DIVING BEHAVIOR AND ECOLOGY OF CUVIER'S (*Ziphius cavirostris*) AND BLAINVILLE'S BEAKED WHALES (*Mesoplodon densirostris*) IN HAWAIʻI

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SUMMARY

Diving habits of beaked whales (Family Ziphiidae) are of management interest for two primary reasons. Firstly, animals which spent long periods of time beneath the water's surface are likely to be missed during shipboard or aerial surveys, and without taking diving patterns into account, abundance estimates may be negatively biased. Based on observational studies, beaked whales are known to dive for very long periods, but collecting detailed surfacing data is problematic. Secondly, beaked whales are known to mass-strand in response to high-intensity sonar. What makes them susceptible to such impacts remains unclear, but received sound pressure levels are thought to be lower than levels that would cause direct physical harm. Theoretically, indirect physical harm could be caused by behavioral reactions in several ways, if whales: 1) surface excessively fast (causing gas bubble formation); 2) stay at the water's surface for too long (if tissues are supersaturated with nitrogen); 3) dive prematurely (if whales spend extended periods at the surface to eliminate nitrogen); or 4) stay at depth for too long, forcing an overly rapid ascent. Given the paucity of information on normal diving behavior of beaked whales, it is not known which of these possibilities is most likely. We studied diving behavior of Cuvier's and Blainville's beaked whales in Hawaiian waters from 2002-2005, using suction-cup attached time-depth recorder/VHF tags. Beaked whales were encountered on 30 occasions in 922 hours of effort (17 sightings of Cuvier's, 11 sightings of Blainville's, and 2 sightings of un-identified beaked whales). Six whales were tagged, two Cuvier's and four Blainville's, and 41 hours of dive data were collected. Several aspects of diving were similar between the species: 1) both dove for 48-68 minutes to depths greater than 800 m (maximum 1,408m for Blainville's, 1,450m for Cuvier's) with one long dive occurring on average every two hours; 2) ascent rates for long/deep dives were substantially slower than descent rates, while for shorter dives there were no consistent differences; and 3) both spent prolonged periods of time (66 – 155 minutes) in the upper 50 m of the water column. We suggest that the frequent extremely long dives push the animals' physiological limits, resulting in behavioral mechanisms (slow ascent rates and prolonged periods of time at the surface to purge excess dissolved nitrogen) to compensate. Indirect physical harm from abnormally rapid ascents or premature dives seem plausible as mechanisms for beaked whale mass-strandings in relation to high-intensity sonar.

INTRODUCTION

Beaked whales (Family Ziphiidae) are one of the least known groups of large mammals. A diverse family (containing 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, behaviors that severely limit the ability of researchers to study them. Until recently, most information available for virtually all beaked whale species came from studies of beach-cast carcasses. Studies of free-ranging beaked whales began in 1988 with northern bottlenose whales (*Hyperoodon ampullatus)* off eastern Canada (Whitehead et al. 1997), and in 1991 with Blainville's beaked whales (*Mesoplodon densirostris)* off the Bahamas (Claridge and

Balcomb 1995), but in recent years, studies of other species and populations in the wild have also been conducted. 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 (Mead 1989; Heyning 1989). However, of the 21 recognized species in the family Ziphiidae, only three species have been tagged with data-logging time-depth recorders, and detailed information on depth-of-dive and sub-surface behavior has only been published for one species, the northern bottlenose whale. Using time-depth recorders attached with suction-cups, Hooker and Baird (1999) collected just over 30 hours of dive data from two *H. ampullatus*, documenting regular dives to over 800 m, with a maximum recorded dive depth of 1,453 m. Dives appeared to fall into two discrete 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)* and Blainville's beaked whales (Baird et al. 2004; Johnson et al. 2005) but have not been reported in detail. Observational information on dive durations is available for several species of beaked whales, with median dive times of 28.6 min for Cuvier's beaked whales, 20.4 min for *Mesoplodon* spp., and 15.5 min for Baird's beaked whales (*Berardius bairdii*) (Barlow 1999).

Diving habits of beaked whales are of interest from both a biological and a management or conservation perspective. Information on diving behavior can be used to examine habitat use and habitat partitioning, foraging ecology, and diel patterns of behavior. From a management perspective, two issues are particularly relevant for beaked whales. Animals which 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 Dept of Commerce and US Navy 2001; Jepson et al. 2003; Fernandez et al. 2005; Cox et al. in press). 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 behavioral reactions to the sounds (Cox et al. in press). In addition, since sound exposure will vary by depth and topography, the depth at which beaked whales spend their time is important in assessing 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. Here, we present results on the diving behavior and ecology of both species based on tagging and observational studies in Hawaiian waters.

