Diving behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales in Hawai'i

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Abstract: Beaked whales (family Ziphiidae) are thought to be among the longest and deepest diving mammals, and some species appear to be prone to mass-strand in response to high-intensity sonar. We studied diving behaviour of Cuvier's (*Ziphius cavirostris* G. Cuvier, 1823) and Blainville's (*Mesoplodon densirostris* (Blainville, 1817)) beaked whales in Hawaiian waters using suction-cup-attached time–depth recorders. Six whales, two Cuvier's and four Blainville's, were tagged and 41 h of dive data were collected. While Cuvier's beaked whales were found in significantly deeper water depths (median depth = 2079 m) than Blainville's beaked whales (median depth = 922 m), several aspects of diving were similar between the two species: (*i*) both regularly dove for 48–68 min to depths greater than 800 m (maximum 1408 m for Blainville's and 1450 m for Cuvier's); (*ii*) ascent rates for long/deep dives were substantially slower than descent rates, while for shorter dives there were no consistent differences; and (*iii*) both spent prolonged periods of time (66–155 min) in the upper 50 m of the water column. Based on time intervals between dives for the Cuvier's beaked whales, such long dives were likely aerobic, but both species appeared to prepare for long dives by spending extended periods of time near the surface.

Résumé : Les baleines à bec (famille Ziphiidae) passent pour les mammifères qui font les plongées les plus longues et les plus profondes et certaines espèces sont portées à s'échouer en groupe en réaction au sonar de forte intensité. Nous avons étudié le comportement de plongée des baleines à bec de Cuvier (*Ziphius cavirostris* G. Cuvier, 1823) et de Blainville (*Mesoplodon densirostris* (Blainville, 1817)) dans les eaux au large d'Hawai'i à l'aide d'enregistreurs de temps–profondeur fixés par une ventouse. Nous avons ainsi suivi six baleines à bec, deux de Cuvier et quatre de Blainville, et récolté 41 h de données de plongée. Bien que les baleines à bec de Cuvier se retrouvent à des profondeurs d'eau significativement plus grandes (profondeur médiane = 2079 m) que les baleines à bec de Blainville (profondeur médiane = 922 m), plusieurs aspects de la plongée sont semblables chez les deux espèces : (*i*) les deux plongent régulièrement pendant 48–68 min à des profondeurs supérieures à 800 m (maximum de 1408 m pour la baleine à bec de Blainville, 1450 m pour celle de Cuvier), (*ii*) les taux de remontée des plongées longues et profondes sont substantiellement plus lents que les taux de descente, alors que, pour les plongées plus courtes, il n'y a pas de différence uniforme et (*iii*) les deux passent de longues périodes de temps (66–155 min) dans les 50 m supérieurs de la colonne d'eau. D'après les intervalles de temps entre les plongées chez les baleines à bec de Cuvier, ces plongées sont vraisemblablement aérobies, mais les deux espèces semblent se préparer pour les plongées prolongées en passant de longues périodes près de la surface.

[Traduit par la Rédaction]

Introduction

Beaked whales (family Ziphiidae) are one of the least known groups of large mammals. A diverse family (consisting of at least 21 species) with members found in all ocean basins, beaked whales typically inhabit deep waters far from shore, often avoid vessels, and stay submerged for extended periods; behaviours that severely limit the ability of researchers to study them. Most information available for virtually all beaked whale species comes from studies of beach-cast carcasses (for exceptions see Claridge and Balcomb 1995; Whitehead et al. 1997). Based on their deep-water distributions, long dive times, and the habits of their prey (documented from stomach contents), beaked whales are thought to be deep divers (Heyning 1989; Mead 1989). However, of the 21 recognized species in the family Ziphiidae, only 3 species have been tagged with data-logging time–depth recorders. Hooker and Baird (1999) collected just over 30 h of dive data from two northern bottlenose whales (*Hyperoodon ampullatus* (Forster, 1770), documenting regular dives to over 800 m, with a maximum recorded dive depth of 1453 m. Dives appeared to fall into two discrete

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categories: short-duration (mean = 11.17 min) shallow dives and long-duration (mean = 36.98 min) deep dives (Hooker and Baird 1999). Dive data have also been collected from Cuvier's beaked whales (*Ziphius cavirostris* G. Cuvier, 1823) and Blainville's beaked whales (*Mesoplodon densirostris* (Blainville, 1817)), but were not reported in detail (Baird et al. 2004; Johnson et al. 2004).

