

Extreme diving of beaked whales

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Summary

Sound-and-orientation recording tags (DTAGs) were used to study 10 beaked whales of two poorly known species, *Ziphius cavirostris* (Zc) and *Mesoplodon densirostris* (Md). Acoustic behaviour in the deep foraging dives performed by both species (Zc: 28 dives by seven individuals; Md: 16 dives by three individuals) shows that they hunt by echolocation in deep water between 222 and 1885 m, attempting to capture about 30 prey/dive. This food source is so deep that the average foraging dives were deeper (Zc: 1070 m; Md: 835 m) and longer (Zc: 58 min; Md: 47 min) than reported for any other air-breathing species. A series of shallower dives, containing no indications of foraging, followed most deep foraging dives. The average interval between deep foraging dives was 63 min for Zc and 92 min for Md. This long an interval may be required for beaked whales to recover from an

oxygen debt accrued in the deep foraging dives, which last about twice the estimated aerobic dive limit. Recent reports of gas emboli in beaked whales stranded during naval sonar exercises have led to the hypothesis that their deep-diving may make them especially vulnerable to decompression. Using current models of breath-hold diving, we infer that their natural diving behaviour is inconsistent with known problems of acute nitrogen supersaturation and embolism. If the assumptions of these models are correct for beaked whales, then possible decompression problems are more likely to result from an abnormal behavioural response to sonar.

Key words: beaked whale, *Ziphius cavirostris*, *Mesoplodon densirostris*, diving, foraging, aerobic dive limit.

Introduction

Marine mammals have remarkable abilities for breath-hold diving. The best known deep divers include the elephant seals, *Mirounga angustirostris* and *M. leonina*, which can dive for up to 2 h to depths over 1500 m (DeLong and Stewart, 1991; Hindell et al., 1991; Le Boeuf et al., 1988), and the sperm whale, *Physeter macrocephalus*, which can dive for >1 h to depths in excess of 1185 m or more (Watkins et al., 1993). Marine mammals that dive so deep usually do so to forage on mesopelagic or benthic prey, but elephant seals are also thought to dive to avoid near-surface predators such as killer whales and sharks (Le Boeuf and Crocker, 1996).

Deep-diving, air-breathing animals face a number of challenges relating to prolonged breath-holding and high hydrostatic pressure (Kooyman, 1989). Animals that prolong apnea must optimize the size and use of their oxygen stores, and must deal with the accumulation of lactic acid if they rely upon anaerobic metabolism. As hydrostatic pressure compresses gases in the body, there are direct mechanical effects, physical effects such as bubble formation during decompression and also possible physiological effects such

as nitrogen narcosis, high pressure nervous syndrome, and shallow water blackout (Bennett, 1982; Bennett and Rostain, 2003). Pathologies related to effects of pressure are well known among human divers (Brubakk and Neuman, 2003), but marine mammals appear to have developed adaptations to avoid most mechanical and physiological effects (Kooyman, 1989). The hazard of bubble formation during decompression is best known for humans breathing compressed gases, but empirical studies (Paulev, 1965; Paulev, 1967; Ridgway and Howard, 1979) and theoretical considerations (Houser et al., 2001; Scholander, 1940) have shown that breath-hold divers can develop supersaturation and possible decompression-related problems when they return to the surface. Supersaturation has not been measured during normal diving behaviour of wild marine mammals but rather in specially designed experiments performed by trained subjects. Nitrogen tensions in the muscles of two dolphins (*Tursiops truncatus*) trained to perform a series of dives to 100 m were estimated to be about three times the ambient pressure (Ridgway and Howard, 1979), a level of supersaturation that did not appear to harm the subjects. By contrast, Scholander (Scholander, 1940) reported abundant gas

bubbles in the arteries of a bladder-nosed seal (*Cystophora cristata*) that died after being forcibly submerged to 300 m in 3 min and drawn to the surface in 9 min. It is not currently known what levels of supersaturation lead to pathological conditions in marine mammals nor if dangerous levels of supersaturation occur in wild animals conducting voluntary dives and, if so, under what conditions.

Air-breathing animals rely upon oxygen for aerobic metabolism; anaerobic metabolism is less efficient and causes the build-up of metabolites, such as lactic acid, that must be processed aerobically. Deep-diving marine mammals extend their dives by an increased ability to store oxygen compared to terrestrial mammals, by increasing their tolerance to hypoxia and by decreasing their metabolism during dives (Butler and Jones, 1997; Kooyman and Ponganis, 1998; Reed et al., 1994; Sparling and Fedak, 2004). Many deep-diving species are able to perform most dives using aerobic metabolism, but must rely increasingly on anaerobic pathways during long dives that cannot be entirely supported aerobically (Butler, 2001; Kooyman, 1985). The duration of apnea at which lactic acid starts to accumulate significantly is called the aerobic dive limit (ADL) (Kooyman et al., 1980) or diving lactate threshold (Butler and Jones, 1997). The measured ADL for Weddell seals, one of the best-studied species, is about 21 min for an adult (Kooyman et al., 1980), but varies as a function of activity level (Davis and Kanatous, 1999). Studies by Kooyman and coworkers (Kooyman et al., 1980) have shown that almost all (>90%) of the dives that the seals undertake are within the ADL. When Weddell seals dive longer than the ADL, up to more than 70 min (Kooyman, 1981), they build up lactic acid and usually do not make another long dive until they have metabolized all or some of it during rest at the surface or during shorter recovery dives (Castellini et al., 1988; Castellini et al., 1992; Kooyman et al., 1980). This increased recovery time required after anaerobic dives reduces the overall fraction of time that can be spent under water compared to a series of aerobic dives (Butler and Jones, 1997; Kooyman and Ponganis, 1998). Models of optimal deep foraging suggest that the cost of dives beyond the ADL would exceed their benefit except in cases where prey are so deep that they cannot be reached otherwise, or the quality of the current prey patch is so high as to outweigh the extra time required to prepare for the next dive (Mori, 1998; Mori, 1999). Although the details are not fully understood, it is likely that the management of gas under pressure and anaerobic metabolism constrains the diving behaviour of marine mammals on a dive-by-dive basis (Butler and Jones, 1997; Kooyman and Ponganis, 1998).

Beaked whales are considered to be deep divers based primarily upon diet inferred from stomach contents (Blanco and Raga, 2000; Mead, 1989; Podesta and Meotti, 1991; Ross, 1984; Santos et al., 2001). This family includes some of the world's most cryptic and difficult to study mammals and little is known about their diving behaviour. Tagging studies have revealed that the northern bottlenose whale, *Hyperoodon ampullatus*, is capable of diving for >1 h to depths in excess of 1500 m (Hooker and Baird, 1999). Recently, Johnson et al.

(Johnson et al., 2004) used acoustic recording tags (DTAGs) to describe echolocation clicks produced by Cuvier's and Blainville's beaked whales (respectively *Ziphius cavirostris* and *Mesoplodon densirostris*) during dives of up to 1270 m depth. Both species were found to produce trains of regular clicks with occasional fast sequences, called buzzes, during deep dives (Johnson et al., 2004). Echoes from targets in the water were recorded by tags on both species, often just before and during buzzes (Madsen et al., 2005), which along with concomitant impact sounds and movements are highly suggestive that buzzes indicate attempts to capture prey (Johnson et al., 2004). It was concluded that both beaked whale species forage by echolocation in deep water.

The diving physiology of Cuvier's and Blainville's beaked whales is of special interest because of reports of the presence of gas and fat emboli in these species during atypical mass strandings associated with the use of naval sonar (Fernandez et al., 2005; Jepson et al., 2003). The atypical mass strandings may involve more than 10 animals distributed over tens of kilometres of coastline within a few hours of sonar transmissions (Cox et al., 2006; D'Amico, 1998; Evans and England, 2001; Frantzis, 1998; Martín et al., 2004; Simmonds and Lopez-Jurado, 1991). Other known causes of stranding have been ruled out in some cases, and sonar sounds spread rapidly enough over broad enough ranges to be a potential trigger for strandings with the observed timing and distribution (D'Amico, 1998; Evans and England, 2001). Jepson et al. (Jepson et al., 2003; Jepson et al., 2005) and Fernandez et al. (Fernandez et al., 2005) report that some stranded cetaceans show indications of gas and fat emboli. They suggest that exposure to sonar sounds may cause a decompression-like syndrome in deep-diving whales either by changing their normal diving behaviour or by a direct acoustic effect that triggers bubble growth (Houser et al., 2001). The latter scenario would, however, only seem to happen for animals with 100–223% supersaturated tissues within tens of meters from a sonar where the received levels exceed 210 dB re 1 μ Pa (Crum and Mao, 1996). Houser et al. (Houser et al., 2001) suggest that beaked whales might have levels of supersaturation as high as 300%, for which bubble growth could occur at lower acoustic exposures than those reported by Crum and Mao (Crum and Mao, 1996). Nonetheless, the geographical pattern of strandings suggests that animals are impacted at ranges significantly greater than those required for acoustically driven bubble growth (Cox et al., 2006), implying that the observed pathologies may follow from a behavioural response that has adverse physiological consequences.

A major limiting factor in determining the probability of *in vivo* bubble formation and risk of decompression is the lack of information on the normal diving patterns of the impacted species of beaked whales. Here we provide the first detailed quantification of the diving behaviour of Cuvier's and Blainville's beaked whales using data obtained from multi-sensor DTAGs on 10 individuals. We show that these animals forage on a food source so deep that the whales on average dive deeper and longer than reported for any air-breathing animal

that dives to forage. We discuss the physiological implications of this extreme diving behaviour in the light of current models of diving physiology and recent theories on decompression sickness and sonar-induced mass strandings.

Materials and methods

Field sites and visual observations

Cuvier's beaked whales (*Ziphius cavirostris* Cuvier, hereafter referred to as *Ziphius* and Zc) were tagged in June of 2003 and 2004 in the Ligurian Sea, Italy. Blainville's beaked whales (*Mesoplodon densirostris* Blainville, hereafter referred to as *Mesoplodon* and Md) were tagged in October 2003 and 2004 off the island of El Hierro in the Canary Islands. Both field sites are in deep (700–2000 m) water with steep bathymetry. In Liguria, 20 m (2003) and 15 m (2004) motor yachts were used as observation vessels whereas a 10 m motor yacht (2003) and a 7 m rigid-hulled inflatable boat (RHIB, 2004) were used in El Hierro. Both vessels towed a small RHIB for tagging. Sighting and tagging of beaked whales usually required sea states of two or less. In El Hierro, a shore observation station with an altitude of about 100 m was used to help locate the whales.

The tag

Beaked whales were tagged with a non-invasive sound and orientation recording tag with overall dimensions 20×10×3 cm (DTAG) (Johnson and Tyack, 2003). Acoustic data were recorded from one or two hydrophones in the nose of the tag sampled at either 96 or 192 kHz using 16-bit resolution sigma-delta analogue-to-digital converters. A pressure sensor and three-axis accelerometers and magnetometers were sampled at 50 Hz to measure the orientation and depth of the tagged whale. The pressure sensor for each tag was calibrated over a 0–2000 m water depth range before and after the experiments in a pressure test facility at WHOI. The orientation sensors were verified after each deployment by measuring their values for a sequence of defined orientations. Data were stored digitally in 3.3 or 6.6 Gb of non-volatile memory and a custom loss-less audio compression algorithm was used to extend the recording time. Tags were attached to whales with a set of four 6 cm diameter silicone suction cups using a handheld pole. Tags were programmed to release from the animal by venting the suction cups at the end of the recording time if they were still attached. A VHF beacon in the tag aided tracking and recovery of the device. Once recovered, the tag data were off-loaded to a computer, checked for errors and archived. Each tag deployment was assigned a code comprising the species initials, the year (two digits), the Julian day, and the tag deployment of the day (a single letter), e.g. Md03_298a.

