STUDIES OF BEAKED WHALE DIVING BEHAVIOR AND

ODONTOCETE STOCK STRUCTURE IN HAWAI'I IN MARCH/APRIL 2006

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SUMMARY

Small-boat surveys were undertaken in March/April 2006 off the west side of the island of Hawai'i for the purposes of obtaining dive data from Blainville's (*Mesoplodon densirostris)* and Cuvier's (*Ziphius cavirostris*) beaked whales, as well as collecting biopsy samples and photo-identification of these and other species of odontocetes for studies of stock structure and residency patterns. There were 157 sightings of 13 species of odontocetes in 4,264 km of effort, with 120 genetic samples from seven species and over 29,000 photographs from 13 species obtained. Photographic matching to existing catalogs is currently underway for eight species. Site fidelity of dwarf sperm whales (*Kogia sima*) was evidenced by a high rate of both within- and between-year photographic re-sightings. Photographs of distinctive individual Cuvier's (3) and Blainville's (11) beaked whales were obtained from 8 encounters (2 with Cuvier's, 6 with Blainville's). One of the three Cuvier's and three of the 11 Blainville's had been previously documented in the area, with matches for two individuals (one of each species) spanning a 15-year period, demonstrating long-term site fidelity for both species. Time-depth recorder/radio tags were deployed on three Blainville's beaked whales, with 30.65 to 64.53 hours of data collected from each individual (sum = 135 hours). Overall dive patterns were similar to the smaller sample of dive data for this species presented by Baird et al. (2006), with dives >800 m occurring an average of once every 2.49 hour and averaging approximately 1,100 m in depth and 54 minutes in duration (maximum 1,520 m, 83.4 minutes). One Blainville's beaked whale was tagged in deep water (>3,000 m) and regularly dove to 1,100 – 1,500 m. Diel patterns were assessed using data from these individuals and from one tagged in 2004 by Baird et al. (2006). Deep (>800 m) dives occurred slightly more often at night (mean = 0.46 h^{-1}, SD = 0.11) than during the day (mean = 0.35 h^{-1}, SD = 0.08), though this difference was not significant, and deep dive depths and durations were similar between the day and night. Dives to mid-water (100-600 m) occurred more than five times as often during the day (mean = 1.74 h^{-1}, SD = 0.44) than at night (mean = 0.32 h^{-1}, SD = 0.23), and whales spent more time in the top 100 m at night than during the day. Dive data collected simultaneously from two individuals in the same group (one adult male, one adult female) indicated whales closely coordinated their dive depths in the top 600 m of the water column (average vertical distance between the pair of 10 m), while below 600 m the whales diverged and likely foraged independently (average vertical distance of 95 m).

INTRODUCTION

The beaked whales (whales of the Family Ziphiidae) are the second-most speciose group of cetaceans, with 21 currently recognized species (Dalebout et al. 2002). While members of the Ziphiidae inhabit all oceans of the world, they are also probably the most poorly-known family of cetaceans, with few studies on free-ranging populations (Heyning 1989; Mead 1989). Most of what is known about the majority of beaked whale species comes from studies of beach-cast animals. In recent years directed studies have been undertaken on free-ranging individuals of three species from three of the six genera of beaked whales, Cuvier's beaked whales (*Ziphius cavirostris*), Blainville's beaked whales (*Mesoplodon densirostris*) and northern bottlenose whales (*Hyperoodon ampullatus*) (Whitehead et al. 1997; Claridge 2006). Despite several directed studies, accumulation of information even on these three species has been slow, as beaked whale populations are typically found in deep water far from shore, densities are low (so encounter rates are low), and individuals are often difficult both to detect and to approach.

Diving habits of beaked whales are of interest from both a biological and a management or conservation perspective. Information on dive depths and durations from three species indicate they are among the deepest- and longest-diving species of cetacean, and are also unusual in that ascent rates from deep dives are considerably slower than descent rates (Hooker and Baird 1999; Johnson et al. 2004; Baird et al. 2006; Tyack et al. in press). 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), and the susceptibility to such impacts may be related to aspects of their behavior (see Cox et al. 2006; Rommel et al. 2006).

In Hawaiian waters, three species of beaked whales have been documented, Cuvier's, Blainville's, and Longman's beaked whales (*Indopacetus pacificus)*, the latter species with only one confirmed sighting and two unconfirmed sightings (Shallenberger 1981; Barlow 2006; McSweeney et al. unpublished manuscript). Studies have been undertaken on the diving behavior of both Cuvier's beaked whales and Blainville's beaked whales in Hawai'i (Baird et al. 2006). However, due to low encounter rates and the difficulty in approaching these species, sample

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sizes from earlier studies are small, and this work is continuing. During surveys for beaked whales there are also opportunities to collect information on other species of Hawaiian odontocetes. There is considerable uncertainty regarding the stock structure and population size of many species of odontocetes in Hawaiian waters (see Carretta et al. 2006), thus information gained on other species may also be of great value for management of populations. Here, we present results on field research undertaken during March and April 2006, briefly summarize information collected on other species of odontocetes, and compare our results on beaked whale diving behavior with our earlier work.

METHODS

Field efforts were undertaken during March and April 2006 off the west coast of the island of Hawai'i (19°-20°N, 156°W), based out of Honokohau Harbor. The primary research vessel was an 8.2-m Boston Whaler with an elevated viewing tower (with observer eye heights of approximately 4 m above water level). On two days a second vessel was also used (a 15.8-m power vessel), with the two vessels generally operating greater than approximately 4 km of each other to minimize overlap in survey coverage. Three to six observers on each vessel scanned 360 degrees, and the study area was transited at 15-30 km h^{-1}. Efforts were made to distribute survey coverage as broadly as possible north, south and offshore (west) of the harbor given fuel and weather constraints, covering depths from less than 500 m out to approximately 5,000 m. Effort data were collected with automatic location information recorded on board each vessel's GPS every 5 minutes. Over the duration of the field project we attempted to minimize overlap in survey tracklines using saved tracks on the GPS, and tried to alternate efforts to the north, south and offshore among days, weather permitting. As the primary goal of the study was to maximize encounters for the purposes of tagging we generally stayed in areas with sea states of Beaufort 2 or less.

In the case of uncommon species (e.g., pygmy killer whale, *Feresa attenuata*, melon-headed whale, *Peponocephala electra)* we also utilized reports from other vessels to occasionally find groups. For each encountered group of odontocetes we recorded species, location and group size, and attempted to obtain photographs (using Canon 10D and 20D digital cameras, with 100-

300 mm lenses) both to confirm species and for individual identification. For beaked whales we attempted to obtain photographs of the head (to confirm sex based on presence/absence of erupted teeth), as well as the back and dorsal fin for individual identification. Skin/blubber samples were obtained from individuals in some groups using a Barnett RX-150 crossbow and Ceta-Dart darts with 25 mm tips or a pole spear.

Tags were the same as those used in previous studies of beaked whale diving (Baird et al. 2006), which included a Mk8 and Mk9 time-depth recorder (Wildlife Computers, Redmond, WA), and a VHF radio transmitter (ATS, Isanti, MN), housed in a custom-made syntactic foam body, and attached to a whale with an 8-cm diameter suction cup. The inner surface of the suction cup was coated with a silicone grease (Dow Corning 111 Valve Lubricant and Sealant), both to increase adhesion, and to help retain sloughed skin (for genetic analyses). 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, and light was recorded at 5-second intervals (in un-calibrated units). The Mk9 TDR also recorded water temperature at 5-second intervals with a temperature sensor extending from the TDR body (to minimize the influence of thermal inertia of the tag body), while the Mk8 TDR recorded swim speed by means of a paddle-wheel (in un-calibrated units).

