

Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution

A. Fais · N. Aguilar Soto · M. Johnson · C. Pérez-González ·
P. J. O. Miller · P. T. Madsen

Received: 7 July 2014 / Revised: 19 January 2015 / Accepted: 19 January 2015
© Springer-Verlag Berlin Heidelberg 2015

Abstract Predators make foraging decisions based upon sensory information about resource availability, but little is known about how large, air-breathing predators collect and use such information to maximize energy returns when foraging in the deep sea. Here, we used archival tags to study how echolocating sperm whales (*Physeter macrocephalus*) use their long-range sensory capabilities to guide foraging in a deep-water habitat consisting of multiple, depth-segregated prey layers. Sperm whales employ a directed search behaviour by modulating their overall sonar sampling with the intention to exploit a particular prey layer. They forage opportunistically during some descents while actively adjusting their acoustic

gaze to sequentially track different prey layers. While foraging within patches, sperm whales adjust their clicking rate both to search new water volumes as they turn and to match the prey distribution. This strategy increases information flow and suggests that sperm whales can perform auditory stream segregation of multiple targets when echolocating. Such flexibility in sampling tactics in concert with long-range sensing capabilities apparently allow sperm whales to efficiently locate and access prey resources in vast, heterogeneous, deep water habitats.

Keywords Sperm whales · Echolocation behaviour · Directed search behaviour · Prior information · Multi-target acoustic scene

Communicated by S. D. Twiss

A. Fais · N. Aguilar Soto
BIOECOMAC, Department of Animal Biology, La Laguna University, Canary Islands, Spain

M. Johnson · P. J. O. Miller
Scottish Ocean Institute, University of St. Andrews, St. Andrews, Scotland

C. Pérez-González
Department of Statistics, Operating Research and Computation, La Laguna University, Canary Islands, Spain

P. T. Madsen
Zoophysiology, Department of Bioscience, Aarhus University, Aarhus, Denmark

P. T. Madsen
MUCRU, Centre for Fish, Fisheries and Aquatic Ecosystems Research, School of Veterinary and Life Sciences, Murdoch University, Perth, Australia

Present Address:

A. Fais (✉)
Institute for Terrestrial and Aquatic Wildlife Research, University of Veterinary Medicine Hannover, Hannover, Germany
e-mail: andrea.fais@tiho-hannover.de

Introduction

When searching for resources such as food, the optimal strategy is determined both by resource distribution and by the sensory and movement capabilities of the searching animal (Bell 1991). Time-efficient prey search and selection strategies are particularly beneficial for predators with short but intense foraging periods as is the case for air-breathing marine predators that must access two vital but spatially separated resources: air at the surface and food at depth (Kramer 1988). Several air-breathing marine animals show anticipatory diving behaviours, using environmental information as priors to strategically accommodate foraging tactics to obtain prey most effectively. For example, Adélie (*Pygoscelis adeliae*) and Macaroni (*Eudyptes chrysolophus*) penguins adjust the time devoted to transit between surface and foraging depth according to the foraging success of the previous dive (Ropert-Coudert et al. 2001; Sato et al. 2004). A steep descent

enables a direct transport to the prey patch depth, whereas descending at shallow angles allows the coverage of a broader horizontal space and thus to extend the search for resources (Sato et al. 2004). Magellanic penguins (*Spheniscus magellanicus*) maintain time spent at foraging depth in deeper dives by increasing dive duration and minimize time spent in transit by adjusting the descend speed to maximum dive depth. These penguins show prey predictability, selecting their new foraging patch based on foraging success in the previous dive, and hence accommodate pre-surface time, i.e. number of breaths, and swim speed on descent to the projected foraging depth layer (Wilson 2003). This behaviour has also been observed in grey seals (*Halichoerus grypus*) (Gallon et al. 2007) and New Zealand sea lions (*Phocarcos hookeri*) (Crocker et al. 2001), which adjust descent swim speed to resource distance in order to spend more time in the foraging layer.

The spatial extent of the environment from which an animal can extract information is defined by the animal's sensory volume (Lima and Zollner 1996), which in turn influences the search effort required to locate resources (Zollner and Lima 1999). Most animals use passive sensing (Nelson and MacIver 2006) to assess environmental parameters via intrinsic visual, chemical or auditory cues. In contrast, animals using active sensing, such as electrolocation or echolocation, emit energy to probe their environment (Nelson and MacIver 2006). As such, echolocators gather sequential but high-resolution information about prey distribution via echoes returning from backscattering targets ensonified with echolocation pulses (Madsen and Surlykke 2013).

Studied species of echolocating bats and toothed whales adjust their clicking rates, and thus their active acoustic gaze (Moss and Surlykke 2010), to match the characteristics of the environment (Moss and Surlykke 2001; Schnitzler et al. 2003), the range to targets of interest (Au and Benoit-Bird 2003; Moss and Surlykke 2010), the density of prey (Madsen et al. 2005) and the rate at which new sensory volumes are encountered (Madsen et al. 2013). Echolocation clicks are typically produced at intervals that are longer than, but often related to, the two-way travel time (TWT) of the sound to the target of interest and back (Au 1993). This makes the inter-click interval (ICI) a useful indicator of the upper bound of the sensing range of an echolocator, i.e. ICI is a proxy for the maximum range over which the animal is focusing its attention (Penner 1988; Verfuß et al. 2005).

The range over which echolocators can detect prey depends upon the source parameters of their biosonar pulses, the reflectivity of prey and the clutter and noise conditions in the habitat. An extreme example is the sperm whale (*Physeter macrocephalus*) whose hypertrophied nasal complex can generate source levels in excess of 235 dB re 1 μ Pa (peak-peak) (Madsen et al. 2002a; Møhl et al. 2003), enabling search ranges for prey aggregations that may exceed water depth in their deep habitat (Madsen et al. 2007). This implies that, in

typical ambient noise conditions, sperm whales may be able to search a large proportion of the water column for prey patches at the start of each foraging dive and so minimize time and energy spent searching for prey, perhaps accounting for their success as a cosmopolitan, mesopelagic predator (Madsen et al. 2002b; Watwood et al. 2006). Male sperm whales off northern Norway exhibit a varied diving behaviour, switching between different prey resources over a wide range of water depths (Teloni et al. 2008). This provides a unique opportunity to uncover whether sperm whales perform random or directed prey search, and how they modify their echolocation sampling both to locate and access spatially separated food resources in the water column and to efficiently locate individual prey once within a patch.

Here, we use sound and movement recordings tags (DTags) to study the echolocation behaviour and search tactics of such male sperm whales, showing that, despite the long sensing range of their biosonar, sperm whales use prior information to guide their foraging within a dive. This directed prey search strategy may explain the high foraging returns achieved by this large air-breathing predator inhabiting the deep waters of all major oceans (Santos et al. 1999).

Methods

Data collection

Field work was performed in the general area of Andøya underwater canyon off Andenes, Norway. Sperm whales were tagged with high-resolution digital archival tags (DTag2), which include a hydrophone, a depth sensor and three-axis accelerometers and magnetometers (Johnson and Tyack 2003). Sounds were recorded with 16-bit resolution at a sampling rate of 96 kHz. Orientation and depth sensors were sampled at 50 Hz and decimated to 5 Hz for analysis using a linear-phase finite-impulse response low-pass filter prior to decimation. In three research cruises performed in the summers of 2005, 2009 and 2010, surfacing whales were approached in an inflatable boat for tagging. Tags with four suction cups were deployed using a cantilevered pole or a handheld pole onto the dorsal surface of the whales. The tags released after a programmed interval and floated to the surface where they were located by VHF radio tracking. Four sperm whales were tagged in July 2005, one animal in June 2009 and three in May 2010. All tag-data analyses were performed with custom scripts in Matlab 7.5 (Mathworks).