Sound data analysis

The sound recording from each tag was evaluated with a custom visualization tool in MATLAB. Apart from a few isolated clicks, vocalizations only occurred during deep dives

and comprised long sequences of regular clicks interspersed with occasional buzzes and short pauses (Johnson et al., 2004; Madsen et al., 2005; Zimmer et al., 2005). The time of each buzz, and the start and end of regular clicking were noted for each dive. Buzzes have a lower apparent level in the tag recording than regular clicks (Madsen et al., 2005) and can be difficult to detect in *Ziphius* if the tag is placed low on the side of the whale or when the ambient noise is unusually high (Aguilar de Soto et al., 2006). In two recordings (Zc03_260a and Zc04_161b) buzzes were not reliably audible whereas in another recording (Zc04_161a) buzzes were not clearly audible after the first dive because of a change in location of the tag on the whale.

Orientation and movement analysis

Signals from the non-acoustic sensors were adjusted according to calibration constants and decimated to a sampling rate of 5 Hz. Orientation signals were corrected for the position of the tag on the whale and then transformed to estimate pitch, roll and heading of the whale using the method described in Johnson and Tyack (Johnson and Tyack, 2003). Changes in the tag position were located in the data by comparing the tag-derived roll and heading at the surface with the actual heading and behavioural observations of the tagged whale made by visual observers. If the tag moved during a dive and the precise time of the move could not be determined from the data, orientation measurements from that dive were excluded from further analysis.

The duration of each dive was timed from when the whale left the surface to when it regained the surface as revealed by the calibrated pressure sensor. The tagged whales swam to depths of a few body lengths in-between respirations at the surface, although logging within a few meters of the surface was also occasionally observed. To avoid counting short shallow submersions in-between individual respirations as dives, only those instances when the whales went deeper than 20 m were classified as a dive. Intervals containing dives to less than 20 m and logging at the surface were scored as surface time. Fluking motion appears in the sensor recordings as cyclic variations in the accelerometer and magnetometer signals. A fluke stroke was counted whenever there was a cyclic variation in the pitch of the whale [i.e. rotation around the transverse axis of the whale (Johnson and Tyack, 2003)] with peak-to-peak magnitude greater than 3° in a time period between 0.3 and 4 s, broadly centred around the nominal fluking period of between 2 and 2.5 s for *Mesoplodon* and *Ziphius*. The fluke count was verified by inspection of random sections of the pitch data. Although the tag does not contain a speed sensor, if it is assumed that the whale swims in the direction of its body axis, swim speed, $s(t)$, can be estimated by:

$$s(t) \approx [1/\sin \rho(t)] \cdot dp(t)/dt, \quad (1)$$

where $dp(t)/dt$ is the rate of change in depth at time t and $\rho(t)$ is the pitch angle at time t . This is only a useful estimate when the absolute pitch angle is not small, i.e. when the whale is ascending or descending steeply. Where swim speed is

reported, this is the average of $s(t)$ over the interval. Where vertical velocity is reported, this is computed as the depth change over the interval divided by the duration.

Statistical testing

Owing to the difficulty in tagging beaked whales, the data set reported here is small both in terms of number of individuals and numbers of dives per individual. Nonetheless, the rarity and utility of these data motivate us to offer some basic statistical inferences about diving behaviour. Comparisons of parameters across different phases of each dive (e.g. descent time *versus* ascent time) for each individual were made using paired two-tailed *t*-tests. When pooling paired parameter data from individuals of the same species, log transforms were used as necessary to ensure homoscedasticity. A significance level of 0.05 was used throughout for hypothesis testing and the estimated probability, *P*, is reported as 0.0 if $P < 0.001$. For several analyses, we performed the same statistical test on several parameters from each individual whale or each dive. The goal of these analyses was to explore the robustness of the pattern for each specific test, not to test the same inferences repeatedly for each parameter across individuals or dives, so within these series of tests, no Bonferroni corrections were made.

Statistical comparisons between the two species were avoided because of the low and unequal sample sizes, and variable number of dives per individual. For correlations, individual means were subtracted from observations which were then log-transformed and pooled within each species. Individuals for which there were fewer than three observations were excluded from correlations. One tag (Md04_287a) was programmed to record audio and sensor data for 9 h, after which sensor recording continued to a reserved section of memory. The data section without audio was included in the dive analyses that did not require breakdown into vocal and non-vocal phases.

Results

Tags were attached to seven *Ziphius* and three *Mesoplodon* over four field efforts in 2003 and 2004, as summarized in Table 1. Two additional short (<15 min) attachments to *Ziphius* were excluded from the table and analyses. All *Ziphius* were tagged in the Ligurian Sea and all the *Mesoplodon* were tagged in the Canary Islands. Attachment durations averaged 8.6 h (Zc) and 12.2 h (Md) with five tags remaining attached to their full memory capacity. Representative dive profiles for each species are given in Fig. 1 with the timing of regular clicking and buzzes superimposed. Each panel in Fig. 1 covers two dives below 500 m extracted from longer recordings. All dives deeper than 500 m were found to contain long sequences of echolocation clicks, and we define these as deep foraging dives (Johnson et al., 2004; Madsen et al., 2005). In comparison, dives shallower than 500 m were apparently silent, excluding a few isolated sounds. The separation of these two classes of dives is apparent in the scatter plots shown in the left column

of Fig. 2 in which dive duration is plotted against maximum depth for all dives recorded from *Ziphius* (top) and *Mesoplodon* (bottom). A gap in dive depths between 450 and 700 m coincides with the break point between silent shallow and deep vocal dives. In line with the likely different functions of the shallow and deep dives, we present results for each dive class separately, following an evaluation of the effects of tagging.

Tagging effects

Beaked whales were observed to respond to tagging by changing heading, diving and swimming rapidly. These responses appeared to be both mild and short-term, but shallow dives immediately following tagging may well be affected. As a precautionary step, we exclude shallow dives and surface intervals preceding the first deep dive from analyses. In order to evaluate whether the first deep dive after tagging was affected by tagging, we compared the duration and depth of the first two deep dives performed by each whale. Two *Ziphius* were excluded from the analysis: one performed only one deep dive while tagged and the other waited 73 min after tagging before performing a deep dive. For the remaining eight whales, neither dive duration nor maximum depth varied significantly between the first and second deep dive (paired *t*-test, $P=0.8$ for duration and $P=0.4$ for depth) although the power to detect an effect is quite low, given the small sample size. Based on this result, we included all deep dives in subsequent analyses.

Diving data set

Table 1 lists descriptive statistics for the data set in terms of individuals whereas Table 2 provides the statistics of dives pooled across all tagged whales within the same species. Given the wide spread in number of deep dives recorded from each animal (1 to 9), no attempt was made to correct the values in Table 2 for individual variation or for number of replicates from each individual. Instead, two standard deviations are reported for each parameter: the standard deviation of the pooled observations (listed as 's.d. total' in Table 2) and the standard deviation of the sample mean of the parameter for each individual (listed as 's.d. means'). If the two measures of variation differ, then one cannot assume that the statistics pooled across dives are a good predictor for other individuals.

Deep foraging dives

Deep dives were recorded from all individuals tagged for more than 15 min, with the depth and duration ranges noted in Table 1. Maximum dive depths and durations of 1888 m and 85 min were recorded for *Ziphius* and 1251 m and 57 min for the smaller *Mesoplodon* (Table 2). We associate deep dives with foraging because of the presence of regular echolocation clicks and buzzes in these dives along with echoes from what appear to be prey (Johnson et al., 2004; Madsen et al., 2005). Although some clicks may also serve a social function, the frequent presence of echoes from items in the water ensounded by the clicks (Johnson et al., 2004) suggests that prey location is a central function of these clicks. We therefore interpret the time during which the animal produced echolocation clicks in

Table 1. Summary dive statistics for all tagged individuals rejecting shallow dives prior to the first deep dive

| Whale ID | Gender/age (*probable) | Record length (h) | Deep foraging dives (DFD) | Length DFD mean (s.d.) (min) | Depth DFD mean (range; in m) | No. SD and depth mean (range; in m) | IDDI (min) mean (s.d.) | # SD in IDDI median (range) |
|-------------------------|---------------------------|----------------------|------------------------------|---------------------------------|---------------------------------|--|---------------------------|--------------------------------|
| Zc03_260a | Unknown | 3.0 | 1 | 50.3 | 824 | 3, 224 (22–343) | – | – |
| Zc03_263a | ♀* | 15.6 | 8 | 55.3 (12.8) | 1145 (1005–1266) | 12, 231 (24–416) | 61.3 (47) | 0 (0–7) |
| Zc04_160a | Adult ♂ | 5.6 | 2 | 84.5 (0.5) | 1322 (756–1888) | 6, 339 (267–420) | 72.9 | 3 |
| Zc04_161a | Sub-adult | 8.9 | 4 | 55.0 (6.4) | 937 (697–1548) | 13, 209 (30–388) | 65.8 (19) | 4 (3–4) |
| Zc04_161b | Sub-adult | 15.8 | 8 | 54.8 (4.9) | 1065 (689–1605) | 27, 197 (33–425) | 56.9 (22) | 3 (1–5) |
| Zc04_175a | Adult ♂* | 7.5 | 3 | 67.9 (0.8) | 1195 (1125–1324) | 3, 182 (148–202) | 66.4 (32) | 1 (0–2) |
| Zc04_179a | Sub-adult | 3.8 | 2 | 50.8 (0.4) | 737 (724–749) | 1, 317 | 98.8 | 1 |
| Total <i>Ziphius</i> | | 60.2 | 28 | 58.0 (11.4) | 1070 (689–1888) | 65, 221 (22–425) | 63.4 (31) | 2† (0–7) |
| Md03_284a | Adult ♂ | 15.4 | 5 | 51.0 (7.7) | 777 (640–855) | 42, 61 (20–240) | 125.1 (46) | 9 (4–12) |
| Md03_289a | Sub-adult | 3.0 | 2 | 47.2 (2.1) | 774 (732–816) | 4, 176 (142–217) | 66.7 | 4 |
| Md04_287a | Adult ♀ | 18.3 | 9 | 43.8 (7.6) | 881 (682–1251) | 54, 72 (22–210) | 76.9 (40) | 6 (1–10) |
| Total <i>Mesoplodon</i> | | 36.7 | 16 | 46.5 (7.6) | 835 (640–1251) | 100, 71 (20–240) | 92.3 (46) | 6† (1–12) |

DFD, deep foraging dive; IDDI, inter-deep-dive-interval; S.D., shallow dive. Either totals or mean (±s.d.) pooling individuals, as appropriate, are given under 'Total'.

†Median number of shallow dives per IDDI, pooling individuals.

a dive as time spent primarily searching for prey [paralleling the usage described by Watwood et al. (Watwood et al., 2006), for sperm whales]. The duration of this vocal phase is shown as a function of dive depth for both species in the left-hand panels of Fig. 2 (unfilled triangles). An average of 33 min (Zc) and 26 min (Md) were devoted to the vocal phase in each dive (Table 2), amounting to an average of 56% (Zc, s.d. 8%) and 53% (Md, s.d. 5%) of the dive duration. In dives with audible buzzes, the average number of buzzes per dive was 30 (s.d. 12) for Zc and 29 (s.d. 9) for Md (Table 2). Although buzzes were produced in a broad depth range from 222 to 1885 m, 95% of all buzzes occurred between 613–1297 m (Zc) and 463–1196 m (Md), showing that foraging was concentrated in a broad layer from mesopelagic to bathypelagic depths.