Tags were deployed using 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, as was the timing of surfacings for calculation of inter-breath intervals. 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). Horizontal movement rates of tagged whales were assessed by calculating distance between locations using the Posdist[1] function in Excel and using time intervals between locations.

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[1] Available from http://nmml.afsc.noaa.gov/Software/ExcelGeoFunctions/excelgeofunc.htm

Temperature-related drift in depth values (see Hooker and Baird 2001) were corrected with the program Instrument Helper Ver. 1.0.0.5 (Wildlife Computers). Rates of descent and ascent were calculated in two ways: as the rate 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 as the rate from the surface to 85% of the maximum depth of each dive (to examine rates over the majority of the dive but excluding time near the bottom engaged in foraging).

For tags that remained on after dark, the time of sunrise and sunset was used to delineate day and night periods for comparison of dive patterns. In addition, dive data from a 22.61 hour deployment in 2004 (*Md*3, a large sub-adult or adult female; Baird et al. 2006) where both day (10.59 hours) and night (12.02 hours) data were obtained were used to increase sample size. For tags which remained on for more than one day/night cycle we calculated the proportion of time spent at different depths in the water column during each day or night period and took an average of them for comparisons among individuals. Dive rates (# dives/hour during the day or at night) for different depth ranges were calculated for each individual using all data from day-time and night-time periods, and statistical comparisons of dive rates between day and night were made using paired t-tests (in Minitab 13.20).

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. For comparison with a previous study (Baird et al. 2006) we examined rates of ascent and descent for dives > 800 m and between 100 and 600 m.

A comparison of diving for two whales that were tagged at the same time was undertaken in several ways. A visual inspection of plots of dive depth of one whale against dive depth for the second whale was used to assess depth ranges where apparent coordination in behavior occurred. Regressions of dive depth of one whale against dive depth of the second whale were undertaken using sub-sets of the data to illustrate periods when whales were coordinating their behavior to different degrees. Because there is no *a priori* reason to choose a dependent or independent variable, we consider only correlation coefficients (r^2) in interpreting the strength of

the relationship. To assess vertical distance between the pair of whales the dive depth of one was subtracted from the dive depth of the other and the average vertical separation was calculated for two different depth ranges (0-600 m, >600 m) using the entire series of overlapping data.

RESULTS

Thirty-four days were spent in the field, with two vessels used simultaneously on two days. A total of 4,264 km of trackline were covered with 257 hours on effort spread over a study area of approximately 4,600 km^2 (Figure 1). In general survey coverage was greater to the south and offshore than to the north due to less favorable sea conditions to the north. Approximately 80% of all survey effort was in sea states of Beaufort 2 or less, and over 95% of all survey effort was in sea states of Beaufort 3 or less. There were 157 sightings of 13 species of odontocetes (Table 1). With the exception of spinner dolphins (*Stenella longirostris*) the seven-most frequently encountered species were all ones that show affinities to deep waters. However, 16 of the 17 groups of spinner dolphins encountered were directly off the mouth of the harbor where our research vessels left from each day (a known resting area for spinner dolphins), thus the encounter rate with that species was artificially inflated.

A total of 120 samples from biopsies or from suction cups were collected from seven species (Table 1). Skin samples were contributed to ongoing studies of stock structure through the Southwest Fisheries Science Center (all species) and Portland State University (for pantropical spotted dolphins, *Stenella attenuata*), and sub-samples of skin/blubber were contributed to studies of stable isotopes/fatty acids through the University of Hawai'i Hilo (all species) and the Pacific Islands Fisheries Science Center (for short-finned pilot whales, *Globicephala macrorhynchus*). When small amounts of muscle tissue were attached to biopsy samples these were contributed to ongoing studies of myoglobin and hemoglobin through Portland State University (for all species) to determine interspecies crosses, an occasional occurrence with spotted dolphins (Duffield et al. 2004).

Over 29,000 photographs were taken of 13 species (Table 1) for species confirmation and for individual photo-identification studies of Hawaiian odontocetes. Photographs were

contributed to existing studies (through Cascadia Research and the Wild Whale Research Foundation) using photo-identification to examine residency and inter-island movements for short-finned pilot whales, false killer whales (*Pseudorca crassidens*), melon-headed whales, pygmy killer whales, rough-toothed dolphins (*Steno bredanensis)*, bottlenose dolphins (*Tursiops truncatus)*, dwarf sperm whales (*Kogia sima)*, Blainville's beaked whales, and Cuvier's beaked whales, as well as to a catalog being established for sperm whales (*Physeter macrocephalus*) through Southwest Fisheries Science Center, and a catalog being established for pantropical spotted dolphins through Portland State University and Cascadia Research. Photographic matching for most of these species is ongoing and will be reported elsewhere; information on beaked whale matches is presented below. Matching for one species, dwarf sperm whales, indicated a high level of within- and between-year re-sightings. Photographs where individual dwarf sperms whales could be recognized based on dorsal fin shape/markings were obtained from 8 of the 10 encounters with that species. Despite relatively poor photo quality in many cases, 13 individuals were documented a total of 27 times, with three individuals with between-year matches (one individual matched from 24 Nov 2004 to 28 March 2006, and two matched from 9 Oct 2003 to 28 Mar 2006), and 11 within-year matches.

Beaked whales were seen on eight occasions, an average of once every 533 km (32 hours) of effort (Figure 1). Two sightings were of Cuvier's beaked whales and six sightings were of Blainville's beaked whales, an encounter rate of one group of Cuvier's beaked whales every 1,132 km (128 hours) and one group of Blainville's beaked whale every 710 km (43 hours). Neither group of Cuvier's beaked whale could be approached closely enough to attempt tagging, though photographs for individual identification were obtained for all three observed individuals. Two of the three individuals had not been previously documented off the island of Hawai'i, though one individual (HIZc029) had been previously photographed off the island of Hawai'i in three different years (1991, 1994, 1995), providing evidence for long-term site-fidelity for this species (McSweeney et al. unpublished manuscript). For Blainville's beaked whales, all individuals present in four of the six groups encountered, and four of five individuals in one group encountered were individually identified based on distinctive markings. Eleven distinctive individuals were documented. Based on comparisons with a long-term photo-identification catalog of this species in Hawai'i, three of these individuals had been previously documented off

the island of Hawaiʻi. One individual (HIMd061) had been previously documented in 1997, one (HIMd007) had been seen and photographed in five years (1997, 2000, 2002, 2003, 2004), and one (HIMd001) had been previously documented in six years (1991, 1994, 1995, 1997, 1999, 2004), providing strong evidence for long-term site fidelity of this species (McSweeney et al. unpublished manuscript).

Tagging attempts were made with three of the six groups of Blainville's beaked whale, and tags were deployed on whales in two groups. In one group (20 April 2006) two whales in the same group were tagged, and this group was re-located on two subsequent days using VHF signals received from one of the tagged whales. No additional tagging was attempted on these subsequent days the group was re-located. For the one remaining encounter (a lone individual), the individual could not be approached closely enough to attempt tagging (or for photo-identification). Based on individual photo-identification, none of the tagged whales were individuals that had been previously tagged in 2002 or 2004 by Baird et al. (2006).

