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RESEARCH ARTICLE

G.D. Hastie · B. Wilson · P.M. Thompson

Diving deep in a foraging hotspot: acoustic insights into bottlenose dolphin dive depths and feeding behaviour

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Abstract To exploit resources in their environment, odontocete cetaceans have evolved sophisticated diving abilities to allow effective foraging. However, data on the diving behaviour and underwater foraging behaviour remains limited. This study made use of echolocation clicks and other calls to study the diving behaviour of bottlenose dolphins. Dolphins used the full water column and consistently dived to depths of around 50 m, close to the seabed. However, the majority of their time appeared to be spent within the surface layers of the water column. In addition, by localising calls that have been associated with prey capture events (Janik, Proc R Soc Lond Ser B 267:923–927, 2000a), it appeared that certain forms of feeding behaviour occurred primarily at depths of between 20 and 30 m. Furthermore, data on the depth of clicks made before and after these feeding calls suggested that during the minute before the calls, dolphins were consistently diving from the surface to depths close to the seabed, and were subsequently returning to the surface after the calls. This passive acoustic technique proved an accurate method for studying the depth distribution of dolphin vocalisations. By exploiting the natural sounds made by these wild odontocetes, this investigation provided a previously unavailable perspective on the the 3D nature of bottlenose dolphins foraging behaviour. It confirmed that while the dolphins spent the majority of time close to the surface, the full water column was exploited during foraging events.

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G.D. Hastie · P.M. Thompson
University of Aberdeen, School of Biological Sciences, Lighthouse Field Station, Cromarty, Ross-Shire, UK

B. Wilson
Dunstaffnage Marine Laboratory,
The Scottish Association for Marine Science,
Argyll, Oban, PA37 1QA, UK

G.D. Hastie (✉)
Marine Mammal Research Unit, AERL,
University of British Columbia, Vancouver, BC, Canada
E-mail: hastie@zoology.ubc.ca
Tel.: +44-604-9316204
Fax: +44-604-8228180

Introduction

Unlike many terrestrial ecosystems, resources in aquatic environments are often distributed in 3D space. To exploit these, air-breathing aquatic predators have evolved sophisticated diving abilities to prolong their time foraging below the surface, and increase the depths they can attain. Nevertheless, for these animals, diving is an energetic expense that must be offset by the benefit of the prey that become available at depth. To understand the habitat use and foraging behaviour of these species, information is therefore required on the depths of dives carried out by individuals and the relationships of these to foraging events underwater.

In contrast to many air-breathing aquatic predator species (e.g. Croxall et al. 1985; Dolphin 1987; Martin et al. 1994; Westgate et al. 1995; Tollit et al. 1998; Hooker and Baird 1999; Georges et al. 2000; Mougin and Mougin 2000), and despite being one of the most intensively studied cetacean species, there is currently little published information on the diving behaviour of free-ranging bottlenose dolphins (*Tursiops truncatus*). As such, interpretation of the underlying functions of habitat relationships, and behavioural patterns for this species is limited.

Bottlenose dolphins in the Moray Firth, NE Scotland exhibit marked preferences for discrete regions of their range; dolphins are sighted most frequently within deep narrow coastal channels (Wilson et al. 1997). Behavioural studies have shown that the functional mechanisms behind these patterns of habitat use are linked to foraging; the probability of observing overt feeding events

[primarily on Atlantic salmon (*Salmo salar*)] at the surface is significantly higher in these deep channels than in surrounding waters (Hastie et al. 2004).

Within these channels, observations of feeding events also exhibit a positive relationship with water depth and seabed gradient (Hastie et al. 2004). This relationship with depth is particularly strong during June and July, those months when the abundance of migratory Atlantic salmon is highest in the area (Menzies 1928; Nall 1937). In addition, Janik (2000a) discovered that specific low frequency calls, termed "brays", made by bottlenose dolphins within the Moray Firth were spatially related to surface observations of the capture of Atlantic salmon. In this previous study (Janik 2000a), the production of "brays" were relatively rare events (2.58 brays h^{-1}). However, they were made during 93% of observed feeding events, suggesting that these calls are exclusively used during feeding and function either as a cue to conspecifics, or act to manipulate the behaviour of prey (Janik 2000a).