METHODS

Field efforts were undertaken during each year from 2002 through 2005 off the west coast of the island of Hawaiʻi (19^{o}-20^{o}N, 156^{o}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 2002 and the latter part of 2003, a 6.4-m and 8.2-m Boston Whaler were used. In the early part of 2003, a 6.4-m Boston Whaler and 18-m power vessel were used. In 2004 and 2005, a single 8.2-m Boston Whaler was used. Two to five observers on each vessel scanned 360 degrees, and the study area was transited at 15-30 km/hr. Effort data were collected with automatic location information recorded on board each vessel's GPS every 5 minutes. Kriging was used to interpolate depths at 5-minute effort locations (and sightings) using *Surfer* Ver. 7.0 (Golden Software) and digital bathymetry data obtained from NOAA. For each encountered group, we recorded species, location and 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 tagging other species of cetaceans, or 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, WA), and a VHF radio transmitter (Telonics, Mesa, AZ or ATS, Isanti, MN), housed in a custom-made syntactic foam body, and attached to a whale with an 8-cm diameter suction cup. Tags weighed either approximately 250 or 450 grams, for units containing a Mk9 or Mk8 TDR, respectively. Depth was recorded at one-second intervals with a depth resolution of 1 m.

Tags were deployed by crossbow (Barnett RX-150) 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. Sex and age of tagged animals were determined based on pigmentation patterns, body scaring, 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: in the top 100 m (to examine near-surface rates) and 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).

RESULTS

Encounters and tag deployments

Between 2002 and 2005, 128 days (922 hours on effort) were spent in the field, covering 13,769 km of trackline (Table 1; Figure 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. Depths of sighting locations were greater for Cuvier's (mean = 2,131 m) than Blainville's (mean = 1,119 m) beaked whales (Table 2), though 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 (3,373 m, 4,224 m), much deeper than we have documented for Blainville's beaked whales. Group sizes ranged from 1-5 for Cuvier's beaked whale and 1-9 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. Twenty-four distinctive individual Blainville's beaked whales were documented, and seven individuals were re-sighted for a total of eight re-sighting occasions[1].

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 behavior with signals from the VHF tag.

Age/sex of tagged individuals and behavioral context

The Cuvier's beaked whale tagged in 2002 (*Zc*1) was an adult female, in a group of five individuals (including one adult male). Group size remained relatively constant (4-5 individuals over a 7 h monitoring period).

The Cuvier's beaked whale tagged in 2004 (*Zc*2) was an adult female in a group of three individuals (with two adult males). This group was observed for 38 minutes prior to tagging and for 1 hour, 51 minutes after tagging. Placement of the tag high up on the body of this individual (Figure 2) allowed for documentation of every surfacing for the period the whale was followed, using the VHF signal. During the entire period, the group size and relative positioning of individuals remained constant, with the two adult males consistently behind and to the sides of the adult female. The males remained separated by approximately 30-100 m on all surfacings. Percussive behavior (two breaches and repeated inverted tail-lobbing) was observed for one of the adult males during the third surfacing period after the tag was attached (Figure 3). Distance between waypoints recorded at the location of the tagging and the surfacing series after a 54.8 min dive was approximately 1.6 km, while distance between waypoints for surfacing series before and after 24.9 minute and 22.5 minute dives were 349 m and 695 m respectively.

The behavioral context of three of the four Blainville's beaked whale taggings was documented for all or part of the tag attachments. An adult male (*Md*1) was tagged in a group of nine individuals and followed for 1.58 h. During this period group size remained constant, direction of travel was inconsistent, and the behavior of the group was considered to be "social".

[1] Additional photographs are available from opportunistic work by D. McSweeney since 1995 and have produced additional re-sightings of individuals.

An adult female (*Md*2) accompanied by an infant estimated to be less than a couple of months old (based on lack of scarring, body size relative to the female, and presence of faint fetal folds) was followed for the entire duration of tag attachment (5.38 h). Group size remained constant, and the infant was not observed at the surface without the adult female. Straight-line distance between the location of tagging and where the tag came off was approximately 10.2 km, though the length of the trackline, taking into account changes in direction during the encounter, was approximately 14 km. One whale (*Md*3), a large sub-adult or adult female, was not seen after tagging, and the tag was recovered 25 hours later approximately 26 km from where the whale had originally been tagged, about two hours after the tag came off. The depth where the tag was recovered was 620 m, though in an area with a very steep slope, and currents could have moved the tag 2-3 km during the interval between when the tag detached and when it was recovered. A juvenile in a group of eight individuals was followed for most of the duration of the tag attachment (0.98 h). The tag for this whale detached at depth (Figure 3) and the whale was not seen again. During the period the group was followed group size remained constant, and direction of travel was inconsistent.

Dive and respiration data

Cuvier's beaked whales

A total of 9.75 hours of dive data was obtained from a single Cuvier's beaked whale (Figure 3). For the 1 hour and 51 minutes the tagged whale was followed, the number and time of all respirations of the tagged individual were recorded, and inter-breath intervals were calculated. Three consecutive surfacing periods were documented, the first after a long dive (54.8 min), the second between two intermediate duration dives (24.9 and 22.5 min), and the third preceding another long dive (67.25 min). In addition, the number of breaths (based on VHF signals heard from land) was recorded for a period following a long dive at approximately 20:06 hrs. Number of breaths per surfacing period was consistent over the four periods (26, 23, 24, 24). Inter-breath intervals during the three surfacing periods while the whale was followed ranged from 3 to 15 seconds (mean = 7 sec, SD = 2.1 sec, 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 minute dives followed by a 68 minute dive, four 23-27 minute dives followed by an 87 minute dive, and three 19-21 minute dives, before the group was left.

