

RESEARCH ARTICLE

Risso's dolphins plan foraging dives

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ABSTRACT

Humans remember the past and use that information to plan future actions. Lab experiments that test memory for the location of food show that animals have a similar capability to act in anticipation of future needs, but less work has been done on animals foraging in the wild. We hypothesized that planning abilities are critical and common in breath-hold divers who adjust each dive to forage on prey varying in quality, location and predictability within constraints of limited oxygen availability. We equipped Risso's dolphins with sound-and-motion recording tags to reveal where they focus their attention through their externally observable echolocation and how they fine tune search strategies in response to expected and observed prey distribution. The information from the dolphins was integrated with synoptic prey data obtained from echosounders on an underwater vehicle. At the start of the dives, whales adjusted their echolocation inspection ranges in ways that suggest planning to forage at a particular depth. Once entering a productive prey layer, dolphins reduced their search range comparable to the scale of patches within the layer, suggesting that they were using echolocation to select prey within the patch. On ascent, their search range increased, indicating that they decided to stop foraging within that layer and started searching for prey in shallower layers. Information about prey, learned throughout the dive, was used to plan foraging in the next dive. Our results demonstrate that planning for future dives is modulated by spatial memory derived from multi-modal prey sampling (echoic, visual and capture) during earlier dives.

KEY WORDS: Predator–prey dynamics, Perceptual range, *Grampus griseus*, Animal decision making, Episodic-like memory, Foraging behaviour

INTRODUCTION

Animals use past experiences to make decisions about future events (Osvath and Martin-Ordas, 2014; Pfeiffer and Foster, 2013). The ability to remember information about resource distribution and use this to plan foraging allows them to reduce their search time and increase foraging efficiency, representing a potential target for natural selection (Benhamou, 1994; Sayers and Menzel, 2012). This ability of an individual to recall temporally dated events and

temporal–spatial relationships among these events is called ‘episodic memory’ in humans (Tulving and Donaldson, 1972). The ability to go back in time (episodic memory) and to project into the future is termed ‘mental time travel’ (Suddendorf and Corballis, 1997; Cheke and Clayton, 2010) and was regarded, until recently, as an exclusively human ability. This remains a contentious subject in comparative cognition (Shettleworth, 2007; Vonk and Shackelford, 2012; Roberts et al., 2012). While challenging to demonstrate in non-linguistic animals, three behavioural criteria, namely content, structure and flexibility, have been proposed for testing episodic-like memory and future planning in animals (Clayton et al., 2003). Research in the last decade has sought to explore the capacity for informed foresight in non-humans, particularly whether an animal's behaviour can be driven by the anticipation of a future need that is different from its current motivational state (Suddendorf and Corballis, 1997).

A series of innovative studies have shown that captive birds learn to provide for upcoming needs, catching food where they have learned that it will not be available when they are hungry in the future (Raby et al., 2007). Rats modify consumption of one food type in anticipation of access to another (Crystal, 2012). Apes trained in the lab to select an object during a short time window can forego selecting an object that would satisfy an immediate motivation and instead select a tool that they plan to use for obtaining something better hours later (Mulcahy and Call, 2006; Osvath and Osvath, 2008).

Air-breathing marine predators that forage at depth must alternate between two spatially segregated resources: food at depth and oxygen at the surface. Thus, we hypothesized that they have the ability to plan their activities according to past experiences and their needs for both resources. Evidence of this is found in penguins and pinnipeds, which increase their oxygen store when they expect to forage deeper (Wilson, 2003; Sato et al., 2011; Gallon et al., 2007). Similarly, male sperm whales in high-latitude habitats adjust their echolocating sampling behaviour at the start of dives relative to the expected range to prey (Fais et al., 2015). While these examples suggest planning in different species, they lack data about both prior exploratory sensing behaviour and the environmental context of animal decisions – specifically, the fine-scale distribution of ephemeral prey – data that are important for experimental demonstrations of future planning.

Echolocating predators acquire sensory information by scanning the environment using directional sonar pulses and evaluating the time delay from pulse to echo to estimate range (Surlykke et al., 2009; Seibert et al., 2013). We call the range associated with the round-trip travel time of the inter-click interval the ‘inspection range’. To avoid pulse–echo overlap, which may result in ambiguous range estimations, echolocating species generally adjust their click rate to allow echoes to arrive before the next pulse is emitted (Simmons, 1973; Kadane and Penner, 1983). This means that through active acoustic sensing, they reveal where they are focusing their attention to navigate and find prey. Moreover, they

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produce fast click series termed ‘buzzes’ when they attempt to capture prey (Miller et al., 2004; Johnson et al., 2004; Arranz et al., 2016), providing an indicator of foraging choices. This makes biosonar an effective sensory system for exploring the manner in which animals actively seek information through their senses and how they process, retain and decide to act on it, when combined with the resulting foraging behaviour and data on prey distribution.

The marine environment is characterized by a high level of patchiness and food resources in shallow waters can be ephemeral and occur at very different densities (Steele, 1976). In contrast, small midwater animals that serve as important prey for many species often form ‘deep scattering layers’ that extend horizontally for tens of kilometres or more within a relatively constant depth range. While predictable, these layers may represent a less-accessible resource for an animal that must hold its breath to forage at depth. The presence of unpredictable shallow resources with more predictable deep prey introduces the problem of decision making for air-breathing marine predators. One solution for these predators would be to sample prey opportunistically (Shettleworth, 1998), then plan their foraging dives accordingly (Dunlap and Stephens, 2012) within the constraints imposed by limited oxygen availability. Echolocating divers may be able to assess current resources using their long-range biosonar (Au, 1993; Arranz et al., 2016), which could be a critical capability needed to decide early in dives where to forage (Au et al., 2000). The maximum sonar range of delphinids is thought to be <100 m for individual prey items (Madsen et al., 2007), but if dense prey layers provide stronger sonar targets, this could allow them to be detected at greater ranges (Au and Lammers, 2016). While search time might be reduced by echolocation on descent, foraging efficiency may be further increased by remembering information about prey location, type and value from the last dive and using it to plan the next forage before starting the next dive (Benhamou, 1994; Sayers and Menzel, 2012; Barraquand et al., 2009). If so, echolocating marine predators represent a promising model for studying whether animals can recall past events to strategize for the future.

We investigated whether the echolocating marine predator Risso’s dolphin, *Grampus griseus* (Cuvier 1812), uses prior information about prey distribution to plan foraging. More specifically, we explored whether these dolphins use information about prey features from previous dives to plan the next foraging dive and how these

plans are affected by prey encounter rates during the foraging dive. As analysis of the relationship between environmental input and behavioural output is required to understand the processes that mediate between them (Shettleworth, 2001), here we used fine-scale predator behavioural data recorded with suction-cup-attached sound-and-motion recording tags (Johnson and Tyack, 2003) coupled with independent and concurrent prey measurements obtained from shipboard and underwater vehicle-based echosounder systems. We present an integrative study linking perception, memory and sensorimotor control information from a free-ranging predator to *in situ* prey fields, providing the context in which animal decisions are executed under natural conditions. We used these data to investigate the underlying cognitive mechanisms predators use to find prey and forage effectively in dynamic environments.