An adult female Blainville's beaked whale (Tag # *Md5*) was tagged on 15 April 2006. This individual was in a group of three (including one adult male and one other adult female), and was encountered in water approximately 3,200 m deep with relatively flat bathymetry. Two tags were deployed on this individual half an hour apart, to increase the likelihood of obtaining a long time-series of dive data and increase the probability of tag recovery. The first tag deployed remained attached 40.13 hours and was recovered two days after deployment (approximately 12 hours after it detached) in water approximately 3,000 m deep, suggesting that the tagged whale may have remained in deep water for all or most of the tag attachment. The second tag remained attached 35.1 hours and was recovered seven weeks after deployment. For the purposes of analyses only data from the longer (40.13 hour) duration tag from this individual was used.

On 20 April 2006 two whales in the same group were tagged, an adult female (Tag # *Md*6) and an adult male *(*Tag #*Md*7). The tag on the adult male remained on for only 1.18 hours, but this individual was re-tagged 1.2 hours after the first tag fell off, and the second tag remained attached for 29.45 hours. For the purposes of analyses, data from these two taggings of the same individual were combined. These two whales were in water approximately 900 m deep when

tagged in an area with steep bathymetry. When these whales were re-located on 21 April 2006 and 22 April 2006 and during the period they were followed on those two days they were in an area with steep bathymetry and water depth was approximately 900 - 1,100 m when first encountered each day. Location information from these whales was obtained over 9.52 hours of tracking over the three days (Table 2; Figure 2) and used for the purposes of calculating horizontal movement rates. A total of 13 within-day rate measurements were obtained, over an average time interval of 0.73 hours (SD = 0.65 hours) and an average distance of 1.49 km (SD = 1.74 km). Mean rate of movement was 1.94 km h⁻¹ (SD = 0.93), with a range from 0.81 to 4.09 km h⁻¹. These values represent minimum horizontal day-time movement rates, as they assume straight-line movements between the two points used in calculations. Based on dive data the tagged whales were foraging during these periods, with four long (>40 minute) dives occurring during the 9.52 h.

A total of 135.3 hours of dive data were obtained, with almost equal amounts during the day (70.2 h) and night (65.1 h). A plot of dive duration versus depth for all dives (Figure 3) indicated a hiatus between dives greater than 800 m and dives less than 400 m (with two exceptions, one dive to 648 m and one dive to 798 m). All dives >800 m had occasional repeated inflections in depth (i.e., changes from descent to ascent and back) in the bottom 20% of the dive, while such inflections in depth for dives <400 m were infrequent (and generally more gradual). The 648 m dive did not have occasional inflections in depth, while the 798 m dive did have such inflections in depth, though they were gradual as in the case of shallower dives. For the purposes of comparisons with previously collected data (Baird et al. 2006) we analyzed and present data separately for dives >800 m and those between 100-600 m in depth (further analyses have excluded the two dives between 600 and 800 m depth).

For the four whales (including one from 2004) with both day- and night-time dive data (Table 4), rates for deep (>800 m) dives were an average of 1.3 times greater at night (mean = 0.46 h⁻¹, SD = 0.11, n = 4) than during the day (mean = 0.35 h⁻¹, SD = 0.08, n = 4), although this was not statistically significant (paired t-test, p = 0.314). Depths and durations of these deep (>800 m) dives were similar between the day and night (Table 4). Rates for dives between 100 and 600 m depths were an average of 5.4 times greater during the day (mean = 1.74 h⁻¹, SD =

0.44, n = 4) than at night (mean = 0.32 h^{-1}, SD = 0.23, n = 4), and this difference was statistically significant (paired t-test, p = 0.003). This greater dive rate to mid-water depths during the day was reflected by a difference in the proportion of time spent in near-surface waters (<100 m), with more time spent in near-surface waters at night than during the day (Figure 4).

All three individuals tagged in 2006 exhibited long (maximum of 65.7 to 83.4 minutes) and deep (maximum of 1,131 to 1,520 m) dives (Figure 5, 6, 7). Dives greater than 800 m in depth occurred an average of once every 2.49 hours (mean = 0.402 dives/hour, SD = 0.047, n = 3 individuals). Based on the bottom depth when tagged, *Md5* was likely diving to mid-water depths at least for the initial period after tagging, and possibly for the entire duration of the tag attachment (based on the water depth where the tag was recovered). The other two tagged whales were seen at the surface within 100 m of each other on all surfacings recorded over 9.5 hours on three different days, and based on bottom depth when first found on each day were likely diving to or close to the bottom on most deep (>800 m) dives.

A plot of dive depths for the two whales with simultaneous dive data (Figure 8) indicated that at dive depths less than approximately 600 m the two whales were diving in a strongly coordinated manner, while there was less coordination in dive depths at depths greater than 600 m. A regression of dive data for depths <600 m for April 21 indicated an almost 1:1 correlation in dive depths (r^2 = 0.997), while a regression of depths >600 m indicated less but still high levels of correlation in dive depths (r^2 = 0.557). A comparison of the relative vertical positions of the two whales by depth indicated that at depths less than approximately 600 m the two whales were within approximately 50 m of each other vertically, while below 600 m the two whales would diverge by up to 440 m, with no consistent relative position between the male and female (Figure 9). For depths greater than 600 m the vertical distance between the two whales averaged 95.3 m (SD = 79.5 m, n = 26,992 depth pairs), while at depths less than 600 m the vertical distance averaged 10.1 m (SD = 13.3 m, n = 78,170 depth pairs).

The thermal environment experienced by one of the tagged whales (*Md6)* was characterized by plotting depth and water temperature (Figure 10). Water in the top 100 m was well mixed with temperatures generally between 24.3°C and 24.9°C. Thermocline depth varied

between approximately 104-141 m, and water temperature decreased steadily to about 12°C at 300 m depth, then decreased more slowly to about 6°C at approximately 600 m depth. Below 1,000 m water temperature decreased slowly from approximately 4.3°C to approximately 3.3°C – 3.5°C at 1,400 m. Water column characteristics were similar for *Md5* tagged on 15 April 2006.

DISCUSSION

Field efforts in March and April 2006 contributed substantial numbers of photographs and genetic samples to ongoing stock structure analyses of a number of poorly-known odontocetes in Hawaiian waters (Table 1). Many analyses are on-going, but matching of individually-distinctive dwarf sperm whales illustrates the value of this work. Despite no sightings of this species from three years of aerial surveys (Mobley et al. 1990), and no sightings from around the main Hawaiian Islands from a large-vessel survey (Barlow 2006), dwarf sperm whales were the fifth-most frequently encountered odontocete in this effort (the fourth most frequently encountered species in waters >100 m deep; Table 1), and photographic matching of individuals indicated both high within-year and between-year re-sightings, suggesting a resident population of this species off the island of Hawai‘i (see also Baird 2005).

