

Sperm whale behaviour indicates the use of echolocation click buzzes 'creaks' in prey capture

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During foraging dives, sperm whales (*Physeter macrocephalus*) produce long series of regular clicks at 0.5–2 s intervals interspersed with rapid-click buzzes called 'creaks'. Sound, depth and orientation recording Dtags were attached to 23 whales in the Ligurian Sea and Gulf of Mexico to test whether the behaviour of diving sperm whales supports the hypothesis that creaks are produced during prey capture. Sperm whales spent most of their bottom time within one or two depth bands, apparently feeding in vertically stratified prey layers. Creak rates were highest during the bottom phase: 99.8% of creaks were produced in the deepest 50% of dives, 57% in the deepest 15% of dives. Whales swam actively during the bottom phase, producing a mean of 12.5 depth inflections per dive. A mean of 32% of creaks produced during the bottom phase occurred within 10 s of an inflection (13× more than chance). Sperm whales actively altered their body orientation throughout the bottom phase with significantly increased rates of change during creaks, reflecting increased manoeuvring. Sperm whales increased their bottom foraging time when creak rates were higher. These results all strongly support the hypothesis that creaks are an echolocation signal adapted for foraging, analogous to terminal buzzes in taxonomically diverse echolocating species.

Keywords: foraging; echolocation; sperm whale; diving

1. INTRODUCTION

The sperm whale (*Physeter macrocephalus*) is a successful deep-sea predator with a cosmopolitan distribution (Rice 1989). Sperm whales consume a wide diversity of prey: squids appear to be their primary food source, with fishes also important in certain locations (Clarke 1980; Martin & Clarke 1986; Rice 1989; Santos *et al.* 1999; Simon *et al.* 2003; Whitehead 2003; Whitehead *et al.* 2003). Even after depletion from whaling, the current world population of sperm whales is estimated to consume a biomass on a par with all human fisheries combined (Whitehead 2002, 2003).

It is widely accepted that sperm whales forage during deep dives that routinely exceed a depth of 400 m and 30 min duration (Watkins *et al.* 2002), but many different hypotheses exist concerning the precise mechanisms by which sperm whales locate and capture prey (Fristrup & Harbison 2002; Whitehead 2003). Early hypotheses suggested that sperm whales employ a sit-and-wait foraging strategy, thought to be more energetically efficient than active pursuit of relatively small prey (Beale 1839; Clarke 1970). Persistent movements of sperm whales followed from the surface or tagged during diving, however, counter this passive foraging hypothesis (Watkins *et al.* 1993; Amano & Yoshioka 2003; Whitehead 2003; Miller *et al.* 2004a).

Following the discovery that sperm whales produce intense broadband clicks during dives (Worthington & Schevill 1957), most researchers have argued that sperm whales forage using echolocation (Norris & Harvey 1972;

Whitehead & Weilgart 1991; Goold & Jones 1995; Jaquet *et al.* 2001; Whitehead 2003). Sperm whales produce regular clicks (called 'usual' clicks by Whitehead & Weilgart (1990)) at inter-click intervals of 0.5–2.0 s during descent from the surface (Jaquet *et al.* 2001; Zimmer *et al.* 2003), until the whale begins its ascent to the surface (Madsen *et al.* 2002a). There is growing evidence that regular clicks produced during foraging dives are directional, with an intense, forward-directed beam (Møhl *et al.* 2000; Madsen *et al.* 2002a,b). Source levels within the beam are estimated to be as high as 236 dB re 1 µPa at 1 m. (Møhl *et al.* 2003). Although some earlier analyses of sperm whale clicks considered that they were unlikely to provide useful echoes from weak targets such as squid (Watkins 1980; Fristrup & Harbison 2002), these more recent data on sperm whale clicks suggest that they are appropriate for echolocation on squid (Madsen *et al.* 2002b). Echoes from both the surface and the seafloor are regularly detected on tags attached to a whale producing regular clicks, suggesting that the whale may use such echoes for orientation and navigation (Johnson & Tyack 2003; Zimmer *et al.* 2003).

Though the evidence that sperm whales use clicks for echolocation is increasingly strong, a variety of other hypotheses have continued to be suggested for sperm whale foraging. Gaskin (1967) repeated the suggestion of Beale (1839) that sperm whales could passively attract squid with the white markings or bioluminescence around their mouths. Fristrup & Harbison (2002) have suggested that a steadily swimming whale may also create a visible bioluminescent field in the water near its open mouth that might attract prey. In addition to these visual 'luring' hypotheses, Fristrup & Harbison (2002) suggest that sperm whales might use vision to detect the silhouette of prey against a

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background of down-welling light or the bioluminescence stimulated by the movement of prey. As noted by Fristrup & Harbison (2002), sperm whales are likely to use any mechanisms available to them, so these hypotheses are not mutually exclusive.