MATERIALS AND METHODS

Data collection

Predators

Grampus griseus, off San Clemente Island, CA, USA, were equipped with high-resolution, sound-and-movement recording tags (DTags; Johnson and Tyack, 2003) between 2011 and 2016. The tagging procedure is described in detail in Arranz et al. (2016). Focal follows of tagged animals were conducted from the tag boat using VHF radio tracking equipment within a minimum range of 25 m. The tracks of tagged dolphins were geo-referenced when possible from visual observations using GPS (Fig. 1). Acoustic data were sampled in stereo with a 16-bit resolution at 240 kHz. Pressure sensor, tri-axial accelerometer and magnetometer data were sampled at 200 Hz per channel and decimated to 25 Hz for analysis. Pitch and depth of the tagged dolphins were derived from orientation and pressure sensors on the tags (Johnson and Tyack, 2003). Tag data processing and analysis were carried out using MATLAB (<http://www.mathworks.es/>), DTag toolbox and custom functions.

Of the 33 tagged dolphins, 18 were exposed to playbacks of acoustic stimuli as part of the Southern California Behavioral Response Study (SOCAL-BRS; Southall et al., 2012), but only behavioural data recorded before the onset of the playbacks were analysed for exposed dolphins. Dives were defined as vertical excursions >20 m depth. Dive bouts were defined as a group of dives ending within 10 min of the start of the next one. These depth

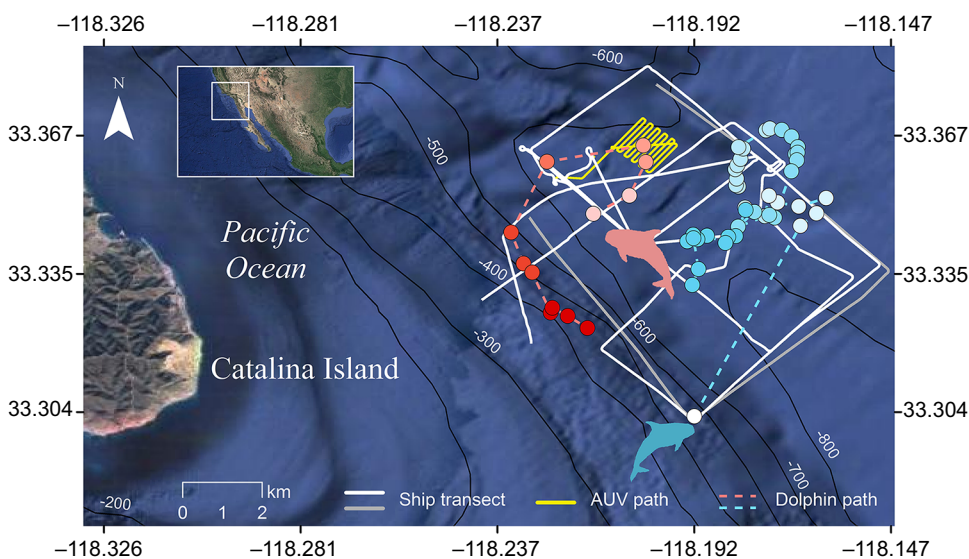


Fig. 1. Map of hydroacoustic survey and dolphin tagging experiments off Catalina Island. Lines represent acoustic transects, white and grey for the ship and yellow for the robot; dotted lines represent the tracks of the tagged dolphins, inferred from surface observations.

and time criteria were selected based on the change of slope of the log-survivorship plot of maximum dive depths and inter-dive intervals, respectively (Slater and Lester, 1982). Dives that started within 15 min of attachment of the tag were excluded to remove data potentially affected by the tagging procedure. Incomplete dives at the start or end of the record were also excluded. Five tag recordings did not have sufficient data to meet our criteria and were not further analysed.

Prey

Synchronous data on the distribution of prey were obtained for two tagged *G. griseus* (gg13_266b and gg13_267) from ship- and autonomous underwater vehicle (AUV)-based hydroacoustic surveys (split-beam Simrad EK60s at 38 and 120 kHz). An echosounder integrated into a REMUS 600 AUV (Moline et al., 2015) sampled at depths where diving predators were feeding, allowing individual prey animals (targets) to be resolved. Instrument specifications and calibration methods were according to those in Moline et al. (2015). Vessel-based echosounder transects were conducted during the daytime at an average speed of 2 m s^{-1} , covering the sides of a square of $\sim 12 \text{ km}^2$ overlapping in space and time with tagged dolphin tracks (Fig. 1). The AUV sampled at a speed of $\sim 1.5 \text{ m s}^{-1}$ at the depths of identified scattering features. Hydroacoustic data were processed using Ecoview (<http://wetlabs.com/software/ecoview-0>). The maximum acoustic intensity at either 38 or 120 kHz was integrated into 50 cm depth by 1 min time bins before the detection of layers. For each bin, a running 25 m median centred on the bin was calculated vertically to define the background scattering. The removal of the background from the maximum acoustic intensity for each bin revealed the depth distribution of scattering layers. The edges of layers were defined as the first and last locations in a contiguous feature that exceeded the background. The upper and lower boundaries of each depth layer over the sampling area were defined as the third quartile of each edge's depth across the samples. Target strength of individual prey within scattering features measured with the AUV was estimated from echoes of single targets (a single return received per acoustic reverberation volume for each pulse; Sawada et al., 1993), at 38 and 120 kHz, which facilitated coarse taxonomic classification (by frequency response) and size estimation. In addition, these data were used to examine inter-individual and inter-group spacing of prey in layers.

Tag data analysis

Data from the two dolphins for which prey data were available were used to define dive classes by looking at the maximum dive depth and the distribution of the scattering features. Most dives had a maximum depth that fell within one of the layers. Dives with a maximum depth that did not fall into one of the layers (15%) were classified as pertaining to the nearest shallower layer. In shallow dives, the descent and ascent phases were not defined because the shallow boundary of the prey layer (25 m) was just 5 m below the 20 m definition of the start of the dive. For buzz rate analysis involving the large data set ($N=174$ dives from 28 dolphins), including the 26 dolphins where the prey layers were not measured, the bottom phase was defined as deeper than 70% of the maximum depth (Arranz et al., 2016). Echolocation clicks and buzzes were isolated on the recordings from the tagged dolphins following the methods described in Arranz et al. (2016). Foraging dives were defined as dives that contained one or more buzzes recorded from the tagged dolphin, because buzzes indicated prey search and capture (Arranz et al., 2016). The inter-click interval of the dolphins

at a certain pitch angle was used to estimate their inspection slant range. The vertical component of this inspection range equalled the slant range times the sin (pitch). The inspection depth was calculated by adding the depth of the dolphin plus the vertical component of the inspection range. When taken from the first clicks in the dive, the inter-click interval can be used as an indicator of the expected range to prey of an echolocating predator based on information gathered on the previous dive, before new information is gained via echolocation (Fais et al., 2015). The initial inspection range was computed from the maximum inter-click interval of the first three clicks emitted in the dive by the tagged dolphin. We used Spearman's rank ρ to check for monotonic correlations between dolphin and prey variables, as the assumption of linearity failed after comparing them with a fitted versus residual plot. Statistical significance was judged at a critical P -value of 5%.