The duration of deep dives is not correlated with maximum depth in *Ziphius* but is significantly correlated in *Mesoplodon* (Zc: 23 dives/4 individuals, $r=-0.2$, $P=0.3$; Md: 14 dives/2 individuals, $r=0.72$, $P=0.004$). Vocal time, a proxy for time spent searching for prey, is correlated with maximum dive depth for both species (Zc: 23 dives/4 individuals, $r=-0.47$, $P=0.02$; Md: 9 dives/2 individuals, $r=0.81$, $P=0.008$), but is negatively correlated in *Ziphius* and positively correlated in *Mesoplodon*. It appears that *Ziphius* must reduce search time as dive depth increases whereas a *Mesoplodon* can prolong deeper dives to accommodate an increased search time, although this determination is based on few individuals. The range of dive depths recorded from *Ziphius* is twice that from *Mesoplodon* even though 95% of buzzes in both species occur in a similar depth range.

For deep dives, we considered the descent to extend from the surface until the whale began to produce regular echolocation clicks. Likewise, the ascent was considered to start at the last regular click and end at the surface. Descents were always performed faster than ascents (paired t -test on vertical speed Zc: $t_{27}=16.5$, $P=0.0$; Md: $t_{10}=22.6$, $P=0.0$). Overall, the mean vertical descent speed was remarkably constant at 1.5 m s^{-1} (s.d. 0.11) for Zc and 1.6 m s^{-1} (0.21) for Md and was uncorrelated with dive depth (Zc: 23 dives/4 individuals $r=-0.1$, $P=0.7$; Md: 9 dives/2 individuals $r=0.2$, $P=0.7$). Descents were steep, with mean pitch angles ranging between 60° to 83° . Fluke rate was high at the start of descent, dropping substantially for all Zc and one Md (Md03_284a) within the first 50 m of descent (fluke rate in the 20–40 m depth bin was greater than in 60–80 m for 27 of 28 Zc descents and all 5 Md03_284a descents) as exemplified by the fluke rate profile in Fig. 3. This reduction in fluke rate was not accompanied by a change in estimated swim speed (paired t -test 20–40 m depth bin vs 60–80 m, Zc: $P=0.4$, Md03_284a: $P=0.1$). The other two Md maintained their initial fluke rate throughout the first 100 m of descent but this was accompanied by a significant increase in swim speed for Md04_287a (same test, $t_6=-5.8$, $P=0.001$).

Unlike the descents, ascents from deep foraging dives were always performed with low overall vertical speed [0.7 m s^{-1} (Zc: s.d. 0.2, Md: s.d. 0.1); see right-hand panels of Fig. 2] and low pitch angle. Because of the low pitch angle, swim speed cannot be estimated accurately for ascents and our analyses are

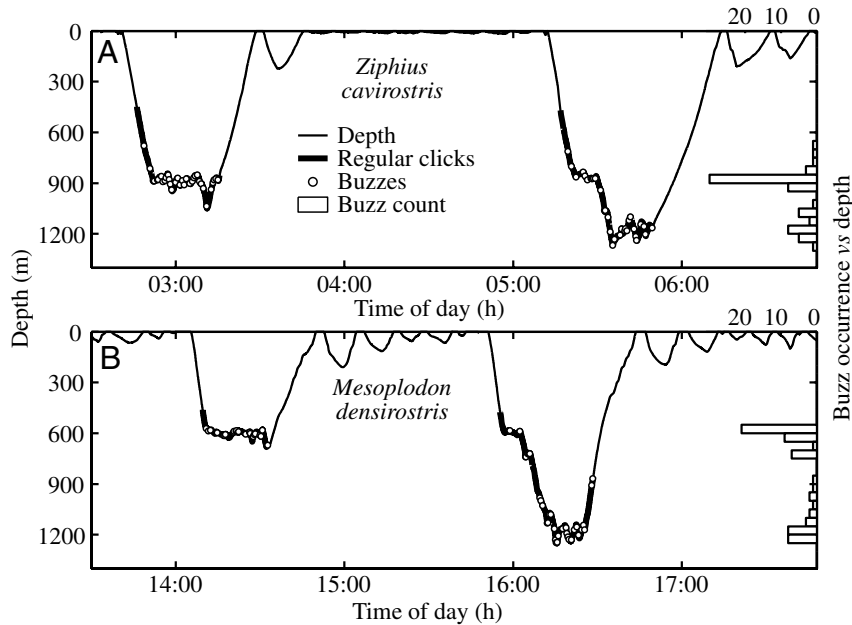


Fig. 1. Representative sections of dive profiles from *Ziphius cavirostris* (A) and *Mesoplodon densirostris* (B). Intervals with regular click vocalizations are indicated by a thicker trace and times of buzzes are indicated by small open circles. The depth of occurrence of buzzes heard in the audio recording during the two dives is shown in the histogram on the right-hand side of each panel. The bin size of the histogram was 50 m.

restricted to vertical speed. The overall vertical speed for ascending *Mesoplodon* was positively correlated with dive depth (9 dives/2 individuals $r=0.8$, $P=0.005$) and the increased ascent speed on deeper dives stabilized overall ascent time: ascent duration was uncorrelated with dive depth for this species. For *Ziphius*, neither ascent duration nor vertical speed were correlated with dive depth, and the ascent strategy of this species is uncertain. However, if the ascents are divided into depth bins, some patterns emerge. In particular, both species showed a strong correlation between dive depth and vertical speed in the deepest 200 m of the ascent immediately after the end of clicking (Zc: 23 dives/4 individuals, $r=0.78$, $P=0.0$; Md:

9 dives/2 individuals, $r=0.87$, $P=0.002$), i.e. both species began their ascent faster from deeper dives. In comparison, there is little or no correlation between ascent speed and dive depth in the top 200 m of the ascent (Zc: 23 dives/4 individuals, $r=-0.1$, $P=0.6$; Md: 14 dives/2 individuals, $r=0.50$, $P=0.07$). (All 14 dives from 2 Md were analysed for final ascent speed whereas only the 9 dives from the same individuals with audio recordings could be analysed for initial ascent speed as the start of ascent is determined by the end of clicking.)

For *Mesoplodon*, the fast initial ascent on deeper dives serves to compensate the longer ascent distance. For *Ziphius*, the picture is more complicated. Regardless of the maximum dive

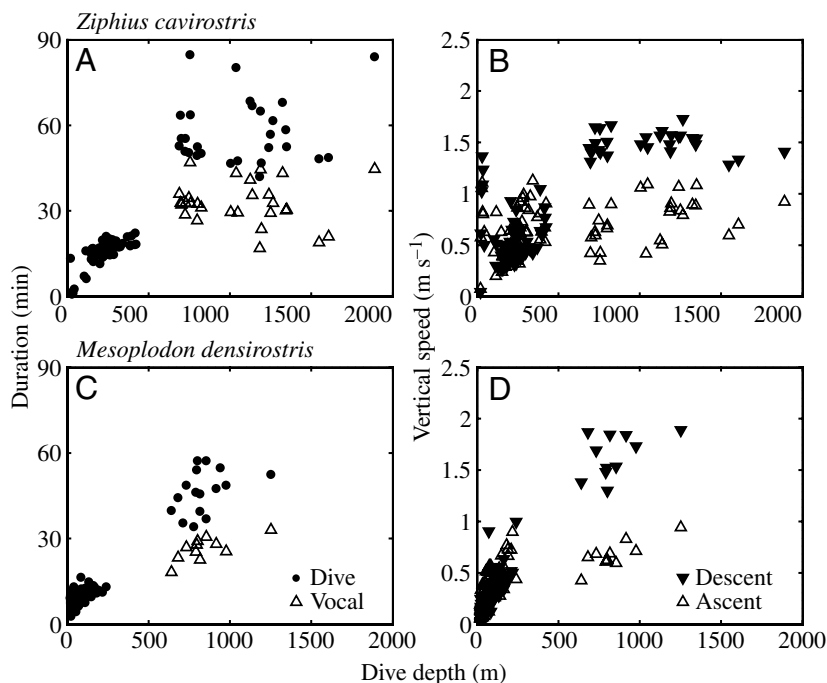


Fig. 2. Scatter plots of dive duration (A,C) and vertical speed (B,D) as functions of dive depth for all dives deeper than 20 m recorded on *Ziphius cavirostris* (A,B) and *Mesoplodon densirostris* (C,D). The plots in A and C show the surface-to-surface dive duration (dots) and the interval from the start to the end of regular clicking (unfilled triangles) in each dive. The absence of dive depths between 450 and 700 m for both species and the observation that only dives deeper than this range have consistent vocalizations leads us to define these as deep foraging dives (DFD). The plots in B and D show vertical speed (i.e. depth rate) as a function of dive depth during descents (downwards pointing black triangle) and ascents (upwards pointing unfilled triangle). The difference between descent and ascent rate for DFDs is apparent.

Table 2. Descriptive statistics of deep and shallow dives, pooling dives from all individuals of the same species

| Parameter | Unit | <i>Ziphius cavirostris</i> | | | | <i>Mesoplodon densirostris</i> | | | | | | | |
|----------------------------|-------------------|----------------------------|------|-----------|---------------------------|--------------------------------|-------|--------------|---------|------|---------------------------|------|------|
| | | N total/ | | Mean | s.d. total/ s.d. means | Min. | Max. | N total/ | | Mean | s.d. total/ s.d. means | Min. | Max. |
| | | N individual | | | | | | N individual | | | | | |
| Deep dive depth | m | 28/7 | 1070 | 317/210 | 689 | 1888 | 16/3 | 835 | 143/61 | 640 | 1251 | | |
| Deep dive duration | min | 28/7 | 58.0 | 11.4/12.4 | 42.0 | 84.9 | 16/3 | 46.5 | 7.6/3.6 | 34.3 | 57.4 | | |
| Depth at start of clicking | m | 28/7 | 457 | 70.4/66.5 | 136 | 531 | 11/3 | 426 | 125/23 | 178 | 554 | | |
| Depth at end of clicking | m | 28/7 | 856 | 270/210 | 588 | 1849 | 11/3 | 738 | 98/44 | 500 | 860 | | |
| Vocal phase duration | min | 28/7 | 32.8 | 7.6/6.2 | 17.0 | 47.0 | 11/3 | 26.4 | 4.1/1.4 | 18.2 | 33.1 | | |
| Buzz count per dive | | 16/5 | 29.8 | 12.4/9.2 | 9 | 52 | 11/3 | 28.6 | 9.1/4.6 | 13 | 45 | | |
| Buzz depth | m | 47/5 | 863 | 238/155 | 233 | 1885 | 322/3 | 724 | 165/56 | 222 | 1244 | | |
| Inter-deep-dive interval | min | 22/6 | 63 | 31/15 | 10 | 142 | 15/3 | 92 | 46/31 | 25 | 181 | | |
| Deep dive descent rate | m s ⁻¹ | 28/7 | 1.5 | 0.1/0.1 | 1.3 | 1.7 | 11/3 | 1.6 | 0.2/0.2 | 1.3 | 1.9 | | |
| Deep dive ascent rate | m s ⁻¹ | 28/7 | 0.7 | 0.2/0.1 | 0.3 | 1.1 | 11/3 | 0.7 | 0.1/0.1 | 0.4 | 0.9 | | |
| Deep dive descent pitch | degrees | 27/7 | 72 | 7/5 | 60 | 83 | 11/3 | 74 | 7/7 | 62 | 82 | | |
| Deep dive ascent pitch | degrees | 27/7 | 35 | 12/10 | 13 | 58 | 11/3 | 28 | 10/9 | 11 | 49 | | |
| Shallow dive depth | m | 65/7 | 221 | 100/61 | 22 | 425 | 100/3 | 71 | 52/64 | 20 | 240 | | |
| Shallow dive duration | min | 65/7 | 15.2 | 5.2/2.3 | 0.9 | 22.3 | 100/3 | 9.3 | 2.4/1.7 | 2.9 | 16.5 | | |
| Shallow dive descent rate | m s ⁻¹ | 65/7 | 0.5 | 0.2/0.1 | 0 | 1.4 | 100/3 | 0.3 | 0.2/0.2 | 0.1 | 1.0 | | |
| Shallow dive ascent rate | m s ⁻¹ | 65/7 | 0.6 | 0.2/0.1 | 0.1 | 1.1 | 100/3 | 0.3 | 0.2/0.2 | 0.1 | 0.9 | | |
| Surfacing duration | min | 85/7 | 7.9 | 16.6/14.7 | 1.0 | 85.6 | 113/3 | 3.8 | 4.6/0.3 | 0.9 | 33.3 | | |

N total, the total number of dives used; N individual, the number of individuals contributing one or more dives; Mean, the mean overall pooled dives; s.d. total, the standard deviation over all pooled dives; s.d. means, the standard deviation of the individual means; Min. and Max. are overall pooled dives. Dives were rejected from pooling only if the parameter in question could not be measured for that dive. Shallow dives prior to the first deep dive were rejected. Depths at start and end of clicking are the depths at which regular clicking commenced and terminated in a deep dive. A few isolated clicks may be produced prior to the start of clicking. Surfacing intervals are defined as continuous time spent at <20 m depth.

depth, *Ziphius* ascended slowly between 600 and 400 m from the surface and then ascended more rapidly during the last 200 m of ascent (paired *t*-test 0–200 m vs 400–600 m depth bins: $t_{27}=5.2$, $P=0.0$). For this species, the mean vertical speed in the last 200 m of ascent was twice that at 400–600 m and the vertical speed in the top 100 m of ascent did not significantly differ from that on descent (paired *t*-test Zc: $t_{27}=-1.5$, $P=0.1$). Thus *Ziphius* tend to ascend rapidly in the first few hundred meters from deeper dives then slow down as they pass 600–400 m and finally speed up again near the surface. This distinctive pattern occurred in 24 of 27 Zc ascents by seven individuals.