Diving habits of beaked whales are of interest from both a biological and a conservation perspective. Information on diving behaviour can be used to examine habitat use and habitat partitioning, foraging ecology, and diel patterns of behaviour. From a management perspective, two issues are particularly relevant for beaked whales. Animals that spend long periods of time beneath the water's surface are likely to be missed during shipboard or aerial surveys. Without taking diving patterns into account, abundance estimates may be negatively biased (see Barlow 1999), and management decisions based on those estimates may be faulty. In addition, beaked whales appear to be susceptible to impacts from high-intensity sonar (Simmonds and Lopez-Jurado 1991; Frantzis 1998; Balcomb and Claridge 2001; US Department of Commerce and US Navy 2001; Jepson et al. 2003; Fernandez et al. 2005; Cox et al. 2006). In several cases where beaked whales have stranded in association with high-intensity sonar, the received sound pressure levels were thought to be lower than levels that would cause direct physical harm. Thus, it seems likely that indirect physical harm may be caused by behavioural reactions to the sounds (Cox et al. 2006). In addition, since sound exposure will vary by depth and topography, the depth at which beaked whales spend their time is important in assessing the risk of exposure to high intensity underwater sounds.

The two primary species involved in the multi-species mass strandings associated with naval activities are Cuvier's beaked whales and Blainville's beaked whales. The purpose of this study was to examine and to compare the diving behaviour and ecology of both species in Hawaiian waters. We also compare diving behaviour of these species with published information from northern bottlenose whales, assess the potential for aerobic versus anaerobic diving, and discuss diving behaviour in relation to potential impacts of high-intensity sonar.

Methods

Field efforts were undertaken during each year from 2002 through 2005 off the west coast of the island of Hawai'i (19°–20°N, 156°W). In the latter part of 2002 and all of 2003, two vessels were operated simultaneously, each independently searching for beaked whales and other species of cetaceans. In 2004 and 2005, a single vessel was used. Two to five observers on each vessel scanned 360° and the study area was transited at 15–30 km/h. GPS data were automatically recorded every 5 min. For each encountered group, we recorded species and location, estimated group size, and attempted to obtain photographs both to confirm species and for individual identification. Efforts during 2002 and the early part of 2003 were primarily focused on photo-identification and genetic sampling, and efforts to tag beaked whales were only undertaken during two encounters. During late 2003 and all of 2004 and 2005, all beaked whale groups were approached for tagging.

Tags were the same as those used in several other studies of cetacean diving (e.g., Hooker and Baird 1999; Baird et al. 2001, 2002), which included a Mk8 (in 2002) or Mk9 (in 2003–2005) time–depth recorder (Wildlife Computers, Redmond, Washington), and a VHF radio transmitter (Telonics, Mesa, Arizona, or ATS, Isanti, Minnesota), housed in a custom-made syntactic foam body, and attached to a whale with an 8 cm diameter suction cup. Tags weighed approximately 250 or 450 g for units containing a Mk9 or Mk8 TDR, respectively. Depth was recorded at 1 s intervals with a depth resolution of 1 m.

Tags were deployed by crossbow (RX-150, Barnett International, Odessa, Florida) or a 5.2 m carbon fiber pole. Once whales were tagged, we attempted to follow them using VHF signals and visual observations. Whenever possible, information on location, group size, distance of the nearest neighbor to the tagged animal, speed, and direction of travel were recorded at each surfacing. The timing of respirations, for the calculation of inter-breath intervals, was recorded for individuals that could be tracked using VHF signals. Sex and age of tagged animals were determined based on pigmentation patterns, body scarring, presence or absence of erupted teeth, and body size (Heyning 1989; Mead 1989). Tags were recovered using VHF signals, and data were downloaded to a PC using Mk8Host or Mk9Host (Wildlife Computers). Temperature-related drift in depth values (see Hooker and Baird 2001) were corrected with the program Instrument Helper (Wildlife Computers). Rates of descent and ascent were calculated in two ways: (1) in the top 100 m (to examine near-surface rates, in depths where the lungs should not yet have collapsed and thus gas exchange may still occur; Ridgway and Howard 1979) and (2) to 85% of the maximum depth of each dive (to examine rates over the majority of the dive but excluding periods near the bottom of dives when rates may change greatly as whales begin foraging). Dives were categorized (e.g., inter-ventilation dives) based on duration, maximum depth, dive "shape" (e.g., the occurrence of multiple inflections in depth along the bottom part of the dive), and temporal patterning of dives.

Bottom depths at effort and sighting locations were derived by overlaying the point location data on a bathymetric raster surface in ArcGIS® version 9.1 (Environmental Systems Research Institute, Inc. 2005). Underlying depth values (in metres) were transferred to point locations using the "intersect point tool" in Hawth's analysis tools (Beyer 2004). We used gridded 3 Arc-Second US Coastal Relief Model bathymetry (~90 m^2) from the National Geophysical Data Center (http://www.ngdc.noaa.gov/mgg/coastal/coastal.html).