Despite the clear links between habitat and foraging in this population (Hastie et al. 2004), direct observations of dolphin feeding behaviour are limited to events close to the surface and are therefore likely to be biased. Inferences of diet from stranded bottlenose dolphins in this region suggest that they also feed on benthic or demersal species, such as haddock (*Melanogrammus aeglefinus*) and saithe (*Pollachius virens*), (Santos et al. 2001). This indicates that dolphins in the Moray Firth can forage close to the seabed. However, there are currently no direct data on the diving and sub-surface foraging behaviour for this species in this type of habitat, which limits our understanding of their habitat use and foraging behaviour. Therefore, to fully understand the mechanisms underlying the dolphins' use of the deep channels, and to understand foraging behaviour by dolphins within such habitats, quantitative data on the diving behaviour of dolphins are required.

Passive acoustic techniques are increasingly being used to locate cetaceans underwater (Clark et al. 1985; Leaper et al. 1992; Freitag and Tyack 1993; Jensen and Miller 1999; Janik et al. 2000). To do this, arrays of hydrophones are used to record vocalisations of free ranging animals and the differences in arrival times of each sound is used to calculate the position of the vocalising animal. A key advantage of using this technique is that it does not rely on the attachment of any animal borne instruments such as dive recorders or sonic transmitters. This is particularly pertinent for bottlenose dolphins in temperate waters as they are known to show particularly strong, adverse reactions to tagging (Schneider et al. 1998; Chilvers and Corkeron 2000), and they are capable of perceiving the frequencies typically used by sonic tags (Richardson et al. 1995). Although passive acoustic techniques have often been used to estimate the positions of dolphins in the horizontal plane (e.g. Janik 2000a, b), they have rarely been used to look directly at the positions of dolphins within the vertical plane (e.g. Watkins and Schevill 1974), and have not been used to place their vertical positions in a foraging context.

In this study, we use passive acoustics to estimate the diving depths of bottlenose dolphins in a deep coastal channel used intensively by dolphins. Our aim was to investigate the relative use of the water column and determine whether dolphins were diving close to the seabed. Furthermore, we investigate the depths that were used for feeding by evaluating the depth related context of feeding related vocalisations.

Materials and methods

Field procedure

The study area we chose was a relatively deep region, reaching 55 m deep, within the narrow channel at the entrance to the Cromarty Firth (57°41′N, 4°00′W). The vertical distribution of dolphin echolocation clicks were used to provide an index of the relative use of the water column by bottlenose dolphins. To establish the depths that specific feeding behaviours occurred, the depth distribution of bray vocalisations (see Janik 2000a) was calculated. To provide further context to the bray calls, the depth of echolocation clicks were estimated during a 1-minute period before and after the brays. The depths of both echolocation clicks and brays were estimated using a passive acoustic localisation technique.

A vertical array of four DOWTY, SSQ906A (D) sonobuoy hydrophones was deployed from a stationary 8.5 m motor vessel with the engine turned off. The hydrophones were positioned in a single, vertical line at depths of 5, 15, 35 and 45 m (Fig. 1). Recordings were made on chrome cassettes using a four-track tape recorder with custom-built pre-amplifiers. This allowed simultaneous recordings from all four hydrophones onto one tape. The frequency response of the whole system was 40 Hz to 12.5 kHz ± 3 dB. Analyses were therefore

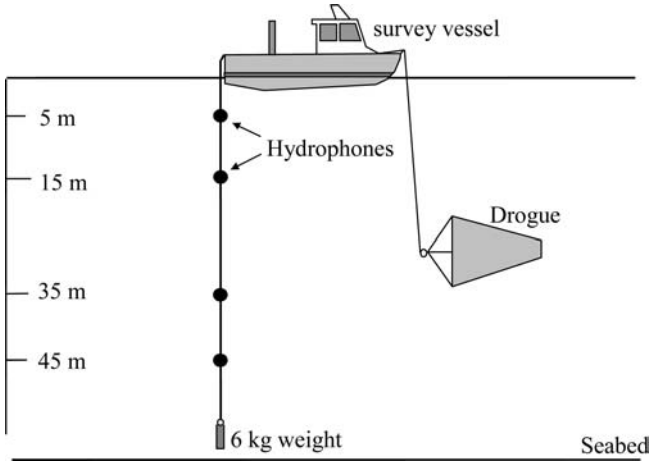

Fig. 1 Design of the vertical 4-hydrophone array, showing the survey vessel, the dimensions of the array and the underwater drogue

carried out on the lower frequency components of the echolocation clicks.