The average pitch angle in the descent of deep foraging dives was steeper than in the ascent for all dives of both species (paired *t*-test Zc: $t_{26}=18$, $P=0.0$; Md: $t_{10}=10$, $P=0.0$). Whereas descents were performed with a uniformly steep pitch, the pitch angle was low and variable during ascents. For both species, ascent pitch angle and vertical ascent speed were persistently correlated [correlations performed separately for each ascent divided into 100 m depth bins: 24 of 27 (Zc) and 12 of 14 (Md) ascents had significant correlations] whereas fluke rate and vertical ascent speed were not [same test: 10 of 27 (Zc) and 2 of 14 (Md) ascents had significant correlations]. Changes in ascent speed are therefore achieved primarily by modulating the pitch angle rather than by changing swimming effort. In fact, as exemplified by Fig. 3, the fluke rate is fairly constant during ascent from deep foraging dives. Over all ascents, the average fluke rate was 10.8 flukes min⁻¹ (s.d. 2.3) for *Ziphius* and 19.6 flukes min⁻¹ (s.d. 3.0) for *Mesoplodon* which, when compared to the typical steady fluking period of 2.3 s (Zc) and 2.1 s (Md), implies that whales were actively swimming during an average of 41% (Zc) and 69% (Md) of each ascent with the remainder being spent in gliding. Gliding and fluking periods were intermixed with a typical burst of 1–3 fluke strokes followed by a glide of similar or shorter length. The fluke rate in the final 40 m of the ascent [Zc: 7.9 per min (s.d. 8.4) and Md: 6.9 min (s.d. 6.3)], although variable, was much lower than during descents [Zc: 31 min⁻¹ (s.d. 0.9) and Md: 33 min⁻¹ (s.d. 6.9)], (paired *t*-test, Zc: $t_{26}=-15$, $P=0.0$; Md: $t_{13}=-15$, $P=0.0$). This suggests that the final meters of the ascent are powered by the buoyancy force of air expanding in the lungs more than by active swimming.

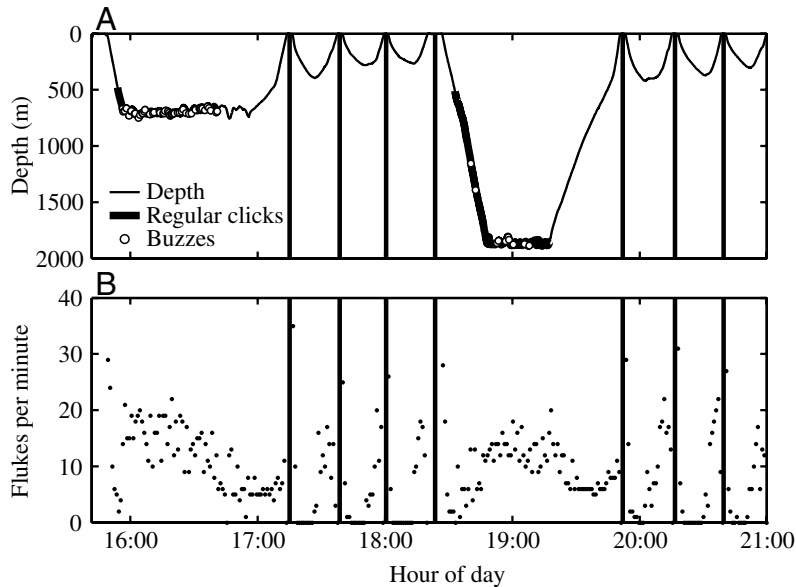


Fig. 3. Dive profile (A) and fluke rate (B) for a *Ziphius*. Vocal phase and buzzes are marked on the dive profile. The average fluke rate in 1 min intervals, measured by counting cyclic variations in the pitch signal from the tag, is shown in the lower panel. The fluke rate is high in the first minute of both deep and shallow dives but then drops markedly during the remainder of the descent. Ascents, in comparison, feature more steady flucking.

To test whether whales tended to swim in a steady horizontal direction during the prolonged ascents, we computed the horizontal distance travelled during ascent assuming a constant swim speed (sensu Johnson and Tyack, 2003) and compared this to the distance that would have been covered at the same speed if the heading had been constant throughout the ascent. By using a ratio of distances like this we avoid the need to estimate swim speed which cannot be done reliably for ascents with low pitch angles. Both species adopted fairly constant headings during ascent with 24 of 27 Zc dives and all 11 Md dives covering more than 50% of the possible horizontal distance and 13 of 27 (Zc) and 8 of 11 (Md) covering more than 80%. The number of buzzes recorded during the bottom phase and the proportion of horizontal distance covered during the following ascent (on 11 Zc and 9 Md dives) were not significantly correlated for either species although this determination is based on just two individuals from each species with clearly audible buzzes in three or more dives.

Foraging dive cycle

We define the inter-deep-dive-interval (IDDI) as the interval between the end of one deep dive and the start of the next deep dive. The IDDI varies widely for both species (Table 2) with mean values of 63 min (Zc) and 92 (Md) min. The duration of deep dives is positively correlated with the preceding IDDI for *Ziphius* (Zc: 17 dives/3 individuals, $r=0.6$, $P=0.01$; Md: $P=0.08$) whereas it is weakly correlated with the following IDDI for *Mesoplodon* (Md: 14 dives/2 individuals, $r=0.6$, $P=0.03$; Zc: $P=0.14$), indicating at least a trend of increased IDDI in compensation for longer bracketing foraging dives.

Combining the IDDI with the deep dive durations, the average foraging dive cycle (i.e. from the start of one deep dive to the start of the next) lasts 121 min (s.d. 36, range 52–222) for *Ziphius* and 139 min (s.d. 51, range 62–236) for *Mesoplodon*. These figures indicate that both species would

perform about 11–12 deep dives per day if diving continues throughout the diurnal cycle at the pace recorded by the tags. In terms of diurnal coverage, tags were on whales from 13.00–07.00 h for *Ziphius* and 09.20–03.40 h for *Mesoplodon*, and so no data are available for the late morning for Zc or early morning for Md.

Shallow dives

A distinctive feature of the dive profiles for both species is the series of shallow dives performed between deep dives. The IDDI contained a median of 2 (Zc) and 6 (Md) shallow dives with 17 of 22 Zc IDDI and all 15 Md IDDI containing at least one shallow dive. The left side of Fig. 2 plots the depth and duration of shallow and deep dives for both species. The duration of shallow dives is strongly correlated with their maximum depth (Zc: 65 dives/7 individuals, $r=0.8$, $P=0.0$; Md: 100 dives/3 individuals, $r=0.6$, $P=0.0$). Although the maximum depths of shallow dives, 425 m (Zc) and 240 m (Md), overlap with the depth range of buzzes recorded in deep dives, there is no evidence of echolocation-mediated foraging in shallow dives. In fact, only three (Zc) and one (Md) buzzes, amounting to about 0.5% of the total, occur during deep dives at depths attained during shallow dives.

For shallow dives, the descent period is defined as the time from leaving the surface until the maximum depth of the dive was reached, and the ascent period is the time from the maximum depth to the surface. This change of definition as compared to deep dives is necessary because of the absence of regular clicks in shallow dives. For both species, the descent period in shallow dives is, on average, 53% (Zc, s.d. 12%; Md, s.d. 14%) of the total dive duration. Vertical speeds in descent and ascent do not differ significantly (Fig. 2). Similar to the finding for deep dives, the flucking rate is higher during descent than ascent through the 0–20 m depth range (paired t -test, Zc: $t_{64}=14$, $P=0.0$; Md: $t_{99}=7$, $P=0.0$). However, after the initial

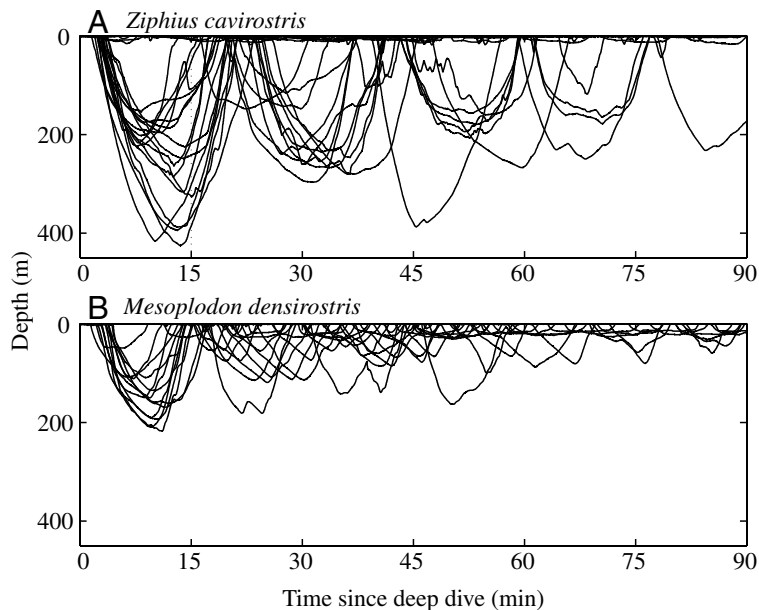


Fig. 4. Aligned dive profiles during inter-deep-dive-intervals (IDDIs) for *Ziphius cavirostris* (A) and *Mesoplodon densirostris* (B). The preceding deep dive ends at minute 0 whereas the following deep dive (not shown) starts after 10–142 min (*Ziphius*) or 25–181 min (*Mesoplodon*). The decreasing trend in the depth of shallow dives with time elapsed since the preceding deep dive is apparent.

burst of fluking in the descent, the trend is reversed with the ascent fluking rate significantly higher than descent (paired t -test, Zc: 100–120 m, $t_{54}=-6$, $P=0.0$; Md: 20–40 m, $t_{63}=-6$, $P=0.0$), although the depth at which this changeover takes place differs for the two species. The lowest fluke rates during the entire tag records occurred during the later part of shallow descents.