Based on dive duration, dive depth, and temporal patterning (Figure 3), dives appeared to fall into four distinct categories. Inter-ventilation dives were of extremely short duration (3-15 seconds), and shallow (depths of 2-3 m), 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. Extremely long duration (>50 min) and very deep (>1,000 m) dives were documented an average of once every two hours (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-~30 min) dives to intermediate depth (292 m – 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 very long duration dives (see Figure 3, between 20.14 and 21.19 hrs) 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 seconds in duration (to 7.5 – 8.5 m), one dive 1.23 minutes in duration to 15.5 m, and four dives from 8.1 – 14.9 minutes in duration (mean = 12.7 min), but of extremely shallow depth (3.5 -6.5 m). After the last very long dive recorded, two dives of intermediate duration (13.8 and 16.9 min) were documented, though the maximum depth of these dives was quite shallow (69 and 15 m, respectively). Maximum dive depth recorded was 1,450 m.

Excluding dives less than 50 m in depth, time intervals between dives ranged from 2.28 min to 65.15 min (mean = 8.3 min, SD = 17.9 min, n = 12). All but one of these intervals was less than 5.1 minutes in duration; excluding the longest interval the range was 2.28 to 5.05 min (mean = 3.14 min, SD = 0.83 min, n = 11). The time interval between dives (excluding the one 65.15 min interval) was regressed against dive duration for both the following and preceding time intervals. There was no relationship between dive duration and the time interval following the dive ($r^2 = 0.02$, $p = 0.66$), though there was a relationship between 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 (~2,900 m), the first and second deep (>800 m) dives were to mid-water. The mean of the ratio of descent/ascent rates was 1.95 for dives > 800 m, when looking at descent/ascent to/from 85% of the maximum depth of dive, though in the top 100 m of the water the ratio was 0.85 (Table 5). For dives between 100 and 600 m in depth, the differences between descent and ascent rates were lower (Table 5). The proportion of time spent at different depths in the water column varied between day and night (Figure 5), although this difference was due to one extended period (66 minutes) 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. Detailed respiration data was recorded for one individual based on VHF signals (*Md*2). The number of breaths for each surfacing period was recorded continuously for 4.3 hours, and the timing of all breaths was recorded (for calculation of inter-breath intervals) for an additional 0.83 hours, 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) 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 sec) 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 seconds (mean = 10.9, SD = 5.51, 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 148 dives greater than 5 m in depth were documented, 144 of which were complete (tags detached at depth for all four whales). Taking into account all complete dives to greater than 5 m, there was a strong positive relationship between dive depth and duration (regression, $r^2 = 0.92$, $p < 0.001$). There were no dives between 300 and 800 m depth, and if dives greater than 300 m are excluded, the relationship between dive duration and depth still exists but is not as strong (regression, $r^2 = 0.37$, $p < 0.001$). Based on plots of depth versus descent and ascent rates (not shown), dives between 6 and 300 m in depth appear to comprise two types: dives less than 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 dives greater than 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. All whales exhibited deep (>800 m) dives, with the shallowest maximum depth recorded for the two whales with the shortest tag attachments. Deep (>800 m) dives were recorded approximately once every two hours. Maximum dive depth recorded for a Blainville's beaked whale was 1,408 m (Table 4), from the female accompanied by the infant (*Md*2). This pair of whales was tracked for the entire duration of tag attachment, and there were no signs of the infant at the surface during the female's long dives. While only 1.28 hours of dive data were obtained from the tagged juvenile (*Md*4; estimated at 1-2 years of age based on body size and scarring patterns), this whale was documented diving to 938 m. The tag came off during the descent, so this likely does not represent the maximum depth that this whale was diving. Based on bottom depth when first tagged and when last seen (~2,000 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 less than 50 m. For *Md*2 time intervals ranged from 2.6 min to 35.5 min (mean = 14.3 min, SD = 10.1 min, n = 9), while for *Md*3 time intervals ranged from 1.58 min to 154 min (mean = 23.6 min, SD = 41.7, n = 28). For *Md*2 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, though for *Md*3 there was a relationship between dive duration and the interval preceding the dive (regression, $r^2 = 0.42$, $p < 0.001$), though not for the interval following the dive ($r^2 = 0.02$, $p = 0.46$).

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 (Figure 6). Proportion of time at depth differed between the day and night (Figure 6), with more time spent in near-surface waters at night. The ratio of descent/ascent rate was 1.38 for dives > 800 m in depth (to 85% of maximum dive depth) and 1.14 in the top 100 m (Table 5). There was little difference in the ratio of descent/ascent rate for dives of 100-600 m in depth (Table 5).

DISCUSSION

Both Cuvier's and Blainville's beaked whales were encountered in deep waters off the west coast of the island of Hawaiʻi, though encounter rates were extremely low, with only 17 and 11 sightings of the two species, respectively, in 922 hours of search effort (one Cuvier's sighting every 54 hours, one Blainville's sighting every 83.8 hours). 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 hours of search effort. Despite low encounter rates, photographic re-sightings of individuals suggest the existence of a somewhat resident population, at least for Blainville's beaked whales.