Orientation and depth

Pitch and heading angles were derived from the accelerometers and magnetometers following Johnson and Tyack (2003). These angles were used to estimate the orientation of the

whales with respect to the navigation frame (Miller et al. 2004b) and to determine their turning rate derived from the time-varying longitudinal vector of the animal (sensu Madsen et al. 2013). To separate surface intervals and shallow silent dives from foraging behaviour, we defined foraging dives as those deeper than 25 m (i.e. about two body lengths Teloni et al. (2008)) and containing echolocation clicks. Within each dive, the descent, bottom and ascent phases were defined by changes in the sign of the pitch angle of the whale (sensu Miller et al. 2004a) lasting at least 5 s.

Clicks, clicking and buzzing

Sounds produced by tagged whales and nearby animals were identified in tag recordings using spectrograms (512 point FFT, Hann window, 50 % overlap). Individual clicks were detected using a supervised click detector. Clicks from tagged whales were recorded with a consistently high received level (RL) and thus were easily distinguished from the lower and variable RL clicks from conspecifics (Zimmer et al. 2005). For each dive, the beginning and end of the clicking phase (termed start of clicking, SOC, and end of clicking, EOC, respectively) were located demarcating the interval when whales are searching for prey with echolocation (Zimmer et al. 2005). Following Teloni et al. (2008), a buzz was defined as a series of clicks with ICIs < 0.1 s, bracketed by ICIs above 0.22 s. As the ICI generally changes rapidly at the start and end of buzzes, the precise value of this threshold had little impact on the timing of buzz starts and ends. To avoid

including slow clicks (an infrequent click type with a presumed communication function (Oliveira et al. 2013)) in the analyses, only ICIs < 2.5 s were considered. The time delay between consecutive buzzes within a dive (the inter-buzz interval (IBI)) was defined as the time between the last click of a buzz and the first click of the following buzz.

Altitude

The altitude of the whale above the seafloor was obtained from bottom echoes generated by the clicks of the whales and recorded by the tags (Thode et al. 2002; Zimmer et al. 2003). Bottom echoes were located using echograms (Fig. 1; see Arranz et al. 2011) constructed from 3.5-s sound segments synchronized to each outgoing click. These enabled detection of seafloor echoes at ranges up to 2580 m from the whale assuming an average sound speed of 1475 m/s (Teloni et al. 2008). Echoes from the seafloor appeared within the echograms as sequences of reverberant echoes with slowly varying TWT. The TWT/2 was multiplied by 1475 m/s to estimate the altitude of the whale above the seafloor, which was then added to the whale depth to estimate the seafloor depth. Seafloor echoes were detected more readily when the whales were pointing downwards, likely directing their sonar beams vertically towards the bottom. The seafloor depths for a whole dive were interpolated using a Kalman filter and Rauch smoother (Bar-Shalom et al. 2004) with water depth and depth rate as states in order to estimate altitude over any short intervals in which no echoes were detected.

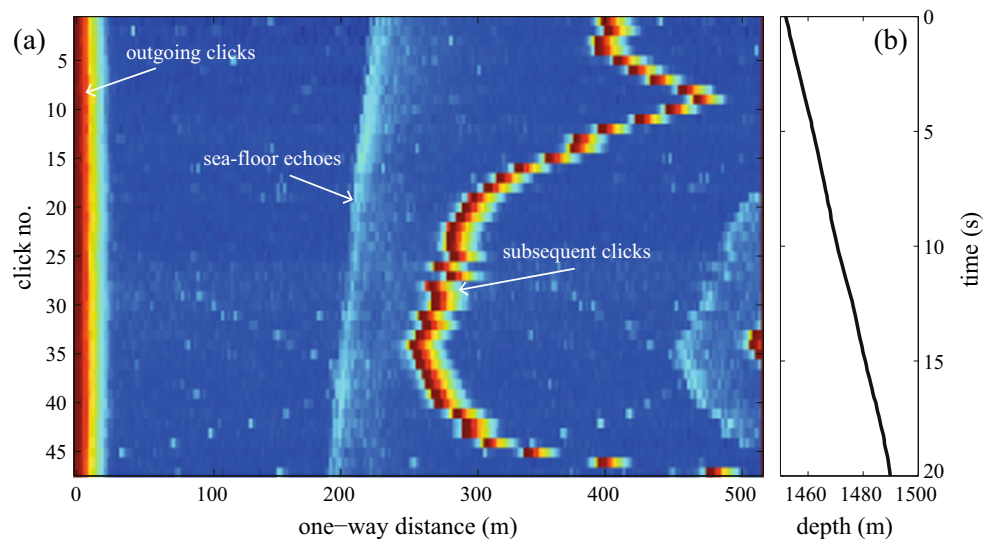


Fig. 1 **a** Echogram based on recordings made with DTag on a free-ranging sperm whales foraging off northern Norway. The echogram was constructed by stacking the envelopes of 0.7-s-long sound segments, expressed as range using sound speed of 1475 m/s, synchronized to outgoing clicks (red line at distance 0). Subsequent clicks appear as red shaded areas around 250–500 m, corresponding to an inter-click interval

around 0.3–0.7 s. Seafloor is shown as a sequence of reverberant echoes with slowly varying two-way travel time, allowing the calculation of the distance from the whale to the bottom. **b** Change in depth of the whale during the time elapsed between the emission of the first and last usual clicks used in the stackplot (colour figure online)

Statistics

For non-linear relations between continuous variables, independent variables were log-transformed. Post hoc analysis in R (R Core Team 2012) was used to examine the influence of individuals on the relationships between response and regressor variables. Individual was included both as a dummy independent variable and as an interaction term with the primary independent variable. The regression model was bootstrapped by treating the regressors as random and selecting bootstrap samples directly from the observations, taking for each individual the same size of samples as in the original data set. The regression coefficients were calculated using a robust estimator (Tukey's biweight) in each bootstrap. To test if the regression coefficient of the interaction term varied across individuals, their bootstrap confidence intervals were calculated using a bias-corrected method (Fox 2002).

To compare means of variables across dive depths, the software PRIMER was used together with distance-based permutational ANOVAs (PERMANOVA). Post hoc pair tests were performed for detected significant differences across grouping factors. Distance-based multiple regression was performed with the DISTLM routine included in PRIMER to assess the relationship between initial clicking after buzzing, IBI and turning rate. In all these analyses, permutation *F* tests were applied, which enable us to obtain the corresponding *p* values avoiding assumptions about the data distribution (Anderson and Braak 2003).

Results

A total of 144 h of combined acoustic and movement data were collected from eight immature and mature male sperm whales between 11 and 16 m long, providing a dataset of 175

complete foraging dives (Table 1). Foraging dives were performed to depths from 48 to 1862 m, alternating, in some cases, between shallow and deep dives within a few hours (Fig. 2a). During shallow dives the whales targeted predominantly epipelagic prey and during deep dives the whales mostly foraged benthopelagically (Fig. 2). Judging by the depth at which buzzes occurred, the tagged whales encountered prey in three broad depth layers. The slope changes of a survivor plot of buzz depth defined these layers as follows: (1) shallow prey, i.e. <220 m; (2) medium, between 220 and 700 m; and (3) deep prey >700 m (Fig. 2b). Regardless of which prey layer the whales exploited, foraging dives were typically U-shaped, consisting of steep descent and ascents bracketing a relatively horizontal bottom phase (Fig. 2a).