The dive profiles during each IDDI, starting at the end of the preceding deep dive, are shown in Fig. 4 for each species. It is evident that shallow dives immediately following the deep dive tend to be deeper and longer than those occurring later in the IDDI. To characterize this dependence in a way that is robust to individual variations in shallow dive sequences, we made a paired comparison of the mean dive depths in the intervals 0 to N and N to $2N$ minutes after each deep dive, where N was chosen as the mean shallow dive duration for each species. The mean dive depths in the two intervals for each IDDI were log-transformed for variance homogeneity and then pooled for all animals of the same species. The results using $N=15$ and 10 min, respectively, for Zc [mean shallow dive duration of 15.2 (s.d. 5.2) min] and Md [mean shallow dive duration of 9.3 (s.d. 2.4) min], indicate a significant difference (paired t -test, Zc: $t_{18}=3.1$, $P=0.006$; Md: $t_{12}=2.8$, $P=0.015$) in mean dive depth in the two intervals. An even stronger result was obtained from a paired comparison of mean dive depth in the N min just prior to a deep dive and the preceding N -min interval (paired t -test, Zc: $t_{18}=-3.7$, $P=0.002$; Md: $t_{12}=-7.6$, $P=0.0$), confirming that the trend of decreasing dive depth with time elapsed since a deep dive continues throughout the interval between deep dives.

Several IDDIs contained protracted surface intervals (i.e. continuous periods at depths <20 m). Three *Ziphius* performed a total of seven surface intervals longer than 30 min (max. 86 min) whereas only one similarly protracted surface interval was observed in *Mesoplodon* (max. 33 min). The mean depth

during these surface intervals varied between 1.6 m for a Zc that logged persistently for 79 min and 10.8 m for the Md that performed a series of very shallow dives.

Discussion

We report data from a limited set of 10 animals of two difficult to study species, and discuss the data in the light of physiological implications for diving physiology and possible decompression problems. The observed diving behaviour in all the tagged animals shows the same pattern, and is similar to that reported by Baird et al. (Baird et al., 2006) for the same species in Hawaiian waters, but we acknowledge that the data set is limited and that the conclusions we reach here should be treated with reservations inherent to a limited sample size. The dives recorded here of up to 1888 m and 85 min are among the deepest and longest recorded for any air-breathing animals. While there are indications of deeper dives in sperm whales[†], this is the deepest dive confirmed by a precise tagging record. Sperm whales typically perform dives of 30–50 min duration to depths between 600 and 1200 m (Watwood et al., 2006; Whitehead, 2003). Hooker and Baird (Hooker and Baird, 1999) tagged *Hyperoodon* and reported dives to 1530 m and for up to 70 min. Hobson and Martin (Hobson and Martin, 1996) reported a 153 min dive from a *Berardius arnuxii* surfacing in a breathing hole in the ice, but they considered that they might have missed a surfacing, so discarded dives lasting longer than 70 min. Elephant seals have been reported to dive to 1500 m for as long as 120 min (Hindell et al., 1991; Stewart and Delong, 1990). However, such extreme diving behaviour is

[†]Watkins et al. reported a depth of >2100 m obtained from a tag telemetering analogue depth measurements acoustically (Watkins et al., 1993) (but this depth was an outlier and could be erroneous), Whitney reported 2250 m based upon acoustic localization (Whitney, 1968), and Clarke inferred 3000 m from stomach contents (Clarke, 1976).

unusual for elephant seals that normally undertake foraging dives lasting about 25–30 min to depths of about 500 m (Hindell et al., 1991; Le Boeuf et al., 1986; Le Boeuf et al., 1988). The important point with the diving behaviour of the beaked whales studied here is, likewise, not what they can maximally achieve, but the fact that they perform the deepest and longest average foraging dives reported to date of any air-breathing animal.

Judging by the vocal and movement data recorded from the tagged beaked whales, deep dives are primarily used for foraging (Johnson et al., 2004; Madsen et al., 2005). Echolocation tends to start at 400–500 m depth while the whales are still descending, presumably to find the patch or depth layer richest in prey, and continues through a vocally active bottom phase. Buzzes, which are associated with feeding, are centred on the broad depth range of 500–1300 m for both species. Echolocation behaviour and frequent prey echoes recorded by the DTAGs (Johnson et al., 2004; Madsen et al., 2005) show that beaked whales hunt individual, probably small, prey items of which they try to catch about 30 per dive. This foraging strategy takes time as each item is selected from the clutter, approached and caught (Madsen et al., 2005). Thus our data strongly suggest that *Ziphius* and *Mesoplodon* perform such deep and long dives to gain access to deep prey, as is the case for the larger and better studied sperm whale. However, whereas sperm whales typically perform consecutive deep dives with short intervening surface intervals for ventilation (Watwood et al., 2006), the tagged beaked whales almost always spent a protracted time between deep dives, often filling this with a sequence of shallower, apparently non-foraging dives. Our objective in the following sections is to explore what this stereotypical behaviour reveals about the diving physiology and potential vulnerability to decompression problems of *Ziphius* and *Mesoplodon*.

Diving behaviour and the aerobic dive limit

In order to maximize foraging time in a deep prey patch, breath-hold divers should minimise the time spent travelling to the surface, breathing, and returning from the surface (Carbone and Houston, 1996; Houston and Carbone, 1992). Increased body size improves the potential for breath-holding since larger animals can store more oxygen, and have lower mass-specific diving metabolic rates (Castellini et al., 1992; Kooyman et al., 1983; Schreer and Kovacs, 1997). Mori (Mori, 2002) predicted that, to forage optimally, smaller divers would rely more heavily on anaerobic metabolism and would push closer to their physiological limits than larger divers. This may require a refractory period between deep dives to clear the lactic acid accumulated from anaerobic catabolism. The aerobic dive limit (ADL) defines how long an animal can dive using aerobic respiration without accumulating significant amounts of lactic acid. The ADL for Weddell seals, one of the few species for which this has been measured, is about 21 min for an adult of 450 kg (Kooyman et al., 1980) and almost all of the dives (>90%) that these seals undertake are shorter than the measured ADL. The average foraging dive time for the larger elephant

seal is less than 30 min (Hindell et al., 1991; Le Boeuf et al., 1988). In comparison, the mean dive time measured by DTAGs during deep dives of *Mesoplodon* is about 47 (s.d. 8) min and, for *Ziphius*, about 58 min (s.d. 11). Considering the high oxygen storage capacity and extreme hypometabolism reported for both of these seal species (Kooyman, 1989), it is relevant to evaluate whether the beaked whales perform such long dives within their ADL.

Diving metabolic rates have never been measured in beaked whales and these species are likely to have specialized metabolic adaptations for deep-diving as found for deep-diving seals. In the absence of other data, we propose a first order approximation for the ADL of beaked whales estimated by extrapolating the mass-specific diving metabolic rate of Weddell seals (Castellini et al., 1992). The large oxygen carrying capacity of up to 93 ml O₂ kg⁻¹ in Weddell seals (Davis and Kanatous, 1999) is among the highest measured in any diving animal (Kooyman, 1989). The mass-specific basal metabolic rate of mammals generally scales by the power of -0.25 (Kleiber, 1975), meaning that the metabolic rate per unit of body mass decreases with increasing size. Assuming that beaked whales can carry as much oxygen per kg body mass as the extreme Weddell seal (Kooyman, 1989), and that the diving metabolic rate of the two species scales with lean body mass (M_b) by the same power as the basal metabolic rate of mammals in general, the ADL of a beaked whale can be estimated by:

$$ADL_{\text{beaked}} = ADL_{\text{Weddell}} (M_{b,\text{Weddell}} / M_{b,\text{beaked}})^{-0.25} \quad (2)$$

Using lean body masses of 630 kg and 2000 kg for adult *Mesoplodon* and *Ziphius*, respectively [21% adipose tissue assumed for both species (Mead, 1989)], the predicted mass-specific diving metabolic rates are 85% (Md) and 64% (Zc) of the rate of an adult Weddell seal with a lean body mass of 330 kg [27% adipose tissue (Davis and Kanatous, 1999)]. These reduced diving metabolic rates as a result of larger size would translate to aerobic dive limits of 25 min for a *Mesoplodon* and 33 min for a *Ziphius* compared to 21 min for the smaller Weddell seal (Kooyman et al., 1980) assuming the same overall activity level during foraging dives. Although such extrapolations must be treated with caution, the observed mean foraging dive times for *Mesoplodon* and *Ziphius* are about twice as long as their estimated ADLs, leaving a considerable margin for error. It seems unlikely that the beaked whale species studied here would be able to carry significantly more oxygen per kg body mass than the already extreme amounts of the Weddell seal, or would deviate sufficiently from the scaling of mass-specific diving metabolic rate to account for such a large discrepancy. Consequently, we infer that most, if not all, foraging dives presented in this paper likely have durations well in excess of the ADL and that the animals return to the surface with an oxygen debt. In comparison, applying the ADL scaling from a Weddell seal to the lean mass for sperm whales estimated to weigh between 8 and 20 tonnes, the estimated ADL would range from 43–54 min, which is close to the mean dive duration of 45 (s.d. 6.3) min reported for sperm whales of this size class (Watwood et al., 2006). A

12 tonne sperm whale is 15 times heavier than *Mesoplodon* and six times heavier than *Ziphius*, yet the average foraging dive duration of *Mesoplodon* is comparable, and that of *Ziphius*, is considerably longer. Whereas sperm whales dive near their ADL, the two beaked whale species appear to exceed their ADLs by a factor of about two. Sperm whales can perform deep dives with inter-deep-dive surface intervals averaging only 9 min (Watwood et al., 2006), but the beaked whales have intervals averaging 63 (Zc) and 92 (Md) min between deep foraging dives. Our explanation for this difference is that the smaller species require protracted periods between deep dives to process lactic acid accumulated during dives, which are partially supported by anaerobic metabolism.

The question that arises is why the beaked whales studied here perform foraging dives that so greatly exceed their ADL when this appears to necessitate prolonged periods between foraging dives and therefore a reduction in the time available for foraging at depth. The depth range of buzzes (Johnson et al., 2004; Madsen et al., 2005) and the stomach contents of stranded individuals (Blanco and Raga, 2000; Mead, 1989; Podesta and Meotti, 1991; Ross, 1984; Santos et al., 2001) both show that these species have specialized to a deep prey niche with mean buzz depths of round 724 m for Md and 863 m for Zc (Fig. 1, Table 2). The transport time to and from this deep foraging zone represents a large fixed cost for each foraging dive. Applying the mean ascent and descent rates measured for the two species in this study, the transport time to and from foraging layers at 724 m (Md) and 863 m (Zc) would be 25 min for *Mesoplodon* and 30 min for *Ziphius*. Consequently, *Mesoplodon* would not be able to spend any time at its foraging depth if it were to stay within its estimated ADL, and *Ziphius* would have 3 min available for foraging. This remarkable outcome is due in part to the slow ascent rate adopted by all of the tagged beaked whales: the average ascent rate was less than 50% of the descent rate for both species. This contrasts with sperm whales which were found to ascend as fast or faster than they descended (Watwood et al., 2006). It therefore seems that these beaked whales must dive well beyond their ADL in order to feed at depth, even though this incurs the cost of a longer time to recover from the oxygen debt. Given an average deep dive cycle of 121 min for *Ziphius* and 139 min for *Mesoplodon*, these species probably can perform about 10–12 dives per day, each one enabling about 28 (Zc) or 22 (Md) min at foraging depth, for a total of between 4 and 5.6 h of foraging per day. In comparison, the sperm whale with its short IDDI can perform more than 20 dives per day achieving a foraging time in excess of 9.5 h per day [based on 28.5 min foraging per dive, after Watwood et al. (Watwood et al., 2006)].