This study aims to relate the diving and movement behaviour of sperm whales to the rapid-click buzzes (named 'creaks' by Gordon (1987)) that are interspersed throughout the period of regular clicking. Clicks during creaks have an initial inter-click interval of *ca.* 0.2 s, which decreases to 0.02 s (Goold & Jones 1995). The amplitude of these clicks also appears to decline rapidly, with clicks at the end of the creak more than 20 dB lower in level than the regular clicks (see figure 2; Madsen *et al.* 2002*b*). A clicking whale often pauses for several seconds following a creak before resuming regular clicking. Based upon the acoustic features of these click sequences, creaks appear to be analogous to the terminal buzzes produced by echolocating bats as they close on targets (Goold & Jones 1995; see fig. 8 in Griffin 1958). Similar high-rate buzz sequences have been described in echolocating dolphins and other odontocetes (Au 1993; Miller *et al.* 1995; Kastelein *et al.* 1995; Johnson *et al.* 2004).

Little information is available on the behaviour of sperm whales while they produce clicks at depth (Jaquet *et al.* 2001). Gordon (1987) noted that whales being tracked by a ship's depth sounder often appeared to modulate their depth profile during creaks. Across a small sample of 12 dives, Jaquet *et al.* (2001) found a positive correlation between creak rates and total dive duration. When a marine mammal is feeding during a dive, it needs to decide when to break off from foraging and return to the surface. If returning to the surface represents leaving a patch, optimal foraging theory suggests that divers should remain in the patch at depth longer when prey density is high (Charnov 1976; Stephens & Krebs 1986). Aerobic divers that abandon poor patches by returning to the surface are predicted to benefit from spending more time in higher-quality patches (Thompson & Fedak 2001). The cost of remaining at depth increases in a nonlinear fashion when dive duration exceeds the aerobic dive limit because energy reserves are used less efficiently in anaerobic respiration and more time is therefore required away from foraging areas subsequently for recovery from lactate build-up (Kooyman 1989). The long and deep dives of sperm whales increase the chance that aerobic limits are approached and that moving to the surface to breathe reduces the ability of a whale to relocate the same patch (Ydenberg & Clark 1989; Kooyman & Ponganis 1998). Within this context, it is predicted that sperm whales should extend the foraging phase of dives with high prey capture rates.

The development of a high-resolution archival tag that can be attached to sperm whales using suction cups (Johnson & Tyack 2003) has enabled the recording of each whale's depth, three-dimensional orientation and sound production during deep foraging dives. To critically test the idea that creaks function in prey capture, similar to 'terminal buzzes', we detail the depth and behaviour of sperm whales during creaks. Presumably, sperm whales dive to depth to access prey resources not available near the surface. Given the cost of diving, we would expect foraging whales to spend most of their bottom time at the depth of good prey layers. This suggests that foraging activity would

be most intense during the bottom phase of deep dives (LeBoeuf *et al.* 1988). If creaks are used in prey capture, they should reflect a similar pattern.

Data collected using tags strongly support the summary of Whitehead (2003) that sperm whales move consistently throughout deep dives. Sperm whales spend most of their bottom time within one or two depth bands apparently feeding in vertically stratified prey layers, though considerable depth excursions occur during the bottom phase of the dive (see fig. 5.14 in Whitehead (2003)). While it seems unlikely, on energetic grounds, that a sperm whale weighing tens of metric tons will engage in prolonged high-speed chases of typically small prey items, we expect that a moving sperm whale will need to manoeuvre to some extent to capture prey in its mouth. This leads us to predict higher rates of changes in body orientation during creaks. If the whale is outside or in the top or bottom of its preferred layer while approaching a prey item, then we predict that it may manoeuvre during prey capture to reorient back to the preferred layer. This leads us to predict that if creaks are synchronized with manoeuvring for prey capture, they may also be associated with dive-inflection points, especially when the whale is on the top or bottom of its preferred layer. We test whether the behaviour of sperm whales matches our predictions of what is expected if creaks are produced during prey capture, and whether sperm whales increase foraging time during dives with higher creak rates.

2. MATERIAL AND METHODS

Groups of sperm whales were followed at sea from a research vessel (R/V Alliance in the Mediterranean, R/Vs Gordon Gunter and Gyre in the Gulf of Mexico). We attached archival tags (called 'Dtags') to the backs of surfacing sperm whales with suction cups using a 12 m cantilevered pole (Moore *et al.* 2001; Johnson & Tyack 2003). The sensors in the Dtag include sound, depth, a 3-axis accelerometer, and a 3-axis magnetometer (Johnson & Tyack 2003). Sound was sampled at 16 or 32 kHz rate, while the other sensors were filtered and down-sampled to obtain a common effective sampling rate of 5.88 Hz. Pressure readings were converted to depth using calibrated values. Magnitude readings on 3-axis accelerometers and magnetometers were converted to pitch, roll and heading of the whale following published techniques (Johnson & Tyack 2003; Miller *et al.* 2004*a*).

The acoustic record of the tag was analysed to determine the start and end time of each creak. All deep dives (greater than 350 m) were broken into descent, bottom and ascent phases. The beginning of descent was the time that a whale left the surface on a deep dive, while the end was the time when the pitch of the diving whale first exceeded 0° (when it was no longer oriented downward). The start of the ascent was defined as the last point in time when an animal's pitch was downward (when it first pointed upward) and ended when the whale reached the surface (Miller *et al.* 2004*a*). The bottom phase was defined from the end of the descent until the start of the ascent.