To estimate the depths of vocalisations, the array was held vertical within the water column using a drogue and weights (Fig. 1). Recordings were only made when winds were light (less than Beaufort state 2) and at slack tide when currents were minimal. Recordings were made whenever dolphins moved to within approximately 200 m of the array, and were made for as long as dolphins remained within this area.

Call localisation

Sound analyses were adapted from the technique described in Janik et al. (2000) and were implemented using the sound localisation module in the software package SIGNAL (Engineering Design, Belmont, USA). The localisation of a sound source using this method is based on the arrival time of a signal at each pair of hydrophones. For the echolocation clicks, the time delay in the signal arrival between all six pairs of hydrophones was calculated by hand from the click waveforms. Sounds were digitised at a sampling rate of 30 kHz. A 10 KHz digital high pass filter was applied to each of the waveforms to reduce low frequency, background noise. The leading edge of the echolocation click was used to measure the time delays, minimising possible anomalous measurement due to signal echo from the water surface or seabed.

Brays are lower in frequency than the echolocation clicks and it was often difficult to identify the signal against background noise in the waveforms. Calculating frequency spectrograms of the waveforms allowed the detection of the signal more clearly. Therefore, to estimate the depths of brays, the time delays between hydrophones were calculated by cross correlating frequency spectrograms. Spectrograms were calculated with a 75% overlap between successive Fast Fourier Transforms (FFT's, *dt*: 10 ms; *df*: 98 Hz; FFT size: 512) resulting in a time resolution of 2.5 ms^{-1}. The cross-correlation functions of the spectrograms between each pair of hydrophones were calculated and, in each case, the time delays were checked manually. For both echolocation clicks and brays, hyperbolic curves corresponding to the possible source locations for each pair of hydrophones were plotted and the point of intersection of all the hyperbolas was estimated to be the sound source location. On occasions when the hyperbolas did not intersect at a single point, the centre of the resultant error polygon was considered to be the call location.

Localisation errors

To test the accuracy of this localisation procedure, a man-made sound source; a Dukane NetMark 1,000 electronic net pinger (Dukane Co. Seacom Division, 2900 Dukane Drive, St Charles, K 60174) was deployed from an inflatable boat at distances of 50, 150 and 300 m from the array and at depths of 10, 20 and 40 m. The pinger produced a 10–11 kHz signal lasting approximately 300 ms. The distance between the array and the inflatable was calculated using an electronic theodolite operated from a cliff overlooking the study area.

Data analyses

Between June and August 1999, 20 independent 5-minute recordings were collected. Because the use of a linear array did not allow us to track individual dolphins for extended periods (Fig. 2), all analyses were carried out with groups of dolphins as the sampling units. As each 5-minute recording was made with a different group of dolphins, we considered each recording to be an independent sample. Furthermore, each sample was taken on a separate day minimising the risk of the same dolphins being present in different samples. A sample duration of 5 min was chosen as it encompasses a large proportion of dive durations of bottlenose dolphins (e.g. Corkeron and Martin 2004), allowing the full range of depths during dives to be estimated within each sample, and it was the average duration that dolphins remained within the study area (within 200 m of the array). The number of dolphins present within the study area during recording periods varied between one and ten.

The samples were used initially to examine the depth distribution of echolocation clicks. Within each sample, 1 s of sound was digitised every 10 s and the first click within this second was selected and localised. This sampling protocol was chosen for practical reasons; it ensured we had a good distribution of depths for each