The apparent reliance on a combination of aerobic and anaerobic metabolism during every foraging dive in beaked whales differs from most marine mammals (Kooyman and Ponganis, 1997), but is similar to some penguins (Ponganis et al., 1997), sea lions (Costa et al., 2001; Chilvers et al., 2006) and fur seals (Mattlin et al., 1998), which seem to exceed their ADL regularly during foraging dives. Kooyman and Ponganis (Kooyman and Ponganis, 1997) suggest that the small body

size of these animals forces them to exceed their ADL in order to access food sources at depths of more than 300 m: they are obliged to make do with a less efficient diving behaviour out of the necessity to reach deep prey to which there is a long two-way travel time (Costa et al., 2001). We propose that the beaked whales studied here, which are relatively small compared to sperm whales, follow the same pattern and that the long periods of acoustically-inactive shallow diving between foraging dives therefore represent a period of recovery from the build-up of metabolites of anaerobic metabolism. Castellini et al. (Castellini et al., 1988) measured a decline in lactate during short shallow dives performed by Weddell seals after long dives in excess of the ADL and argued that this kind of dive serves a recovery function. In terrestrial mammals, moderate exercise after anaerobic lactate build up, termed active recovery, enhances lactate clearance by increased perfusion of the lactate-producing tissues and by increased oxidative metabolism (Bangsbo et al., 1996). The fluking record during the beaked whale shallow dives shows a mixture of gliding in the descent and steady fluking in the ascent with active swimming during about 50% of the dive duration. This exercise could improve foraging efficiency by speeding up recovery from the oxygen debt. Thus, both physiological considerations and the characteristic diving behaviour with long IDDI are consistent with the hypothesis that these comparatively small animals exceed their ADL to forage deeper on average than any other marine mammal studied so far.

It is worth noting here that *Ziphius* and *Mesoplodon* are so difficult for humans to observe because of their brief surface time. If these species are at risk of predation from predators that spend most of their time near the surface or that use vision, then the shallow dives may serve for predator avoidance as well as recovery, perhaps explaining the 'shallow' dives of up to 425 m depth performed by the *Ziphius*. The most likely predator of these species is the killer whale, *Orcinus orca*, which spends >70% of its time shallower than 20 m (Baird et al., 1998). Mead (Mead, 1989) reported rake marks on *Mesoplodon* produced by *Orcinus* or *Pseudorca*, and Notarbartolo-di-Sciara (Notarbartolo-di-Sciara, 1987) reported a killer whale feeding on a fresh *Ziphius* carcass near our Ligurian Sea study site, suggesting predation. Le Boeuf and Crocker (Le Boeuf and Crocker, 1996) consider deep-diving in elephant seals as an adaptation to reduce encounters with near-surface predators such as killer whales and great white sharks. Killer whales and other large mammal-eating odontocetes have sensitive hearing and the fact that tagged beaked whales only produced their directional high-frequency echolocation clicks at depths >200 m may be viewed as an adaptation to avoid acoustic detection by a predator that seldom dives so deep.

Implications for supersaturation and embolism

Jepson et al. (Jepson et al., 2003)[‡] and Fernandez et al. (Fernandez et al., 2005) have reported gas and fat emboli in deep-diving beaked whales that stranded soon after naval sonar

[‡]Gas-filled cavities were also reported for delphinids stranded in Britain, with no known concurrent sonar activity.

exercises. They conjectured that bubble formation in supersaturated tissues may have been caused by acoustically driven bubble growth or by a disruption of normal diving behaviour such as accelerated ascent rates. The process of decompression is quite different for breath-hold divers than for divers who breathe compressed gases. During descent, as the ambient pressure increases, the lungs of breath-hold divers collapse as the fixed amount of air diffuses from alveoli to blood or moves into the more rigid and thick-walled trachea and nasal apparatus (Scholander, 1940). Lung collapse is estimated to occur at 25–60 m for seals that exhale before diving (Falke et al., 1985; Kooyman et al., 1972) and at 70 m in a bottlenose dolphin that dives on inhalation to have air available for sound production at depth (Ridgway and Howard, 1979; Ridgway et al., 1969). The assumption that beaked whales also dive upon inhalation is consistent with the observation that the fluke rate decreased after the first 20–40 m of descents by both species without loss of speed, presumably due to a reduction in buoyancy as the lungs compressed. The depth of lung collapse is not known for beaked whales, but if it is assumed, as with dolphins, that the comparatively rigid volume of the bronchi, trachea, bony nasal passages, and air spaces of the nasal complex represent more than 9% of the total surface air volume in beaked whales, there should be no more air in the alveoli at a depth of 100 m (Scholander, 1940)[¶].

According to Fick's law, the diffusion rate of a gas per unit time across a tissue barrier is a product of the difference in partial pressures, the diffusion area, and the inverse of the barrier thickness (Dejours, 1975). The partial pressure gradient of nitrogen between the airspaces and the blood increases with increasing hydrostatic pressure, promoting diffusion of gas. However, when air moves out of the alveoli (which have a large perfused surface area and a thin one cell layer between air and blood) and into the airspaces of the trachea and the head, the drastically reduced surface areas and much increased barrier thickness will result in a very slow diffusion rate (Crystal et al., 1997). Thus, when marine mammals dive deeper than the depth of alveolar collapse, there is no effective interface left for gas diffusion into the blood (Falke et al., 1985; Irving, 1935; Kooyman et al., 1972; Scholander, 1940) and the nitrogen tensions in the blood and muscle stabilize or drop despite increasing hydrostatic pressure, as has been observed in diving seals (Falke et al., 1985; Kooyman et al., 1972) and dolphins (Ridgway and Howard, 1979). Accordingly, no significant amount of nitrogen can be expected to diffuse from airspaces to the blood during the portions of dives that are deeper than the depth of lung collapse.

Nonetheless, observations consistent with DCS and embolism have been made in stranded beaked whales of the genera *Ziphius* and *Mesoplodon* (Jepson et al., 2003; Jepson et

al., 2005; Fernandez et al., 2005) and, as shown in this paper, these animals employ an extreme diving behaviour with a stereotypical form unusual in diving air-breathers. In the following we examine three peculiar aspects of this diving behaviour for indications that these species of beaked whales have a heightened risk of DCS. The three behaviours are: (1) the occasional protracted periods near the surface, (2) the sequences of shallow dives following deep dives, and (3) the slow ascents from deep dives.

A breath-holding animal, submerged at a depth shallower than that of lung collapse, will have a nitrogen influx to the blood, due to the high partial pressures of the compressed air in the lungs. If submergence is maintained for long enough, the blood will be supersaturated with nitrogen (i.e. N_2 tissue tension > atmospheric partial pressure of N_2) upon returning to the surface (Brubakk and Neuman, 2003; Falke et al., 1985; Kooyman et al., 1972). However, the high rate of lung perfusion and low carrying capacity of nitrogen in the blood will provide rapid equilibration of the nitrogen tensions at the surface (Cross, 1965; Falke et al., 1985; Fahlman et al., 2006) unless shallow dives are repeated over and over with short surface intervals (Paulev, 1965; Paulev, 1967; Ridgway and Howard, 1979) to supersaturate the tissues such as fat and muscles of higher carrying capacity. Cox et al. (Cox et al., 2006) speculated that the characteristic short surface intervals of beaked whales may indicate that they are chronically supersaturated with nitrogen to a level at which remaining near the surface for more than a few minutes could be a risk factor for emboli. Our observations of beaked whales spending up to 86 min (Zc) and 33 min (Md) at mean depths of less than 11 m from the surface (including prolonged logging directly at the surface) after deep foraging dives do not support this contention. Rather it seems that these whales, like other diving animals, equilibrate to normal nitrogen tensions during surface intervals.

Despite the lack of evidence for dangerous levels of chronic supersaturation, it is tempting to regard the characteristic sequence of increasingly shallow dives following deep foraging dives (Fig. 4) as recompression dives, i.e. as serving to prevent emboli by slowly equilibrating the gas tensions in the tissues, analogous to the recompression process adopted by human divers (Brubakk and Neuman, 2003; Paulev, 1967). If shallow dives function for decompression, one would hypothesize that the animals would descend rapidly to a depth close to lung collapse where the pressure difference between the supersaturated tissue and the compressed air in the alveoli is smaller, and then slowly return to the surface, allowing gas to diffuse back from the blood and the tissues with little risk of bubble formation (Brubakk and Neuman, 2003). Our finding that the descent phase of shallow dives takes, on average, a little longer than the ascent, is contrary to this prediction and suggests that shallow dives if anything would facilitate supersaturation, not prevent it. In addition, many of the short dives (especially of *Ziphius*) are considerably deeper than the 100 m expected maximum depth of lung collapse. There is accordingly little support for the hypothesis that the shallow

[¶]If the relative volume of the upper airways is the same for beaked whales as for dolphins, the above estimate is conservative since the relative lung volume of a beaked whale is estimated to be about half that of a dolphin (Scholander, 1940), so it is likely that the depth of lung collapse is shallower than 100 m and possibly 70 m in beaked whales. This estimate may also be biased deep because it ignores gas that diffuses from the alveoli into circulation.

dives after deep, foraging dives serve as recompression dives at least within the mechanisms known for dolphins (Ridgway and Howard, 1979; Ridgway et al., 1969), seals (Falke et al., 1985; Kooyman et al., 1972) and humans (Brubakk and Neuman, 2003; Paulev, 1967). On the contrary, the shallow dives of beaked whales would seem to pose a greater risk for the generation of supersaturated tissue and subsequent decompression stress than the deep, long foraging dives, where the alveoli are collapsed for most of the dive. The highest nitrogen tensions in the muscles of a dolphin were measured after a long series of dives to 100 m, whereas deeper dives yielded lower nitrogen tensions (Ridgway and Howard, 1979).

The third enigmatic aspect of beaked whale dive behaviour that may have a bearing on the risk of DCS is the consistent slow ascent from deep dives. Given that these animals most likely exceed their ADL during deep foraging dives and must spend protracted times at the surface between such dives to recover, it is puzzling that the ascent rate in deep dives is, on average, one half that of the descent rate. To maximize time spent foraging, one would expect either a rapid return to the surface at the end of foraging, or that foraging would continue during a slower ascent. However, all tagged whales, without exception, made slow silent ascents from deep foraging dives suggesting that this behaviour is either physiologically mandated or behaviourally important. In the following, we consider a number of hypotheses for slow ascents culled from the literature, and discuss why none of these seem to fit the behaviour observed in the tagged beaked whales.

One possible explanation for the slow ascent rate is that a whale, already at or near its ADL by the end of the foraging phase of a deep dive, might seek to minimize the cost of transport by performing a long duration, but metabolically cheap, gliding ascent as described for Weddell seals (Sato et al., 2003) and sperm whales (Miller et al., 2004). However, tagged beaked whales swam with consistent fluking effort at a shallow pitch angle during the long ascents (Fig. 3), resulting in a swimming speed probably comparable to that of the descent, but with a smaller vertical component.

Sato et al. (Sato et al., 2004) reported that foraging penguins sometimes extend their ascent, returning to the surface at a low pitch angle, and suggested that this behaviour may serve to increase horizontal displacement from a poor food patch. Tagged beaked whales always ascended at a low pitch angle and consistently covered more than 50% of the possible horizontal displacement during ascent. No correlation was found between horizontal displacement and buzz count with the small data set available, suggesting that the ascent behaviour is decoupled from variation in food patch quality and that the whales employ this behaviour for other reasons. It is possible that the consistently high horizontal displacements achieved during the silent ascents could impede a near-surface predator from tracking these cryptic species after they stop vocalizing at depth.

Slow ascents from deep dives have also been reported for another beaked whale species, the northern bottlenose whale, *Hyperoodon ampullatus* (Hooker and Baird, 1999), and for

beluga whales, *Delphinapterus leucas* (Martin and Smith, 1992). Both of these species reduced their vertical velocity in the top 200 m of ascents from deep dives. The authors noted that the changes in gas volume with depth are greatest near the surface and suggested that the whales they studied might slow the final phase of their ascents to reduce the risk of gas bubbles forming in the blood or tissues, or to avoid fast expansion of gas in confined and possibly constricted airspaces such as sinuses. Enigmatically, the beaked whales studied here ascended slowly at the start or in the middle of their ascent, depending on dive depth, where changes in gas volume with depth are small. In the top 100 m, where gas expansion is most rapid, ascent rates were variable but often comparable to descent rates. This pattern is inconsistent with the hypothesis that slow ascents serve to reduce the negative effects of gas expansion in the lungs or other tissues.