Blainville's beaked whales were typically sighted in shallower water than Cuvier's beaked whales (Table 2), though the maximum dive depths of the two species were similar (Table 4). Both Cuvier's and Blainville's beaked whales regularly dove to depths greater than 800 m, with a maximum recorded dive depth of 1,408 m for a Blainville's beaked whale and 1,450 m for a Cuvier's beaked whale. Diving behavior for these species was similar to the diving behavior documented for northern bottlenose whales (Hooker and Baird 1999), suggesting that such extreme diving behavior may be typical for the Family Ziiphidae. In settings where obtaining samples to examine lactic acid buildup or blood oxygen concentrations are not possible, assessments of whether dives are aerobic or anaerobic typically examine the relationship between 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. For the Cuvier's beaked whale, the number of breaths immediately following a long (54.8 min) dive was similar (26) 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), though 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 dive duration and the time interval after dives, for one of the two Blainville's beaked whales there was a positive relationship between 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, again, similar to the findings for northern bottlenose whales (Hooker and Baird 1999). Little is known of the diet of Blainville's beaked whales (see review by MacLeod et al. 2003), but they are thought to feed on deep-water squid and fish, while Cuvier's beaked whales feed primarily on deep-water squid. 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). There were diel differences in the proportion of time spent in the upper few hundred meters of the water column for both the Cuvier's beaked whale and the one Blainville's beaked whale with night-time data. In both cases extended periods were found when the whales did not dive below 50 m.

For deep dives of both species, overall descent rates were faster than ascent rates, while for shallower dives (100-600 m) descent and ascent rates were similar, but much lower than for deep dives (Table 5). 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 suggested 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 5). 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. (in press) outlined several scenarios whereby behavioral 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 deep dives and the existence of prolonged periods of time (66-155 minutes) 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 behavioral 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 abnormally rapid ascents 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 sub-set of age/sex classes. Further deployments of tags are necessary to assess how typical these patterns of diving are, and what the implications of such diving behavior is to impacts of naval sonars.

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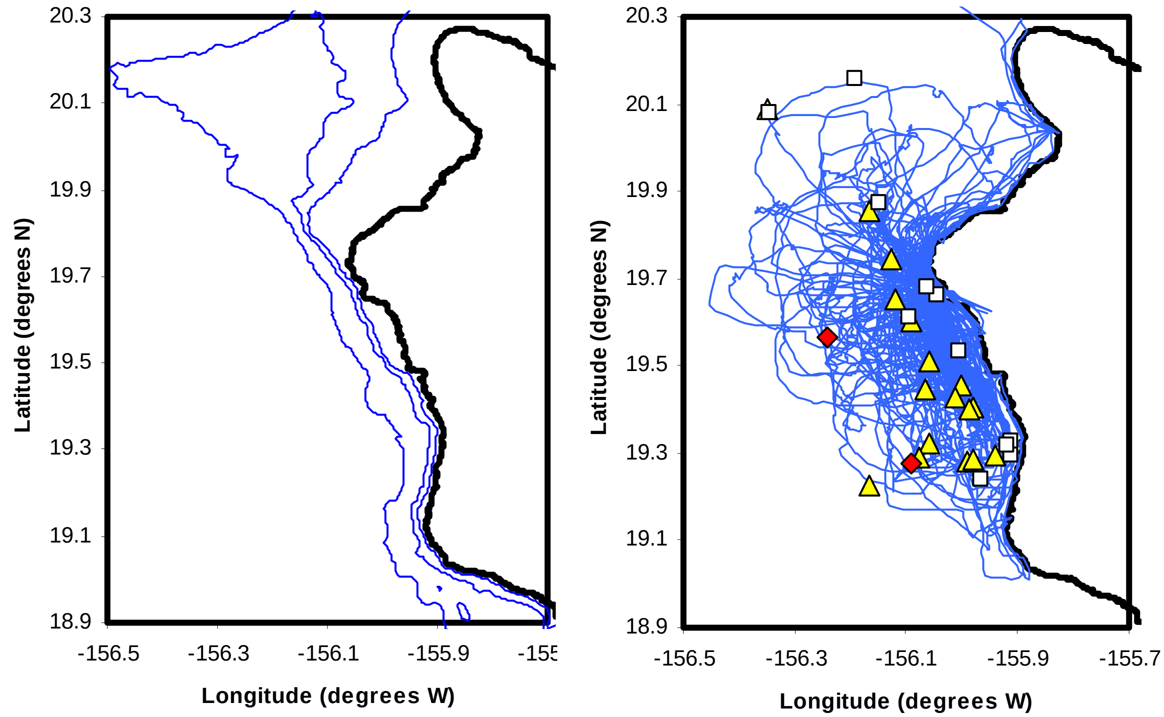

Figure 1. Study area off the island of Hawaiʻi showing 2,000 m, 1,000 m and 500 m depth contours (left), and tracklines from search effort with sightings of Cuvier's beaked whales (triangles), Blainville's beaked whales (squares), and un-identified beaked whales (diamonds).