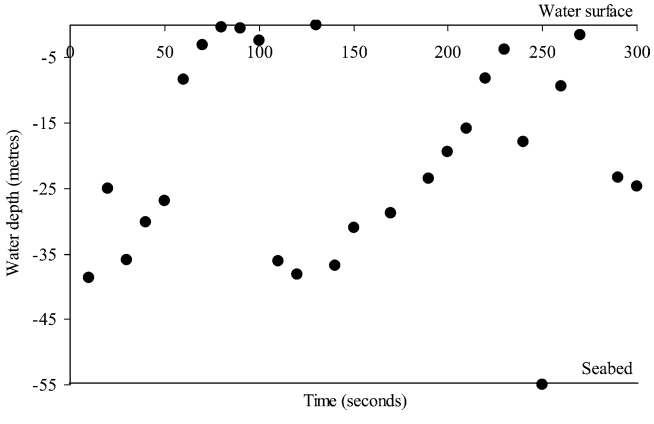

Fig. 2 An example of the progression of localised echolocation clicks every 10 s within a 5-minute sample for a group of four dolphins. Each point represents the depth of a localised click. In this example, the maximum depth of a click was 55 m, and the number of clicks in the depth classes (0–10, 10–20, 20–30, 30–40, 40–50 and 50–60 m) were 9, 3, 6, 7, 0 and 1, respectively. Although, it is possible that consecutive localised clicks were made by the same individual during some periods, it is clear that on others, several dolphins were simultaneously at different depths. This precluded attempts to track the dive profiles of individual dolphins

sample whilst being carried out in a reasonable analytical timeframe. This resulted in a total of approximately 30 localised positions for each sample. The depths of 544 clicks were estimated using passive acoustic localisation. Fifty-six of the 1-second digitised sound sequences contained no echolocation clicks. A total of 45 clicks were localised more than 5 m above the water surface. These were considered anomalous and were removed from the analyses. Clicks localised less than 5 m above the surface were assumed to be within the top 10 m of the water column. Brays were detected in eight of the samples. To ensure independence of the depth estimations of these vocalisations, the depth of a single bray was localised from each sample.

The physical presence of the survey vessel and the array could potentially have affected the depths to which dolphins dived. To test this, the median depth of echolocation clicks was compared at distances of 0–50, 50–100, 100–150 and 150–200 m from the vessel using a non-parametric Kruskal–Wallis test.

To examine the variation in the use of the water column, the number of clicks within each vertical 10 m water depth class i.e. 0–10, 10–20, 20–30, 30–40, 40–50 and >50 m, was calculated for each 5-minute samples. The median numbers of clicks within each depth class were compared using a non-parametric Kruskal–Wallis test. To estimate the maximum dive depth during each 5-minute sample, the frequency distribution of the maximum depth that a click was detected was evaluated. To determine the depth distribution of brays, the total number of these calls detected in each depth class, was plotted. To examine the variation in the use of the water column before and after brays were made, the median depth of clicks was evaluated during 30-second periods up to 1-minute before and after the brays. To avoid potential psuedo-replication, a single click from each of the 30-second periods before and after brays in each of the 5-minute samples was chosen at random to represent the depth of dolphins during that period. These values were compared using a non-parametric Kruskal–Wallis test.

Results

The results of this study indicate that there was differential use of the water column, and that echolocating dolphins consistently dived close to the seabed. Feeding related calls were made predominantly between 20 and 30 m depth, with dive depths before these calls being deeper than after the calls.

Dive depths

There were no significant differences in the depth that echolocation clicks were detected with varying distance from the hydrophone array (Kruskal–Wallis, $H=3.42$, $df=3$, $P=0.331$). The maximum depth at which a click was localised was 58.5 m. There was significant variation in the number of clicks localised at different depth classes within the water column (Kruskal–Wallis, $N=20$, $H=63.97$, $df=5$, $P<0.0001$); the highest number of clicks were detected within the top 10 m of the water column, and decreased to a minimum at depths greater than 50 m (Fig. 3). The maximum depth that a click was detected, during individual 5-minute samples varied from 12 to 59 m. The distribution of maximum click depth per 5-minute sample peaked in the depth class 40–50 m (Fig. 4).

Feeding calls

Brays were detected at depths between 9.6 and 33.4 m. The majority (50%) were detected in depths between 20 and 30 m (Fig. 5). The median depth of clicks varied significantly before and after the time of the production of each bray. (Kruskal–Wallis, $H=9.3637$, $df=3$, $P=0.025$). Click depth increased from a minimum of -1.95 m, 60 s before the bray to a maximum of 35.2 m 30 s before the bray. After the bray, the median depth of clicks decreased from 14.45 m, 30 s after the bray to 8.1 m, 60 s after the bray (Fig. 6).

Localisation errors

There was no significant difference between the localised depths and the actual depths of 33 man made sounds up to 300 m from the array (Paired samples t-test; $t=0.88$, $df=32$, $P=0.385$). The overall mean error in depth estimation was 1.42 m (SE = 0.31 m). The maximum error in depth estimation was 8.53 m.

