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

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Abstract

Predators make foraging decisions based upon prior and 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

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 strategies, using environmental information as priors to strategically accommodate foraging behaviour. For example, Adélie (*Pygoscelis adeliae*) and Macaroni (*Eudyptes chrysolophus*) penguins adjust the time devoted to transit between the surface and the foraging depth according to the foraging success of the previous dive (Ropert-Coudert et al. 2001; Sato et al. 2004). A steep descend enables a direct transport to the prey patch depth, whereas descending at shallow angles allows extending the search for resources to a broader swath of the water column (Sato et al. 2004). Moreover, Magellanic penguins (*Spheniscus magellanicus*) adapt pre-surfacing periods and vertical speeds to foraging depth, showing prey predictability (Wilson 2003). Gallon and colleagues (2007) demonstrated that grey seals (*Halichoerus grypus*) anticipate dive performance by adjusting swim speed to resource accessibility in order to spend more time within the prey patch.

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 (Wisniewska et al. 2012), 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 range over which the animal is focusing its attention (Wisniewska et al. 2012).

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 230 dB re 1μPa (peak-peak) (Madsen et al. 2002b; 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. 2002a; 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 (Santos et al. 1999) achieved by this large air-breathing predator inhabiting the deep waters of all oceans.

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 3-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. 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 of the tag 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 *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 1.5 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 five seconds.

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 (Møhl et al. 2003, Madsen et al. 2002a). 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 inter-click intervals (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 sea-floor 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 (Figure 1; see Arranz et al. 2011) constructed from 3.5 s sound segments synchronized to each outgoing click. These enabled detection of sea-floor echoes at ranges up to 2580 m from the whale assuming an average sound speed of 1475 m/s in this roughly iso-velocity region (Teloni et al. 2008). Echoes from the sea-floor appeared within the echograms as sequences of reverberant echoes with slowly varying two-way travel time (TWT). The TWT/2 was multiplied by 1475 m/s to estimate the altitude of the whale above the sea-floor, which was then added to the whale depth to estimate the sea-floor depth. To estimate altitude over short intervals in which no echoes were detected, the sea-floor 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.

Statistics

Log transformations were donefor non-linear relations between continuous variables. *Post hoc* analysis in R (R Development 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 hours of combined acoustic and movement data were collected from eight physically mature (>12 m) male sperm whales, 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 (Figure 2A). During shallow dives the whales targeted predominantly epipelagic prey and during deep dives the whales mostly foraged benthopelagically (Figure 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: (1) shallow prey, i.e. <220 m; (2) medium, between 220 and 700 m; and (3) deep prey >700m (Figure 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 (Figure 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). If sperm whales rely primarily on sensory information gained during the descent to decide on where to forage, 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<<0.001, n=161 dives with buzzes, 8 whales) (Figure 3A), revealing that sperm whales started clicking later when foraging on deep prey (Figure 3B). The initial ICI (inspection range) and the SOC depth were also significantly positively correlated (Spearman's ρ: 0.81, p<<0.001, n=175 dives, 8 whales) (Figure 3C), with whales clicking faster at the start of shallower dives (Figure 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 sea-floor 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 sea-floor to avoid range ambiguity from this strong reflector, and should reduce accordingly as the whale descends so as to track the sea-floor (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 sea-floor 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.

Sea-floor echoes were found in 170 dives. Visual inspection of the data showed two distinct ICI patterns (Figure 4). Dives to depths < 1200 m (n=158, 8 individuals) had widely varying ICIs throughout the descent (mean ICI: 0.84 s; std 0.22) that did not appear to consistently track either targeted prey layers (Spearman's ρ=0.13) or the sea-floor (Spearman's ρ=0.02) (Figure 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.

In contrast, in all dives exceeding 1200 m (n=17, 3 individuals), whales produced distinctive sawtooth-patterned ICIs during descents, comprising intervals with consistently decreasing ICIs bracketed by occasional step increases (Figure 4E and F). This pattern indicated that the ICI was tracking different depth layers between 500 and 1300 m sequentially throughout the descent, evidenced by the depth of the acoustic gaze during the descents as exemplified in Figure 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 (Figure 4E). In all 17 deep dives, the final tracked depth layer coincided with the sea-floor. During much of the bottom phase of these dives the three whales foraged within the benthic boundary layer (nominally 0-200 m above the sea-floor, (Angel and Boxhall 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 sea-floor. 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 the behaviour is only beneficial during deep dives which may pass several depth layers of prey.