To compare relative movements of the animals at the bottom phase of dives associated with foraging in different prey layers, we reconstructed the dead-reckoned track of the dolphins (*sensu* Johnson and Tyack, 2003). Swim speed was approximated from the vertical velocity (rate of change of depth) and pitch angle of the dolphins using a Kalman filter. The track was generated by combining swim speed during the bottom phase of the dive with the pitch and heading of the dolphin at a 1 Hz sampling rate. The average pitch angle at the bottom phase of dives was small (7 ± 5 deg, mean \pm s.d.). We acknowledge that the reliability of this speed estimate decreases at such low pitch angles and that we are ignoring water currents that may affect the speed of the animal over the ground. However, as we were comparing relative movements across scattering features, the effect of currents may be negligible and variations in the absolute values may have little impact on the overall conclusions.

Permit details

Experiments were performed under the US National Marine Fisheries Service (NMFS; permit no. 14534-2), Channel Islands National Marine Sanctuary (permit no. 2010-003) (B.L.S., principal investigator for both) and IACUC permits issued to the project investigators.

RESULTS

A total of 9 h of synchronous predator and prey data, comprising sound and movement DTag recordings from 37 dives performed by two dolphins and hydroacoustic mapping of prey within their foraging area, were analysed. Additional DTag data from 26 *G. griseus* tagged in the same general area, amounting to 83.2 h of data and 174 dives, were used to investigate predator search behaviour in relation to foraging rates. A dive was considered as starting the first time the dolphins exceeded 20 m depth after a surfacing and ending at the next surfacing. Dives with one or more buzzes, i.e. prey capture attempts (Arranz et al., 2016), from the tagged dolphins, henceforth referred to as foraging dives, lasted for 1–10 min and contained on average 5 (range: 1–11) buzzes.

Dive and prey data integration

Hydroacoustic surveys concurrent with tag data revealed a strong segregation of biomass vertically in scattered patches 50–150 m across between 100 and 200 m depth, and in three sound-scattering layers, each of which was horizontally continuous (Fig. 2). The three scattering layers were identified as follows: 'shallow' (30–90 m minimum and maximum depths of the layer boundaries averaged for the two datasets, rounded to the nearest 10); 'midwater' (200–300 m, migrating vertically in 24 h cycles) and 'deep'

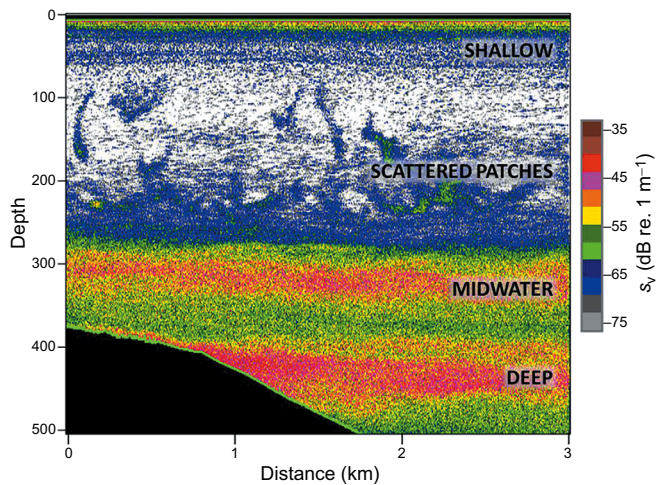


Fig. 2. Longitudinal section of the acoustic backscatter volume off Catalina Island, CA, USA, showing relative distribution and composition of prey aggregations. The colour map for acoustic backscatter uses grey to represent low values, blue for intermediate, and green and red for high values. From shallow to deep waters, based on target strength measurements, there was a fairly dilute shallow layer of small nekton, a zone of scattered patches of unknown composition, and midwater and deep sound-scattering layers composed of organisms of larger sizes.

(350–450 m, no diurnal migration). Although the vertical distribution of these layers remained relatively constant over the duration of the two tag deployments, when monitored over longer time scales, the presence of the shallow layer varied in an unpredictable fashion when compared with the more reliable midwater and deep scattering layers. In the horizontal domain, midwater and deep layers had a ubiquitous distribution over a scale of tens of kilometres with a complex heterogeneous inner structure composed of small-scale, discrete aggregations of animals of similar sizes and taxonomic groups approximately 100 individuals across, and adjacent to aggregations of animals of a different size and/or group (Benoit-Bird et al., 2017). The scattered patches found between 100 and 200 m depth (taxonomy and size of animal within unknown) represented only 5% of the water volume within these depths and had a less predictable occurrence than the patches that formed discrete layers at greater depths.

Dive types

Dolphins foraged in bouts of 7–11 dives covering a wide depth range, with only 1–3 min spent at the surface between dives within the same bout. The maximum depth of dives varied by 260 m across bouts and 120 m within bouts (median of 3 dive bouts per tag). The maximum depth of most dives fell within the boundary of one of the four observed prey features (corresponding to either layers or scattered patches; Fig. 3). Dives were classified into four dive types based on the deepest scattering feature visited. Overall, dolphins performed 57% of dives to no deeper than the shallow layer, 30% to the scattered patches, 17% to the midwater layer and 12% to the deep layer (Fig. 3). Each dive was divided into three phases based on the boundary of prey features: (i) descent – the period between when the dolphin left the surface and entered the deepest prey layer visited during the dive; (ii) ascent – the period from when the dolphin left the deepest prey layer visited to when it reached the surface; and (iii) bottom – the period between the end of the descent and start of the ascent, except for shallow dives where there was no descent or ascent and the whole dive was considered a bottom phase. Most

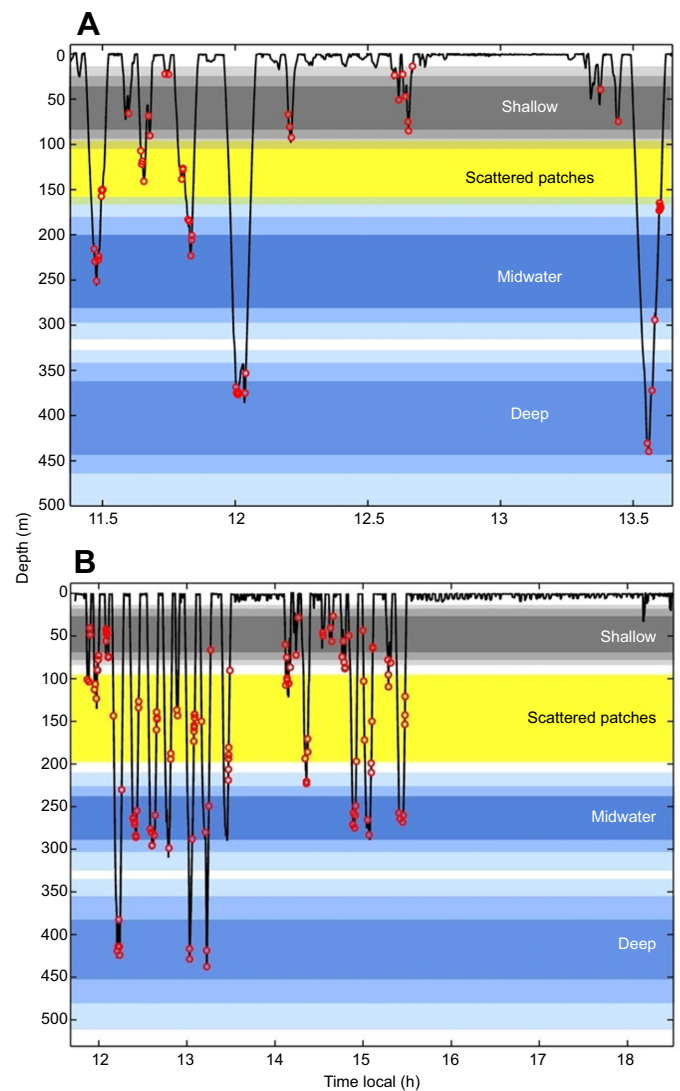


Fig. 3. Foraging activity of the dolphins and synchronous time–depth distribution of prey aggregations. The coloured layers represent, from darker to lighter blue, the mean depth, third quartile and 95% confidence interval of each edge's depth layer integrated across the sampling area. The dive profile (black) is shown with buzzes (red circles) that indicate attempts to capture prey for dolphin one (A) and two (B).