There were no significant differences in the depth estimation error in relation to the distance from the array (up to 300 metres) that the sound source was located (GLM; $F=0.07$, $df=1$, $P=0.801$) and there were no significant differences in the error with respect to the

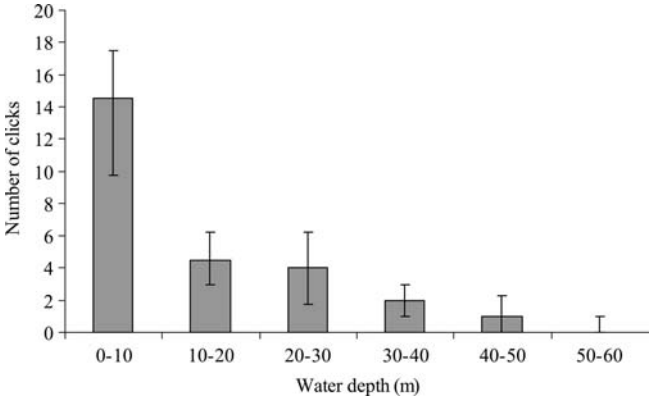

Fig. 3 The median number of clicks localised in each water depth class ± inter-quartile range. There was a significant difference in the number of clicks localised in each depth class (Kruskal–Wallis, $N=20$, $H=63.97$, $df=5$, $P<0.0001$)

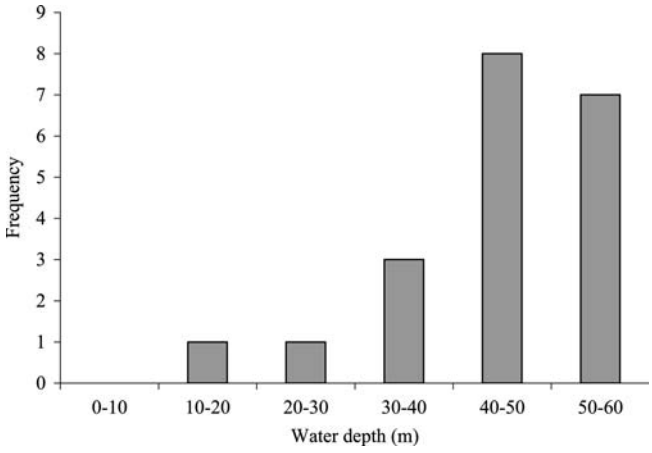

Fig. 4 The frequency distribution of the maximum depth at which clicks were localised, during each individual 5-minute recordings, $N = 20$

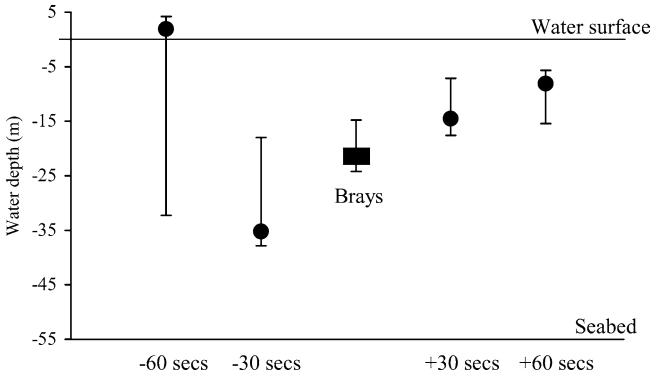

Fig. 6 The median depths of clicks localised during 30-second periods around each bray ± inter-quartile ranges. There was a significant difference in the depth of clicks throughout this period (Kruskal–Wallis, $H = 9.3637$, $df = 3$, $P = 0.025$). The black rectangle denotes the time and median depth ± inter-quartile range of the brays

depth at which the sound source was located (GLM; $F = 0.84$, $df = 1$, $P = 0.443$).

Discussion

This study has shown that within a coastal region that is used intensively by bottlenose dolphins for feeding, dolphins used the full water column and consistently dived to depths of around 50 m. As the maximum depth is 55 m, this would suggest that they were diving close to the seabed. However, the majority of their time appeared to be spent within the surface layers of the water column. In addition, it appeared that a specific feeding vocalisation occurred primarily at depths of between 20 and 30 m. Furthermore, data on the depth of clicks made before and after these feeding calls suggested that during the minute before the brays, dolphins were consistently diving from the surface to depths close to the seabed, and were subsequently returning to the surface after the brays.