Dive inflections were identified as points where the vertical velocity of the whale changed sign, with an ensuing net vertical change of at least 10 m (approximately one body length) before the next inflection. The 10 m criterion removes minor inflections that could result from thrusting oscillations or other minor changes in body orientation. We determined the number of creaks that each whale produced within 10 s of an inflection. To compare the observed value to that expected by chance, we randomized

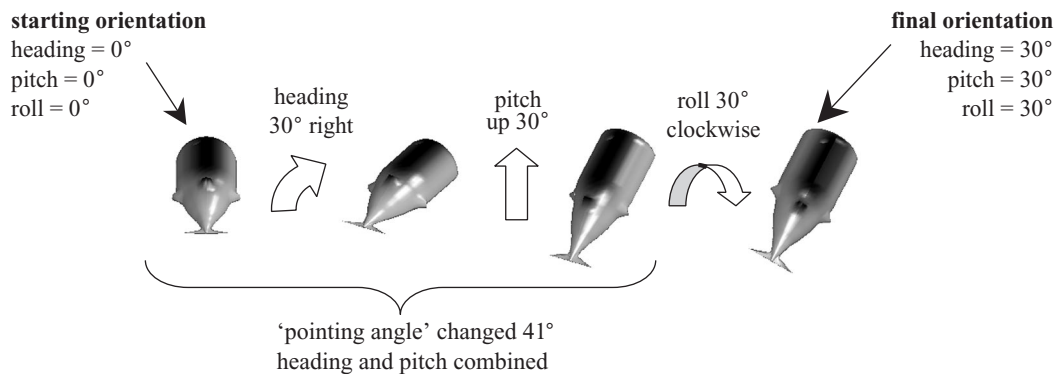


Figure 1. Orientation changes in a sperm whale model broken into separate components. The three-dimensional orientation of the whale is described fully by three variables: heading (0: due north, +90: due east), pitch (0 when body is flat, +90 when rostrum pointed up), and roll (0 when back is up, +90 when rotated clockwise). Heading and pitch both reflect changes in the orientation of the whale axis itself, whereas roll reflects rotational movements around the axis of the whale. We combined changes in pitch and heading as changes to the 'pointing angle' of the whale axis.

the alignment of the dive profile and acoustic records by joining the start and end of the creak time-series and rotating it a random amount of time while holding the dive profile time series constant (Miller *et al.* 2004b). For each random rotation, the number of creaks within 10 s of a give inflection was re-calculated. By performing this rotation 10 000 times for each dive record (Adams & Anthony 1996), we generated an expected distribution of the number of creaks that would occur within 10 s of a dive-inflection point under the null hypothesis that the timing of the two sequences was independent.

We analysed each whale's rate of orientation change to assess whether sperm whales manoeuvre more during creaks (see electronic Appendix A). The absolute value of the change in each whale's roll, pitch and heading was calculated at three-second intervals (figures 1 and 2b). Pitch and heading give a three-dimensional description of the angle of the whale's axis, so changes in these two values were combined into 'pointing angle'. Changes in whale pointing angle and roll were calculated for 3 s intervals centred on the beginning of each creak, the end of each creak and a control period halfway between each creak. The control interval for the first creak of each dive was set at 30 s before the creak. Data distributions were checked for normality using the one-sample Kolmogorov–Smirnov test, and non-parametric statistics were employed if the assumptions of ANOVA were not met (Zar 1984).

3. RESULTS

Between 2000 and 2002, at least one entire deep dive was recorded from each of 23 sperm whales (5 in the Ligurian Sea in the Mediterranean and 18 in the Gulf of Mexico), and three or more deep dives from 15 whales (four from the Ligurian Sea; see table 1 in Miller *et al.* (2004a)). Typical surface reactions to approach and tagging were minor and of short duration, such as a brief startle response followed by an arch-out dive. The first dive made by a tagged sperm whale tends to be shorter than subsequent dives (P.J.O. Miller, unpublished data). This is probably caused by the whale diving earlier during the surfacing sequence than normal, in reaction to the approach and tagging operation. This effect does not extend beyond the first dive. We therefore excluded the first dive after tag attachment from duration and creak-rate analyses.

From inspection of dive records, these sperm whales appeared to dive to preferred depth layers (figure 2a). Regular clicks start fairly early in descent and cease once the

whale begins to ascend, in close agreement with Madsen *et al.* (2002a). Creaks were produced within sequences of regular clicks during deep dives only, and generally during the deepest part of dives. Fast series of clicks were recorded only four times when the tagged whale was near the surface. These fast series had longer durations than typical creaks, and did not have the same click timing or amplitude pattern that were common to creaks (Whitehead 2003). We therefore did not include in our analyses these relatively uncommon fast series recorded while the whale was at the surface, though they might represent the use of echolocation in a non-foraging context.

During 129 h of tag recordings, these 23 animals produced a total of 1670 creaks, out of which 1589 were produced during the 103 complete dives recorded. The deepest and shallowest creaks were recorded at 1169 m and 288 m, respectively. Talled by individual whale, creaks had a mean duration of 8.7 s (± 7.6 s.d.), and 88.9% ($\pm 13.5\%$) of creaks were followed by a pause in clicking of 4.8 s (± 2.4 s). Creaks were produced at a mean depth of 616 m (± 126 m).