Using prior information: expectations of vertical prey distribution

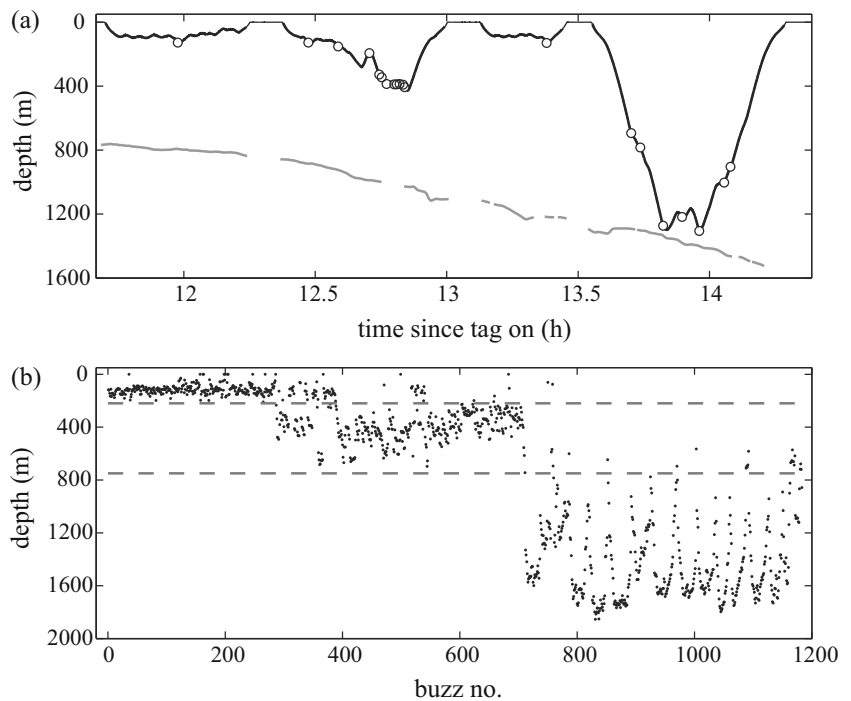
The choice of prey layer(s) within which to invest time during each dive may depend upon both (1) prior information obtained during preceding dives and (2) sensory feedback during the descent phase of the current dive. The usual clicks from the tagged whales were consistently clipped in the recordings; therefore, the analyses focused on signal timing, rather than level. The depth at which whales begin searching for prey (echolocating) in a dive, together with the initial ICI, are strong indicators of the depth range within which they expect to find prey before getting updated information via echolocation (Thode et al. 2002; Zimmer et al. 2003). Given that sperm whales descend at steep angles and do so at steady swimming speeds around 1.5–2 m/s (Miller et al. 2004a), the depth at which the whales start echolocating is closely related to the time elapsed from leaving the sea surface to the start of clicking. If sperm whales rely primarily on sensory information gained during the descent to decide on where to forage,

Table 1 Information on tag placements

Whale code	Year	Time recording	No. of foraging dives	No. of shallow dives	No. of medium dives	No. of deep dives	No. of clicks
# 196a	2005	24 h 17'	29	24 (83 %)	5 (17 %)	0	51,860
# 199a	2005	20 h 42'	28	20 (72 %)	4 (14 %)	4 (14 %)	55,945
# 199b	2005	16 h 46'	17	10 (59 %)	2 (12 %)	5 (29 %)	37,977
# 199c	2005	16 h 47'	11	2 (18 %)	1 (9 %)	8 (73 %)	22,108
# 153a	2009	12 h 34'	15	10 (67 %)	5 (33 %)	0	31,625
# 147a	2010	18 h 29'	19	2 (10 %)	17 (90 %)	0	28,613
# 149a	2010	17 h 31'	27	15 (55 %)	8 (30 %)	4 (15 %)	46,528
# 150a	2010	16 h 59'	29	1 (3 %)	28 (97 %)	0	30,875
Total		144 h 5'	175	84 (48 %)	70 (40 %)	21 (12 %)	305,531

Whale codes were formed by the Julian day and the deployment order of the tag in that day. Foraging dives were defined as echolocation dives with a maximum depth greater than 25 m. Based on the distribution of buzz depth, dives were divided according to their maximum depth in shallow (<220 m), medium (<700 m) and deep (>700 m)

Fig. 2 **a** Section of a dive profile recorded from a male sperm whale off northern Norway showing how whales switched between different prey layers in the water column in successive foraging dives. The *thick black line* marks the echolocating period of the dives, and each *open circle* marks a prey capture attempt (buzz). The *thick grey line* shows the estimated location of the seafloor. **b** Depth of buzzes of all tags, arranged according to dive type (i.e. shallow, medium and deep) and plotted one by one ordered according to their occurrence within the dives. *Grey dashed lines* represent the threshold depths used to differentiate among shallow and medium dives at 220 m, and among medium and deep dives at 700 m



they should sample the entire water column or at least the depth range over which prey can be detected, beginning early in the dive. Alternatively, if choices are based on prior experience, whales do not need to begin sampling until they have descended closer to their previously chosen target layer. Following the same reasoning, a short initial ICI is expected when whales target a nearby food resource.

The depth at which sperm whales started searching for prey, i.e. the SOC depth, was compared with (1) the median buzz depth of the dive and (2) the mean ICI of the first ten clicks in that dive. The median buzz depth was a robust indicator of the main depth layer eventually targeted during a dive, while the mean ICI of the first ten clicks was a proxy for the initial maximum inspection range. The depth of SOC varied widely, from 3 to 215 m. Pooling the data from all whales ($n=175$ dives), there was a significant linear relationship between the median buzz depth and the SOC depth (Spearman's ρ 0.89, $p \ll 0.001$, $n=161$ dives with buzzes, eight whales) (Fig. 3a), revealing that sperm whales started clicking later when foraging on deep prey (Fig. 3b). The initial ICI (inspection range) and the SOC depth were also significantly positively correlated (Spearman's ρ 0.81, $p \ll 0.001$, $n=175$ dives, eight whales) (Fig. 3c), with whales clicking faster at the start of shallower dives (Fig. 3d).

Sampling strategies during descents

Once whales have started clicking and thus may have gained new information about prey distribution during their current

dive, it is expected that they will adapt their acoustic sampling to track either the current location of prey or the furthest limit of inspection, i.e. the seafloor for a steeply descending whale. We assume that the ICIs of the tagged sperm whales exceed the TWT to the target of interest, as observed in small-toothed whales studied in the wild (Madsen et al. 2013) and in captivity (Wisniewska et al. 2012). If a whale is sampling the full water column, the ICI should exceed the TWT from the whale to the seafloor to avoid range ambiguity from this strong reflector and should reduce accordingly as the whale descends so as to track the seafloor (Thode et al. 2002). Alternatively, if attention is focused on a closer prey layer, a shorter ICI that decreases as the whale approaches the layer is expected (Zimmer et al. 2003). To test these hypotheses, the ICI during the descent phase was compared with (1) the TWT to the seafloor and (2) the TWT to the closest indication of where prey were expected or actually encountered, i.e. the depth at the end of the descent phase or the depth of the first buzz, whichever occurred earlier.

Seafloor echoes were found in 170 dives. Visual inspection of the data showed two distinct ICI patterns (Fig. 4). Dives to depths <1200 m ($n=158$, eight individuals) had widely varying ICIs throughout the descent (mean ICI 0.84 s; sd 0.22) that did not appear to consistently track either targeted prey layers (Spearman's $\rho=0.13$) or the seafloor (Spearman's $\rho=0.02$) (Fig. 4a–d). There were few buzzes (median of 1) during the descent phase in these dives, only occurring in 40 of 158 dives near the end of the descent.