Figure 2. Adult female Cuvier's beaked whale tagged in 2004 showing location of tag placement. Photo by R.W. Baird.

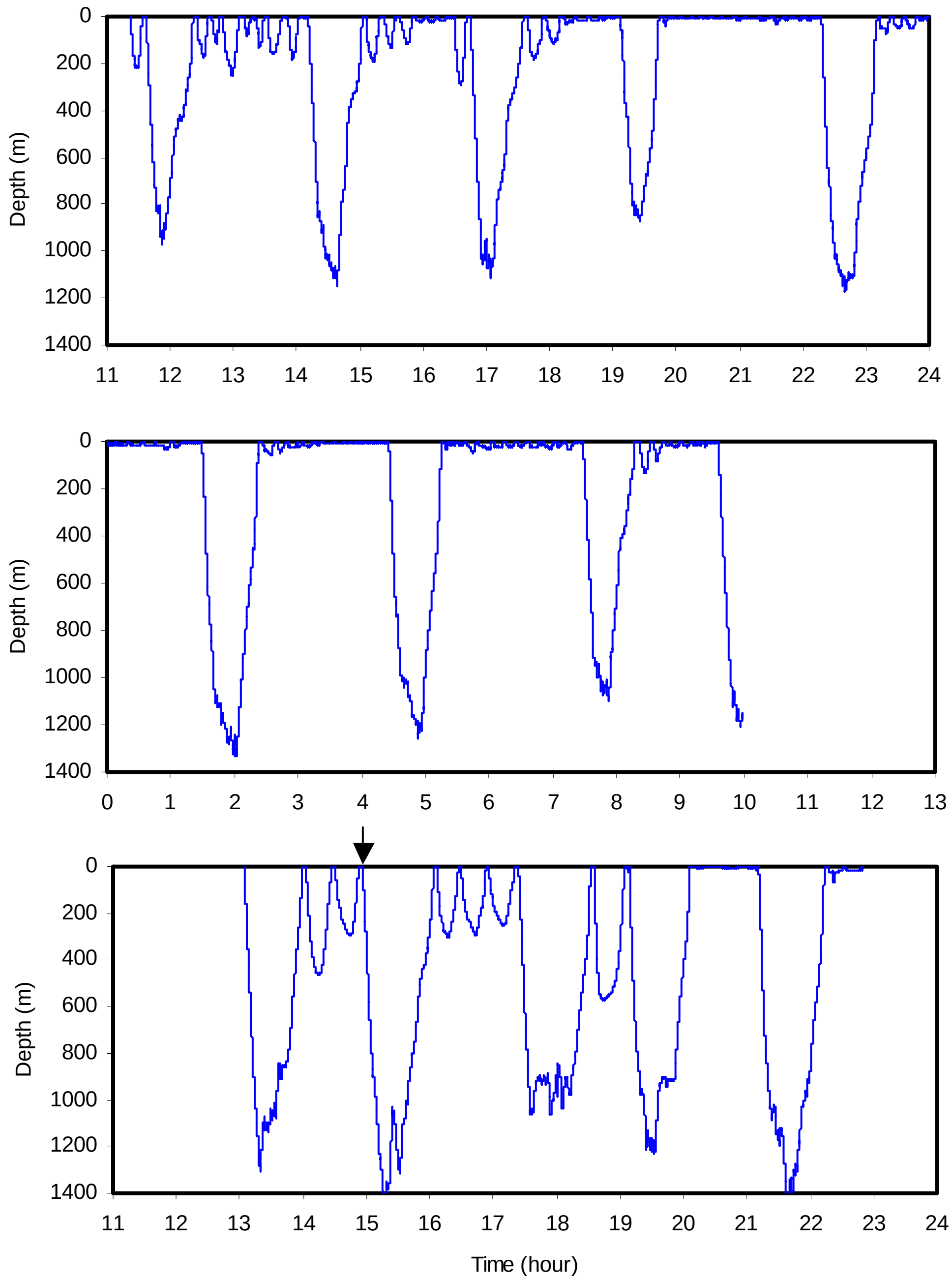

Figure 3. Depth data from a 22.6 h deployment on a Blainville's beaked whale (top, middle, tag number *Md*3) from 27 and 28 September 2004 (time of sunset 18.25 hrs, time of sunrise 6.23 hrs), and a 9.75 h deployment on a Cuvier's beaked whale (bottom, tag number *Zc*2) from 28 November 2004 (time of sunset 17.73 hrs). The approximate point when percussive behavior 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.