(a) Depth of creak production

All 23 whales produced most of their creaks during the bottom phase of their dives (figure 2a). Creak rates were significantly higher during the bottom phase (27.7 ± 12.7 creaks h^{-1}) than during descent (3.7 ± 4.1 creaks h^{-1}) or ascent (6.3 ± 3.7 creaks h^{-1} ; $F_{2,66} = 62.1$, $p < 0.0001$). To test the depth distribution of creaks, we calculated the creak rate in four depth bins (<50%, 50–70%, 70–85%, and > 85% of maximum dive depth) in which sperm whales spent roughly equivalent amounts of time during deep dives. Tallying by individual whale, mean (\pm s.d.) creak rates within these depth bins were 0.02 (± 0.05), 3.76 (± 6.12), 9.91 (± 8.18) and 17.97 (± 11.46) per hour (Kruskal–Wallis $H_3 = 62.9$, $p < 0.0001$). Non-parametric Tukey *post hoc* contrasts showed that creak rates differed at $p < 0.05$ between all bins except for the 70–85% versus more than 85% contrast. Out of the 1589 creaks observed during full dives, 0.25% were produced in the shallowest 50% of dive depths. By contrast, 57% of all creaks were produced in the deepest 15% of dives.

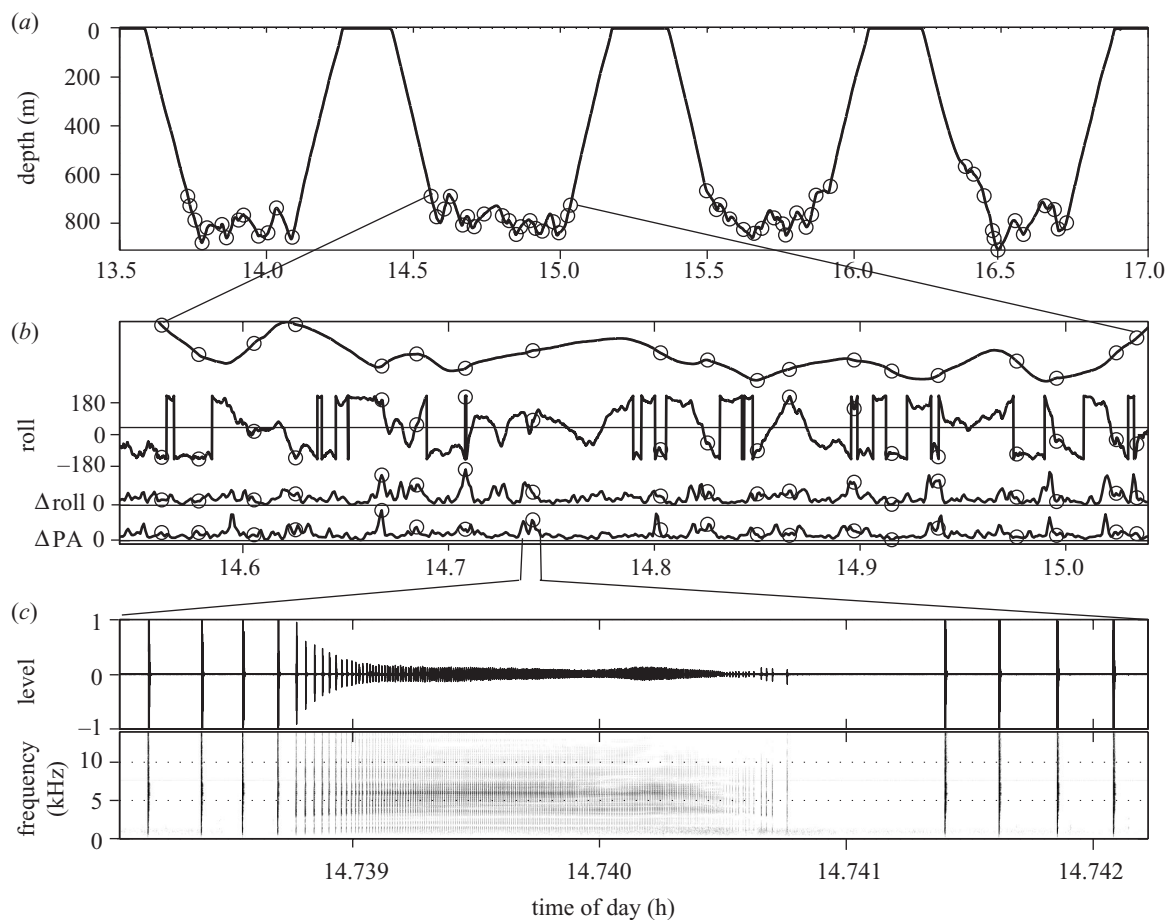


Figure 2. Sample data analysis of sperm whale sw265 tagged on 22 September 2001 in the Ligurian Sea. (a) Time–depth profile of four recorded dives with the end times of creaks marked with a circle. Note that the whale spent time and produced creaks primarily within a preferred depth range. (b) Detailed time–depth profile of the second dive with the animal's roll throughout the dive, the change in roll (Δ roll) and change in pointing angle (Δ PA) measured over 3 s intervals and with creaks marked as circles. Note that creaks are often associated with inflections in the dive profile, as well as with peaks in Δ roll and Δ PA. (c) Waveform and spectrogram of the eighth creak produced during the second dive. Note that the level of the creak clicks as recorded by the tag on the animal's back is $\times 10$ (or 20 dB) lower than the regular clicks. The 5.9 s creak is followed by a 2.3 s pause before the resumption of regular clicking. The three-dimensional movement of the whale is linked to the sounds it produced during this creak in an animation presented as electronic Appendix A. In this animation, the increased manoeuvring by the whale during the creak is clear.