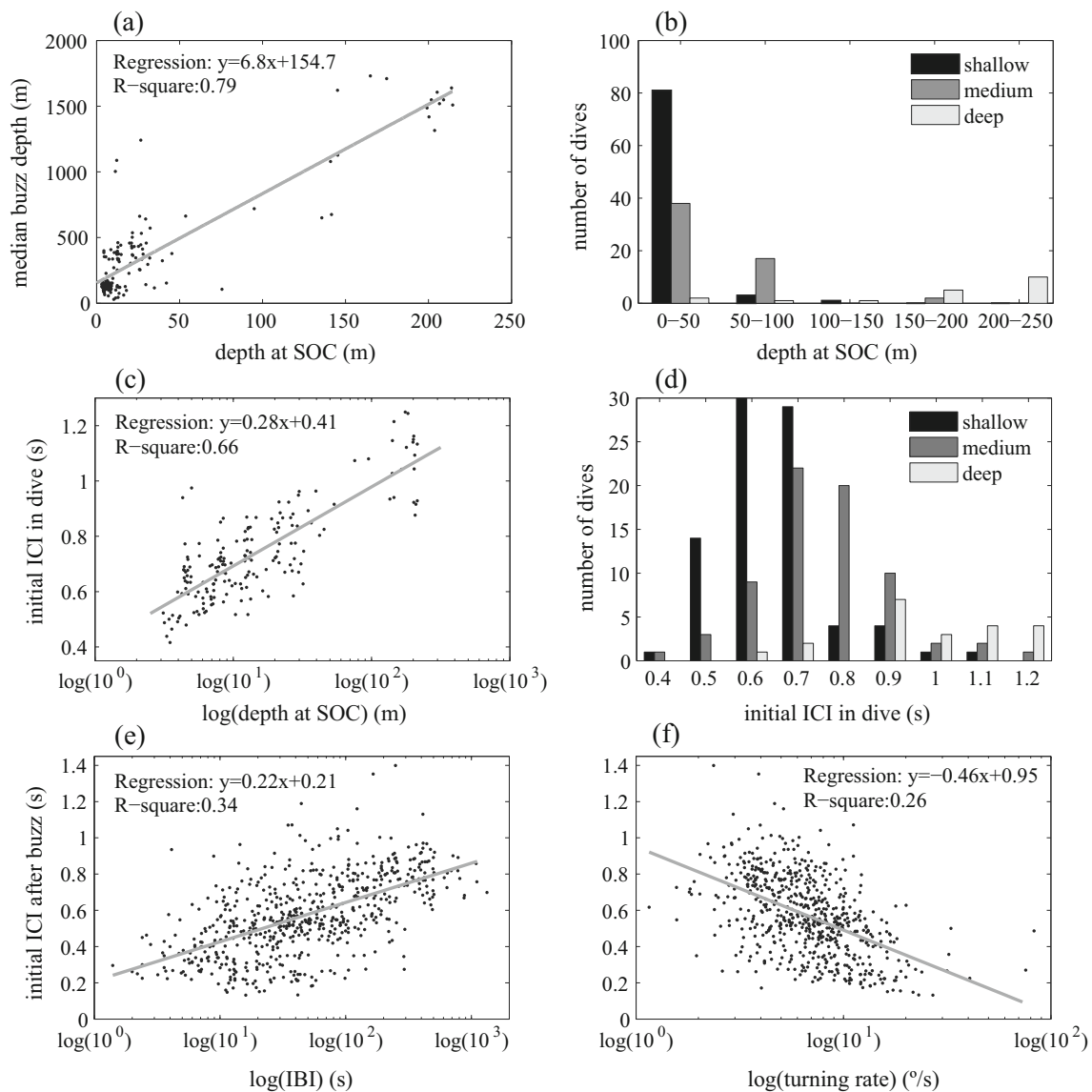


Fig. 3 **a** Relation between median buzz depth and depth of SOC for each dive ($n=161$); **b** histogram of SOC in 50-m depth bins, colour coded according to the targeted prey depth layer. **c** Relation between mean ICI of the ten first clicks of a dive and depth at SOC ($n=175$). **d** Histogram of initial ICI in a dive colour coded according to the targeted prey depth

layer. **e** Relation between mean ICI of the first ten clicks after a buzz, during the bottom phase of dives and time between consecutive buzzes (IBI) ($n=615$). **f** Relation between initial ICI after each buzz of the bottom phase and mean turning rate over the first 5 s after each buzz ($n=615$)

In contrast, in all dives exceeding 1200 m ($n=17$, three individuals), whales produced distinctive sawtooth-patterned ICIs during descents, comprising intervals with consistently decreasing ICIs bracketed by occasional step increases (Fig. 4e, f). This pattern indicated that the ICI was tracking different depth layers between 500 and 1300 m sequentially throughout the descent, as evidenced by the depth of the acoustic gaze during the descents exemplified in Fig. 4e. On average, one quarter of the buzzes in these deep dives were produced during the descent phase, with the depth of buzzes consistently coinciding with the layer previously tracked by echolocation (Fig. 4e). In all 17 deep dives, the final tracked depth layer coincided with the seafloor. During much of the

bottom phase of these dives, the three whales foraged within the benthic boundary layer (nominally 0–200 m above the seafloor (Angel and Boxshall 1990): 119 of 274 buzzes with bottom echoes 60 s before or after each buzz (sensu Arranz et al. 2011) occurred less than 200 m from the seafloor. All of these deep dives were performed by whales 199a-c which were tagged on the same day and in the same area, confounding evaluation of whether the ICI tracking is specific to deep dives or pertains to a particular prey type or location. Lack of ICI tracking during descents of shallower dives performed by the same whales ($n=39$) suggests that the behaviour is only beneficial during deep dives which may pass several depth layers of prey.