The results presented here illustrate that this technique is an effective method of localising echolocation clicks made within the water column by bottlenose dolphins, thus providing estimates of the minimum depths used by diving dolphins. With a mean error in depth estimation of only 1.42 m, the localisation procedure proved to be accurate and showed little bias to either shallower or deeper estimates. Although, previous tests suggest that estimated positions obtained when localising low and high frequency sounds are not significantly different (van Parijs et al. 2000) and the technique provides a sufficiently accurate method of localising these lower frequency calls (Janik et al. 2000), it should be noted that localising the brays generally produced larger error polygons than the echolocation clicks or man-made sound source. The use of passive acoustics to estimate the depths of dolphins in our study suggests that it can present a viable alternative to tagging where the attachment of telemetry devices is unfeasible for political reasons or where adverse behavioural reactions have been observed (Schneider et al. 1998). Furthermore, the passive acoustic method allows researchers to examine the diving behaviour of dolphins in a particular area of interest. However, the use of passive acoustics to estimate the depths of dolphins underwater clearly has a number of limitations associated with it; it is limited to a relatively short range around the hydrophone array, it is reliant on the dolphins being vocal, and it is currently not possible to track individual dolphins for extended periods.

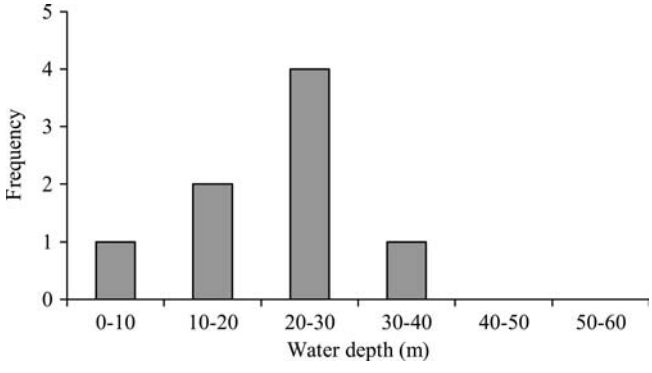

Fig. 5 The frequency distribution of the localised depths of bray vocalisations, $N = 8$

Despite these caveats, this study has provided the first quantitative data on the routine diving depths of this species in coastal habitats. There were no significant differences in the depth distributions of clicks up to 200 m distance from the array, indicating that up to this range, the physical presence of the array had no measurable effect on the diving behaviour of the dolphins. Although, it was not possible to track the dive profiles of individuals in our study (Fig. 2), the use groups of dolphins as sample units allowed us to estimate a depth distribution of dolphins for each group. Each sample

was collected on a separate day and there is evidence (University of Aberdeen, unpublished data) to show that this ensures that the risk of the same dolphins being present in different samples is minimised. Despite this, with a population of only 130 dolphins (Wilson et al. 1999), it is clear that there is still the potential that some dolphins may have been re-sampled during the study.

The depth distribution of echolocation clicks (Fig. 3) suggests that in their core region for foraging (Hastie et al. 2004), echolocating dolphins spent a significant proportion of their time within the surface layers of the water column. Relatively little time appeared to be spent below 10 m, with the least time at depths close to the seabed. Perhaps more importantly however, although these results suggest that relatively little time was spent at deeper depths, the distribution of the maximum click depth (Fig. 4) during each 5-minute recording shows that dolphins were routinely diving to depths greater than 40 m. Although, this may not be surprising considering that these depths are well within the diving capabilities of this species (Ridgway et al. 1969), this provides the first quantitative evidence that wild bottlenose dolphins in this kind of coastal habitat consistently dive, and presumably forage, close to the seabed.

The depth distribution of clicks is, however, intrinsically linked to the echolocating behaviour of the dolphins and it is unclear whether this pattern has arisen due to differential use of the water column or from variation in click rate at different depths. Despite this caveat, the distribution of clicks shows a strikingly similar pattern to the depth use found in other species of coastal small cetaceans. For example, Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) tagged with time-depth recorders spent around two-thirds of their time in the surface 5 m of the water column (Corkeron and Martin 2004), a tagged Dall's porpoise (*Phocoenoides dalli*) spent approximately 60% of its time within the surface 10 m (Baird and Hanson 1996), a tagged Atlantic spotted dolphin (*Stenella frontalis*) spent approximately 75% of its time within the surface 10 m (Davis et al. 1996), and in coastal waters off Canada, tagged narwhals (*Monodon monoceros*) spent approximately 60% of their time within the surface 10 m of the water column (Martin et al. 1994). The close parallels between the results from these other studies and those obtained in this acoustic study support that the localised echolocation clicks are a good index of usage and that they are representative of the amount of time dolphins are spending at different depths.