(b) Association of creaks and dive-inflection points

Numerous inflection points, and the close association of many creaks to these inflections, can be seen on the dive profiles (figure 2). We excluded one dive record in which a large male (sw208b) foraged along the seafloor with no dive inflections during the bottom phase. The remaining 22 sperm whales made primarily bathypelagic dives, although several whales made benthic excursions for portions of dives. Tallying by individual, these 22 whales made a mean (\pm s.d.) of 12.5 (± 4.0) depth inflections, and 13.1 (± 6.1) creaks during the bottom phase of their dives.

A mean of 4.2 (± 2.6) creaks per dive, or 32.1% of all creaks, were produced within 10 s of an inflection point during the bottom phase. There was no difference in the mean number of creaks within 10 s of up-to-down (2.11 ± 1.2) versus down-to-up (2.07 ± 1.9) inflections (paired $t_{21} = 0.13$, $p = 0.90$). Creaks were equally likely to be produced 10 s before ($51.2\% \pm 23.5\%$) as 10 s after an inflection point. Based on 10 000 random rotations of the creak time-series (holding the inflections constant), the mean expected number of creaks within 10 s of a dive

inflection was 0.32 (± 0.22) creaks per dive. The observed value exceeded the mean expected value for all 22 whales (binomial $p < 0.001$). Averaging by whale, we observed 13.3 (± 8.9) times more creaks within 10 s of a dive inflection point than would be expected by chance if the two sequences were independent of each other.

For each dive, we scored the depth of inflection points as the percentage depth between the minimum and maximum obtained by each whale during the bottom phase of that dive. Dive-inflection points were quite evenly spread throughout the depth range covered in the bottom phase of dives. A statistically equal number ($47.8 \pm 13.0\%$) of all dive inflections occurred in the central 50% depth band as in the two extreme 25% bands. While, in some cases, sperm whales moved to shallow or deep extremes and then inflected back to the preferred depth layer (figure 2), just as many dive inflections were produced within the central depth band of the bottom phase. Though inflection points were equally distributed across the depth range of the bottom phase, creaks were roughly twice as likely to occur within 10 s of a dive inflection in the outer 25% depth

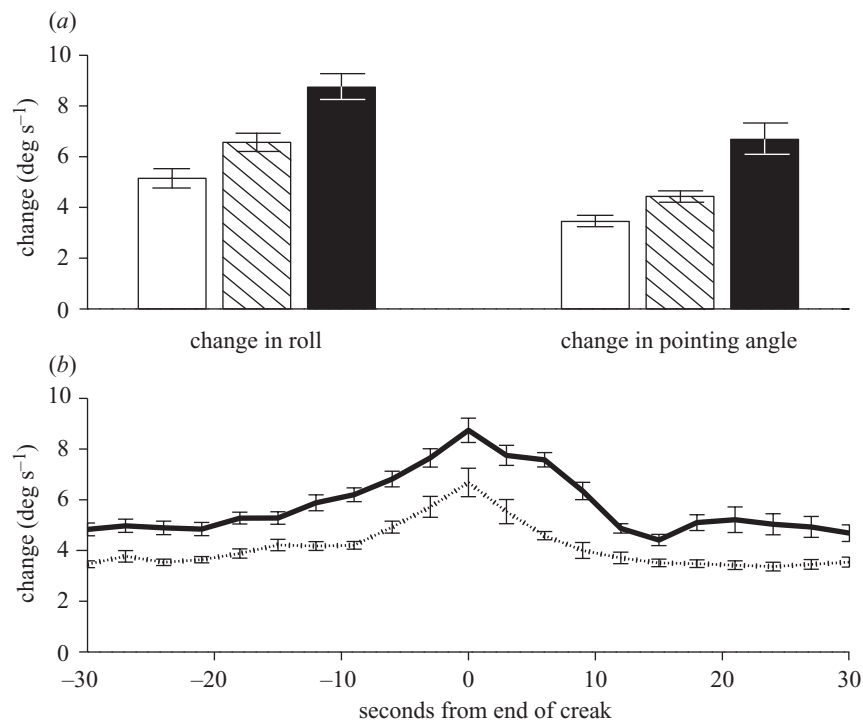


Figure 3. (a) Mean (\pm s.e.) change per second in roll and three-dimensional pointing angle measured over a 3 s interval centred on a control period halfway between creaks (open bars), the start of creaks (hatched bars) and the end of creaks (black bars). Roll and pointing angle change increased during the start of creaks and again at the end of creaks. (b) Mean (\pm s.e.) change in roll (solid line) and pointing angle (dotted line) over 3 s intervals before, during, and after the end of all creaks, which were centred at zero. Note that the whales increased both roll and pointing-angle activity *ca.* 12 s before the end of the creak, and returned to baseline within 12 s of the end of the creak; $n = 23$ whales (1670 creaks).

bands of the bottom phase. Tallying by individual whale, 23.8% ($\pm 12.4\%$) of 753 total creaks in the central 50% depth band of the bottom phase were within 10 s of an inflection point, versus 43.6% ($\pm 22.4\%$) of 659 total creaks in the extreme depth bands (arcsine-transformed paired $t_{21} = -4.24$, $p < 0.001$).