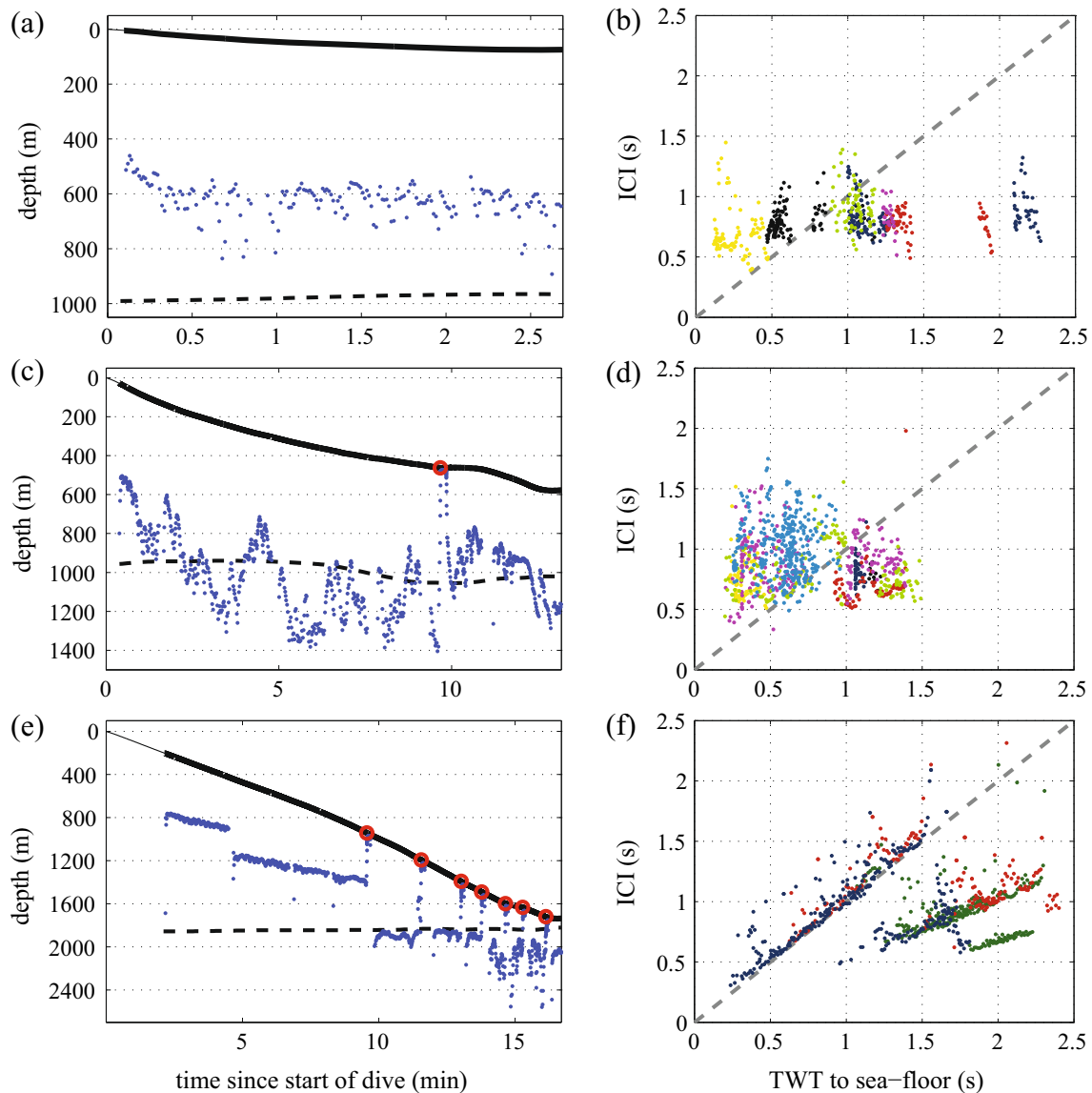


Fig. 4 ICI as indicator of inspection range in a shallow dive (<220 m) (a), in a medium dive (up to 1200 m) (c) and in a deep dive (>1200 m) (e). The inspection range (blue dots) is given by $\frac{1}{2}$ ICI*c added to the whale depth during the steep descent of the dives. The dive profile is shown as a thin grey line with the time that the whales spent clicking as a black thick line and the location of the buzzes as red circles. The depth of the seafloor (deeper dashed black line) was estimated from the TWT of seafloor

echoes. Relation between ICI and the TWT to the seafloor for the descent phase of shallow dives (<200 m, 17 dives randomly selected from a total of 84 dives performed by eight animals) (b), medium dives (up to 1200 m, 17 dives randomly selected from a total of 74 dives performed by eight animals) (d) and the deepest dives (>1200-m depth, 17 dives performed by three animals) (f), with colour indicating whale ID. The dashed grey line marks the relation ICI=TWT to the seafloor

Search within the prey layer

Assuming that a new prey is targeted during each buzz (Wisniewska et al. 2012; Madsen et al. 2013), the time lapse between consecutive buzzes (i.e. the IBI) gives an indication of how frequently prey are encountered. The median IBI was 171 s (IQR 95–354 s) for shallow dives (<220-m dive depth), 17 s (8–54 s) for medium (220–700 m) dives, and 36 s (21–59 s) for deep (>700 m) dives. Although significant differences across individuals were found (PERMANOVA, $p < 0.01$, $n = 615$), IBIs were

longer during shallow dives than in medium and deep dives (PERMANOVA, $p < 0.05$, $n = 615$).

After finishing a buzz, sperm whales reopened their sensory volume by increasing the ICI of subsequent regular clicks. To test whether this ICI was adapted to their perception of how closely prey were spaced (Madsen and Surlykke 2013), the mean ICI of the ten first clicks after each buzz was used as a proxy for the maximum inspection range used by the whale when attempting to locate the next prey and was compared with the following: (1) the time to the next buzz (IBI) and (2) the mean turning rate over the first 5 s after each buzz. The IBI

is a proxy for prey density within the prey layer, while the turning rate is an indicator of patchiness: for the whale to remain within a small patch, it must turn at a high rate following each buzz (Johnson et al. 2008; Madsen et al. 2013). The relationship between initial clicking rate and IBI was significant (Spearman's ρ 0.58, $p \ll 0.001$, $n=615$, eight whales), but given the r^2 value of 0.34 (Fig. 3e), other factors also contributed to the ICI variation. Turning rate similarly explained some 30 % of the ICI variation, showing a significant negative correlation that was followed by all whales, although with different slopes (Spearman's ρ -0.5, $p \ll 0.001$, $n=615$, eight whales; Fig. 3f). No strong correlation between turning rate and IBI was found ($r^2=0.1$, Spearman's ρ -0.3, $p \ll 0.001$, $n=615$, eight whales); thus, a multiple linear regression analysis was performed to determine the variation in ICI explained by both predictor variables. The overall model fit was $r^2=0.45$.

Echolocation during ascents

In most dives (165 of 175 foraging dives), sperm whales did not stop clicking until near the end of the ascent phase, regardless of the prey depth layer targeted during the dive. Whales switched to shallower dives after approximately 30 and 57 % of medium ($n=21$) and deep ($n=12$) dives, respectively (Fig. 2). In dives <1200 m ($n=158$) sperm whales performed buzzes during the ascent phase of 26 dives, with a median of 1 buzz. In contrast, in dives >1200 m ($n=17$), whales produced around 17 % of the total buzzes while ascending. As a result, prey capture attempts occurred over a wide depth range in the deepest dives (Fig. 2).

Discussion

For animals exploiting patchy resources, prior experience may be an important source of information to guide search behaviour (Dall et al. 2005). Nevertheless, it seems reasonable to expect that prior experience may be less important for predators such as sperm whales that are able to gather real-time information about the distribution of resources over long distances. This study investigated how such an animal with long-range sensory capabilities combines both current information and priors to exploit spatially segregated prey resources. We show that sperm whales rely upon information obtained during previous dives to decide where to invest searching and foraging effort in the next dive. In the following, we discuss how these top predators modulate their sensor sampling rate to the variable distribution of their prey in a directed search enabling them to collect sufficient prey within a limited dive time.

Dimensionality reduction

Resources in the open ocean are not uniformly distributed across depth but tend to concentrate within several broad depth layers (Steele 1989). Male sperm whales in high-latitude waters feed over a wide depth range and may switch between prey layers several times per day (Fig. 2a). Although the whales occasionally switched between shallow and medium prey within a dive (Fig. 2a), the 10 % of U-shaped shallow and medium dives without prey capture attempts, suggest that it may be more economical to continue foraging within a poor layer than to begin searching for a new layer mid-dive. If so, it is critical for whales to choose a productive foraging layer at the beginning of each dive before incurring the transport costs of a deep dive (Thompson and Fedak 2001). In a habitat with vertical resource stratification, U-shaped dive profiles effectively reduce the three-dimensional search problem into successive one-dimensional (i.e. depth) and two-dimensional (i.e. within a horizontal depth layer) searches during dives. This may explain why U-shaped dives are performed by many marine mammal species (Watwood et al. 2006; Kuhn et al. 2009; Arranz et al. 2011). However, the ability to study dive depth choices in air-breathing marine predators is greatly restricted by the limited knowledge on the available sensory inputs for even well-studied species, which mainly includes several pinniped species (Dehnhardt et al. 2001; Vacqu e-Garcia et al. 2012). Male sperm whales off northern Norway present a unique combination of data that include the range over which they are sensing while performing variable depth dives. This allows us to test if foraging decisions in a long-range sensing species rely on expectations from priors or within dive sensory information flow.