Jepson et al. suggest that a rapid ascent from a deep dive may heighten the risk of nitrogen supersaturation and subsequent bubble formation (Jepson et al., 2003). Under this argument, the slow ascents could provide time for gas to diffuse back into the airspaces and so avoid embolism. For this to be the case, there must be a positive gradient from the blood to the gas phases and an interface over which diffusion can happen effectively within the duration of the slow part of the ascent. Given that *Ziphius* ascend most slowly between 600 and 400 m, spending an average of 6 min in this depth range, the whale would need some tissues saturated with nitrogen at tensions greater than 35 000 mmHg (61 ATA \times 580 mmHg of N₂ at the surface) at the end of the foraging phase to have a positive diffusion gradient from the blood to the air spaces at 600 m depth. Considering the time available for diffusion, the interface and barrier thickness problems and the half time of nitrogen exchange in tissues (Ridgway and Howard, 1979), we regard such high N₂ tensions as inconceivable. On the contrary, we argue that, if beaked whales actually do have significant nitrogen flux between airspaces and the blood at great depths, ascending slowly from 600 to 400 m will only facilitate higher tissue tensions of nitrogen, not prevent them. In this case, it would be better to move quickly up to the depth of lung collapse where there is an effective interface and larger partial pressure gradient in the re-inflating alveoli, and then ascend slowly from there to the surface, as described for *Hyperoodon* and beluga. We did not observe such behaviour and conclude that the slow ascent at depth and the faster, but variable ascent in the upper 100 m is inconsistent with mediating the effects of nitrogen supersaturation. The slow ascent is costly and must serve a critical behavioural or physiological purpose, but, given current models of breath-hold diving, mitigating decompression problems cannot in our view explain this unusual behaviour. The simple model for nitrogen diffusion considered here does not take into account the role of other tissues in the body in absorbing and releasing nitrogen, since we have no information about perfusion rates of such tissues in beaked whales during diving. However, given the current lack of evidence for severe supersaturation in the blood, it seems unlikely that nitrogen stored in other compartments

would radically change the risk of emboli under normal diving conditions.

Several aspects of the diving behaviour of beaked whales remain enigmatic: we cannot offer an explanation for the slow ascents observed from deep dives nor for the sequences of shallow dives with decreasing depth following a deep dive. The diving behaviour of beaked whales must fit within physiological constraints but also must meet ecological and behavioural needs related to foraging, social interactions and predator avoidance. Although our analysis of the normal dive behaviour of beaked whales does not identify an obvious risk factor for decompression problems, the enigmatic elements of diving behaviour and the apparent vulnerability of beaked whales to anthropogenic sound may not correspond exclusively to physiological limitations, but could also be related to behavioural issues, such as problems maintaining social cohesion given the limited range of their acoustic signals, or the strategies they use to avoid predation.

Scenario for development of decompression sickness in beaked whales

Even though beaked whales are extreme divers, our analysis above does not suggest that these animals run a risk of decompression stress and embolism during normal diving behaviour. However, an aberrant behaviour can be envisioned, for which decompression sickness might be an issue. Houser et al. (Houser et al., 2001) modelled the nitrogen levels in the tissues of a diving bottlenose whale based on a set of assumptions including lung collapse at a depth of 70 m. They concluded that diving speed and depth are the primary determinants of tissue nitrogen accumulation, with slower rates of ascent/descent and dives within lung collapse depths leading to supersaturation. Thus, considerable time spent close to, but within, lung collapse depth should cause the highest risk for supersaturation and thereby bubble formation. The highest influx of nitrogen does not happen just before the depth of complete alveolar collapse, because the process of alveolar collapse is gradual. So while the partial pressure gradient between nitrogen in the lungs and the blood perfusing the alveoli increases with depth, the surface area over which the diffusion takes place decreases with the reducing lung volume. The so-called invasion rate of nitrogen (Scholander, 1940) is therefore estimated to be highest at depths about half-way between the surface and the depth of complete alveolar collapse. Beaked whales with a lung collapse depth shallower than 100 m will therefore probably experience the highest influxes of nitrogen when they are at depths between 30 and 80 m.

This line of reasoning suggests that the most risky behaviour in terms of decompression sickness for beaked whales would be repeated dives at depths between 30 and 80 m. If a whale responded to a noise source by repeating several long dives in this depth range with short intervening surface durations, such a response could facilitate tissue supersaturation levels of up to 400 to 900% (corresponding to 5–10 ATA) compared to the partial pressures of nitrogen at the surface. Supersaturation at

that level could lead to embolism and symptoms of DCS (Brubakk and Neuman, 2003) when the animals return to the surface (*sensu* Paulev, 1965; Paulev, 1967) for long periods of time, e.g. because of fatigue or stranding. Thus if exposure to sonar pings provokes a response of the sort described here, it could lead to DCS-like symptoms in line with the pathological findings in the stranded animals, but it does not explain why beaked whales seem at higher risk than the other species. The critical question in this context is how these beaked whale species respond to sounds of sonars and whether these responses pose a physiological risk that can ultimately cause the animals to strand and die.

Conclusion

The two species of beaked whales studied here, *Ziphius cavirostris* and *Mesoplodon densirostris*, undertake long, deep dives to predate on a deep water food source. Diving is highly stereotypical with most deep foraging dives being followed by an extended period of shallow dives and slow travel/resting near the surface. All foraging dives of both species are considerably longer than the estimated aerobic dive limits, suggesting that the whales return to the surface with an oxygen debt. We propose that the shallow dives and the long periods in-between foraging dives are needed to repay the oxygen debt before the next deep dive. Despite the extreme diving of these species, the long periods spent at or close to the surface are inconsistent with the hypothesis that beaked whales are chronically supersaturated at high levels. Likewise, the equal durations of ascent and descent found in the shallow recovery dives are contrary to what would be required for recompression. Another consistent feature of the dive profiles, the slow ascent from deep foraging dives, remains a puzzle. The long ascents, which are acoustically inactive but involve active swimming, appear to divert substantial time away from foraging, suggesting that the animals are constrained by some physiological requirement or behavioural need that prevents them from optimizing foraging performance. However, since the slowest phase of the ascent occurs well below the depth of lung collapse, we argue against it representing an adaptation to prevent bubble formation. Rather we argue that the deep-diving behaviour of beaked whales is unlikely, under current models of nitrogen diffusion, to heighten the risk of embolism. We suggest that emboli observed in animals exposed to naval sonar exercises (Jepson et al., 2003; Jepson et al., 2005; Fernandez et al., 2005) could stem instead from a behavioural response that involves repeated dives shallower than the depth of lung collapse. Regardless of the precise cause of the strandings, it is a pressing issue to develop effective mitigation protocols so as to reduce the accidental exposure of beaked whales to navy sonar. The stereotyped dive cycle and acoustic behaviour of *Ziphius* and *Mesoplodon* described in this paper provide critical data for the design of efficient acoustic and visual detection methods for the at-risk species.

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References

- Aguilar Soto, N., Johnson, M., Madsen, P. T., Tyack, P. L., Bocconcelli, A. and Borsani, J. F. (2006). Does intense ship noise disrupt foraging in deep-diving Cuvier's beaked whales (*Ziphius cavirostris*). *Mar. Mamm. Sci.* **22**, 690-699.
- Baird, R. W., Dill, L. M. and Hanson, M. B. (1998). Diving behaviour of killer whales. In *World Marine Mammal Science Conference*, p. 9. Monaco: Society for Marine Mammalogy.
- Baird, R. W., Webster, D. L., McSweeney, D. J., Ligon, A. D., Schorr, G. S. and Barlow, J. (2006). Diving behavior and ecology of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales in Hawaii. *Can. J. Zool.* **84**, 1120-1128.
- Bangsbo, J., Graham, T., Johansen, L. and Saltin, B. (1996). Muscle lactate metabolism in recovery from intense exhaustive exercise: impact of light exercise. *J. Appl. Physiol.* **77**, 1890-1895.
- Bennett, P. B. (1982). The high pressure nervous syndrome in man. In *The Physiology and Medicine of Diving and Compressed Air Work* (ed. P. B. Bennett and D. H. Elliot), pp. 262-296. London: Balliere-Tindall.
- Bennett, P. B. and Rostain, J. C. (2003). High pressure nervous syndrome. In *Bennett and Elliott's Physiology and Medicine of Diving* (ed. A. Brubakk and T. Neuman), pp. 323-357. Edinburgh: Saunders.
- Blanco, C. and Raga, J. A. (2000). Cephalopod prey of two *Ziphius cavirostris* (Cetacea) stranded on the western Mediterranean coast. *J. Mar. Biol. Assoc. U.K.* **80**, 381-382.
- Brubakk, A. O. and Neuman, T. S. (ed.) (2003). *Bennett and Elliott's Physiology and Medicine of Diving*. Edinburgh: Saunders.
- Butler, P. J. (2001). Diving beyond the limits. *News Physiol. Sci.* **16**, 222-227.
- Butler, P. J. and Jones, D. R. (1997). Physiology of diving of birds and mammals. *Physiol. Rev.* **77**, 837-899.
- Carbone, C. and Houston, A. I. (1996). The allocation of time over the dive cycle: an approach based on aerobic and anaerobic respiration. *Anim. Behav.* **51**, 1247-1255.
- Castellini, M. A., Davis, R. W. and Kooyman, G. L. (1988). Blood chemistry regulation during repetitive diving in Weddell seals. *Physiol. Zool.* **61**, 379-386.
- Castellini, M. A., Kooyman, G. L. and Ponganis, P. J. (1992). Metabolic rates of freely diving Weddell seals: correlations with oxygen stores, swim velocity and diving duration. *J. Exp. Biol.* **165**, 181-194.
- Chilvers, B. J., Wilkinson, I. S., Duignan, P. J. and Gemmill, N. J. (2006). Diving to extremes: are New Zealand sea lions (*Phocarcos hookeri*) pushing their limits in a marginal habitat? *J. Zool.* **269**, 233-240.
- Clarke, M. R. (1976). Observation on sperm whale diving. *J. Mar. Biol. Assoc. UK* **56**, 809-810.
- Costa, D. P., Gales, N. J. and Goebel, M. E. (2001). Aerobic dive limit: how often does it occur in nature? *Comp. Biochem. Physiol.* **129A**, 771-783.
- Cox, T. M., Ragen, T. J., Read, A. J., Vos, E., Baird, R. W., Balcomb, K., Barlow, J., Caldwell, J., Cranford, T., Crum, L. et al. (2006). Why beaked whales? Report of workshop to understand the impacts of anthropogenic sound. *J. Cetacean Res. Manag.* **7**, 177-187.
- Cross, E. R. (1965). Taravana diving syndrome in the Tuamotu diver. In *Physiology of Breath-Hold Diving and the Ama of Japan* (ed. H. Rahn and T. Yokoyama), pp. 207-219. Washington DC: National Academy of Sciences, National Research Council.
- Crum, L. A. and Mao, Y. (1996). Acoustically enhanced bubble growth at low frequencies and its implications for human diver and marine mammal safety. *J. Acoust. Soc. Am.* **99**, 2898-2907.
- Crystal, R. G., West, J. B., Weibel, E. R. and Barnes, P. J. (1997). *The Lung: Scientific Foundations*. New York: Raven Press.
- D'Amico, A. (1998). *Summary Record SACLANTCEN Bioacoustic Panel*. La Spezia, Italy: Saclant Centre for Undersea Research.
- Davis, R. W. and Kanatous, S. B. (1999). Convective oxygen transport and tissue oxygen consumption in Weddell seals during aerobic dives. *J. Exp. Biol.* **202**, 1091-1113.
- Dejours, P. (1975). *Principles of Comparative Respiratory Physiology*. Amsterdam: Elsevier.
- DeLong, R. L. and Stewart, B. S. (1991). Diving patterns of northern elephant seal bulls. *Mar. Mamm. Sci.* **7**, 369-384.
- Evans, D. L. and England, G. R. (2001). *Joint Interim Report, Bahamas Marine Mammal Stranding, Event of 15-16 March 2000*. Washington, DC: US Department of Commerce and Secretary of the Navy.
- Fahlman, A., Olszowka, A., Bostrom, B. and Jones, D. R. (2006). Deep diving mammals: dive behavior and circulatory adjustments contribute to bends avoidance. *Respir. Physiol. Neurobiol.* **153**, 66-77.
- Falke, K. J., Hill, R. D., Qvist, J., Schneider, R. C., Guppy, M., Liggins, G. C., Hochachka, P. W., Elliott, R. E. and Zapol, W. M. (1985). Seal lungs collapse during free diving: evidence from arterial nitrogen tensions. *Science* **229**, 556-558.
- Fernandez, A., Edwards, J. F., Rodriguez, F., Espinosa de los Monteros, A., Herraiz, P., Castro, P., Jaber, J. R., Martin, V. and Arbelo, M. (2005). "Gas and fat embolic syndrome" involving a mass stranding of beaked whales (family Ziphiidae) exposed to anthropogenic sonar signals. *Vet. Pathol.* **42**, 446-457.
- Frantzis, A. (1998). Does acoustic testing strand whales? *Nature* **392**, 29.
- Hindell, M. A., Slip, D. J. and Burton, H. R. (1991). The diving behaviour of adult male and female southern elephant seals, *Mirounga leonina* (Pinnipedia: Phocidae). *Aust. J. Zool.* **39**, 595-619.
- Hobson, R. P. and Martin, A. R. (1996). Behaviour and dive times of Arnoux's beaked whales, *Berardius arnuxii*, at narrow leads in fast ice. *Can. J. Zool.* **74**, 388-393.
- Hooker, S. K. and Baird, R. W. (1999). Deep-diving behaviour of the northern bottlenose whale, *Hyperoodon ampullatus* (Cetacea: Ziphiidae). *Proc. R. Soc. Lond. B Biol. Sci.* **266**, 671-676.
- Houser, D. S., Howard, R. and Ridgway, S. H. (2001). Can diving-induced tissue nitrogen supersaturation increase the chance of acoustically driven bubble growth in marine mammals? *J. Theor. Biol.* **213**, 183-195.
- Houston, A. I. and Carbone, C. (1992). The optimal allocation of time during the diving cycle. *Behav. Ecol.* **3**, 255-265.
- Irving, L. (1935). The protection of whales from the danger of caisson disease. *Science* **81**, 560-561.
- Jepson, P. D., Arbelo, M., Deaville, R., Patterson, I. A. P., Castro, P., Baker, J. R., Degollada, E., Ross, H. M., Herraiz, P., Pocknell, A. M. et al. (2003). Whales, sonar and decompression sickness. *Nature* **425**, 575-576.
- Jepson, P. D., Deaville, R., Patterson, I. A. P., Pocknell, A. M., Ross, H. M., Baker, J. R., Howie, F. E., Reid, R. J., Colloff, A. and Cunningham, A. A. (2005). Acute and chronic gas bubble lesions in cetaceans stranded in the United Kingdom. *Vet. Pathol.* **42**, 291-305.
- 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. Ocean. 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**, S383-S386.