Beaked whales were encountered an average of once every 533 km of trackline, similar to our long-term average for beaked whale encounter rates off the island of Hawai‘i (1 encounter every 513 km of trackline; Baird unpublished). However two of the six Blainville's sightings were cued by signals from attached radio transmitters and these two groups would not have been detected without the presence of the radio tags. Excluding these two Blainville's sightings our encounter rates for Blainville's alone were still similar to our long-term average (one group every 1,066 km in this effort versus one every 1,148 km in the long-term), while encounters with Cuvier's beaked whales were lower than average (one group every 2,132 km in this effort versus one every 1,027 km in the long-term). Overall our encounter rates for Blainville's beaked whales off the island of Hawai‘i are about one-third of the encounter rates for that species from the Bahamas (Claridge 2006), suggesting that the overall density is relatively low. Despite the low density, the between-year re-sighting of individuals documented in 2006, and the limited movements of one group of Blainville's beaked whales over a three-day period (Figure 2)

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indicate that both species exhibit a high degree of site fidelity to the area (McSweeney et al. unpublished manuscript).

We were able to collect an additional 135 hours of dive data from three individual Blainville's beaked whales in 2006. These additional data allow us to both confirm several trends suggested with the relatively small sample of data (n = 4 individuals with 31 hours of dive data) presented by Baird et al. (2006), and address several new questions regarding the diving behavior and diel cycle of this species. As with the earlier sample, all whales exhibited both long (maximum durations of 65.7 to 83.4 minutes) and deep (maximum depths of 1,126 to 1,520 m) dives (Table 4), and dives > 800 m occurred an average of once every 2.5 hours. Not surprisingly, maximum depths and durations recorded in 2006 were greater than those documented in the smaller sample of dive data previously available (Baird et al. 2006), although overall patterns of diving were similar. All three whales also spent extended periods of time in near-surface (<50 m) waters (Table 3), and these periods occurred both during the day and at night (Figure 5, 6).

Baird et al. (2006) noted that both Cuvier's and Blainville's beaked whales had substantially slower ascent rates than descent rates for deep (>800 m) dives, while for shallower dives there were no consistent differences. Our results from 2006 support these findings (Table 5). In fact, the differences between descent and ascent rates for deep dives from the 2006 data are greater than found for our earlier (smaller) sample (ratio of descent to ascent for dives > 800 m of 2.09 and 1.43 for rates to/from 85% of maximum depth and in the top 100 m, respectively in 2006, versus 1.38 and 1.14 from Baird et al. 2006). As noted above, such reduced ascent rates have also been reported for northern bottlenose whales (Hooker and Baird 1999), and for deep-diving beluga whales, *Delphinapterus leucas* (Martin and Smith 1992), and may be a behavioral mechanism to compensate in some way for depth-related physiological processes, such as reducing the rate at which gas bubbles form.

The collection of simultaneous dive data from two individuals in the same group indicated that whales closely coordinated their diving behavior in the top 600 m of the water column, with less coordination at depths greater than 600 m (Figure 8, 9). Blainville's beaked

whales generally do not vocalize above about 400 m in depth on descents, and above about 700 m on ascents (Tyack et al. in press), so it may be that whales need to remain close to each other to maintain contact, either through physically touching, being close enough to feel water movements, or hearing sounds generated by companion whales swimming. There are few reports of simultaneously recorded dive data on two whales (of any species) in the same group to compare these results. Simultaneous data collected from two pairs of cooperatively hunting mammal-eating killer whales (*Orcinus orca*) indicated strong concordance in dive durations and depths (r^2 of 0.87 and 0.68; Baird et al. unpublished manuscript), with the two pairs of whales traveling and presumably foraging in the top 100 m of the water column. Simultaneous data collected from 11 different pairs of fish-eating killer whales indicated various degrees of concordance in dive depths and durations (r^2 values ranging from 0.0001 to 0.7517 for short periods; Baird and Hanson unpublished manuscript), with the highest degree of concordance reflecting periods when the whales were thought to be resting. With our beaked whale data, dive depths, durations and dive shapes (e.g., the occurrence of numerous inflections in depth on the deep dives) indicated the two whales were foraging on all deep (>800 m) dives (see also Tyack et al. in press). During these periods of overlap the whales were separated vertically by an average of 95 m, while at depths <600 m (on the way to/from greater depths and in shallower dives) the whales were separated vertically by an average of only 10 m. Although vertical separation was not reported, Zimmer et al. (2005) noted such coordinated behavior of two tagged Cuvier's beaked whales, with the two whales diving together, separating by about 200-400 m while at depth, and then approaching each other and surfacing with a nearly parallel track. Hooker and Baird (1999) also reported that more than one northern bottlenose whale were often recorded diving together on sonar traces, suggesting some coordination of sub-surface behavior at least on descents. Based on the distance between the two individuals in this study and what is known about diet in this species (MacLeod et al. 2003) it is unlikely that the two whales were foraging cooperatively, but instead were foraging in similar water depths while staying relatively close to each other, and re-joining on the way to the surface. Given the harem-like mating system of this species (Claridge 2006) it seems most likely that the male would maintain contact between the pair.

One of the tagged whales in 2006 was in deep (>3,000 m) water and regularly dove to

depths of 1,300 to 1,500 m, similar to the whales tracked in shallower (1,000-1,500 m) water. One of the Blainville's beaked whales tagged previously was also in deep (~2,000 m) water and regularly dove to similar depths as in this study (Baird et al. 2006), though the longer duration sample from 2006 (40 hours versus 5.38 hours) lends considerable support to the suggestion that Blainville's beaked whales in deep (>2,000 m) waters are feeding in mid-water.

Baird et al. (2006) reported on one Blainville's beaked whale with both day- and night-time data, noting that there were no obvious differences in maximum dive depths between the day and night, but that more time was spent shallower than 50 m in depth at night. Our larger sample of four individuals with day- and night-time data (including the one reported by Baird et al. 2006) allows us to examine diel patterns with more confidence. On average, rates of deep diving were higher at night than during the day, though not consistently so for all four individuals (Table 4). However, characteristics (depths, durations) of these deep dives were similar during the day and at night (Table 4), providing evidence that Blainville's beaked whales are likely foraging as often at night as they are during the day, and on prey that are not vertically migrating. However, as was reported by Baird et al. (2006) it appears that use of the upper portions of the water column varies between the day and night, with more time spent in near-surface (<100 m) waters at night (Figure 4), and more time spent at mid-water depths (100 to 600 m) during the day. Given the lack of diel variation in the deep foraging dives, the reason or reasons for such variation in use of the upper portions of the water column are unclear. If whales needed to behaviorally thermoregulate they could do this by spending more or less time below the thermocline (see Figure 10), though we know of no reason why the need for thermoregulation should vary between the day and night. Regardless such diel variation in use of the water column may have important implications for predicting and mitigating exposure to high-intensity underwater sounds such as naval sonars, as well as potentially influencing detection probabilities using acoustic detection systems.