Results

Encounters and tag deployments

Between 2002 and 2005, 128 days (922 h on effort) were spent in the field, covering 13 769 km of trackline in a study area of approximately 5 000 km^2 (Table 1, Fig. 1). Beaked whales were encountered 30 times, with 17 sightings of Cuvier's beaked whales, 11 sightings of Blainville's beaked whales, and 2 sightings of unidentified beaked whales. Search effort covered depths from <100 m to almost 5000 m, with approximately 50% of the search effort between 700 and 2300 m in depth (Fig. 2). Cuvier's beaked

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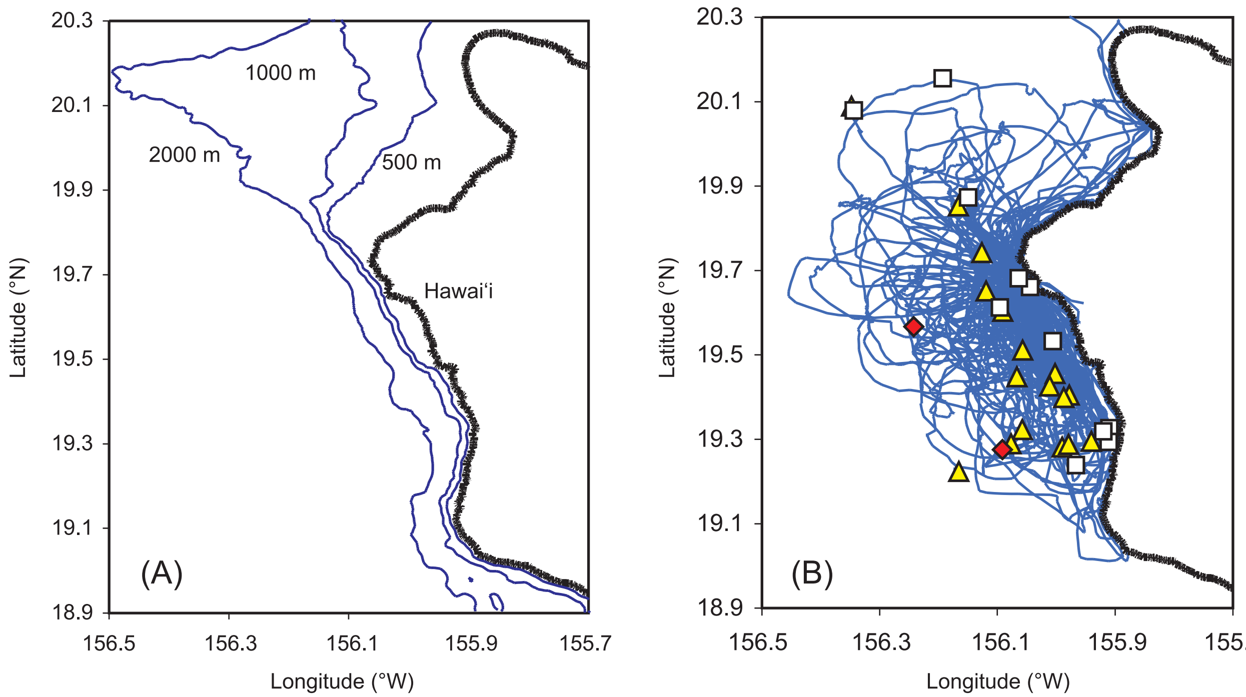
Table 1. Summary of effort, based on three measures, by field project off the island of Hawai‘i.

Year	Dates	No. of vessel days on water*	No. of kilometres on effort	No. of hours on effort	No. of beaked whale sightings	Vessels
2002	3–13 Apr.	10	1 089	75	1	6.4 m whaler
2002	24 Sept. – 5 Oct.	20	1 649	154	5	6.4 and 8.2 m whalers
2003	4–12 May	15	1 791	108	1	6.4 m whaler and 18 m striker
2003	8–20 Oct.	24	2 495	173	6	6.4 and 8.2 m whalers
2004	12 Sept. – 9 Dec.	42	4 656	290	10	8.2 m whaler
2005	19 Jan. – 5 Feb.	17	2 089	122	7	8.2 m whaler
Total		128	13 769	922	30	

Note: Number of beaked whale sightings include both Blainville’s beaked whales (*Mesoplodon densirostris*) and Cuvier’s beaked whales (*Ziphius cavirostris*), as well as unidentified beaked whales.
*When two vessels were used simultaneously in 1 day, they are counted as two “vessel days”.