buzzes (112/181) occurred during the bottom phase of dives; overall, 31% occurred in the shallow layer, 21% in the scattered patches, and 33% and 15% in the midwater and deep layers. These proportions differed from the percentage of dives to each of these prey features. Dives that reached the midwater and deep layers regularly featured buzzes on the ascent, accounting for 30% of the total number of buzzes, most of them (66%) within scattered patches, with 26% and 7% in shallow and midwater layers, respectively. The remaining 7% of buzzes (13/181) were performed on dive descents, primarily in the shallow layer ($N=6$) and scattered patches ($N=6$).

Advanced selection of foraging layer

To explore whether dolphins planned foraging within a specific depth range before gaining new information by sensing the environment in the current dive, we first investigated whether planning would cause animals to wait to start clicking until they swam closer to the planned layer rather than near the surface.

Pooling data from two dolphins, the mean depth of the first click in dives was 23 ± 13 m, indicating that the dolphins always started echolocating early in dives, regardless of how deep they started foraging. Moreover, the depth at which the first click occurred was only weakly correlated to the mean depth of the scattering feature in which the first foraging attempt of the dive was recorded (Spearman's $\rho=0.27$, $P=0.11$, $N=33$ dives). This suggested that even when dolphins planned to forage at depth, they still started sampling in shallower layers.

Second, we investigated whether the inspection range of the first clicks on descent correlated with the depth of the first foraging attempt. The initial inspection range occurred over a wide breadth (50–460 m) and showed a significantly positive correlation with the depth of the furthest edge of the first prey layer where buzzes were recorded (Spearman's $\rho=0.64$, $P=0.0001$, $N=33$ dives), consistent with our planning hypothesis.

Sampling adjusted to prey features

Based on the distribution of potential prey, we predicted three types of search patterns each characterized by how the inspection range varied over the course of descents. If a dolphin planned to forage in a shallow layer or shallow scattered patches and found the expected prey there, then we predicted a short inspection range that would not change as a function of depth. If dolphins planned to forage in a shallow prey feature but encountered fewer prey or lower quality prey than expected, we predicted they may switch their attention to a new, deeper prey layer, resulting from remembering the depth of other prey features. A sudden increase in the inspection range was expected if such a decision was made, comparable to the range of the new expected prey layer. Alternatively, if a dolphin was planning at the beginning of a dive to forage on a medium or deep layer, we predicted that the inspection range would start at long ranges and reduce gradually as the dolphin descended to track the scattering feature on which it planned to forage. To test this hypothesis, we first took the descent phase of individual dives as the unit of analysis and, for each dive type, assessed the correlation between the

maximum depth searched by the dolphin and the depth of the deepest prey layer visited. In shallow dives ($N=12$), dolphins exhibited a relatively short and constant inspection range over the dive (mean inspection range before the first buzz, 97 ± 52 m). In 11 of the 12 shallow dives, the inspection range in the period from the emission of the first echolocation click and the first buzz was not associated with the distance to the furthest edge of the shallow scattering layer (mean Spearman's $\rho=0.1$, $P>0.05$, $N=12$ dives). Similarly, in 7 of 8 dives targeting scattered patches, the dolphins employed a relatively short inspection range (112 ± 60 m) and there was no correlation with the distance to the further edge of the depth range of scattered patches (mean Spearman's $\rho=0.03$, $P>0.05$, $N=8$ dives; Fig. 4A). A review of midwater and deep dives revealed two distinctive patterns: one pattern (Fig. 4B) suggested the intention to dive to deeper depths from the outset, while the other (Fig. 4C) was consistent with the dolphin initially planning a shallow dive but later switching its attention to a deeper layer. Midwater and deep dives with Spearman's $\rho<0.5$ ($N=6$) had an initially short inspection range (140 ± 90 m) and often featured buzzes during the descent (1 ± 1 buzz recorded in 5 of 8 dives). In the descent phase of these dives, dolphins maintained a relatively constant and short inspection range, roughly equivalent to that observed in dives targeting the shallow layer and scattered patches, until the first prey capture attempt occurred, usually between 100 and 200 m depth (85% of the buzzes). Shortly after the buzz, the dolphins increased their inspection range. This distance was comparable to the range of the layer ultimately targeted during the dive and the inspection range employed within the same depth range in dives in which layer tracking was apparent (i.e. dives with strong correlations of initial inspection range and distance to the further edge of the chosen prey layer) (Fig. 4C). In these cases, the dolphins ended up foraging at the bottom phase of the dive in a deeper layer. This switch from short to long searches during the descent and subsequent deeper foraging was observed in 40% of the midwater and deep dives. In contrast, in midwater and deep dives with Spearman's $\rho>0.5$ ($N=8$), the initial inspection range was long