ACKNOWLEDGEMENTS

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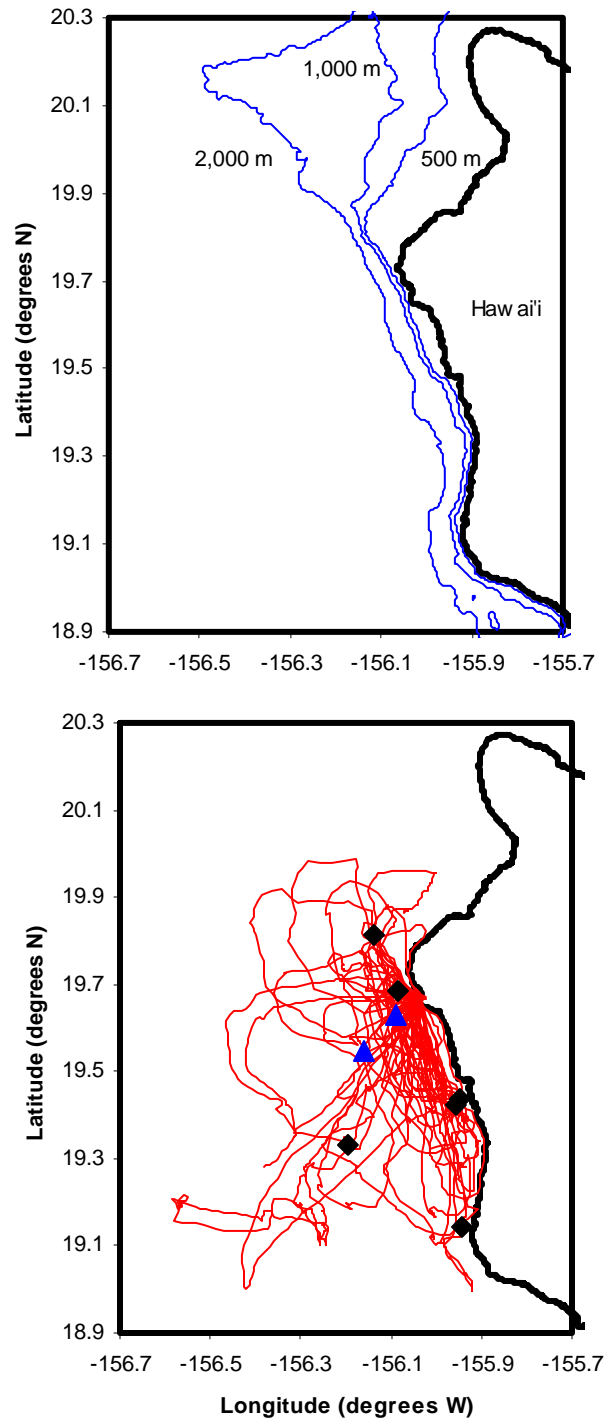
Figure 1. Study area off the island of Hawaiʻi showing 2,000 m, 1,000 m and 500 m depth contours (top), and tracklines from search effort (bottom) with sightings of Cuvier's beaked whales (blue triangles) and Blainville's beaked whales (black diamonds).
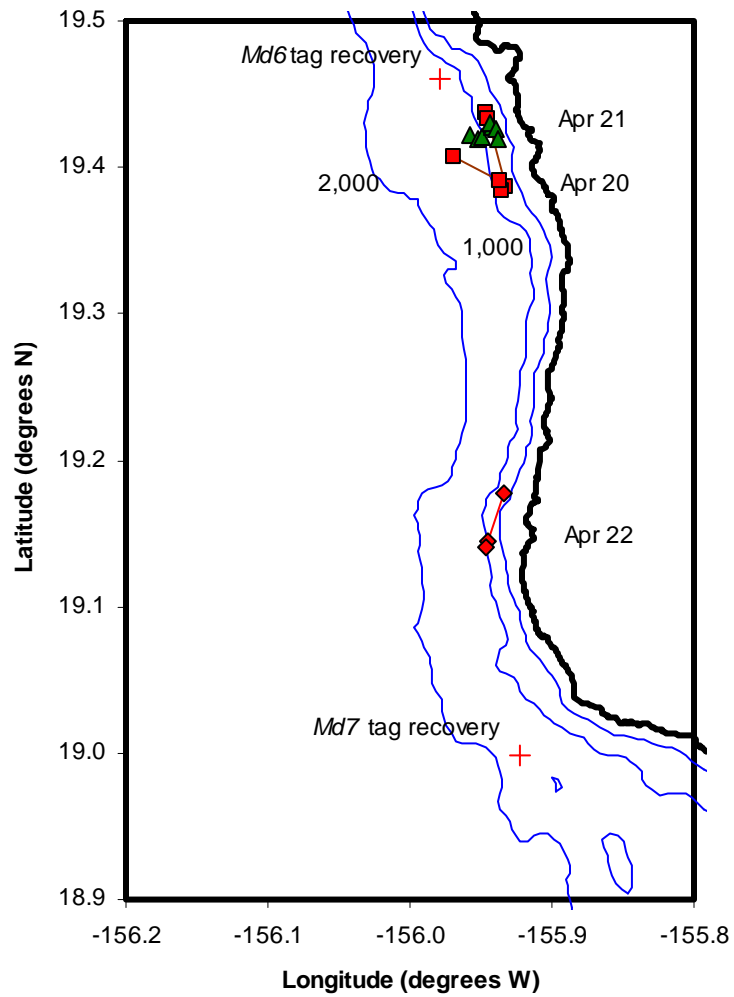
Figure 2. Re-sighting locations of tagged Blainville's beaked whales *Md6* and *Md7* on April 20 (squares), April 21 (triangles), and April 22 (diamonds). Tag recovery locations (+) for *Md6* (on April 23) and *Md7* (on April 22) also indicated. The 2,000 m, 1,000 m and 500 m depth contours are shown.
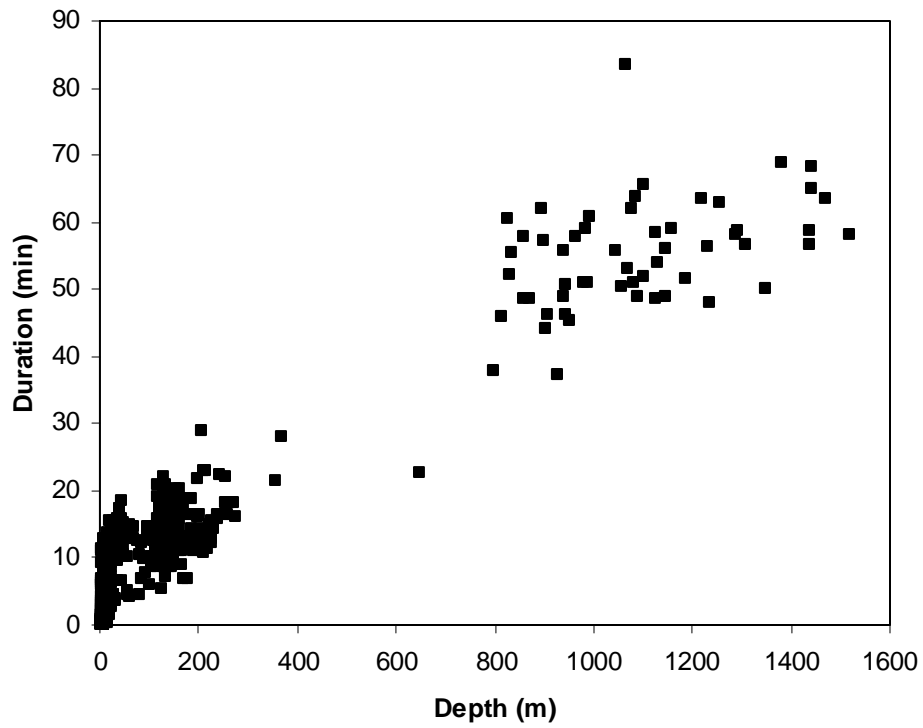