Search within the prey layer

Assuming that a new prey is targeted during each buzz (Wisniewska et al. 2012a; Madsen et al. 2013), the time lapse between consecutive buzzes (i.e., the inter-buzz interval, 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: (1) the time to the next buzz (IBI), and (2) the mean turning rate over the first five seconds 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 (Madsen et al. 2013). The relationship between initial clicking rate and IBI was significant (Spearman's ρ: 0.58, $p<<0.001$, $n=615$, 8 whales), but given the r^2 value of 0.34 (Figure 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, $p<<0.001$, $n=615$, 8 whales; Figure 3F). No strong correlation between turning rate and IBI was found ($r^2=0.1$, Spearman's ρ:-0.3, $p<<0.001$, $n=615$, 8 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 (Figure 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 (Figure 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 that expectations should be less important for predators such as sperm whales that are uniquely 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 (Figure 2A). Although the whales occasionally switched between shallow and medium prey within a dive (Figure 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 3-dimensional search problem into successive 1-dimensional (i.e., depth) and 2-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; Arranz et al. 2011; Kuhn et al. 2009). 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, such as several pinnipeds (Dehnhardt et al. 2001; Vacquié-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 sensory range. 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 (Figure 3C and D). Further, when performing deep dives sperm whales did not begin echolocating until they had passed the depth of shallow prey (Figure 3A and B). Sperm whales are potentially able to profile the vertical distribution of prey resources out to a range in excess of 1000 m (Møhl 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 sea-floor (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 (Naito et al. 2013; Aguilar Soto et al. 2008). 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 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. (2002b) 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 are apparently non-social animals and that they generally forage several km apart (Letteval et al. 2002), suggesting that male sperm whales mainly usetheir own information to make foraging decisions. In contrast to passive sensing, echolocation provides larger sensory volumes, resulting in more extensive information gathering in light-limited environments than is possible with vision or tactile senses (Costa and Gales 2003). Given their long-range sensory capabilities, sperm whales may glean information about prey while sampling within but also before arriving at a prey patch (Louâpre 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 degrees (Møhl 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 target slow 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 sea-floor nor the prey layer (Figure 4A-D), while whales performing dives to >1200 m tracked sequentially discrete layers, making repetitive downward ICI adjustments (Figure 4E and 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 (Figure 2) with widely spaced prey, as indicated by the long IBIs. In these dives, whales started clicking immediately upon leaving the surface (Figure 3A and B) and dove at a relatively shallow angle (as evidenced by the low vertical rate in shallow descents, Figure 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 (Figure 4A and B). Long ICIs allow long-range target detection, appropriate for detecting the sparsely distributed prey encountered in these shallow dives.

During the deepest dives (>1200m depth) sperm whales foraged opportunistically during descents (Figure 2), actively changing their acoustic gaze by modulating ICIs to sequentially track discrete prey layers (Figure 4E and F). When swimming vertically towards a prey layer, whales receive echoes from a discrete delay window corresponding to the depth range of the layer. As exemplified in Figure 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; Figure 4C and D) is more difficult to explain. Sperm whales appeared to forage over a broad depth range in these dives (Figure 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 (Figure 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 sea-floor 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 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 sea-floor were recorded by the tags as soon as whales started echolocating, indicating that when whales are pointing downwards, they inevitably ensonify the sea-floor 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 sea-floor ensonified by preceding clicks (Figure 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 sea-floor, they adjusted their ICI to track the range to the sea-floor (Figure 4E and F). This suggests that sea-floor echoes may be so strong that whales are no longer able to decode prey echoes among the reverberation (Moss and Surlykke

2010; Moss and Surlykke 2010). Further, attention to sea-floor 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 sea-floor 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 (Figure 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 2-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 Harbinson 2002). Although this hypothesis cannot be rejected from the data at hand, the small, laterally placed eyes of sperm whales and 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 (Figure 3E and F). 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. Fast turns imply the encounter of larger water volumes compared to straight-line swimming, and whales need to sample fast enough to have a complete coverage of their surroundings (Madsen et al. 2013). Hence, 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 showed that sperm whales employ directed search behaviour, using priors to guide foraging decisions. They actively modulated 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 sea-floor 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.