Using priors: expectations of vertical prey distribution

Echolocating predators exert control over the timing of their pulse emission, thus determining both when they search and the potential sensory volume. The sperm whales in this study adjusted their initial search range (as indicated by the ICIs) to the distance to the targeted depth layer before gaining information via echolocation of the actual resource distribution in the water column (Fig. 3c, d). Further, when performing deep dives, sperm whales did not begin echolocating until they had passed the depth of shallow prey (Fig. 3a, b). Sperm whales are potentially able to profile the vertical distribution of prey resources out to a range in excess of 1000 m (M ohl et al. 2003; Madsen et al. 2007) at low energetic costs (Nelson and MacIver 2006), enabling them to plan dives from close to the surface based on current sensory information. However, in this study, the whales employed a directed search behaviour focusing their search on a subset of the water column from the beginning of the dive. Such directed search behaviour may be more efficient for these animals, making a conscious decision on where to

forage before committing effort. Other air-breathing marine predators also direct their search for prey by swimming through shallower layers of potential prey when foraging near the seafloor (Costa and Gales 2003). However, their passive sensing system provides limited cues from which to infer search tactics and use of priors. Conversely, echolocation provides robust cues to when and where predators are searching for prey, in this case, revealing an adaptation in the start depth and subsequent sampling rates of the biosonar to the location of preferred prey.

Most deep foraging marine mammals show the ability to adapt their foraging behaviour to exploit different depths (Kuhn et al. 2009; Arranz et al. 2011) and different prey types (Aguilar Soto et al. 2008; Naito et al. 2013). These modifications of foraging patterns are often related to circadian variations in vertical distribution of resources, constituting a predictable aspect of the marine environment (McNamara et al. 2006). In contrast, male sperm whales off northern Norway need to respond to short-term environmental changes, given the general lack of temporal structure in high latitude waters (Blachowiak-Samolyk et al. 2006). When foraging in a dynamic prey landscape, the most reliable source of information to plan a dive a priori is information collected during previous dives. Madsen et al. (2002a) hypothesised that sperm whales could use eavesdropping to locate suitable prey patches, and the occasional click trains from non-tagged conspecifics in the recordings analysed here suggest acoustic contact between the whales. However, the use of eavesdropping information to directly assess foraging patches on a dive-to-dive basis seems unlikely given that male sperm whales generally forage several kilometres apart (Lettevall et al. 2002) in a canyon area in which the bathymetry, and therefore presumably the prey communities, can vary markedly with location. This suggests that male sperm whales primarily rely on their own information to make foraging decisions. In contrast to passive sensing, echolocation enables inspection of larger sensory volumes, resulting in more extensive information gathering in light-limited environments than is possible with vision or tactile senses (Naito et al. 2013). Given their long-range sensory capabilities, sperm whales may glean information about prey while sampling within, but also before arriving at, a prey patch (Lou  pre et al. 2011). In half of the switches from deep and medium to shallow dives sperm whales echolocated during the ascent phase until close to the surface. Hence, decisions about where to forage in subsequent dives may be based not only on foraging success but also on echo information gathered during ascents, providing a timely update on the location and quality of prey in the water column.

Sampling strategies during descents

Sperm whales produce clicks in a very narrow sound beam, with a half-power width of around 4° (M  hl et al. 2003). This beamforming increases the range at which prey can be

detected but at the expense of a broad acoustic field of view for closer prey. Thus, the whales face a trade-off between (1) failing to sample water volumes as they manoeuvre if they click slowly to accommodate targets at long ranges and (2) range ambiguity and spatial aliasing from distant targets when clicking at a high repetition rate to get frequent updates on closer water volumes (Madsen et al. 2013). Hence, echolocation clicking rates provide inherent information about the exploratory tactics of echolocating predators. Sperm whales off northern Norway seem to prey on fast moving fish during shallow dives but seem to target slower moving squid at greater depths (Martin and Clarke 1986). The current study found a bimodal sampling behaviour during descents: in dives to <1200-m depth, sperm whales sampled with a varying ICI not tracking either the seafloor nor the prey layer (Fig. 4a–d), while whales performing dives to >1200 m tracked sequentially discrete layers, making repetitive downward ICI adjustments (Fig. 4e, f), potentially suffering from pulse-echo overlap. These different echolocation tactics suggests that these long-range sensing predators adjust their sensory input stream to accommodate variations in prey distribution while descending towards a preferred depth.

In shallow dives (<220 m), sperm whales fed within an epipelagic layer (Fig. 2) with widely spaced prey, as indicated by the long IBIs. In these dives, whales started clicking immediately upon leaving the surface (Fig. 3a, b) and dove at a relatively shallow angle (as evidenced by the low vertical rate in shallow descents, Fig. 4a), thus ensonifying a broad swath of the epipelagic prey layer throughout the descent. This strategy facilitates detection of echoes from multiple targets at different ranges immediately upon start of clicking. Sperm whales clicked rapidly during the initial descent of these dives but opened their depth of gaze by slowing down their sampling rate while descending within the foraging layer (Fig. 4a, b). Long ICIs allow long-range target detection, appropriate for detecting the sparsely distributed prey encountered in these shallow dives.

During the deepest dives (>1200-m depth), sperm whales foraged opportunistically during descents (Fig. 2), actively changing their acoustic gaze by modulating ICIs to sequentially track discrete prey layers (Fig. 4e, f). When swimming vertically towards a prey layer, the whales receive echoes from a discrete delay window corresponding to the depth range of the layer. As exemplified in Fig. 4e, the depth of the acoustic gaze decreased sequentially as the whale descended with prey capture attempts coinciding with the shortest inspection ranges. This suggests that the clicking rate during the descent phase of the deepest dives is adjusted to maximize the sampling rate on nearby prey to increase interception probability. Previous studies (Thode et al. 2002; Zimmer et al. 2003) have reported stereotyped monotonically decreasing ICI patterns during descents of sperm whales in tropical waters, but this study shows that, when multiple prey layers are available,

sperm whales adjust their acoustic gaze to sequentially track these layers. This gives rise to a sawtooth pattern in the ICI with step changes in the ICI signalling a switch in acoustic gaze to a further prey layer.

The echolocation behaviour in the descents of medium depth dives (up to 1200 m; Fig. 4c, d) is more difficult to explain. Sperm whales appeared to forage over a broad depth range in these dives (Fig. 2) on prey that were aggregated in patches, as indicated by the short IBIs. The slow sampling rate and the lack of ICI tracking of a prey layer during these descents may help maintain a broad auditory scene to accommodate targets spread over a wide depth range and so facilitate prey patch selection. Although the buzz depths in medium dives (mostly in four dives with depth >700 m) overlapped with the depth of some buzzes during the descents of deep dives (Fig. 2b), there may be a difference in intention underlying the different biosonar sampling behaviour. If whales intend to dive deep, there may be no need to compare prey patches within the same auditory scene while descending, rather it may be more useful to maximise the update rate of prey locations for opportunistic capture. Conversely, whales performing medium dives tended to commit to a narrow range of foraging depths and so should compare prey availability in different vertical layers carefully during descents.