Figure 3. Plot of dive duration versus depth for all dives of all three tagged Blainville's beaked whales, indicating general hiatus in depths/durations between approximately 400-800 m.
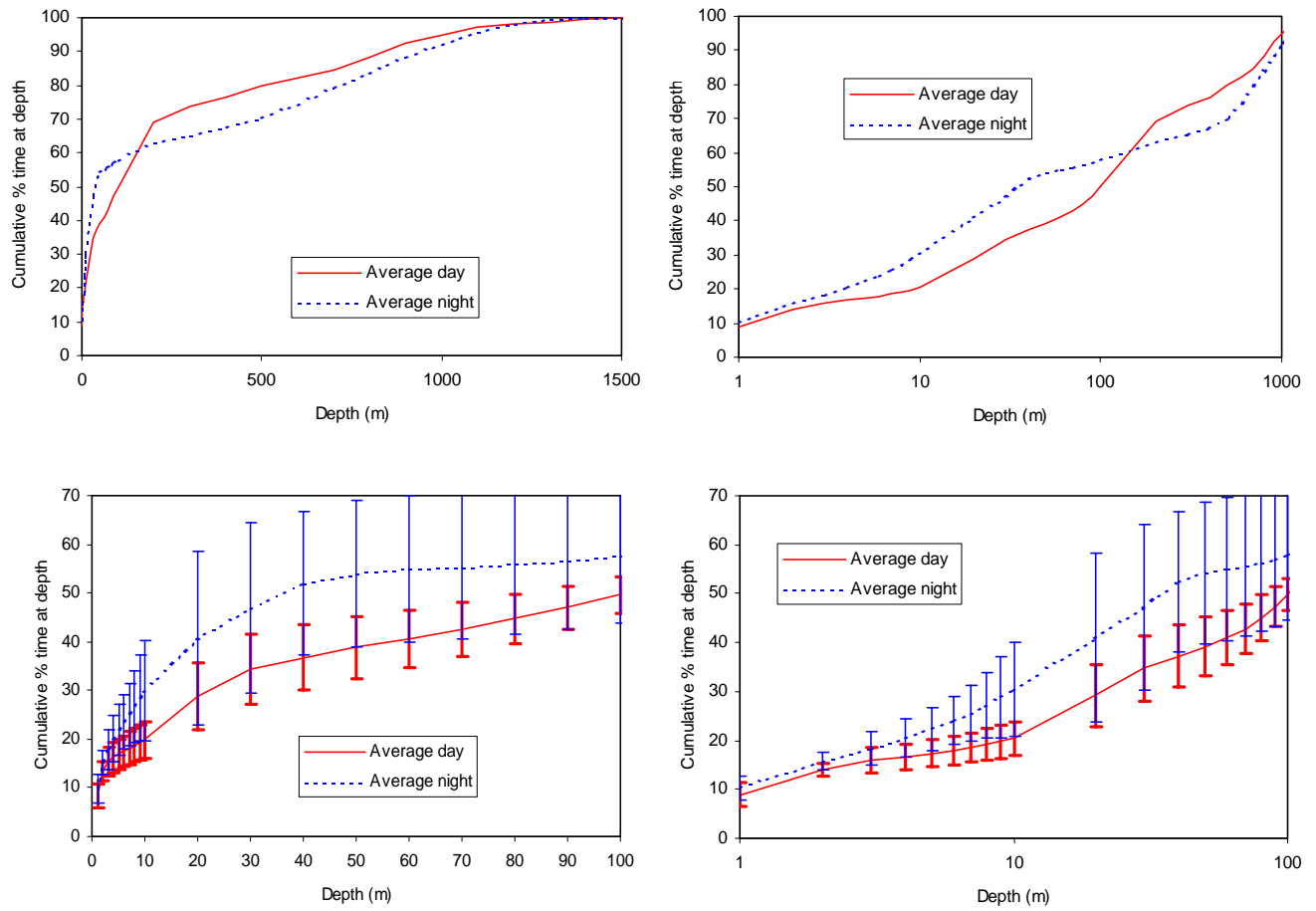
Figure 4. Cumulative percentage of time at or less than specified depths during the day (solid red line) or at night (dashed blue line) for all four Blainville's beaked whales with both day- and night-time data. Upper panels show entire water column (linear and log scales) while lower panels show the top 100 m and bars represent +/- 1 SD (linear and log scales).
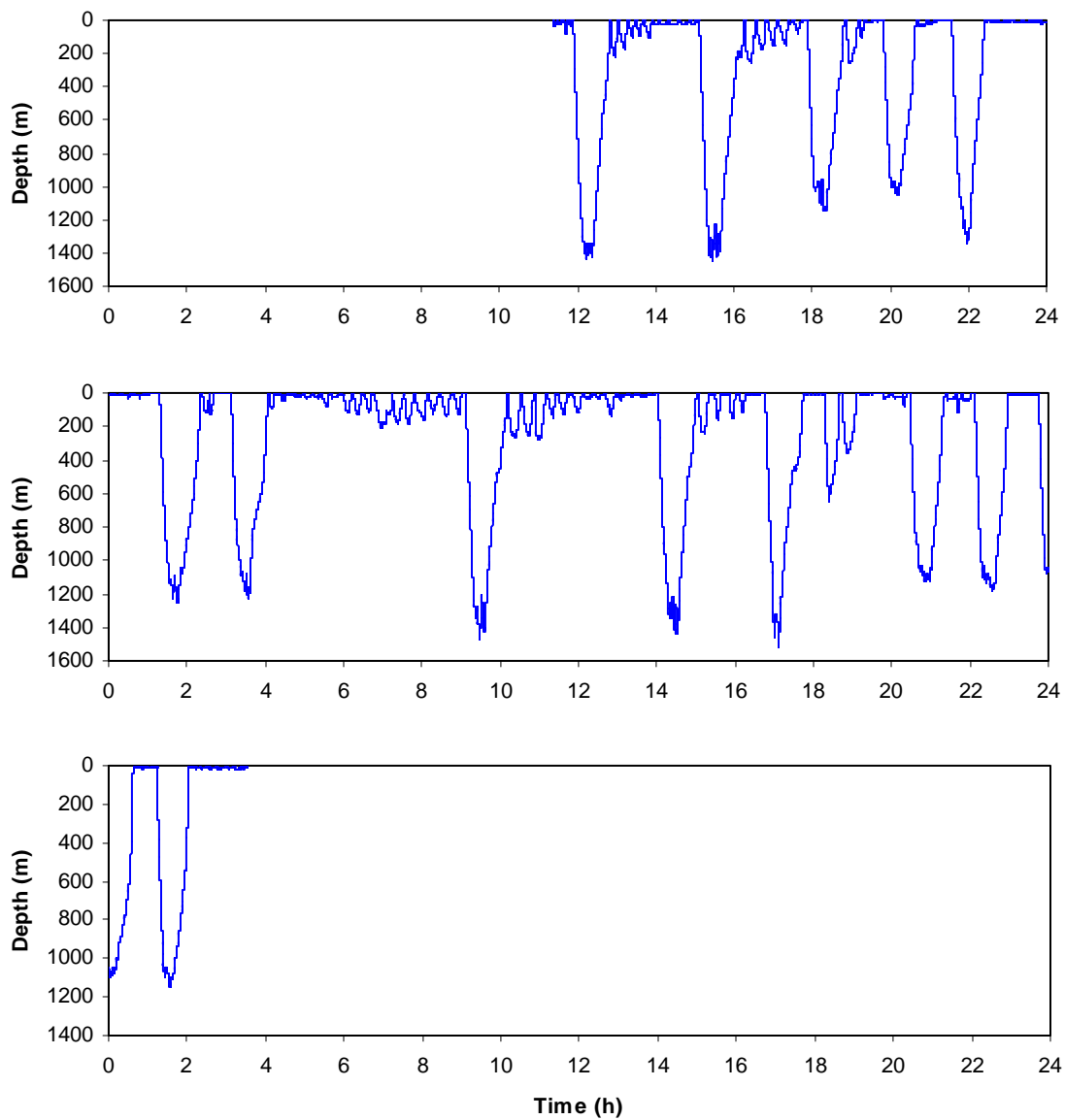
Figure 5. Dive data from adult female Blainville's beaked whale (*Md*5). Top panel - 15 April 2006. Middle panel – 16 April 2006. Bottom panel – 17 April 2006. Sunrise was approximately 0606 hrs, and sunset was approximately 1842 hrs.
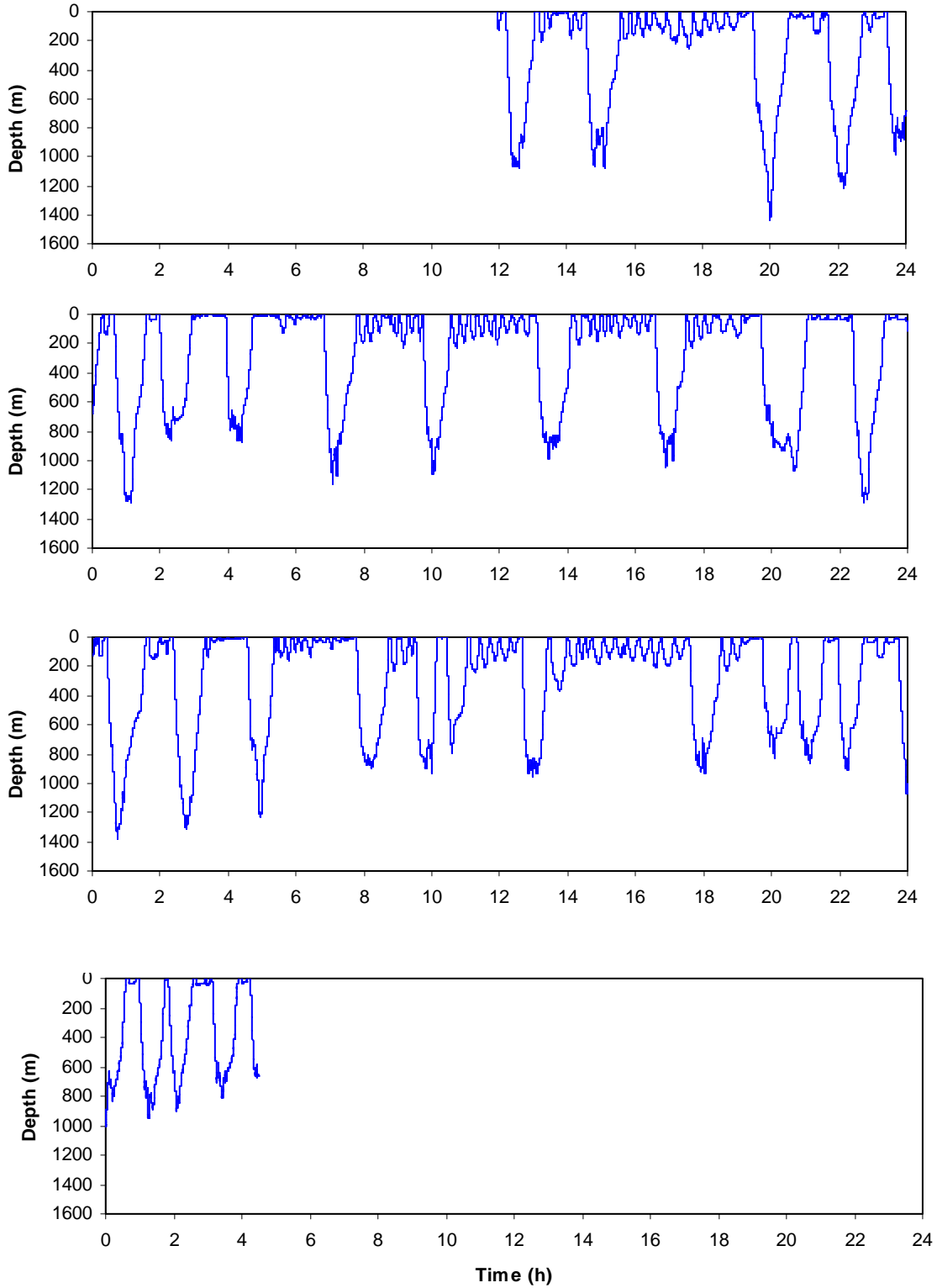