Fig. 1. (A) Study area off the island of Hawai‘i showing 2000, 1000, and 500 m depth contours. (B) Tracklines from search effort and sightings of Cuvier’s beaked whales, *Ziphius cavirostris* (triangles), Blainville’s beaked whales, *Mesoplodon densirostris* (squares), and unidentified beaked whales (diamonds).



whales were generally seen in deeper areas (median depth = 2079 m), whereas Blainville’s beaked whales were generally seen in shallow areas (median depth = 922 m) (Fig. 2, Table 2; Mann–Whitney *U* test, $p = 0.0014$); however, there was some overlap in sighting depths, and on one occasion both species were seen within 400–500 m of each other in similar water depths. Both of the sightings of unidentified beaked whales were in very deep water (3373 and 4224 m), much deeper than we have documented for Blainville’s beaked whales. Group sizes ranged from 1 to 5 for Cuvier’s beaked whale and from 1 to 9 for Blainville’s beaked whale (Table 2). Twenty-four distinctive individual Cuvier’s beaked whales were photo-identified, and two of the individuals were re-sighted on one occasion each, both within a year.[2] Twenty-three distinctive individual Blainville’s beaked whales were documented, and seven individuals were re-sighted for a total of eight re-sighting occasions, all between years.[2]

Tags were deployed on six individuals: four Blainville’s beaked whales and two Cuvier’s beaked whales. Although one of the tags from a Cuvier’s was not recovered, we followed this individual for 7 h and monitored its surfacing behaviour with signals from the VHF tag. Information on the age and sex of tagged whales is presented in Table 3. During the period that tagged whales were followed, group size for all remained constant.

Dive and respiration data

Cuvier’s beaked whales

For the Cuvier’s beaked whale *Zc*2 (Fig. 3), the time of

[2] Additional photographs are available from opportunistic work by D. McSweeney since 1986 and have produced additional re-sightings of individuals (not included in this study).

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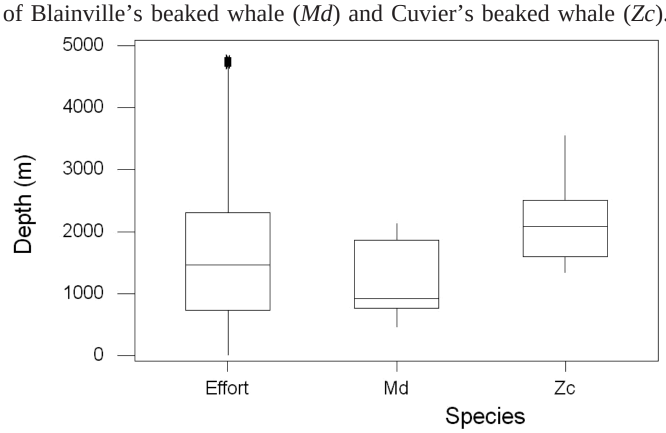
Table 2. Sighting characteristics of Blainville's and Cuvier's beaked whales off the island of Hawai'i, April 2002 through February 2005.

Species (no. of sightings)	Group size	Sighting depth (m)
Blainville's beaked whale (*n* = 11)	3.6±3.0 (1–9)	1119±527 (633–2050)
Cuvier's beaked whale (*n* = 17)	2.6±1.3 (1–5)	2131±667 (1381–3655)

Note: Values in the last two columns are means ± SD, with the range in parentheses.

Fig. 2. Boxplot showing depth distributions of effort and sightings of Blainville's beaked whale (*Md*) and Cuvier's beaked whale (*Zc*).



all respirations were recorded and inter-breath intervals were calculated for three consecutive surfacing periods — after a 54.8 min dive, between a 24.9 and a 22.5 min dive, and before a 67.25 min dive. In addition, the number of breaths was recorded following a long dive at approximately 20:06 h. Number of breaths per surfacing period was consistent over the four periods (26, 23, 24, 24). Inter-breath intervals during the three consecutive surfacing periods ranged from 3 to 15 s (mean = 7 s, SD = 2.1 s, *n* = 70). While only long-dive durations are available from the Cuvier's beaked whale (*Zc*1) where the tag was lost, duration and temporal patterning of long dives were similar to *Zc*2. The series of long dives for *Zc*1 included three 20–22 min dives followed by a 68 min dive, four 23–27 min dives followed by an 87 min dive, and three 19–21 min dives, before we left the group.

Based on dive duration, dive depth, dive shape, and temporal patterning (Fig. 3), dives appeared to fall into four distinct categories. Inter-ventilation dives were of short duration (3–15 s), shallow (depths of 2–3 m), had a parabolic shape, and occurred in extended bouts (e.g., 23–26 based on VHF data) in between longer/deeper dives. Two or three "types" of longer duration dives were documented that went below 5 m in depth. Long duration (>50 min) and deep (>1000 m, maximum 1450 m) dives were documented, on average, once every 2 h (*n* = 5 over the deployment duration). The bottom portion of these dives had occasional repeated inflections in depth (i.e., changes from descent to ascent and back), likely representing prey chases (see Discussion). One to three intermediate duration (~20 to ~30 min) dives to intermediate depth (292–568 m) were documented in three of the four intervals between the very long duration dives. These dives were "U-shaped" in vertical profile (i.e., there were no repeated inflections in depth). In the last interval between long (>50 min) duration dives (see Fig. 3, between 20.14 and 21.19 h), a variety of dive "types" were documented. Dives during this period included several series of short duration inter-ventilation dives, three dives between 25 and 35 s in duration (to 7.5–8.5 m), one dive at 1.23 min in duration to 15.5 m, and four dives from 8.1 to 14.9 min in duration (mean = 12.7 min), but of extremely shallow depth (3.5–6.5 m). After the last long dive recorded, two dives of intermediate duration (13.8 and 16.9 min) were documented, although the maximum depth of these dives was relatively shallow (69 and 15 m, respectively). All of these dives were relatively flat-bottomed (i.e., there were no large vertical excursions similar to those found in dives >800 m).