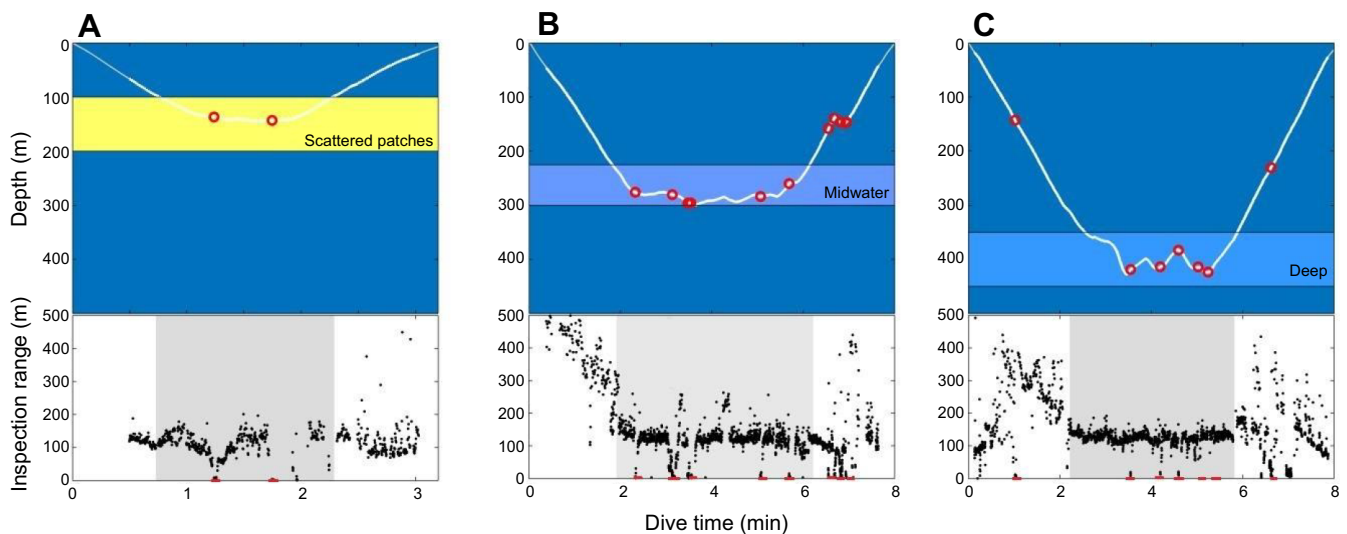


Fig. 4. Examples of the sampling strategies of the dolphins in relation to prey layers in three dive types. Upper panel: dive profile with clicks (white) and buzzes (red), and mean depth of the boundaries of the prey layer targeted, (A) scattered patches, (B) midwater and (C) deep layers. Lower panel: dolphin inspection range (black dots) taken from the inter-click interval multiplied by one/half the speed of sound as a function of dive time. The grey area represents the bottom phase of the dive and the red lines indicate buzzes. The correlation between inspection range and range to the deeper boundary of the first prey layer with foraging buzzes was assessed visually to exemplify dives with none (A), weak (C) and strong (B) correlations. Note the buzz during the descent of the deep dive (C) and associated changes in the inspection range afterwards.

(400±100 m) and gradually decreased as they approached the forage layer in a pattern consistent with initially planning to forage in the deep layers. Dolphins did not produce buzzes during the descent of these dives.

For midwater and deep dives in which dolphins switched their attention to a new prey layer over the course of the descent (i.e. dives with buzzes during descent, $N=5$), we measured whether dolphins could have detected the new expected layer based upon clicking while at shallow depths or in scattered patches. The average difference between the range to the shallowest edge of the new foraging layer and the maximum inspection depth before the first buzz recorded over the descent was -348 ± 108 m. This suggested that the dolphins were sampling the new foraging layer before the last buzz in shallower layers rather than simply relying on information from previous deep dives.

Sampling adjusted to prey patch

Once entering the foraging layer, dolphins adopted a mean inspection range that was similar for scattered patches (127 ± 15 m), midwater (127 ± 22 m) and deep dives (127 ± 7 m) and tended to decrease in shallow dives (105 ± 7 m). On average, this range was roughly similar to the horizontal distance covered by the dolphins while foraging in the layer (99 ± 47 m). Both were comparable to the mean size, in the horizontal dimension, of mono-specific aggregations (Scalabrini et al., 1996) containing the largest available prey in each layer (113 ± 34 m), suggesting that dolphins use echolocation to select prey within these aggregations. As reported in Benoit-Bird et al. (2017), the target strength of individual prey in the shallow layer was significantly lower than that in deeper aggregations and shallow prey were generally in smaller aggregations, which correlates with the use of shorter inspection ranges by the dolphins.

Ascent sampling based on prey expectations

Optimal foraging theory predicts that breath-hold divers would maximize the time spent foraging at depth and minimize the time spent in transit (Mori, 1998). This led us to presume that dolphins will forage for as long as possible in their chosen foraging layer and cease searching for prey on the dive ascent once they have left the layer. Alternatively, dolphins may echolocate all the way up for orientation, or because they expect to gain from capturing shallower prey during the ascent, or to gain new information about prey for planning the next dive. To test these hypotheses, we examined the depth of the last click in dives and the sampling strategy used by the dolphins on dive ascents in relation to prey features and buzz occurrences. Pooling data from the two dolphins for which prey data were available, the mean depth of the last click in a dive was 37 ± 36 m, indicating they echolocated almost all the way up to the surface, irrespective of the type of dive. Furthermore, the buzz rates, i.e. number of buzzes per minute, during dive ascents were up to six times higher than those during descents (signed-rank $P=0.005$, $N=14$ paired comparisons of buzz rate during descent versus ascent phases). Dolphins emitted buzzes during the ascent in 40% of dives. In those dives, clicking continued after the last buzz recorded on the ascent. All midwater and deep dives with no buzz on ascent and one with buzz on ascent had buzzes on descent (4 of 14 dives). Average ascent duration was 58 ± 31 and 76 ± 42 s for dives without and with buzzes on the ascent, respectively, whereas bottom time was reduced from 158 ± 61 to 110 ± 50 s during the same dives. To test whether, on ascent, dolphins were seeking more efficient foraging in upper layers, we explored whether the buzz rate during the bottom phase was higher than that during the ascent.

Buzz rates at the bottom phase were two times higher than those during ascent (signed-rank $P=3.2e-9$, $N=130$ paired comparisons of buzz rate during bottom versus ascent phases), suggesting that dolphins were foraging more efficiently at the bottom of the dive compared with foraging on ascent.

During ascents of most dives, an inspection range consistent with tracking the next prey feature was observed, suggesting the dolphins focused their search on expected shallower scattering features. There was only one deep dive (out of 4) during which the dolphin did not produce buzzes on the ascent and this was the only dive for which the initial ascent inspection range was adjusted to a range consistent with tracking the surface. The five buzzes recorded at the bottom phase of this dive were comparable to the average number of buzzes recorded at the bottom phase of deep dives in which buzzes on ascent were also recorded (3.5 ± 1.5 buzzes). For midwater dives, we tested whether the dolphins were more likely to switch to a longer search range at the start of ascent than while they were searching for prey within the layer. For this test, we compared the mean maximum inspection range of the last three clicks recorded at the bottom phase (177 ± 86 m) with the first three clicks of the ascent phase (366 ± 160 m). The same variables measured in deep dives were 198 ± 44 and 370 ± 244 m, respectively. Both in midwater and in deep dives, there was a strong correlation between the vertical inspection range measured from the first three clicks of the dolphins emitted on the ascent and the depth difference between the dolphin and the shallower edge of the next shallower layer where buzzes were recorded (Spearman's $\rho=0.66$, $P=0.01$, $N=14$ dives). The absolute difference between these two variables was small (16 ± 14 and 17 ± 11 m in midwater and deep dives, respectively), supporting the hypothesis that dolphins were sampling prey at a particular depth, on their way up to the surface.

To explore whether dolphins sensed prey located above them during the bottom phase of the dive or remembered their location from before that phase, we tested whether the vertical inspection range of long-range clicks (i.e. estimated inspection range >200 m) recorded over the bottom phase of the dive matched the depth difference between the dolphin, when emitting the click, and the shallower edge of the next shallower layer where buzzes were recorded on ascent. The average absolute difference between the two variables was 5 ± 78 m in midwater dives and 40 ± 85 m in deep dives, suggesting that dolphins could sense shallower prey features located above them while at the bottom of the dives.