Figure 6. Dive data from adult female Blainville's beaked whale (*Md*6). Top panel - 20 April 2006. Second panel – 21 April 2006. Third panel – 22 April 2006. Bottom panel – 23 April 2006. Sunrise was approximately 0601 hrs, and sunset was approximately 1844 hrs.
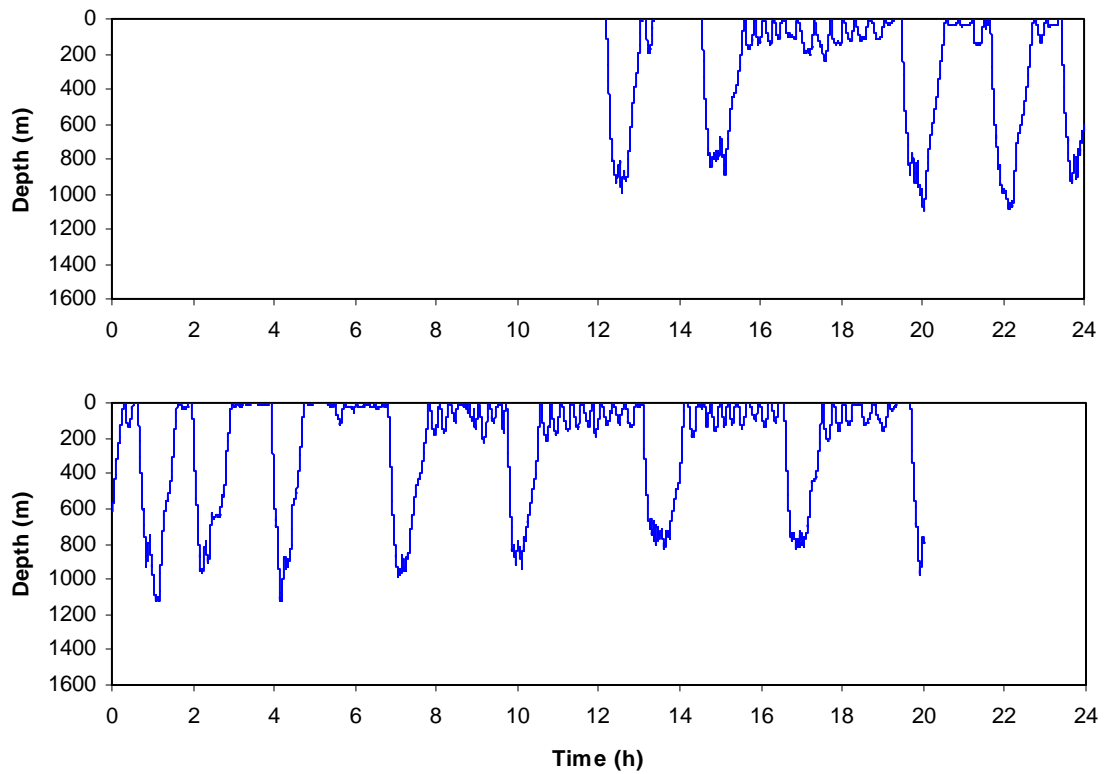
Figure 7. Dive data from adult male Blainville's beaked whale (*Md*7*)*. Top panel – 20 April 2006. Bottom panel - 21 April 2006. Note data from 20 April 2006 includes two tag deployments with a gap between. Sunrise was approximately 0602 hrs, and sunset was approximately 1843 hrs.
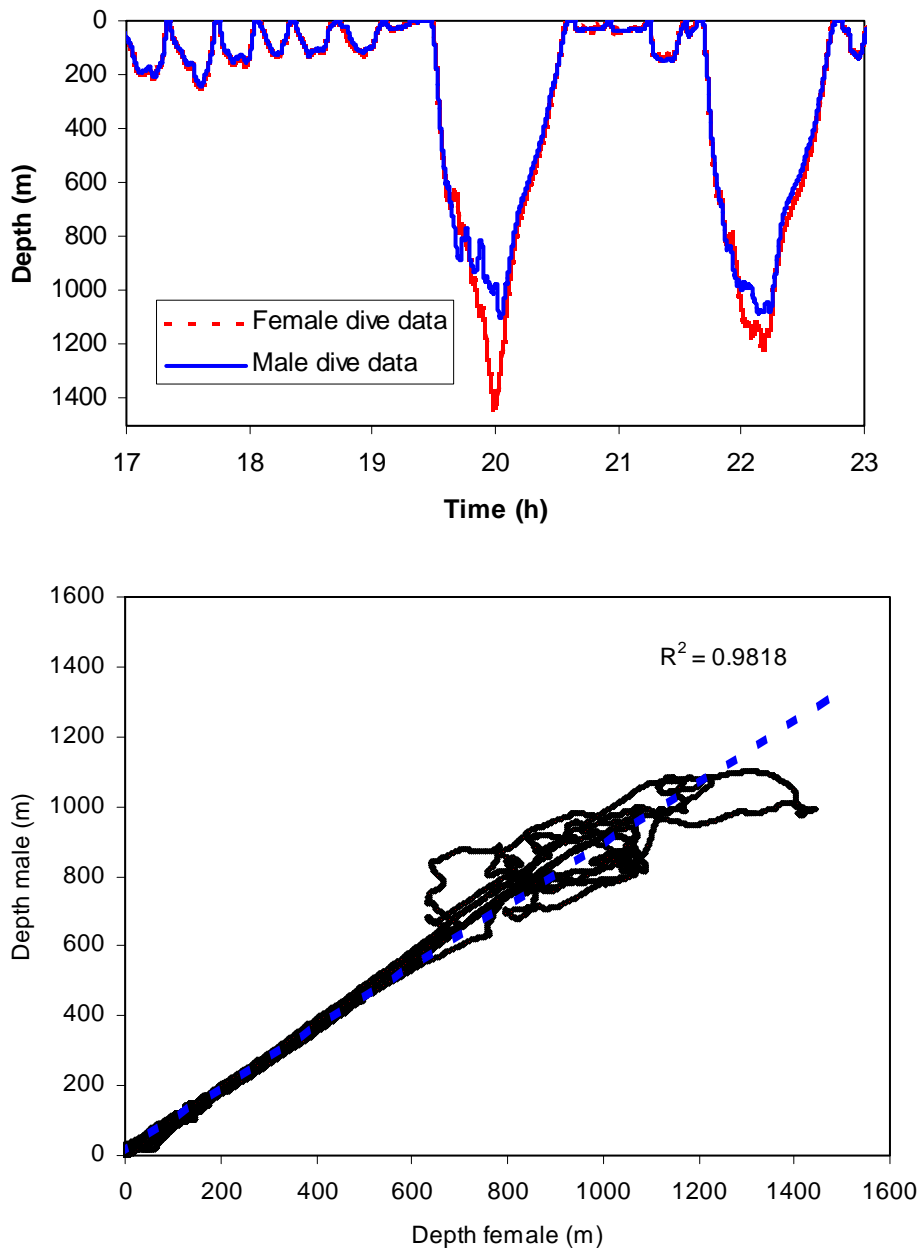
Figure 8. Comparison of dive depths of adult female (*Md*6) and adult male (*Md*7) Blainville's beaked whale with dive data collected simultaneously on 20 April 2006. Top panel shows a 6-hour period with data from both whales. Bottom