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Ethical standards

The study complied with the laws of Norway. The whales were tagged under permits no. 2005/7720-1 to PTM and no. S-2007/61201 to P. Kvadsheim from the Norwegian Animal Research Authority.

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Legends

Figure 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 out-going 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. Sea-surface and sea-floor are shown as sequences of reverberant echoes with slowly varying two-way travel time, allowing the calculation of the distances from the whale to each surface. 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.

Figure 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 white dot marks a prey capture attempt (buzz). The thick grey line shows the estimated location of the sea-floor. 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 220m, and among medium and deep dives at 700m.

Figure 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 10 first 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 seconds after each buzz (n=615).

Figure 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 is given by ½ ICI added to the whale depth (blue dots) 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 sea-floor echoes. Relation between ICI and the TWT to the sea-floor for the descent phase of shallow dives (< 200 m, 17 dives randomly selected from a total of 84 dives

performed by 8 animals) (B), medium dives (up to 1200 m, 17 dives randomly selected from a total of 74 dives performed by 8 animals) (D) and the deepest dives (>1200 m depth, 17 dives performed by 3 animals) (F), with colour indicating whale ID. The dashed grey line marks the relation ICI = TWT to the sea-floor.

Table 1

Information on tag placements. 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 25m. Based on the distribution of buzz depth dives were divided according to their maximum depth in shallow (<220 m), medium (<700m) and deep (>700m).

Whale code	Year	Time Recording	# Foraging Dives	# Shallow Dives	# Medium Dives	# Deep Dives	# Clicks
# 196a	2005	24h 17'	29	24 (82.8%)	5 (17.2%)	0	51860
# 199a	2005	20h 42'	28	20 (71.4%)	4 (14.3%)	4 (14.3%)	55945
# 199b	2005	16h 46'	17	10 (58.8%)	2 (11.7%)	5 (29.4%)	37977
# 199c	2005	16h 47'	11	2 (18.2%)	1 (9.1%)	8 (72.7%)	22108
# 153a	2009	12h 34 ’	15	10 (66.7%)	5 (33.3%)	0	31625
# 147a	2010	18h 29’	19	2 (10.5%)	17 (89.5%)	0	28613
# 149a	2010	17h 31’	27	15 (55.6%)	8 (29.6%)	4(14.8%)	46528
# 150a	2010	16h 59’	29	1 (3.4%)	28 (96.6%)	0	30875
Total		144h 5’	175	84 (48%)	70 (40%)	21 (12%)	305531

Figures:

Figure 1.