Prey-dependent planning

To test whether dolphins plan the layer in which to forage based on perceived prey profitability in the previous dive, we looked at the relationship between the buzz rate at the bottom phase of the previous dive and the initial inspection range in the next dive, pooling data for 28 dolphins. If a previous dive suggested the best patches were shallow, and the animal used this information to plan the next dive, then we expected that it would start sampling at a short range. In contrast, if past experiences indicated that shallow patches were of low profit, we expected the animal would start searching at a longer range. The results supported this hypothesis; after shallow dives when buzz rates were moderate to high (>3 buzzes min^{-1}), dolphins started sampling at a short range (169 ± 158 m) during the next dive (Fig. 5). After shallow dives with low buzz rates (<3 buzzes min^{-1}), dolphins, on average, chose to sample at longer ranges during the next dive (249 ± 204 m). A reverse pattern was observed after deep dives: when buzz rates were moderate to high (>3 buzzes min^{-1}), dolphins started sampling at a long range (414 ± 157 m) during the next dive (Fig. 5); when buzz rates were

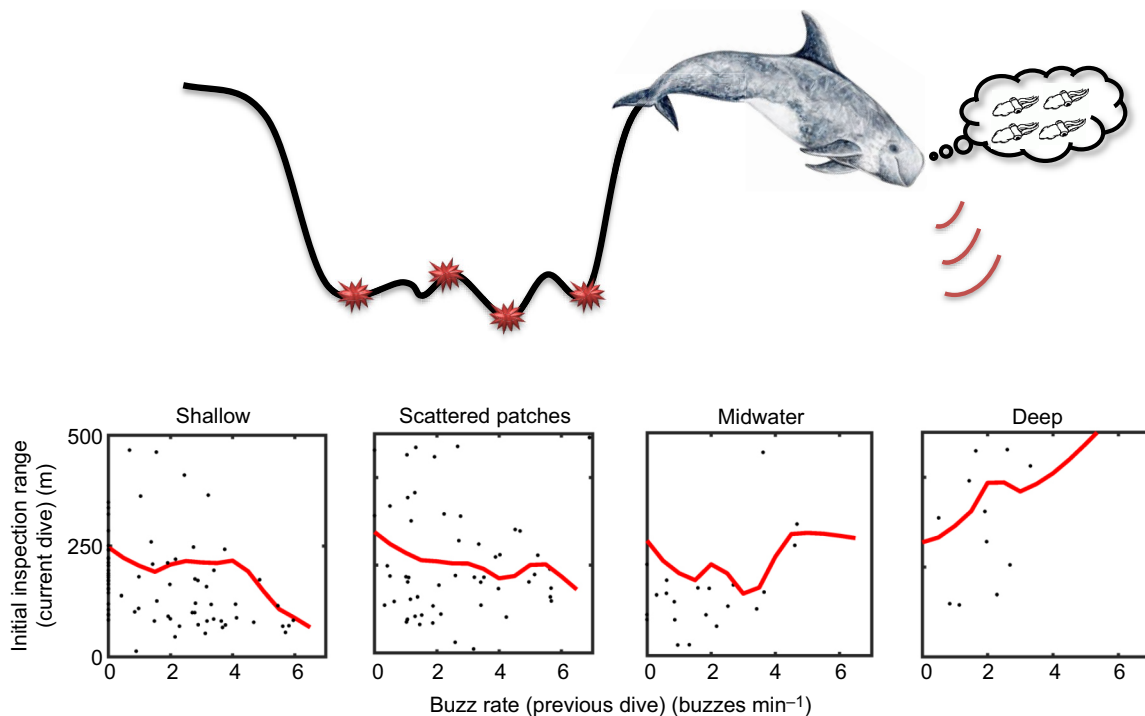


Fig. 5. Initial inspection range adapted to the best foraging depth encountered on the previous dive, from 174 dives by 28 dolphins. (A) Illustration of an individual's foraging scenario showing buzzes (red stars) emitted in the previous dive in a given prey feature and the inspection range at the start of current dive. (B) Initial inspection range of the current dive (y-axis) as a function of buzz rate in the last dive (x-axis). Note the tendency of the dolphin to target the depth layer where it had the highest buzz rate on the previous dive. Dive types are classified using the depth distribution of prey features described in Fig. 1.

low (<3 buzzes min^{-1}), dolphins sampled at shorter ranges (181 ± 110 m) in the next dive, consistent with dolphins using information on prey from a previous dive to plan the foraging depth in the next one.

DISCUSSION

Each time an air-breathing aquatic animal dives to forage, it must make decisions to adjust its physiology for different lengths and depths of dives. In environments with ephemeral patches of prey at close shallow ranges and predictable resources at more costly deeper ranges, the animal may benefit from using information from previous dives to plan the next foraging dive. Yet, we rarely can obtain evidence of how an individual's decisions are affected by prior knowledge and modulated by comparisons of real-time information and balancing available alternatives, and this has narrowed progress in studies of animal planning and decision making under natural settings.

Echolocating divers are a good taxon to use to address these questions because they provide us with information on their search ranges (i.e. what information is available in order to make a decision) and when and where prey capture attempts occur (i.e. actual choices). Integration of this information with contemporaneous fine-scale data from the prey fields, sampled at the same depths and times where the predators occur, provides a unique perspective on the choices available to a predator in a three-dimensional marine system. Here, we shed light on how predators adjust their search based upon sensing the current distribution of prey or using information gathered in previous dives or from earlier phases of the same dive. These processes were viewed from sub-mesoscales (i.e. how they plan and choose to forage on different prey aggregations) to microscales (i.e. how they adjust their acoustic gaze to search within a patch).

The dolphins explored their environment based on past experiences to inform upcoming foraging decisions of dive-time allocation and prey choice. They used a long inspection range for dives when they were planning to forage in the stable deep patches, and switched to a short inspection range once they located a patch in which to forage. Once this decision was made, the inspection range remained roughly constant and comparable to the scale of prey patches containing the largest prey, suggesting that inspection range was adjusted to select prey within the expected size of prey patches. When dolphins performed well in one patch, as judged by high buzz rates, they planned to target the same layer in the next dive. Observed differences in maximum dive depth of dives within bouts were probably driven by variations in prey selection by the dolphins on a dive-by-dive basis. There was an apparent mismatch between the proportion of dives and buzzes performed within each prey layer, as judged by the gradual decrease in the percentage of dives performed per prey feature against the more Gaussian distribution of buzz counts. This may be because the latter is related to the relative capture rate in each layer, whereas the former may be driven by energetic costs of diving to different depths. Larger deep-diving odontocetes, such as sperm or beaked whales, emit between 3 and 5 times more buzzes than *G. griseus* at the bottom phase of dives (Arranz et al., 2011; Watwood et al., 2006; this study). This apparent, higher foraging efficiency of larger species probably reflects differences in foraging requirements as well as their greater diving capacity and lower cost of transport (Williams et al., 1999). *Grampus griseus* are small- to medium-sized delphinids for which extending the time foraging at depth to compensate for long transit times (Thompson and Fedak, 2001) may be limited by the available oxygen stores.

Animals considering potential prey alternatives with variable benefits as well as variable costs of locomotion to travel to these patches may need to track the environment relatively closely to

update existing information in order to respond quickly to short-term changes in cost and benefit (Dunlap and Stephens, 2012; Mori, 1998). Here, in contrast to other deep-diving odontocetes (Arranz et al., 2011; Watwood et al., 2006), the dolphins started echolocating early and throughout the dives, probably to gain information on the depth distribution and availability of prey and to respond swiftly to rapid changes in habitat structure at different depths. We found evidence that dolphins updated their foraging plans based on information about prey gathered during the dive, suggesting that animals were revisiting plans regularly, comparing alternatives based on memory with those based on current assessment of resource distribution via sensory information acquired from sampling throughout the dive. Before ascent, dolphins planned when to forage on the way up and when not to, as evidenced by their inspection range at the start of the ascent. Sampling during descents to foraging depths may guide initial decisions about which prey features to sample on ascent, as demonstrated by the jump in the inspection range when dolphins decided to leave the bottom foraging layer. Strikingly, when dolphins attempted to catch prey (demonstrated by the production of buzzes) on descent, they did not produce buzzes on ascent, perhaps because the increased time on descent interfered with opportunities to forage on ascent, given the time constraints imposed by breath-hold diving. Dolphins at times slowed down their ascent, taking 20% longer in order to search for and capture prey in shallower layers. These results suggest that while dolphins may sample prey on descent, they make a decision about whether to shorten foraging at the bottom to forage on ascent based upon information about prey and oxygen availability. The tendency for dolphins to forage on ascent versus descent may result from the stability of prey patches and the ability of an individual foraging in the bottom layer to weigh the benefits lost by breaking off from foraging at the bottom to forage on ascent.