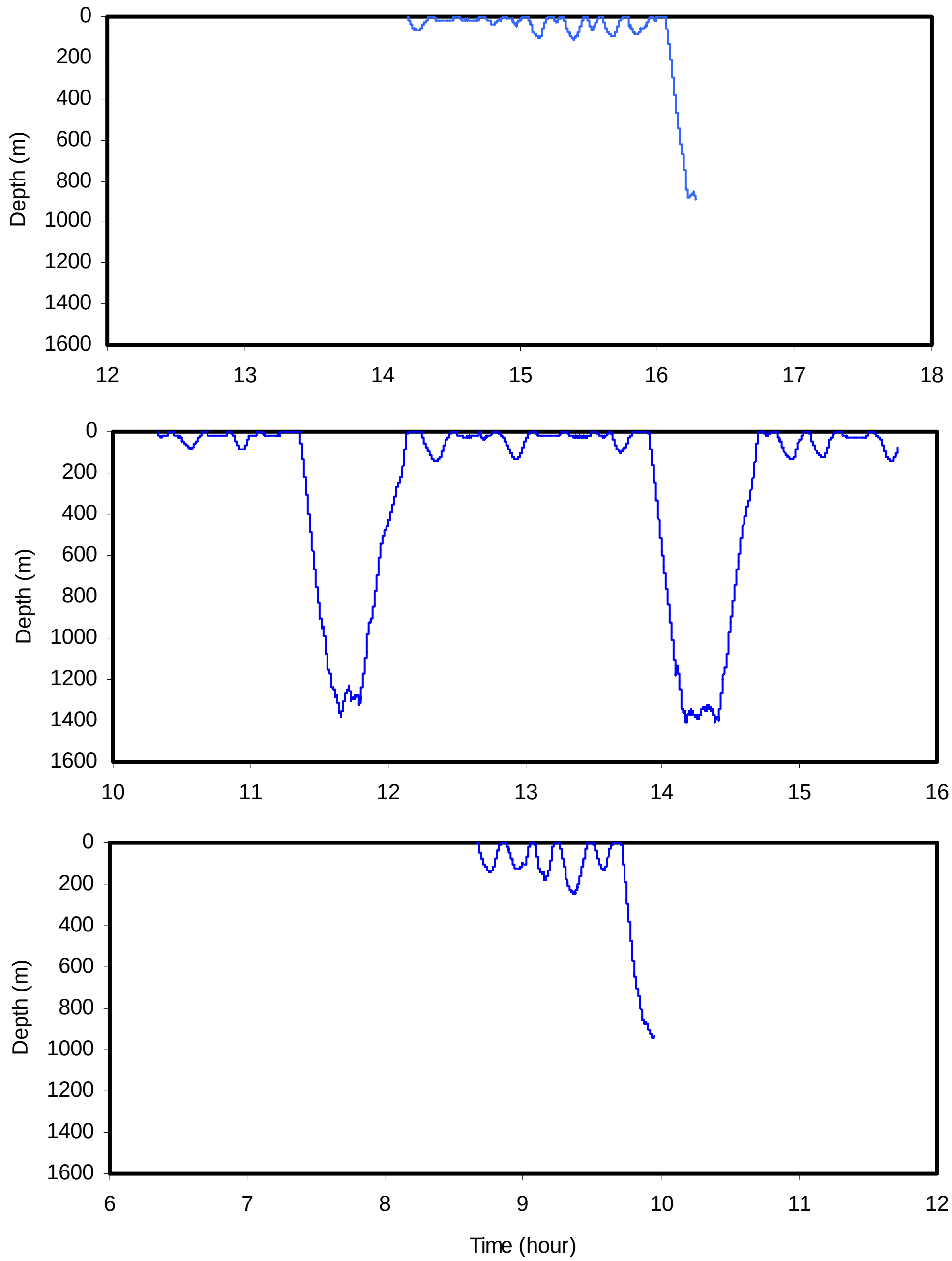

Figure 4. Depth data from three tag deployments on Blainville's beaked whales. Top, a 2.09 h deployment on an adult male (24 Sep 2002, tag number *Md*1); Middle, a 5.38 h deployment on an adult female with young calf (15 Sep 2004, tag number *Md*2); Bottom, a 1.28 h deployment on a juvenile (23 Nov 2004,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