Excluding dives <50 m in depth, time intervals between dives ranged from 2.28 to 65.15 min (mean = 8.3 min, SD = 17.9 min, *n* = 12). All but one of these intervals was <5.1 min in duration; excluding the longest interval, the range was 2.28–5.05 min (mean = 3.14 min, SD = 0.83 min, *n* = 11). The time interval between dives (excluding the 65.15 min interval) was regressed against dive duration for both the following and preceding time intervals. There was no relationship between the dive duration and the time interval following the dive (r^2 = 0.02, *p* = 0.66), although there was a relationship between the dive duration and the preceding time interval (r^2 = 0.49, *p* = 0.017).

Based on bottom depth during the period when the Cuvier's beaked whale was tagged and followed (~2900 m), the first and second deep (>800 m) dives were to mid-water. For dives >800 m, descent rates to 85% of the maximum depth were significantly greater than ascent rates (Mann–Whitney *U* test, *p* = 0.012), with a mean ratio of descent/ascent rates of 1.95. In the top 100 m of the water for these dives, the rates were not significantly different (Mann–Whitney *U* test, *p* = 0.66), and the mean ratio of descent/ascent rates was 0.85 (Table 4). For dives between 100 and 600 m in depth, the differences between descent and ascent rates were lower (Table 4) and not statistically significant (Mann–Whitney *U* test, *p* = 0.69 to 85% of maximum depth, *p* = 0.57 in top 100 m). The proportion of time spent at different depths in the water column varied between day and night, although this difference was due to one extended period (66 min) when the whale did not dive below 50 m.

Blainville's beaked whales

Thirty-one hours of dive data were obtained from the four Blainville's beaked whales (Figs. 3, 4). Detailed respiration data were recorded for one individual based on VHF signals (*Md*2). The number of breaths for each surfacing period was recorded continuously for 4.3 h and the timing of all breaths was recorded (for calculation of inter-breath intervals) for an additional 0.83 h, representing all 19 surfacing periods in between dives. The number of breaths per surfacing series ranged from 3 to 41 (mean = 18, SD = 11.3, *n* = 19 series). However, the two series preceding the two deep (>800 m)

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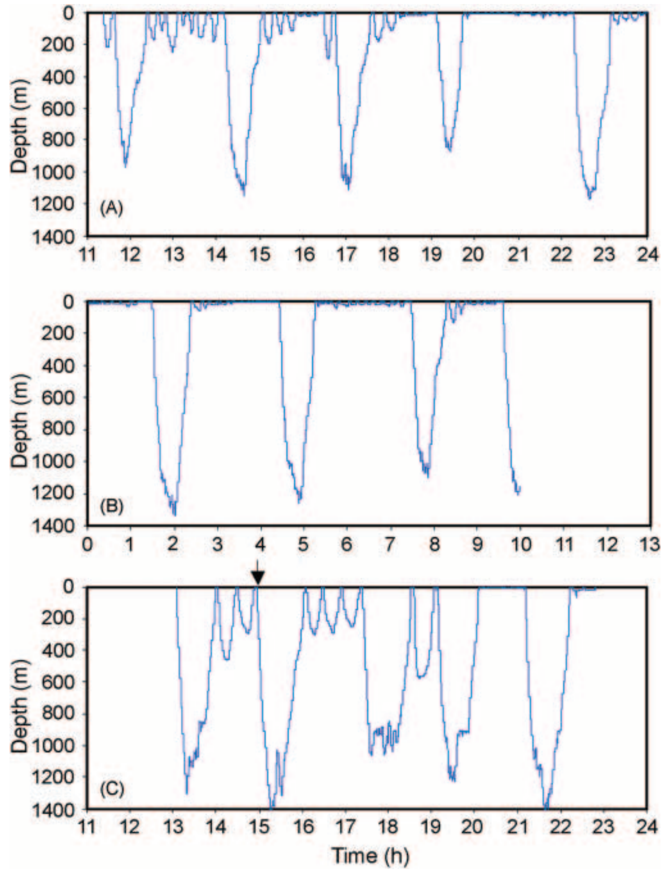
Table 3. Details of tag attachments on Blainville's and Cuvier's beaked whales off the island of Hawai'i.