Foraging on ascent contradicts most foraging theories, which emphasize minimizing the time in dive transits to and from foraging depths to extend bottom time and therefore the probability of finding prey (Mori, 1998; Thompson and Fedak, 2001). Most diving mammals studied to date, including sperm, beaked, blue and humpback whales, do not show foraging activity on the dive ascent (Arranz et al., 2011; Watwood et al., 2006; Hazen et al., 2015; Doniol-Valcroze et al., 2011). Moreover, most deep-diving echolocating species stop clicking early in the ascent. However, there is considerable selection pressure for search strategies that increase the encounter rate with food and therefore their foraging efficiency (Cowie, 1977; Friedlaender et al., 2016; Ydenberg and Hurd, 1998). Sperm whales foraging in high-latitude habitats have been observed searching for and capturing prey on dive ascents (Fais et al., 2015), as the Risso's dolphins did in this study. This suggests that such a strategy might represent an adaptive behaviour of air-breathing predators in multi-layered habitats containing both shallow- and deep-water prey of variable predictability.

In this paper, we have shown that at the start of a foraging dive, dolphins selected an echolocation range that targeted the best foraging depth encountered on the last dive. This can be interpreted as dolphins recalling information from the previous dive to plan the next foraging dive (i.e. episodic-like memory). Alternatively, one can argue that having spatial memory abilities is sufficient to allow such behaviour (i.e. semantic knowledge). However, further convincing evidence of planning comes from situations in which an animal behaves in a way that ignores its current motivational state in order to meet a need for an expected future motivational state (Naqshbandi and Roberts, 2006). Here, we found that dolphins emit

clicks throughout their ascent to the surface after feeding at the bottom layer, when the dolphins have lower motivation to feed and higher motivation to breathe. The function of this behaviour appears to be to sample prey at different layers in anticipation of their future dive in order to update their knowledge on prey distribution, supporting the flexible deployment of information in novel situations (Clayton et al., 2003). In this situation, the dolphins appeared to ignore their more urgent motivation to breathe in order to improve their foraging on the next dive, by potentially modifying their search strategy; however, after breathing, their primary motivation again became to forage.

The data presented here on the spatial distribution of prey and durations over which distribution was stable, coupled with our data on how breath-hold divers make use of sensory information to make foraging decisions, provide unique insight into how these animals plan dynamically, with a balance of strategy and flexibility, to cope with varying predictability in the distribution of their food.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: P.A., K.J.B., B.L.S., P.L.T.; Methodology: K.J.B., B.L.S.; Software: K.J.B.; Validation: P.L.T.; Formal analysis: P.A., K.J.B.; Investigation: P.A., K.J.B., J.C., A.S.F.; Resources: J.C., A.S.F.; Data curation: P.A., K.J.B.; Writing - original draft: P.A.; Writing - review & editing: P.A., K.J.B., B.L.S., J.C., A.S.F., P.L.T.; Supervision: P.L.T.; Project administration: B.L.S., J.C., P.L.T.; Funding acquisition: K.J.B., B.L.S., J.C., P.L.T.

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Data availability

Data are available from the Dryad Digital Repository (Arranz et al., 2017): <https://doi.org/10.5061/dryad.48vq4>

References

- Arranz, P., Aguilar de Soto, N., Madsen, P. T., Brito, A., Bordes, F. and Johnson, M. P. (2011). Following a foraging fish-finder: diel habitat use of Blainville's beaked whales revealed by echolocation. *PLoS ONE* **6**, e28353.
- Arranz, P., DeRuiter, S. L., Stimpert, A. K., Neves, S., Friedlaender, A. S., Goldbogen, J. A., Visser, F., Calambokidis, J., Southall, B. L. and Tyack, P. L. (2016). Discrimination of fast click-series produced by tagged Risso's dolphins (*Grampus griseus*) for echolocation or communication. *J. Exp. Biol.* **219**, 2898-2907.
- Arranz, P., Benoit-Bird, K. J., Southall, B. L., Calambokidis, J., Friedlaender, A. S. and Tyack, P. L. (2017). Data from: Risso's dolphins plan foraging dives. Dryad Digital Repository. <https://doi.org/10.5061/dryad.48vq4>
- Au, W. L. (1993). *The Sonar of Dolphins*. New York, US: Springer.
- Au, W. L. and Lammers, M. O. (2016). Biosonar detection range of mesopelagic patches by spinner dolphins in Hawaii. *J. Acoust. Soc. Am.* **140**, 3130-3130.
- Au, W. L., Popper, A. N. and Fay, R. R. (2000). *Hearing by Whales and Dolphins*. New York, US: Springer-Verlag.
- Barraquand, F., Inchausti, P. and Bretagnolle, V. (2009). Cognitive abilities of a central place forager interact with prey spatial aggregation in their effect on intake rate. *Anim. Behav.* **78**, 505-514.
- Benhamou, S. (1994). Spatial memory and searching efficiency. *Anim. Behav.* **47**, 1423-1433.