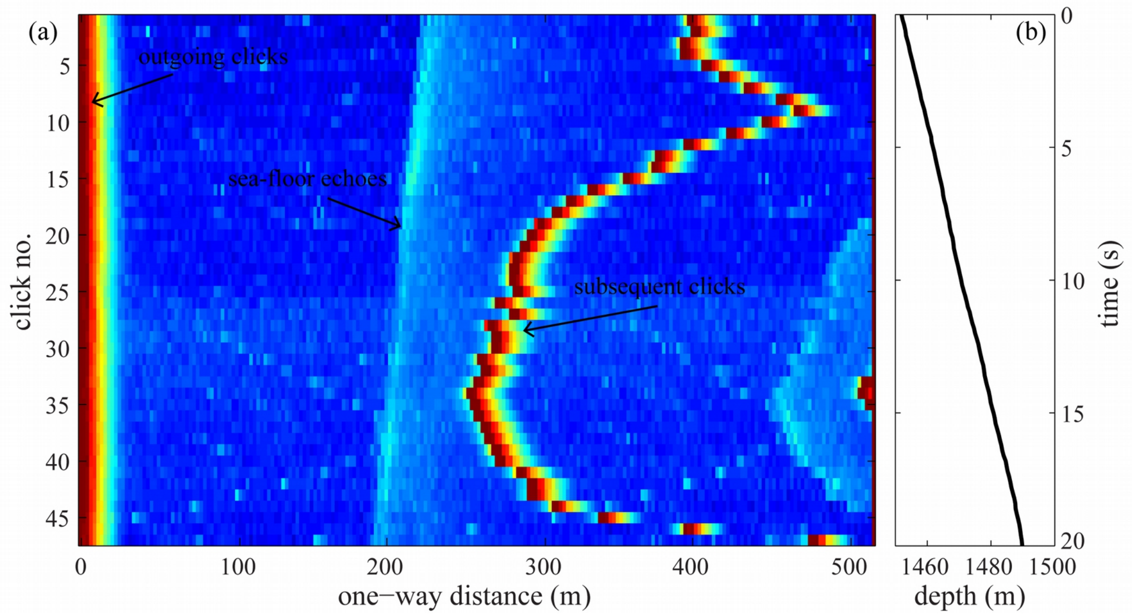


Figure 2.

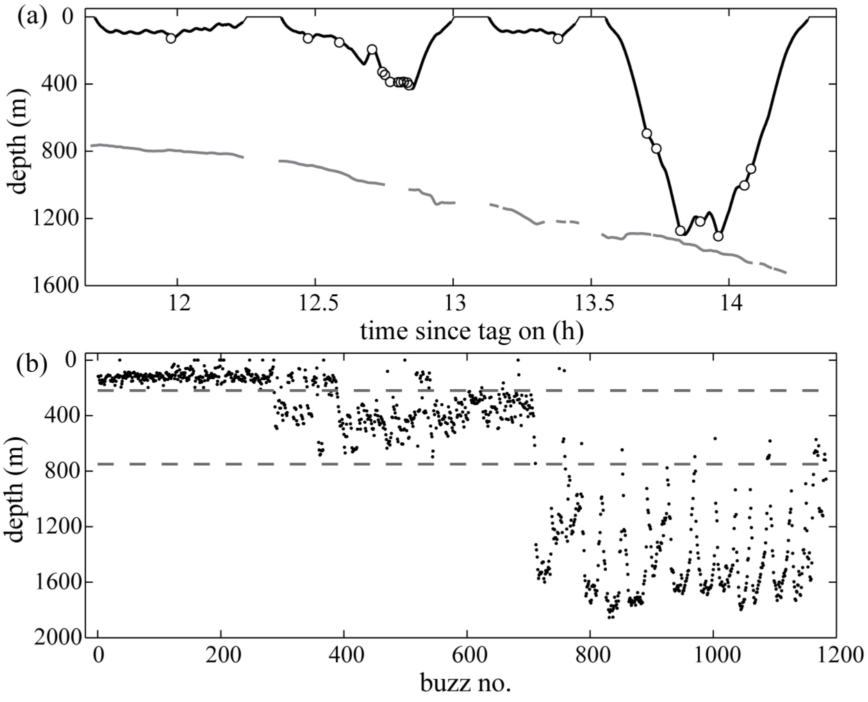


Figure 3.