Tag No.	Species	Date	Time tag on (hh.hh)	Time tag off (hh.hh)	Tag duration (hh.hh)	Duration followed after tagging (h.hh)	Age and sex	Group size when tagged
*Md*1	Blainville's	24 Sept. 2002	14.19	16.28	2.09	1.58	Adult male	9
*Md*2	Blainville's	15 Sept. 2004	10.32	15.7	5.38	5.38	Adult female (with young calf)	2
*Md*3	Blainville's	27 Sept. 2004	11.37	9.98	22.61	0	Large sub-adult or adult female	2
*Md*4	Blainville's	23 Nov. 2004	8.67	9.95	1.28	0.98	Juvenile (1–2 years old?)	8
*Zc*1	Cuvier's	27 Sept. 2002			—*	7	Adult female	5
*Zc*2	Cuvier's	28 Nov. 2004	13.08	22.83	9.75	1.85	Adult female	3

*Tag not recovered, respiration data only.

Fig. 3. Depth data from a 22.6 h deployment on a Blainville's beaked whale (A and B, tag number *Md*3) between 27 and 28 Sept. 2004 (time of sunset 18.25 h, time of sunrise 6.23 h) and from a 9.75 h deployment on a Cuvier's beaked whale (C, tag number *Zc*2) on 28 Nov. 2004 (time of sunset 17.73 h). The approximate point when percussive behaviour by an adult male Cuvier's beaked whale, associated with the tagged animal, was observed is indicated by an arrow. All graphs shown to same scale.



dives had the largest number of breaths (41 and 38). The number of breaths following the first long dive was 35. The second long dive was followed by a series of 15 breaths, a short (2 min 54 s) dive to 15 m depth, and another series of 17 breaths. Inter-breath intervals were calculated for all breaths within five surfacing periods and ranged from 5 to 42 s (mean = 10.9 s, SD = 5.51 s, $n = 71$).

Based on dive depth, dive duration, and temporal patterning, three or four types of dives are apparent. Inter-ventilation dives were typically only to 2–4 m depth. A total of 144 complete dives ≥5 m in depth were documented. As expected, there was a strong positive relationship between dive depth and duration (regression, $r^2 = 0.92$, $p < 0.001$). Dives between 6 and 300 m in depth appear to comprise two dive types: (1) dives <50 m in depth with no strong relationship between depth and either ascent (regression, $r^2 = 0.053$, $p = 0.024$) or descent (regression, $r^2 = 0.0007$, $p = 0.80$) rates and (2) dives >50 m in depth with strong positive relationships between depth and descent (regression, $r^2 = 0.55$, $p < 0.001$) and ascent (regression, $r^2 = 0.63$, $p < 0.001$) rates. Deep (>800 m) dives were recorded approximately once every 2 h. Maximum dive depth recorded for

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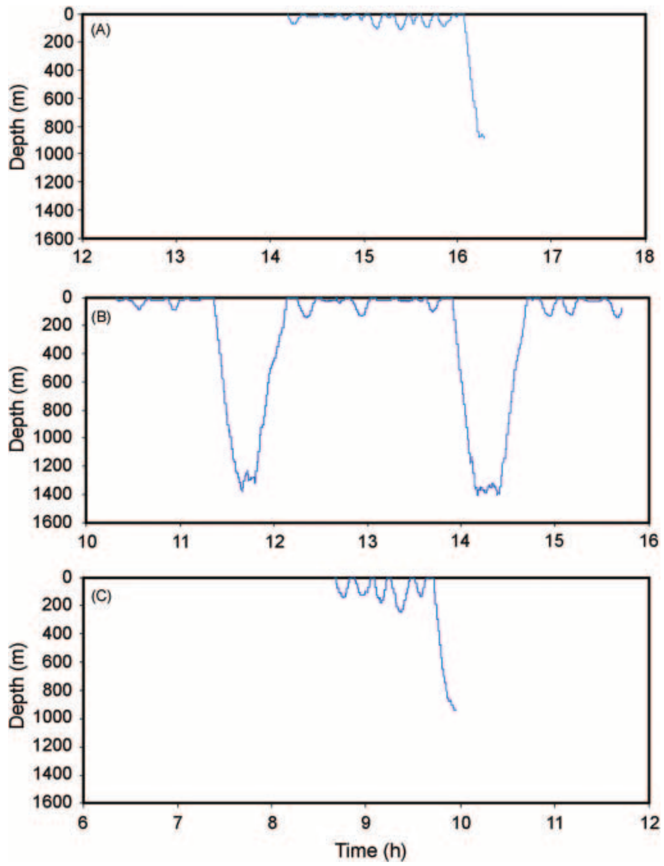
Table 4. Rates (mean ± SD; m/s) of descent and ascent of Blainville's and Cuvier's beaked whales tagged off the island of Hawai'i.