(c) *Manoeuvring by the whales in relation to creaks*

Diving sperm whales made steady changes in both their roll and pointing angle throughout dives, with occasional spikes that were often associated with creaks (figure 2b). Overall, the 23 sperm whales in our sample changed both their roll ($F_{2,66} = 23.5$, $p < 0.0001$) and pointing angle ($F_{2,66} = 21.8$, $p < 0.0001$) significantly more during creaks than during control periods halfway between creaks (figure 3a). Roll movements over the 3 s centred on the start and end of creaks were 28% and 70% greater than during control periods, respectively (Tukey $p < 0.001$ for end of creak versus control and start of creak, $p < 0.05$ for control versus start of creak). Similarly, change in pointing angle increased by 29% and 93% at the start and end of creaks, respectively (Tukey $p < 0.001$ end of creak versus control and start of creak, $p = 0.13$ for control versus start of creak).

Because increased changes in roll and pointing angle were also observed in association with dive inflections, we tested whether association with a dive inflection influenced the change in roll and pointing angle. Excluding whale sw208b, which made no dive inflections at the bottom, two-way ANOVA models showed no interaction between condition and association with a dive inflection point for changes in roll (interaction $F_{2,126} = 0.38$, $p = 0.68$) or

pointing angle (interaction $F_{2,126} = 0.88$, $p = 0.42$). This reflects the gradual change in orientation during most dive inflections, so the whale's orientation did not change significantly more during a creak when a dive inflection was present.

To assess the timing of manoeuvring by the whale in relation to creaks graphically, changes in roll and pointing angle over 3 s were averaged for each whale from 30 s before to 30 s after the end of each creak. Thus, the movements of each of the 23 whales in the study were weighted equally. The result shows a clear peak in roll and pointing angle change over the 3 s centred on the end of creaks (figure 3b). The primary interval of increased manoeuvring activity occurs between *ca.* 12 s before and after the end of creaks, suggesting a fairly brief period of increased activity.

(d) *Creak rates and duration of bottom phase of dives*

After eliminating the first dive made by each whale after tagging, we had two or more dives from 15 whales, for a total of 79 complete dives. Over these 79 dives, creak rates averaged (\pm s.d.) 32.3 (± 15.6) creaks h^{-1} during the bottom phases of 27.2 ± 6.7 min duration. If there were no link between creak rate and bottom time, we would expect each whale to have a positive or negative correlation of creak rate versus bottom time with equal probability. Instead, creak rate and bottom time were positively correlated for 12 out of the 15 whales, which strongly deviates from an equal probability binomial distribution ($p = 0.014$). Pooling the data for all individuals after subtracting their mean creak rate and bottom time duration, regression showed that creak rate during the bottom phase

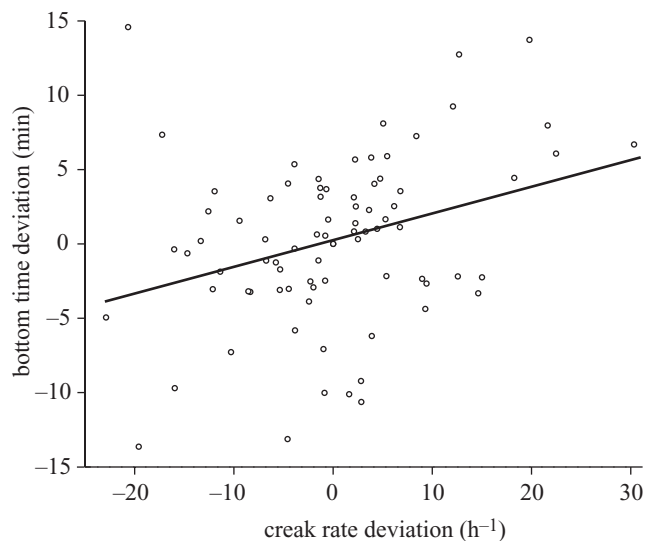


Figure 4. Deviation in the duration of the bottom phase versus deviation in creak rate during the bottom phase. The mean rate and duration for each whale were subtracted from its dives. The first dive after tag attachment was eliminated from this analysis, so we included only 79 dives from 15 whales from each of which we recorded three or more dives. The positive slope of the regression line ($0.18, F_{1,63} = 9.14, p < 0.01$) demonstrates that sperm whales remained in the bottom phase of dives for longer when their creak rates were higher.

of dives was positively correlated with bottom time duration (figure 4; $F_{1,63} = 9.14, p < 0.01$).