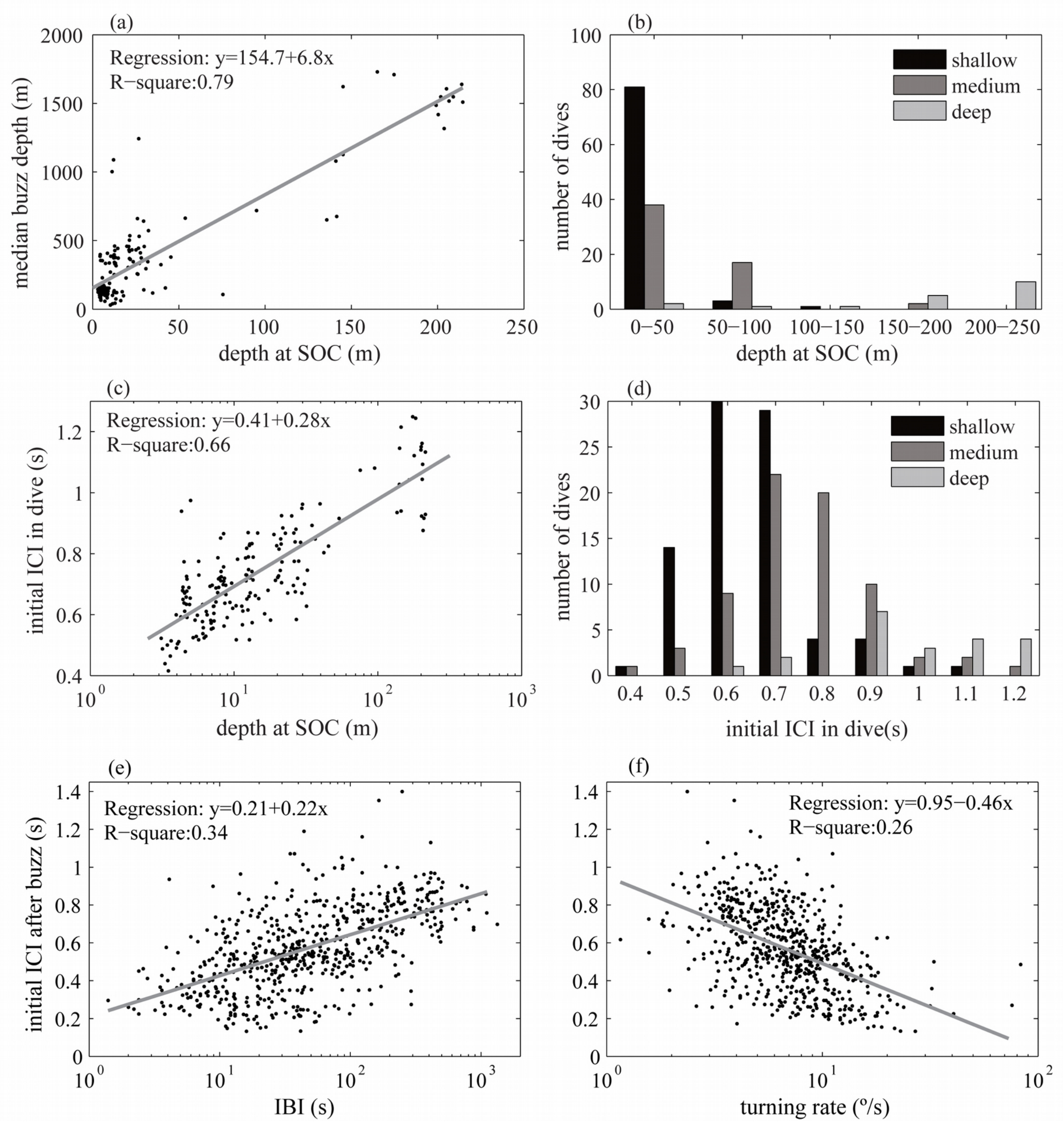
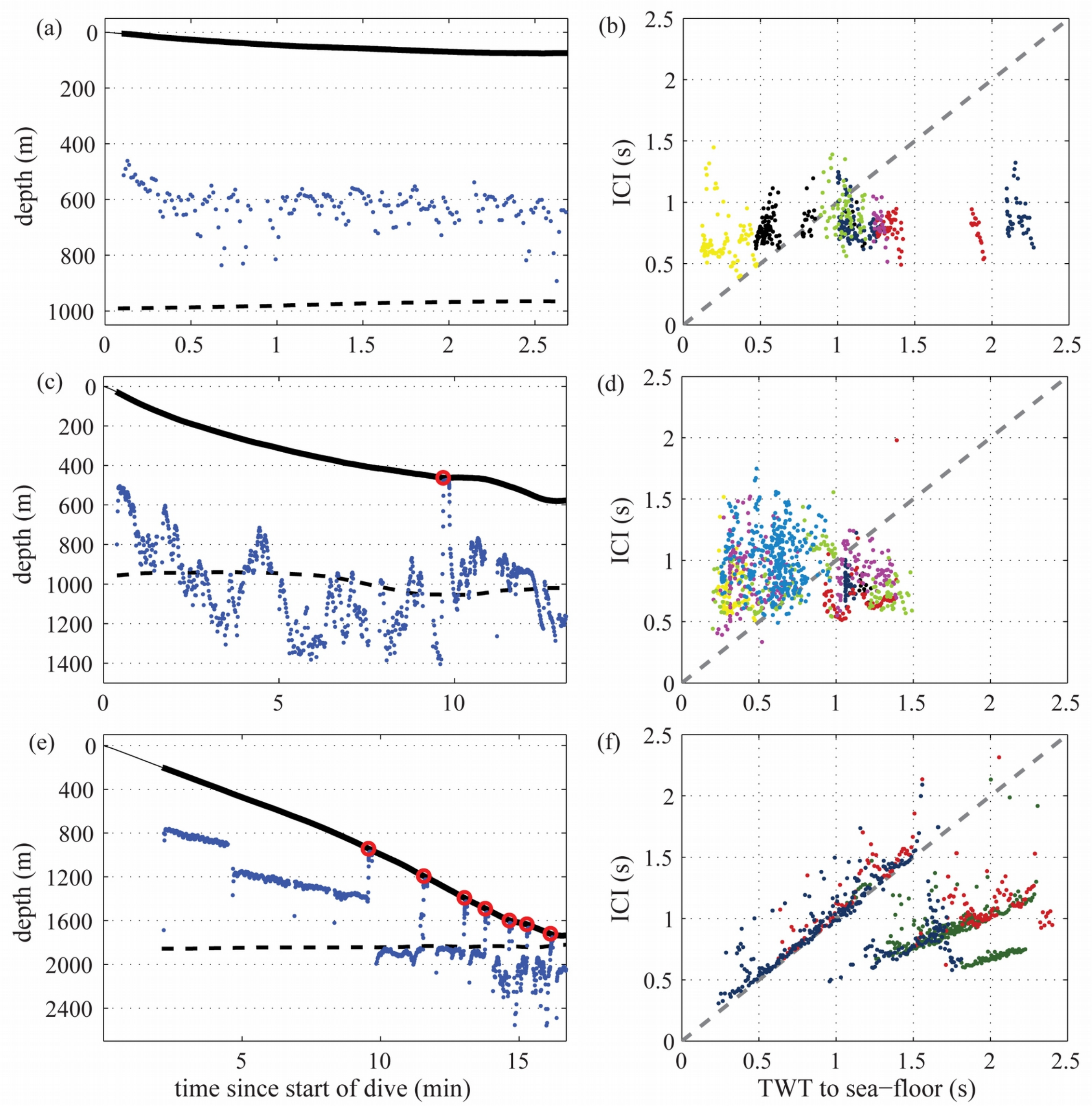

