possible to sample individual behaviour for longer intervals in more species, a greater variety of echolocation tactics will be uncovered.

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