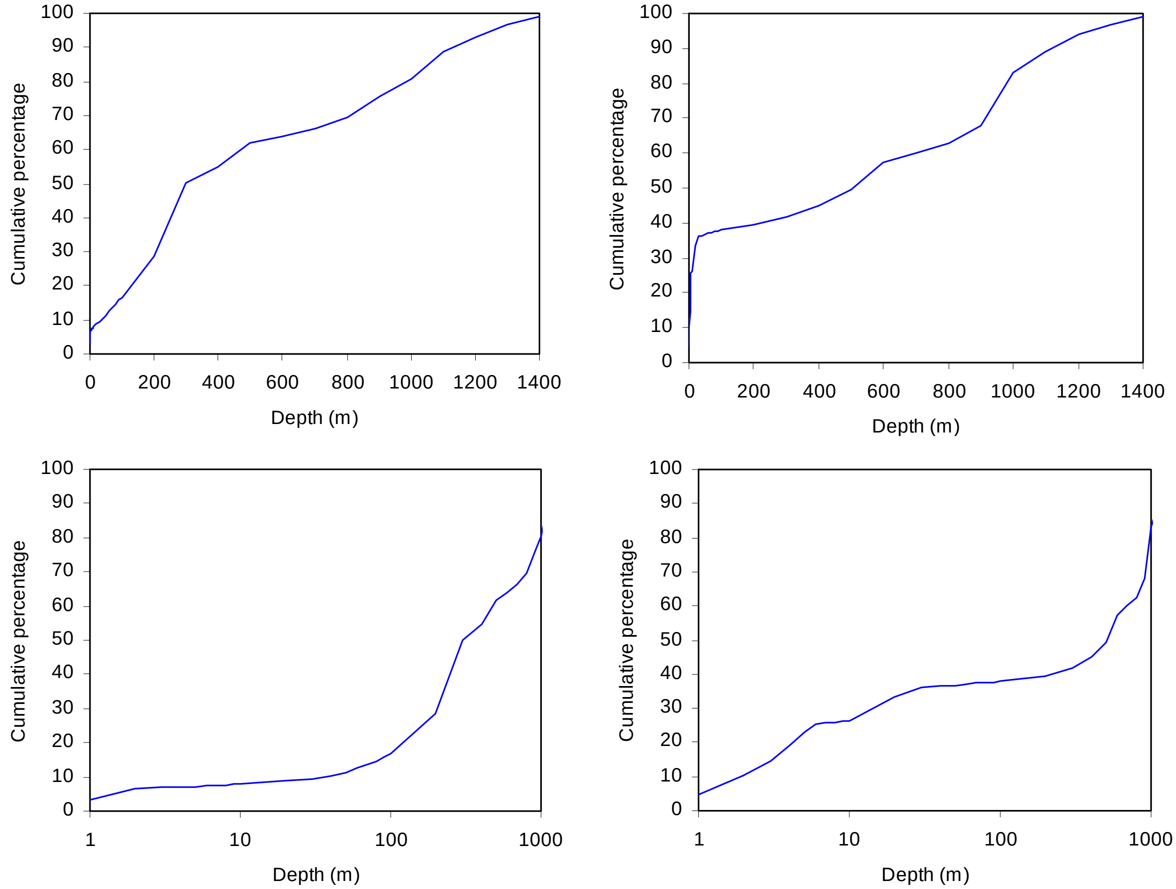

Figure 5. Cumulative percentage of time spent at or less than specified depths for an adult female Cuvier's beaked whale (*Zc*2) during the day (left) and at night (right), with depth shown on a log scale for lower pair of graphs.

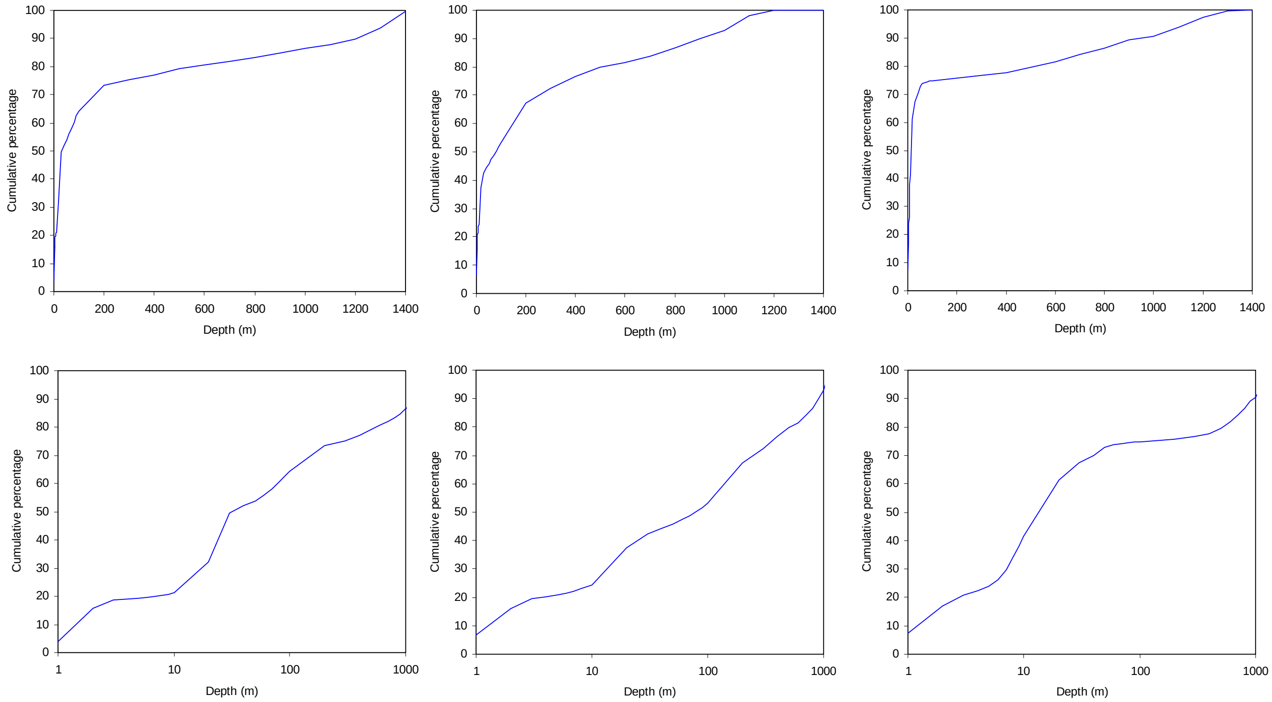

Figure 6. Cumulative percentage of time spent at or less than specified depths for Blainville's beaked whales: left, an adult female with young calf (*Md*2); middle, day-time data for a large sub-adult or adult female (*Md*3); right, night-time data for *Md*3. Depth is shown on a log scale for lower graphs.