A powerful biosonar enables the location of prey at long ranges, but each click also ensonifies a large volume of water as well as seafloor and sea surface interfaces, leading to a potentially complex and slowly decaying auditory scene for the animal to decode. It is conventionally assumed that echolocators faced with rich auditory scenes attempt to avoid range ambiguity of strong echoes from distant targets by clicking slowly enough to encompass the strong reflectors in the ensonified scene (Wisniewska et al. 2012). This clicking behaviour, however, would not provide rapid updates on the immediate surroundings. Echoes from the seafloor were recorded by the tags as soon as whales started echolocating, indicating that when whales are pointing downwards, they inevitably ensonify the seafloor with their long-range sonar. The sperm whales studied here focused their attention on nearby layers of prey while descending, despite ambiguous echoes from the seafloor ensonified by preceding clicks (Fig. 4e). This implies that sperm whales employ auditory stream segregation to organize ambiguous echoes when encountering pulse-echo overlap, a capacity that may be crucial for predators with long-range biosonar to focus their attention on nearby targets while operating in a complex reverberant auditory scene. As the whales approached within about 1000 m of the seafloor, they adjusted their ICI to track the range to the seafloor (Fig. 4e, f). This suggests that seafloor echoes may be so strong that whales are no longer able to decode prey echoes among the reverberation (Moss and Surlykke 2001, 2010). Further, attention to seafloor echoes may be important in near-bottom deep dives, given that relatively weak prey

echoes must be distinguished from the closely following bottom echoes and a collision with the seafloor while manoeuvring must be avoided.

Search within the prey layer

Once arrived at the selected prey layer, sperm whales navigated within it to locate individual prey (Fig. 2a). Optimal foraging theory predicts that predators put a premium on maximizing net energy gain during foraging to increase fitness (McArthur and Pianka 1966). Hence, the echolocation sampling behaviour throughout the two-dimensional search within a layer should maximize biosonar information flow to minimize search time. It has been hypothesised that sperm whales benefit from visual cues, such as bioluminescence to find prey at depth (Fristrup and Harbison 2002). Blind sperm whales are known to forage successfully (Berzin 1972); however, in general, it is possible that sperm whales use visual cues to find prey. Nevertheless, the consistent use of usual clicking throughout the dives is a strong indicator that the whales are gathering information about prey distribution via echolocation to inform search behaviour. We found that the depth of the search volume, as given by the ICI, immediately after a prey capture attempt was related both to the time between consecutive buzzes (IBI) and the rate at which whales turned after a buzz (Fig. 3e, f). Fast turns imply the encounter of larger water volumes compared to straight-line swimming, where whales need to sample fast enough to have a complete coverage of their surroundings (Madsen et al. 2013). This suggests that the tagged whales adjusted their echolocation sampling rate to their perception of prey distribution either directly based on echoes acquired before the last buzz or indirectly by meeting the sampling requirements set by their own movements as they manoeuvre to stay within a patch. In either case, sperm whales seem to simultaneously track several targets for sequential capture and perceptually organize a multi-target auditory scene formed by echo information. Studies on smaller toothed whales show that they can also handle multi-target acoustic scenes. Porpoises can accurately adjust their sampling rates to new target locations when switching between targets (Wisniewska et al. 2012), and beaked whales sample faster when executing large-scale motor patterns adjusted to several prey items in a patch (Madsen et al. 2013).

Conclusion

Analysis of acoustic and movement data of sperm whales tagged off northern Norway provide a unique insight into the sampling tactics employed by deep sea, endothermic predators with long-range sensing capabilities when searching for and selecting between foraging options with varying exploitation costs. Here, we show that sperm whales employ

directed search behaviour, using priors to guide foraging decisions. They actively modulate their echolocation behaviour to the prey distribution and environmental constraints which change in time and space. The long-range sonar capabilities of sperm whales potentially inform them about multiple prey items in a sensory volume far ahead of them, but such capabilities come at the cost of very low biosonar sampling rates if echoes from distant surfaces such as the seafloor are to arrive before the next ensonification. To solve that trade-off between high rate tracking of nearby prey and avoiding range ambiguity, sperm whales seem to have developed active auditory stream segregation to deal with ambiguous echoes, allowing them to track nearby and fast-moving prey using short ICIs in challenging reverberant conditions. Further, they appear to adjust their sampling rates to both the spatial relationships with individual prey and prey patches, and also to the rate with which they encounter new and unsampled water volumes as they manoeuvre. In combination, these capabilities enable sperm whales to perform directed searches of prey, improving their efficiency and probably contributing to the foraging success of this widely distributed large marine predator.

Acknowledgments We dedicate this paper to Bertel Møhl who has pioneered studies of sperm whale echolocation. We thank all captains and crew during the research cruises for their dedicated assistance. The fieldwork was funded by a grant from the Carlsberg Foundation to B. Møhl and ONR, SERDP and FNU grants to MJ, PJOM and PTM. PJOM was supported by a Royal Society Fellowship, NAS by the International Campus of Excellence of the Canary Islands, MJ by the Marine Alliance for Science and Technology for Scotland and AF partly by project CETOBAPH (grant number CGL2009-1311218).

Ethical standards The study complied with the laws of Norway. The whales were tagged under permit no. 2005/7720-1 to PTM and no. S-2007/61201 to P. Kvadheim from the Norwegian Animal Research Authority. The tagging methodology was approved by the Woods Hole Oceanographic Institution animal use and care committee.