To a certain extent, the depth distribution of clicks is undoubtedly governed by the physiological constraints of dolphins and all air breathing diving animals. A certain proportion of their time must be spent at the surface between dives replenishing oxygen stores, readjusting blood pH and processing metabolites. In addition, because diving animals have a limited time to spend underwater, the steady decrease in the proportion of time spent in deeper waters may in part be a function of the time available to them at each depth after transit time has been taken into consideration. This pattern would be particularly apparent for short duration divers such as bottlenose dolphins whose dives rarely exceed 8 min (Corkeron and Martin 2004). For example, during a 2-minute dive and assuming a descent/ascent velocity of 2 ms^{-1} (Williams et al. 1999), transit time accounts for only 8% of a dive to 10 m, and 42% of a dive to 50 m. Correspondingly, the dolphin would have 110 s available for foraging at 10 m and only 53 s at 50 m. Once these physiological limitations have been considered, it is also possible that, in part, the pattern of depth use is suggestive that a significant proportion of foraging is carried out close to the surface. Alternatively, for bottlenose dolphins in this type of habitat, given the range of their echolocation clicks (Murchison 1980), it is possible that dolphins close to the surface are capable of detecting fish throughout the water column, and much of their prey searching can be carried out close to the surface.

Although sample sizes are small, the depth distribution of brays is interesting, as it is markedly different to that of the echolocation clicks (Fig. 5) and of previous diving studies. This suggests that the depth distribution of these calls is not simply a function of the amount of time spent at these depths. Furthermore, analyses of the depth of echolocation clicks before and after the brays suggest that a distinctive diving pattern exists around the foraging events with dolphins utilising the full water column; dolphins were primarily at the surface one minute before brays are produced and appeared to dive quickly to depths of 30–40 m around 30 s before each bray. After the brays, dolphins appeared to return to the upper half of the water column, between 10 and 20 m.

Janik (2000a) showed that brays clearly occur within a feeding context, primarily on large fish such as Atlantic salmon (*S. salar*). This is supported by the observation that in all cases during this present study, the production of brays was closely associated with dolphins subsequently at the surface with large fish. Relatively little is known about the swimming depths of Atlantic salmon within this area. However, evidence from Atlantic salmon in freshwater (Gowans et al. 1999), and Pacific salmon (Yano et al. 1984) in coastal regions suggest that although these species do occasionally dive to depth, they primarily swim within the surface layers of the water column.

Although the behaviour of salmon and the mechanisms underlying prey capture in this current study remain unknown, the results presented here provide an interesting insight into the routine diving depths of bottlenose dolphins in a discrete coastal habitat that provides a core region for foraging, and the depths of dolphins in close proximity to overt feeding events on large fish. The low rate of bray production (Janik 2000a) suggests that this vocal related foraging strategy is only a small part of the foraging repertoire of bottlenose dolphins in this population. Furthermore, it is clear that by using passive acoustics to understand the diving behav-

iour around foraging events, our study is limited to those individuals that utilise brays during prey capture. Nevertheless, our study provides a solid basis for future studies into the movements of dolphins in this discrete coastal habitat, their diving behaviour upon encountering salmon, and the mechanisms of capture by dolphins in this population. Further studies into the mechanisms of prey capture, individual differences in vocal behaviour and foraging strategies, and the spatial and temporal patterns of bray calls are needed to fully understand this foraging mechanism.

Conclusions

This study showed that in a core foraging region, dolphins used the full water column and frequently dived close to the seabed, to depths of around 50 m. However, the majority of their time appeared to be spent within the surface layers of the water column. In addition, it appeared that vocalisations associated with particular feeding behaviour occurred primarily at depths of between 20 and 30 m. This was supported by data on the depth of clicks made before and after these feeding calls suggested that during the minute before the calls, dolphins were consistently diving from the surface to depths close to the seabed, and were subsequently returning to the surface after the calls.

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