Tag No.*	Dives >800 m				Dives 100–600 m				No. of dives	
	Descent to 85% of maximum depth	Ascent from 85% maximum depth	Descent in top 100 m	Ascent in top 100 m	Descent to 85% of maximum depth	Ascent from 85% of maximum depth	Descent in top 100 m	Ascent in top 100 m	>800 m	100–600 m
*Md*2	1.48±0.01	1.24±0.17	1.48±0.02	1.44±0.07	0.44±0.07	0.47±0.03	0.45±0.09	0.47±0.29	2	4
*Md*3	1.26±0.24	0.80±0.16	1.41±0.41	1.12±0.27	0.61±0.21	0.69±0.21	0.76±0.35	0.71±0.20	9	14
*Zc*2	1.29±0.29	0.66±0.16	1.73±0.40	2.01±0.33	0.90±0.72	0.73±0.21	1.21±0.70	0.89±0.41	5	6

Note: Information presented only for those individuals with both shallow and complete deep dive records.
*Tag numbers correspond to individuals listed in Table 3.

Fig. 4. Depth data from three tag deployments on Blainville's beaked whales. (A) A 2.09 h deployment on an adult male (24 Sept. 2002, tag *Md*1); (B) a 5.38 h deployment on an adult female with young calf (15 Sept. 2004, tag *Md*2); (C) a 1.28 h deployment on a juvenile (23 Nov. 2004, tag *Md*4). All graphs shown to same scale (though note difference in scale from Fig. 3).



a Blainville's beaked whale was 1408 m (Table 5), from the female (*Md*2) accompanied by a calf estimated to be less than a couple of months old (based on the lack of scarring, body size relative to the female, and presence of faint fetal folds). This pair of whales was tracked for the entire duration of tag attachment (5.38 h), and there were no signs of the calf at the surface during the female's long dives. Based on bottom depth when first tagged and when last seen (~2000 m), both of the deep dives for *Md*2 were to mid-water. Two of the tagged whales (*Md*1, *Md*3) likely dove to or close to the bottom on deep (>800 m) dives, based on the timing of the dives relative to bottom depth.

Time intervals between dives were calculated excluding dives <50 m. Time intervals ranged from 2.6 to 35.5 min (mean = 14.3 min, SD = 10.1 min, n = 9) for *Md*2, whereas time intervals ranged from 1.58 to 154 min (mean = 23.6 min, SD = 41.7 min, n = 28) for *Md*3. There was no significant relationship between dive duration and time intervals between dives for either the interval preceding (regression, $r^2 = 0.01$, $p = 0.82$) or following ($r^2 = 0.13$, $p = 0.34$) dives for *Md*2; however, there was a relationship between the dive duration and the interval preceding the dive (regression, $r^2 = 0.42$, $p < 0.001$), though not for the interval following the dive ($r^2 = 0.02$, $p = 0.46$), for *Md*3.

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Table 5. Details on bottom depth, maximum dive depth and duration, dive rates, and longest period of time spent <50 m in depth for Blainville's and Cuvier's beaked whales off the island of Hawai'i.

Tag No.*	Depth when first tagged (m)	Depth when last seen (m)	Maximum dive depth (m)	No. of dives >800 m	No. of dives >800 m / h	Longest time <50 m (min)	Maximum dive duration (min)
*Md*1	692	914	890†	1	0.48	48.1	>13.58†
*Md*2	2003	3004	1408	2	0.37	39.0	48.36
*Md*3	1047	1047	1333	9	0.40	155.4	54.06
*Md*4	2043	1806	>938†	1	0.78	6.0	>14.53†
*Zc*2	2849	2667	1450	5	0.51	66.2	68.7

*Tag numbers correspond to individuals listed in Table 3.
†Tag off during dive.

Despite similar maximum dive depths as the Cuvier's beaked whale, in general the Blainville's beaked whales spent more time in the upper portion of the water column. Proportion of time at depth differed between day and night, with more time spent in near-surface waters at night. For dives >800 m, descent rates to 85% of the maximum depth were significantly greater than ascent rates (Mann–Whitney U test, $p = 0.0025$), with a mean ratio of descent/ascent of 1.38. There was no significant difference in descent and ascent rates in the top 100 m for dives >800 m (Mann–Whitney U test, $p = 0.12$) or for dives of 100–600 m in depth (Mann–Whitney U tests, $p = 0.26$ to 85% of maximum depth, $p = 0.66$ in top 100 m).

Discussion

Both Cuvier's and Blainville's beaked whales were encountered in deep waters off the west coast of the island of Hawai'i, although encounter rates were extremely low with only 17 and 11 sightings of the two species, respectively, in 922 h of search effort (one Cuvier's sighting every 54 h, one Blainville's sighting every 83.8 h). For comparison, MacLeod and Zuur (2005) reported an encounter rate of Blainville's beaked whales off Great Abaco in the Bahamas of one group every 12.7 h of search effort, with similar survey conditions. Despite low encounter rates in our study, high between-year re-sighting rates of individual Blainville's beaked whales (7 of 23 photo-identified individuals were seen in >1 year) suggest the existence of a resident population.