(a)
Regression: y=154.7+6.8x
R−square:0.79
median buzz depth (m)
2000
1500
1000
500
0
0
50
100
150
200
250
depth at SOC (m)
(b)
100
80
60
40
20
0
number of dives
shallow
medium
deep
0−50
50−100
100−150
150−200
200−250
depth at SOC (m)
(c)
Regression: y=0.41+0.28x
R−square:0.66
initial ICI in dive (s)
1.2
1
0.8
0.6
0.4
10^0
10^1
10^2
10^3
depth at SOC (m)
(d)
30
25
20
15
10
5
0
number of dives
shallow
medium
deep
0.4
0.5
0.6
0.7
0.8
0.9
1
1.1
1.2
initial ICI in dive(s)
(e)
Regression: y=0.21+0.22x
R−square:0.34
initial ICI after buzz (s)
1.4
1.2
1
0.8
0.6
0.4
0.2
0
10^0
10^1
10^2
10^3
IBI (s)
(f)
Regression: y=0.95−0.46x
R−square:0.26
1.4
1.2
1
0.8
0.6
0.4
0.2
0
10^0
10^1
10^2
turning rate (°/s)

Figure 4.


(a)
depth (m)
0
200
400
600
800
1000
0
0.5
1
1.5
2
2.5
(b)
ICI (s)
2.5
2
1.5
1
0.5
0
0
0.5
1
1.5
2
2.5
(c)
depth (m)
0
200
400
600
800
1000
1200
1400
0
5
10
(d)
ICI (s)
2.5
2
1.5
1
0.5
0
0
0.5
1
1.5
2
2.5
(e)
depth (m)
0
400
800
1200
1600
2000
2400
5
10
15
time since start of dive (min)
(f)
ICI (s)
2.5
2
1.5
1
0.5
0
0
0.5
1
1.5
2
2.5
TWT to sea−floor (s)