References

- Aguilar Soto N, Johnson MP, Madsen PT, Díaz F, Domínguez I, Brito A, Tyack P (2008) Cheetahs of the deep sea: deep foraging sprints in short-finned pilot whales off Tenerife (Canary Islands). *J Anim Ecol* 77:936–947
- Anderson MJ, Braak C.J.F. (2003) Permutation test for multi-factorial analysis of variance. *J Stat Comput Simul* 73:85–113
- Angel M, Boxshall G (1990) Life in the benthic boundary layer: connections to the mid-water and sea floor [and Discussion]. *Phil Trans R Soc A* 331:15–28
- Arranz P, Aguilar Soto N, Madsen PT, Brito A, Bordes F, Johnson MP (2011) Following a foraging fish-finder: diel habitat use of Blainville's beaked whales revealed by echolocation. *PLoS ONE* 6:e28353
- Au WWL (1993) *The sonar of dolphins*. Springer, New York
- Au WWL, Benoit-Bird KJ (2003) Automatic gain control in the echolocation system of dolphins. *Nature* 423:861–863
- Bar-Shalom Y, Li XR, Kirubarajan T (2004) *Estimation with applications to tracking and navigation: theory algorithms and software*. Wiley, New York
- Bell WJ (1991) *Searching behaviour—the behavioural ecology of finding resources*. Chapman and Hall, London
- Berzin AA (1972) *The sperm whale*. Israel Program for Scientific Translations, Jerusalem
- Blachowiak-Samolyk K, Kwasniewski S, Richardson K, Dmoch K, Hansen E, Hop H, Falk-Petersen S, Mouritsen LT (2006) Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Mar Ecol Prog Ser* 308:101–116
- Costa DP, Gales NJ (2003) Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecol Monogr* 73:27–43
- Dall SRX, Giraldeau L, Olsson O, McNamara JM, Stephens DW (2005) Information and its use by animals in evolutionary ecology. *Trends Ecol Evol* 20:187–193
- Crocker DE, Gales NJ, Costa DP (2001) Swimming and foraging strategies of New Zealand sea lions (*Phocarctos hookeri*). *J Zool* 254: 267–277
- Dehnhardt G, Mauck B, Hanke W, Bleckmann H (2001) Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). *Science* 293:102–104
- Fox J (2002) *An R and S-Plus companion to applied regression*. Sage, CA
- Fristrup KM, Harbison GR (2002) How do sperm whales catch squids? *Mar Mamm Sci* 18:42–54
- Gallon SL, Sparling CE, Georges J-Y, Fedak MA, Biuw M, Thompson D (2007) How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. *J Exp Biol* 210:3285–3294
- Johnson MP, Tyack PL (2003) A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J Ocean Eng* 28:3–12
- Johnson MP, Hickmott LS, Aguilar Soto N, Madsen PT (2008) Echolocation behaviour adapted to prey in foraging Blainville's beaked whale (*Mesoplodon densirostris*). *Proc R Soc Lond B* 275: 133–139
- Kramer DL (1988) The behavioral ecology of air breathing by aquatic animals. *Can J Zool* 66:89–94
- Kuhn CE, Crocker DE, Tremblay Y, Costa DP (2009) Time to eat: measurements of feeding behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris*. *J Anim Ecol* 78:513–523
- Lettevall E, Richter C, Jaquet N, Slooten E, Dawson S, Whitehead H, Christal J, Howard PM (2002) Social structure and residency in aggregations of male sperm whales. *Can J Zool* 80:1189–1196
- Lima SL, Zollner PA (1996) Towards a behavioural ecology of ecological landscape. *Trends Ecol Evol* 11:131–135
- Louâpre P, Baaren J, Pierre JS, Alphen JJM (2011) Information gleaned and former patch quality determine foraging behavior of parasitic wasps. *Behav Ecol* 22:1064–1069
- Madsen PT, Surlykke A (2013) Functional convergence in bat and toothed whale. *Physiology* 28:276–283
- Madsen PT, Wahlberg M, Møhl B (2002a) Male sperm whale (*Physeter macrocephalus*) acoustics in a high-latitude habitat: implications for echolocation and communication. *Behav Ecol Sociobiol* 53:31–41
- Madsen PT, Payne R, Kristiansen NU, Wahlberg M, Kerr I, Møhl B (2002b) Sperm whale sound production studied with ultrasound time/depth-recording tags. *J Exp Biol* 205:1899–1906
- Madsen PT, Johnson M, Aguilar Soto N, Zimmer WMX, Tyack P (2005) Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J Exp Biol* 208:181–194
- Madsen PT, Wilson M, Johnson MP, Hanlon RT, Bocconcelli A, Aguilar Soto N, Tyack PL (2007) Clicking for calamari: toothed whales can echolocate squid *Loligo pealeii*. *Aquat Biol* 1:141–150
- Madsen PT, Aguilar Soto N, Arranz P, Johnson M (2013) Echolocation in Blainville's beaked whales (*Mesoplodon densirostris*). *J Comp Physiol A* 1–19

- Martin AR, Clarke MR (1986) The diet of sperm whales (*Physeter macrocephalus*) captured between Iceland and Greenland. *J Mar Biol Assoc UK* 66:779–790
- McArthur RH, Pianka ER (1966) On the optimal use of a patchy environment. *Am Nat* 100:603–610
- McNamara JM, Green RF, Olsson O (2006) Bayes' theorem and its applications in animal behaviour. *Oikos* 112:243–251
- Miller PJO, Johnson M, Tyack PL, Terray EA (2004a) Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J Exp Biol* 207:1953–1967
- Miller PJO, Johnson MP, Tyack PL (2004b) Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proc R Soc Lond B* 271:2239–2247
- Møhl B, Wahlberg M, Madsen PT, Heerfordt A, Lucas A (2003) The monopulsed nature of sperm whale clicks. *J Acoust Soc Am* 114:1143–1154
- Moss CF, Surlykke A (2001) Auditory scene analysis by echolocation in bats. *J Acoust Soc Am* 110:2207–2226
- Moss CF, Surlykke A (2010) Probing the natural scene by echolocating bats. *Front Behav Neurosci* 4:1–16
- Naito Y, Costa DP, Adachi T, Robinson PW, Fowler M, Takahashi A (2013) Unravelling the mysteries of a mesopelagic diet: a large apex predator specializes on small prey. *Funct Ecol* 27:710–717
- Nelson ME, MacIver MA (2006) Sensory acquisition in active sensing systems. *J Comp Physiol A* 192:573–586
- Oliveira C, Wahlberg M, Johnson M, Miller PJ, Madsen PT (2013) The function of male sperm whale slow clicks in a high latitude habitat: communication, echolocation, or prey debilitation? *J Acoust Soc Am* 133:3135–3144
- Penner RH (1988) Attention and detection in dolphin echolocation. In: Nachtigall PE, Moore PWB (eds) *Animal sonar process and performance*. Plenum Press, New York and London, pp 707–713
- R Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Ropert-Coudert Y, Kato A, Baudat J, Bost C, Le Maho Y, Naito Y (2001) Time/depth usage of Adélie penguins: an approach based on dive angles. *Polar Biol* 24:467–470
- Santos M, Pierce G, Boyle P, Reid R, Ross H, Patterson I, Kinze C, Tougaard S, Lick R, Piatkowski U (1999) Stomach contents of sperm whales *Physeter macrocephalus* stranded in the North Sea 1990–1996. *Mar Ecol Prog Ser* 183:281–294
- Sato K, Charrassin J, Bost C, Naito Y (2004) Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J Exp Biol* 207:4057–4065
- Schnitzler H-U, Moss CF, Denzinger A (2003) From spatial orientation to food acquisition in echolocating bats. *Trends Ecol Evol* 18:386–394
- Steele JH (1989) The ocean 'landscape'. *Landscape Ecol* 3:185–192
- Teloni V, Johnson M, Miller PJO, Tyack PL (2008) Shallow food for deep divers: dynamic foraging behavior of male sperm whales in a high latitude habitat. *J Exp Mar Biol Ecol* 354:119–131
- Thode A, Melling DK, Stienessen S, Martinez A, Mullin K (2002) Depth-dependent acoustic features of diving sperm whales (*Physeter macrocephalus*) in the Gulf of Mexico. *J Acoust Soc Am* 112:308–321
- Thompson D, Fedak M (2001) How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Anim Behav* 61:287–296
- Vacquié-Garcia J, Royer F, Dragon AC, Viviant M, Bailleul F, Guinet C (2012) Foraging in the darkness of the southern ocean: influence of bioluminescence on a deep diving predator. *PLoS ONE* 7:e43565
- Verfuß UK, Miller LA, Schnitzler H-U (2005) Spatial orientation in echolocating harbour porpoises (*Phocoena phocoena*). *J Exp Biol* 208:3385–3394
- Watwood SL, Miller PJO, Johnson M, Madsen PT, Tyack PL (2006) Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J Anim Ecol* 75:814–825
- Wilson RP (2003) Penguins predict their performance. *Mar Ecol-Prog Ser* 249:305–310
- Wisniewska DM, Johnson M, Beedholm K, Wahlberg M, Madsen PT (2012) Acoustic gaze adjustments during active target selection in echolocating porpoises. *J Exp Biol* 215:4358–4373
- Zimmer WMX, Johnson MP, D'Amico A, Tyack PL (2003) Combining data from a multisensor tag and passive sonar to determine the diving behavior of a sperm whale (*Physeter macrocephalus*). *IEEE J Ocean Eng* 28:13–28
- Zimmer WMX, Madsen PT, Teloni V, Johnson M, Tyack PL (2005) Off-axis effects on the multipulse structure of sperm whale usual clicks with implications for sound production. *J Acoust Soc Am* 118:3337–3345
- Zollner PA, Lima SL (1999) Search strategies for landscape-level interpatch movements. *Ecol Soc Am* 80:1019–1030