- Benoit-Bird, K. J., Moline, M. A. and Southall, B. L.** (2017). Prey in oceanic sound scattering layers organize to get a little help from their friends. *Limnol. Oceanogr.* **62**, 2788-2798.
- Cheke, L. G. and Clayton, N. S.** (2010). Mental time travel in animals. *Wiley Interdiscip. Rev. Cogn. Sci.* **1**, 915-930.
- Clayton, N. S., Bussey, T. J. and Dickinson, A.** (2003). Can animals recall the past and plan for the future? *Nat. Rev. Neurosci.* **4**, 685-691.
- Cowie, R. J.** (1977). Optimal foraging in great tits (*Parus major*). *Nature* **268**, 137-139.
- Crystal, J. D.** (2012). Prospective cognition in rats. *Learn. Motiv.* **43**, 181-191.
- Doniol-Valcroze, T., Lesage, V., Giard, J. and Michaud, R.** (2011). Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behav. Ecol.* **22**, 880-888.
- Dunlap, A. S. and Stephens, D. W.** (2012). Tracking a changing environment: optimal sampling, adaptive memory and overnight effects. *Behav. Process.* **89**, 86-94.
- Fais, A., Aguilar Soto, N., Johnson, M., Pérez-González, C., Miller, P. J. O. and Madsen, P. T.** (2015). Sperm whale echolocation behaviour reveals a directed, prior-based search strategy informed by prey distribution. *Behav. Ecol. Sociobiol.* **69**, 663-674.
- Friedlaender, A. S., Johnston, D. W., Tyson, R. B., Kalteneberg, A., Goldbogen, J. A., Stimpert, A. K., Curtice, C., Hazen, E. L., Halpin, P. N., Read, A. J. et al.** (2016). Multiple-stage decisions in a marine central-place forager. *R. Soc. Open. Sci.* **3**, e160043.
- Gallon, S. L., Sparling, C. E., Georges, J.-Y., Fedak, M. A., Biuw, M. and Thompson, D.** (2007). How fast does a seal swim? Variations in swimming behaviour under differing foraging conditions. *J. Exp. Biol.* **210**, 3285-3294.
- Hazen, E. L., Friedlaender, A. S. and Goldbogen, J. A.** (2015). Blue whales (*Balaenoptera musculus*) optimize foraging efficiency by balancing oxygen use and energy gain as a function of prey density. *Sci. Adv.* **1**, e1500469.
- Johnson, M. P. and Tyack, P. L.** (2003). A digital acoustic recording tag for measuring the response of wild marine mammals to sound. *IEEE J. Oceanic Eng.* **28**, 3-12.
- Johnson, M. P., Madsen, P. T., Zimmer, W. M. X., Aguilar de Soto, N. and Tyack, P. L.** (2004). Beaked whales echolocate on prey. *Proc. R. Soc. Lond. B Biol. Sci.* **271** Suppl. 6, S383-S386.
- Kadane, J. and Penner, R.** (1983). Range ambiguity and pulse interval jitter in the bottlenose dolphin. *J. Acoust. Soc. Am.* **74**, 1059-1061.
- Madsen, P. T., Wilson, M., Johnson, M., Hanlon, R. T., Bocconcelli, A., Aguilar de Soto, N. and Tyack, P. L.** (2007). Clicking for calamari: toothed whales can echolocate squid *Loligo pealeii*. *Aquat. Biol.* **1**, 141-150.
- Miller, P. J. O., Johnson, M. P. and Tyack, P. L.** (2004). Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture. *Proc. R. Soc. Lond. B Biol. Sci.* **271**, 2239-2247.
- Moline, M. A., Benoit-Bird, K., O'Gorman, D. and Robbins, I. C.** (2015). Integration of scientific echo sounders with an adaptable autonomous vehicle to extend our understanding of animals from the surface to the bathypelagic. *J. Atmos. Oceanic. Tech.* **32**, 2173-2186.
- Mori, Y.** (1998). Optimal choice of foraging depth in divers. *J. Zool. Lond.* **245**, 279-283.
- Mulcahy, N. J. and Call, J.** (2006). Apes save tools for future use. *Science* **312**, 1038-1040.
- Naqshbandi, M. and Roberts, W. A.** (2006). Anticipation of future events in squirrel monkeys (*Saimiri sciureus*) and rats (*Rattus norvegicus*): tests of the Bischof-Kohler hypothesis. *J. Comp. Psychol.* **120**, 345-357.
- Osvath, M. and Martin-Ordas, G.** (2014). The future of future-oriented cognition in non-humans: theory and the empirical case of the great apes. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **369**, 20130486.
- Osvath, M. and Osvath, H.** (2008). Chimpanzee (*Pan troglodytes*) and orangutan (*Pongo abelii*) forethought: self-control and pre-experience in the face of future tool use. *Anim. Cogn.* **11**, 661-674.
- Pfeiffer, B. E. and Foster, D. J.** (2013). Hippocampal place-cell sequences depict future paths to remembered goals. *Nature* **497**, 74-79.
- Raby, C. R., Alexis, D. M., Dickinson, A. and Clayton, N. S.** (2007). Planning for the future by western scrub-jays. *Nature* **445**, 919-921.
- Roberts, W. A., McMillan, N., Musolino, E. and Cole, M.** (2012). Information seeking in animals: metacognition? *Comp. Cogn. Behav. Rev.* **7**, 85-109.
- Sato, K., Shiomi, K., Marshall, G., Kooyman, G. L. and Ponganis, P. J.** (2011). Stroke rates and diving air volumes of emperor penguins: implications for dive performance. *J. Exp. Biol.* **214**, 2854-2863.
- Sawada, K., Furusawa, M. and Williamson, N. J.** (1993). Conditions for the precise measurement of fish target strength in situ. *Fish. Sci.* **20**, 15-21.
- Sayers, K. and Menzel, C. R.** (2012). Memory and foraging theory: chimpanzee utilization of optimality heuristics in the rank-order recovery of hidden foods. *Anim. Behav.* **84**, 795-803.
- Scalabrin, C., Diner, N., Weill, A., Hillion, A. and Mouchot, M. C.** (1996). Narrowband acoustic identification of monospecific fish shoals. *ICES J. Mar. Sci.* **53**, 181-188.
- Seibert, A.-M., Koblitz, J. C., Denzinger, A. and Schnitzler, H.-U.** (2013). Scanning behavior in echolocating common pipistrelle bats (*Pipistrellus pipistrellus*). *PLoS ONE* **8**, e60752.
- Shettleworth, S. J.** (1998). *Cognition, Evolution and Behaviour*. New York, US: Oxford University Press.
- Shettleworth, S. J.** (2001). Animal cognition and animal behaviour. *Anim. Behav.* **61**, 277-286.
- Shettleworth, S. J.** (2007). Animal behaviour: planning for breakfast. *Nature* **445**, 825-826.
- Simmons, J. A.** (1973). The resolution of target range by echolocating bats. *J. Acoust. Soc. Am.* **54**, 157-173.
- Slater, P. J. B. and Lester, N. P.** (1982). Minimising errors in splitting behaviour into bouts. *Behaviour* **79**, 153-161.
- Southall, B. L., Moretti, D., Abraham, B., Calambokidis, J., DeRuiter, S. L. and Tyack, P. L.** (2012). Marine mammal behavioral response studies in southern California: advances in technology and experimental methods. *Mar. Technol. Soc. J.* **46**, 48-59.
- Steele, J. H.** (1976). *Patchiness*. Philadelphia, US: Saunders Company.
- Suddendorf, T. and Corballis, M. C.** (1997). Mental time travel and the evolution of the human mind. *Genet. Soc. Psych.* **123**, 133-167.
- Surlykke, A., Ghose, K. and Moss, C. F.** (2009). Acoustic scanning of natural scenes by echolocation in the big brown bat, *Eptesicus fuscus*. *J. Exp. Biol.* **212**, 1011-1020.
- Thompson, D. and Fedak, M. A.** (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.
- Tulving, E. and Donaldson, W.** (1972). Episodic and semantic memory. In *Organization of Memory* (ed. E. Tulving, W. Donaldson and G. H. Bower), pp. 381-403. Cambridge, MA, USA: Academic Press.
- Vonk, J. and Shackelford, T. K.** (2012). *Oxford Handbook of Comparative Evolutionary Psychology*. New York, US: Oxford University Press.
- Watwood, S. L., Miller, P. J. O., Johnson, M., Madsen, P. T. and Tyack, P. L.** (2006). Deep-diving foraging behaviour of sperm whales (*Physeter macrocephalus*). *J. Anim. Ecol.* **75**, 814-825.
- Williams, T. M., Haun, J. E. and Friedl, W. A.** (1999). The diving physiology of bottlenose dolphins (*Tursiops truncatus*) I. Balancing the demands of exercise for energy conservation at depth. *J. Exp. Biol.* **202**, 2739-2748.
- Wilson, R. P.** (2003). Penguins predict their performance. *Mar. Ecol. Prog. Ser.* **249**, 305-310.
- Ydenberg, R. and Hurd, P.** (1998). Simple models of feeding with time and energy constraints. *Behav. Ecol.* **9**, 49-53.