- Kleiber, M.** (1975). *Fire of Life: An Introduction to Animal Energetics*. New York: Krieger.
- Kooyman, G. L.** (1981). *Weddell Seal: Consummate Diver*. Cambridge: Cambridge University Press.
- Kooyman, G. L.** (1985). Physiology without restraint in diving mammals. *Mar. Mamm. Sci.* **1**, 166-178.
- Kooyman, G. L.** (1989). *Diverse Divers: Physiology and Behavior*. Berlin: Springer-Verlag.
- Kooyman, G. L. and Ponganis, P. J.** (1997). The challenges of diving to depth. *Am. Sci.* **85**, 530-539.
- Kooyman, G. L. and Ponganis, P. J.** (1998). The physiological basis of diving to depth: birds and mammals. *Annu. Rev. Physiol.* **60**, 19-32.
- Kooyman, G. L., Schroeder, J. P., Denison, D. M., Hammond, D. D., Wright, J. J. and Bergman, W. P.** (1972). Blood nitrogen tensions of seals during simulated deep dives. *Am. J. Physiol.* **223**, 1016-1020.
- Kooyman, G. L., Wahrenbrock, E. A., Castellini, M. A., Davis, R. W. and Sinnett, E. E.** (1980). Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *J. Comp. Physiol. B* **138**, 335-346.
- Kooyman, G. L., Castellini, M. A., Davis, R. W. and Maue, R. A.** (1983). Aerobic diving limits of immature Weddell seals. *J. Comp. Physiol. B* **151**, 171-174.
- Le Boeuf, B. J. and Crocker, D. E.** (1996). Diving behavior of elephant seals: implications for predator avoidance. In *Great White Sharks, The Biology of Carcharodon carcharias* (ed. A. P. Klimley and D. G. Ainley), pp. 193-205. San Diego: Academic Press.
- Le Boeuf, B. J., Costa, D. P. and Huntley, A. C.** (1986). Pattern and depth of dives in Northern elephant seals, *Mirounga angustirostris*. *J. Zool. Lond.* **208**, 1-7.
- Le Boeuf, B. J., Costa, D. P., Huntley, A. C. and Feldkamp, S. D.** (1988). Continuous, deep diving in female northern elephant seals, *Mirounga angustirostris*. *Can. J. Zool.* **66**, 446-458.
- Madsen, P. T., Johnson, M., Aguilar de Soto, N., Zimmer, W. M. X. and Tyack, P. L.** (2005). Biosonar performance of foraging beaked whales (*Mesoplodon densirostris*). *J. Exp. Biol.* **208**, 181-194.
- Martin, A. R. and Smith, T. G.** (1992). Deep diving in wild, free-ranging beluga whales, *Delphinapterus leucas*. *Can. Bull. Fish. Aquat. Sci.* **49**, 462-466.
- Martín, V., Servidio, A. and García, S.** (2004). Proceedings of the workshop on active sonar and cetaceans. Mass strandings of beaked whales in the Canary Islands. *Eur. Cetacean Newsl.* **42** [special issue], 33-36.
- Mattlin, R. H., Gales, N. J. and Costa, D. P.** (1998). Seasonal dive behavior of lactating New Zealand fur seals (*Arctocephalus forsteri*). *Can. J. Zool.* **76**, 350-360.
- Mead, J. G.** (1989). Beaked whales of the genus *Mesoplodon*. In *Handbook of Marine Mammals* (ed. S. H. Ridgway and R. Harrison), pp. 349-430. London: Academic Press.
- Miller, P. J. O., Johnson, M. P., Tyack, P. L. and Terray, E. A.** (2004). Swimming gaits, passive drag and buoyancy of diving sperm whales *Physeter macrocephalus*. *J. Exp. Biol.* **207**, 1953-1967.
- Mori, Y.** (1998). The optimal patch use in divers: optimal time budget and the number of dive cycles during bout. *J. Theor. Biol.* **190**, 187-199.
- Mori, Y.** (1999). The optimal allocation of time and respiratory metabolism over the dive cycle. *Behav. Ecol.* **10**, 155-160.
- Mori, Y.** (2002). Optimal diving behaviour for foraging in relation to body size. *J. Evol. Biol.* **15**, 269-276.
- Notarbartolo-di-Sciara, G.** (1987). Killer whale, *Orcinus orca*, in the Mediterranean Sea. *Mar. Mamm. Sci.* **3**, 356-360.
- Paulev, P.** (1965). Decompression sickness following repeated breath-hold dives. *J. Appl. Physiol.* **20**, 1028-1031.
- Paulev, P.** (1967). Nitrogen tissue tensions following repeated breath-hold dives. *J. Appl. Physiol.* **22**, 714-718.
- Podesta, M. and Meotti, C.** (1991). The stomach contents of a Cuvier's beaked whale, *Ziphius cavirostris*, and a Risso's dolphin, *Grampus griseus*, stranded in Italy. *Eur. Res. Cetaceans* **5**, 58-61.
- Ponganis, P. J., Kooyman, G. L., Starke, N., Kooyman, C. A. and Kooyman, T. G.** (1997). Post-dive blood lactate concentrations in emperor penguins, *Aptenodytes forsteri*. *J. Exp. Biol.* **200**, 1623-1626.
- Reed, J. Z., Chambers, C., Fedak, M. A. and Butler, P. J.** (1994). Gas exchange of captive freely diving grey seals (*Halichoerus grypus*). *J. Exp. Biol.* **191**, 1-18.
- Ridgway, S. H. and Howard, R.** (1979). Dolphin lung collapse and intramuscular circulation during free diving: evidence from nitrogen washout. *Science* **206**, 1182-1183.
- Ridgway, S. H., Scronce, B. L. and Kanwisher, J.** (1969). Respiration and deep diving in the bottlenose porpoise. *Science* **166**, 1651-1654.
- Ross, G. J. B.** (1984). The smaller cetaceans of the south-east coast of southern Africa. *Ann. Cape Prov. Mus. Nat. Hist.* **15**, 173-410.
- Santos, M. B., Pierce, G. J., Herman, J., Lopez, A., Guerra, A., Mente, E. and Clarke, M. R.** (2001). Feeding ecology of Cuvier's beaked whale (*Ziphius cavirostris*): a review with new information on the diet of the species. *J. Mar. Biol. Assoc. U.K.* **81**, 687-694.
- Sato, K., Mitani, Y., Cameron, M. F., Siniff, D. B. and Naito, Y.** (2003). Factors affecting stroking patterns and body angle in diving Weddell seals under natural conditions. *J. Exp. Biol.* **206**, 1461-1470.
- Sato, K., Charrassin, J.-B., Bost, C.-A. and Naito, Y.** (2004). Why do macaroni penguins choose shallow body angles that result in longer descent and ascent durations? *J. Exp. Biol.* **207**, 4057-4065.
- Scholander, P. F.** (1940). Experimental investigations on the respiratory function in diving mammals and birds. *Hvalradets Skrifter* **22**, 1-131.
- Schreer, J. F. and Kovacs, K. M.** (1997). Allometry of diving capacity in air-breathing vertebrates. *Can. J. Zool.* **75**, 339-358.
- Simmonds, M. P. and Lopez-Jurado, L. F.** (1991). Whales and the military. *Nature* **351**, 448.
- Sparling, C. E. and Fedak, M. A.** (2004). Metabolic rates of captive grey seals during voluntary diving. *J. Exp. Biol.* **207**, 1615-1624.
- Stewart, B. S. and Delong, R. L.** (1990). Sexual differences in migrations and foraging behavior of northern elephant seals. *Am. Zool.* **30**, 44A.
- Watkins, W. A., Daher, M. A., Fristrup, K. M. and Howald, T. J.** (1993). Sperm whales tagged with transponders and tracked underwater by sonar. *Mar. Mamm. Sci.* **9**, 55-67.
- Watwood, S. L., Miller, P. J. O., Johnson, M., Madsen, P. T. and Tyack, P. L.** (2006). Deep-diving foraging behavior of sperm whales (*Physeter macrocephalus*). *J. Anim. Ecol.* **75**, 814-825.
- Whitehead, H.** (2003). *Sperm Whales: Social Evolution in the Ocean*. Chicago: University of Chicago Press.
- Whitney, W.** (1968). *Observations of Sperm Whale Sounds from Great Depths*. La Jolla: Scripps Institution of Oceanography, Marine Physical Laboratory.
- Zimmer, W. M. X., Johnson, M. P., Madsen, P. T. and Tyack, P. L.** (2005). Echolocation clicks of Cuvier's beaked whales (*Ziphius cavirostris*). *J. Acoust. Soc. Am.* **117**, 3919-3927.