4. DISCUSSION

Visual and acoustic observations of sperm whales from the surface have demonstrated a strong correlation between surface behaviour and the types and rates of various click sounds heard (Whitehead & Weilgart 1990, 1991). As Whitehead (2003, p. 156) states: 'We think we have a reasonable understanding of their behaviour during surface periods, but what happens at depth is probably more significant and certainly more mysterious'. Though we understand the general behavioural context within which various click sounds are produced, their possible functions remain untested because it has been difficult to ascribe sounds to a specific individual or link them to a particular part of the dive cycle (Jaquet *et al.* 2001). Our study overcomes this limitation through the use of short-term archival tag attachment, allowing us to describe in detail the behaviour of sperm whales in relation to the sounds they produce throughout the dive cycle. Our results show that several key aspects of the behaviour of sperm whales are consistent with the hypothesis that creaks are produced during prey capture.

First, we show that creaks are predominantly produced during the bottom phase of dives where feeding is expected to occur (figure 2), with almost no creaks occurring in the top 50% of each dive. That these long and deep dives are foraging behaviour is supported by an analysis of stomach contents that largely consist of bathypelagic or benthic prey (Clarke 1980; see Whitehead (2003) for review). Observations of defecation by fluking whales followed for several days confirm that those whales were feeding during

observation periods when deep diving dominated their behaviour (Whitehead *et al.* 1989). Click sounds produced near the surface include codas and slow click series, probably produced for communication (Watkins & Schevill 1977; Weilgart & Whitehead 1993). Regular clicks are heard during the bottom phase of dives, but also during descent, probably as part of a search behaviour (Thode *et al.* 2002; Zimmer *et al.* 2003). Creaks were heard only after the onset of regular clicking.

The association of creaks with increased movement of sperm whales is the second line of evidence demonstrated in this study. Sperm whales increased the manoeuvring of their body orientation during creaks, with the strongest activity occurring at the end of the creak (see figures 3 and 4 and electronic Appendix A). This finding was equally strong for creaks that were and were not within 10 s of a dive inflection, showing that more rapid changes in body orientation during creaks was not a by-product of the whale making a dive inflection. Given the diverse diet of sperm whales, the 23 whales in our study undoubtedly fed on multiple prey types, with varying degrees of mobility and escape behaviour (Whitehead 2003). However, sperm whales are likely to need to manoeuvre to capture even the most quiescent prey (Simon *et al.* 2003) as final adjustments are made during the final approach phase. The time-sequence of changes in orientation during creaks shows a clear peak at the end of creaks, with higher activity *ca.* 12 s before and after the end of the creak. This timing of manoeuvring seems consistent with the final stages of prey localization and capture.

Almost a third of all creaks (32.1%) ended within 10 s of an inflection point during the bottom phase of dives, which is far more than predicted by chance alignment of these behavioural sequences. Although dive inflections were just as likely to occur in the central 50% depth band as in the two extreme 25% bands of the bottom phase of a dive, creaks were twice as likely to occur within 10 s of an inflection point when the whale was in the extreme depth bands. Although dive inflections may have multiple functions, these findings suggest that creaks often mark the end of a period of directed movement, expected during the approach or pursuit of prey (Whitehead 2003). We restricted our analysis to vertical as opposed to horizontal excursions by the whale during the bottom phase, because the tag records depth with great precision. It is possible that the whale also made horizontal excursions during the bottom phase of dives that were not considered in this analysis. Creaks were equally likely to be associated with up versus down inflections, suggesting that the whale foraged in both directions in the water column.

As it moves toward a detected prey item, a sperm whale will move vertically to some extent depending on its approach angle. At the end of one or more approaches, the whale may end up outside its preferred depth layer and turn back, creating a dive inflection. This interpretation is supported by the result that creaks are twice as likely to be associated with dive-inflection points when they occur in the outer 50% depth range covered during the bottom phase of the dive. The whale could either turn and redirect its tens of tons of mass back to the layer independent of the movements required to capture prey, or it may save energy if it can orient its feeding manoeuvres during the creak in order to head back towards the middle of the layer (an

equal proportion of creaks occurred in the 10 s before and after an inflection point). Approximately one-third of creaks associated with inflection points occur within the central 50% depth range. In this case, the depth inflection point may reflect the whale turning to remain in the highest density of prey or turning toward a detected prey target. After the whale manoeuvres to capture a prey item, it may save energy by simply continuing along the resulting trajectory when it is within its preferred layer. Our understanding of the function of sperm whale movements during foraging will remain uncertain until more information on the distribution and behaviour of their prey is available.

The third line of evidence associating creaks with foraging is that the sperm whales in our study increased the duration of time spent at the foraging depth of dives when creak rates were higher. The 15 whales that made three or more dives increased the duration of the bottom phase of dives by 1.8 min for an increase in creak rate of 10 creaks h^{-1} . This result confirms and extends those of Jaquet *et al.* (2001) with a larger dataset, and we were also able to subtract descent and ascent time from dive duration. This is important to control for the possibility that creaks are simply produced at a constant rate during the bottom phase of dives for some function other than prey capture. If this were the case, creak rate would not be correlated with bottom-phase duration, but longer dives could have a higher creak rate simply owing to a greater proportion of dive time spent in the bottom phase. Instead, we demonstrate that sperm whales modulate the duration of the bottom phase itself with creak rate.