Table 1. Summary of effort by field project off the island of Hawaiʻi. Three measures of effort are shown (# vessel days on water, # km on effort, # of hours on effort).

Year	Dates	# vessel days on water[1]	# km on effort	# hours on effort	Vessels
2002	Apr 3-13	10	1,089	75	6.4-m Whaler
2002	Sep 24-Oct 5	20	1,649	154	6.4-m and 8-m Whaler
2003	May 4-12	15	1,791	108	6.4-m Whaler & 18-m Striker
2003	Oct 8-20	24	2,495	173	6.4-m and 9-m Whaler
2004	Sep 12 - Dec 9	42	4,656	290	8.2-m Whaler
2005	Jan 19 - Feb 5	17	2,089	122	8.2-m Whaler
Total		**128**	**13,769**	**922**	

[1]When two vessels were used simultaneously on one day they are counted as two "vessel days".

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

Species (# of sightings)	Group size Mean (SD), range	Sighting depth (m) Mean (SD), range
Cuvier's beaked whale (n = 17)	2.6 (1.3), 1-5	2,131 (667), 1,381-3,655
Blainville's beaked whale (n =11)	3.6 (3.0), 1-9	1,119 (527), 633-2,050

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

Tag #	Species	Date	Time tag on (hh.hh)	Time tag off (hh.hh)	Tag duration (h.hh)	Duration followed after tagging (h.hh)	Age/sex	Group size when tagged
*Md*1	Blainville's	24-Sep-02	14.19	16.28	2.09	1.58	Adult male	9
*Md*2	Blainville's	15-Sep-04	10.32	15.7	5.38	5.38	Adult female (with young calf)	2
*Md*3	Blainville's	27-Sep-04	11.37	9.98	22.61	0	Large sub-adult or adult female	2
*Md*4	Blainville's	23-Nov-04	8.67	9.95	1.28	0.98	Juvenile (1-2 years old?)	8
*Zc*1	Cuvier's	27-Sep-02			-[1]	7	Adult female	5
*Zc*2	Cuvier's	28-Nov-04	13.08	22.83	9.75	1.85	Adult female	3

[1]Tag not recovered, respiration data only

Table 4. Details on bottom depth, maximum dive depth and duration, dive rates, and longest period of time spent less than 50 m in depth for Blainville's and Cuvier's beaked whales off the island of Hawaiʻi.

Tag #[1]	Depth when first tagged (m)	Depth when last seen (m)	Max dive depth (m)	# dives > 800 m	# dives > 800 m/ h	Longest time < 50 m (min)	Max. duration (min)	Comments
*Md*1	692	914	890	1	0.48		-	Tag off during dive
*Md*2	2,003	3,004	1,408	2	0.37	39	48.36	
*Md*3	1,047	1,047	1,333	9	0.40	155.4	54.06	Tag off during dive
*Md*4	2,043	1,806	>938*	1	0.78		-	*Tag off during descent
*Zc*2	2,849	2,667	1,450	5	0.51	66.2	68.7	

[1]Tag #s correspond to individuals listed in Table 3.

Table 5. Rates of descent and ascent (in m/sec) from Blainville's and Cuvier's beaked whales tagged off the island of Hawai'i. Mean and standard deviation (SD) are presented for each. Information presented only for those individuals with dive records with complete deep and shallow dives.

Tag #[1]	**Dives > 800 m**		**Dives 100 – 600 m**		**Dives > 800 m**		**Dives 100 – 600 m**		**n (dives > 800 m)**	**n (dives 100 – 600 m)**
	Descent to 85% of max. depth	**Ascent from 85% max. depth**	**Descent to 85% of max. depth**	**Ascent from 85% of max. depth**	**Descent in top 100 m**	**Ascent in top 100 m**	**Descent in top 100 m**	**Ascent in top 100 m**		
*Md*2	1.48 (0.01)	1.24 (0.17)	0.44 (0.07)	0.47 (0.03)	1.48 (0.02)	1.44 (0.07)	0.45 (0.09)	0.47 (0.29)	2	4
*Md*3	1.26 (0.24)	0.80 (0.16)	0.61 (0.21)	0.69 (0.21)	1.41 (0.41)	1.12 (0.27)	0.76 (0.35)	0.71 (0.20)	9	14
*Zc*2	1.29 (0.29)	0.66 (0.16)	0.90 (0.72)	0.73 (0.21)	1.73 (0.40)	2.01 (0.33)	1.21 (0.70)	0.89 (0.41)	5	6

[1]Tag #s correspond to individuals listed in Table 3.