Blainville's beaked whales were typically sighted in shallower water than Cuvier's beaked whales (Fig. 2, Table 2), and dive profiles (see below) suggest that both species were using these areas for foraging. Both Cuvier's and Blainville's beaked whales regularly dove to depths >800 m, with a maximum recorded dive depth of 1408 m for a Blainville's beaked whale and 1450 m for a Cuvier's beaked whale. Diving behaviour for these species was similar to the diving behaviour documented for northern bottlenose whales (Hooker and Baird 1999), suggesting that such extreme diving behaviour may be typical for the family Ziphiidae. When it is impossible to sample lactic acid buildup or blood oxygen concentrations, assessments of whether dives are aerobic or anaerobic can be done by examining the relationship between the dive duration and the duration of the following surface interval. The number of breaths within a surface interval, as well as its duration, should be indicators of gas exchange and recovery from long dives. In theory, gas exchange could be increased through an increase in tidal volume, although there is relatively little scope for increase in beaked whales (Slijper 1976), and at least for gray whales, *Eschrichtius robustus* (Lilljeborg, 1861), tidal volume is relatively constant between breaths (J. Sumich, personal communication). For the Cuvier's beaked whale, the number of breaths immediately following a long (54.8 min) dive was similar (26 breaths) to the number following shorter (24.9 and 22.5 min) dives (23 and 24 breaths, respectively). Based on the time intervals between dives for the Cuvier's beaked whale, we infer that long dives were aerobic (i.e., there were no extended time intervals following longer dives), although time intervals prior to long dives were extended in duration, suggesting that the animals prepare for longer dives by spending more time near the surface. For Blainville's beaked whales, increased number of respirations before and after very long dives both suggest a recovery period after and a preparatory period before long dives. While there was no significant relationship between the dive duration and the time interval after long dives, for one of the two Blainville's beaked whales there was a positive relationship between the dive duration and the time interval preceding the dive, again suggesting a preparatory period before long dives.

For the two whales (one of each species) where tags remained attached into the night, there was no evidence of obvious differences in maximum dive depths between day and night, suggesting that their prey are likely not vertically migrating, which again is similar to the findings for northern bottlenose whales (Hooker and Baird 1999). Both individuals did spend more time above 50 m in depth at night. Little is known of the diet of Blainville's beaked whales, but they are thought to feed on squid and fish typically found between 200 and 2000 m, while Cuvier's beaked whales feed primarily on squid found in the same depth range (MacLeod et al. 2003). Foraging likely occurs primarily on the deepest dives, based both on dive shape and results of a study on echolocation use by depth in these species (Johnson et al. 2004), and may occur in mid-water, rather than only at or near the bottom as suggested by MacLeod et al. (2003).

For dives >800 m for both species, overall descent rates were faster than ascent rates (to/from 85% of maximum depth of each dive); for flat-bottomed dives between 100 and 600 m, descent and ascent rates were similar, but much lower than for the >800 m dives (Table 4). Hooker and Baird (1999) reported similar findings for northern bottlenose whales. They further showed that ascent rates on deep dives slowed as the whales approached the surface and sug-

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gested that the decrease in ascent rate might be a response to the higher relative pressure changes in the upper portions of the water column (Hooker and Baird 1999). No similar decrease in ascent rates in the top 100 m were found for Cuvier's or Blainville's beaked whales in this study (Table 4). In fact, ascent rates in the top 100 m, from deep (>800 m) dives, were consistently greater than the overall ascent rates (from 85% of the maximum dive depth) for these dives.

Cox et al. (2006) outlined several scenarios whereby behavioural responses by beaked whales to high-intensity sounds could lead to tissue damage and possibly death. These include surfacing excessively fast, causing gas bubble formation (see Fernandez et al. 2005); staying at the water's surface for too long, if tissues are supersaturated with nitrogen; diving prematurely, if whales spend extended periods at the surface to eliminate nitrogen; or staying at depth for too long, forcing an overly rapid ascent. We found slow ascent rates from dives >800 m and the existence of prolonged periods of time (66–155 min) spent in the upper 50 m of the water column for both Cuvier's and Blainville's beaked whales, the two species involved in mass strandings in relation to naval sonar. We suggest that the frequent extremely long dives push the animals' physiological limits, resulting in such behavioural mechanisms (slow ascent rates and prolonged periods of time at the surface to purge excess dissolved nitrogen in their tissues) to compensate. Indirect physical harm from surfacing excessively fast, or premature dives, seem most plausible as mechanisms for beaked whale mass strandings in relation to high-intensity sonar. Only a small number of individuals have been tagged, however, for relatively short periods and these represent only a subset of age and sex classes. Further deployments of tags are necessary to assess how typical these patterns of diving are, and what the implications of such diving behaviour is, to impacts of naval sonars.

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