Though statistically significant, the effect of creak rate on bottom time was small: a 31% increase above the average bottom phase creak rate increased bottom time by only 7%. Thompson & Fedak (2001) suggested that patch quality might have a reduced influence on deep-diving foragers as the benefit of spending more time in a high-quality patch is offset by longer travel times to depth. Alternatively, if the whales have used their oxygen store and begun anaerobic metabolism, the benefit of remaining in a high-quality patch may be rapidly exceeded by the cost of remaining at depth. A final consideration is that the dive duration of females may be modulated by social demands such as the care of young (e.g. Whitehead 1996).

One objection to the hypothesis that creaks are used in prey capture is that the number of creaks detected from the surface seems too low to provide adequate food resources for sperm whales (Madsen *et al.* 2002b). Based on the heart weight of sperm whales and the food value of cephalopod prey, Lockyer (1981) estimated that sperm whales should consume *ca.* 3% of their body weight in squid per day. The Gulf of Mexico whales were typically estimated to weigh *ca.* 10 MT, while the larger males in the Mediterranean were *ca.* 25 MT (Miller *et al.* 2004a). Over our entire sample, sperm whales were engaged in a deep dive for a total of 86 h out of 129 h when a tag was attached (66% of time). This is similar to the summary of Whitehead (2003) in which sperm whales in most locations forage for *ca.* 75% of the time, of which less than 20% is spent at the surface. Though there was variability across dives and individuals, the average creak rate per dive was 20.1 and 22.4 creaks h^{-1} in the Mediterranean and Gulf of Mexico, respectively, after eliminating the first dive after tagging.

Thus, the number of creaks produced daily can be estimated at *ca.* 320 in the Mediterranean and *ca.* 360 in the Gulf of Mexico. To match the 3% prediction, average prey size in the Gulf of Mexico should be *ca.* 0.8 kg, whereas those in the Mediterranean should be 2.3 kg assuming that each creak led to a successful prey capture. These size estimates are within the range of sizes of typical squid prey consumed by sperm whales worldwide, but the predicted prey size for the Mediterranean is somewhat large compared with that in most studies (see table 2.2 in Whitehead (2003)). Given the inherent inaccuracy of estimated feeding requirements of a species for which metabolic rates have never been measured (Lavigne *et al.* 1986), the daily creak rates are not inconsistent with the probable feeding requirements of sperm whales, even if not every creak leads to successful prey capture.

This study describes the best current information on the behaviour of only half of the predator-prey interaction in relation to creak production. Ideally, we would directly observe both predator and prey to demonstrate a foraging event and show how the behaviour of the predator relates to prey capture (e.g. Nowacek 2002). Though echoes from prey targets have been detected on tags attached to beaked whales, none are apparent on sperm whales (Johnson *et al.* 2004). This is probably owing to the relatively large head of the sperm whale, which blocks the sound path from a prey target near the mouth to the tag on the whale's back. Direct detection of sperm whale prey during feeding is ultimately necessary to estimate the percentage of creaks that result in successful prey capture, and also to identify whether prey is taken without the whale producing a creak sound. More information on the diet of sperm whales in these oceans is also needed to more accurately estimate the ecological role of sperm whales in those ecosystems (Gannier *et al.* 2002; Roberts 2003).

It would be a useful research tool to be able to identify feeding events based on an acoustic cue provided by foraging sperm whales. Other possible methods to observe prey capture would be difficult at best, and expensive to carry out in any routine fashion. By tracking the number of feeding events that occur, we can extrapolate an animal's feeding rates, which could be used to test whether defecation rates accurately reflect feeding success (Whitehead *et al.* 1989). Overall feeding rates measured by defecation are linked to oceanographic conditions (reviewed in Whitehead (2003)), but use of creaks would allow individual variation in feeding success to be measured and related to animal condition or the presence of sources of behavioural disturbance. Food intake per creak produced is likely to vary by prey type owing to variation in prey size, success rate of creaks and the proportion of prey taken in the absence of creaks. Nonetheless, our results suggest that overall creak rates are an indicator of feeding success across a series of successive dives, during which prey type should be fairly stable. Unfortunately, it appears to be difficult to detect creaks from the surface. Jaquet *et al.* (2001) reported that it was often difficult to distinguish creaks from pauses when recording isolated diving males from the surface. Madsen *et al.* (2002b) found that creaks could often be identified from single animals in apparent pauses through careful acoustic filtering and amplification. Acoustic tags clearly provide a means to detect creaks along with concurrent feeding behaviour. With careful ground-truthing,

remote observation of creaks may prove to be a fruitful means to monitor the feeding success of sperm whales.

This study provides strong support for the hypothesis that sperm whales use echolocation to capture prey, and that creaks function in a manner analogous to terminal buzzes during echolocation by foraging bats and other odontocete cetaceans. The increase in the click repetition rate probably reflects the need for more rapid updating on the position of prey during the final capture phase than is obtained with the $0.5\text{--}2\text{ s}^{-1}$ rate of regular clicks. Of course, creaks may have other functions in addition to strictly echolocation. Sounds produced by an approaching sperm whale might stimulate prey to move, which might make them visible via stimulated bioluminescence (Fristrup & Harbison 2002). Creaks may also play a role in communication between sperm whales since they represent a cue of feeding to conspecifics in the area (Barclay 1982; Gordon & Tyack 2002).

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