panel shows plot of dive depths of adult male plotted against dive depth of adult female with regression line (dashed blue) and R^2 value shown.
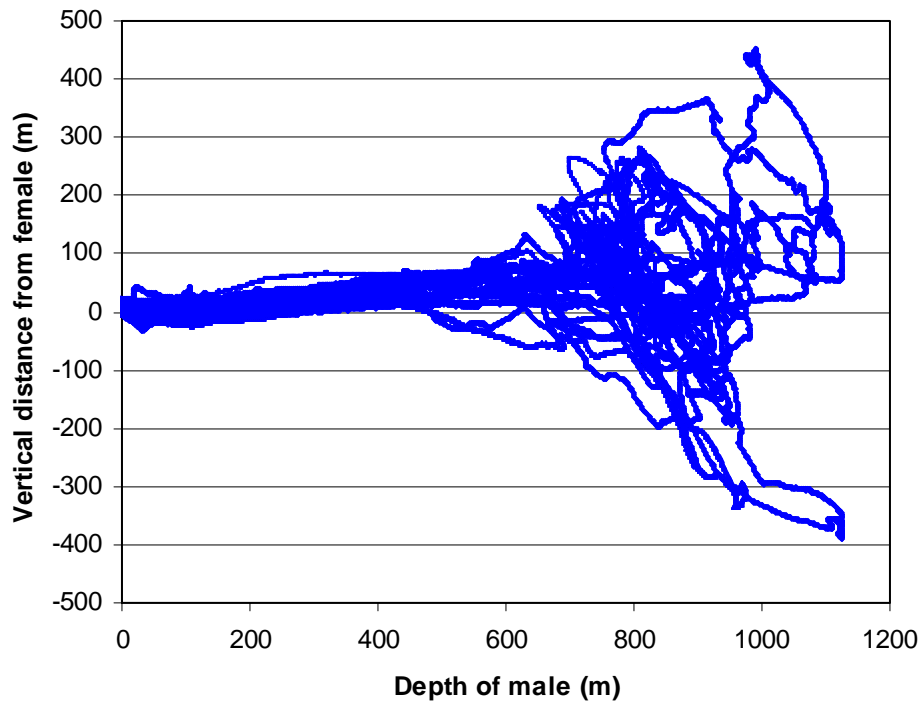
Figure 9. Vertical distance of male from female in relation to the depth of the male Blainville's beaked whale during period with simultaneous dive data collection. Negative values indicate periods where the male is deeper than the female, while positive values indicate periods when the male is shallower than the female. Within the top approximately 600 m of the water column the two whales were generally within 50 m of each other in vertical distance (mean vertical distance =10.1 m, SD =13.3 m).

Figure 10. Characterization of thermal environment for Blainville's beaked whale *Md6* over 64 hour period from April 20, 2006 through April 22, 2006.
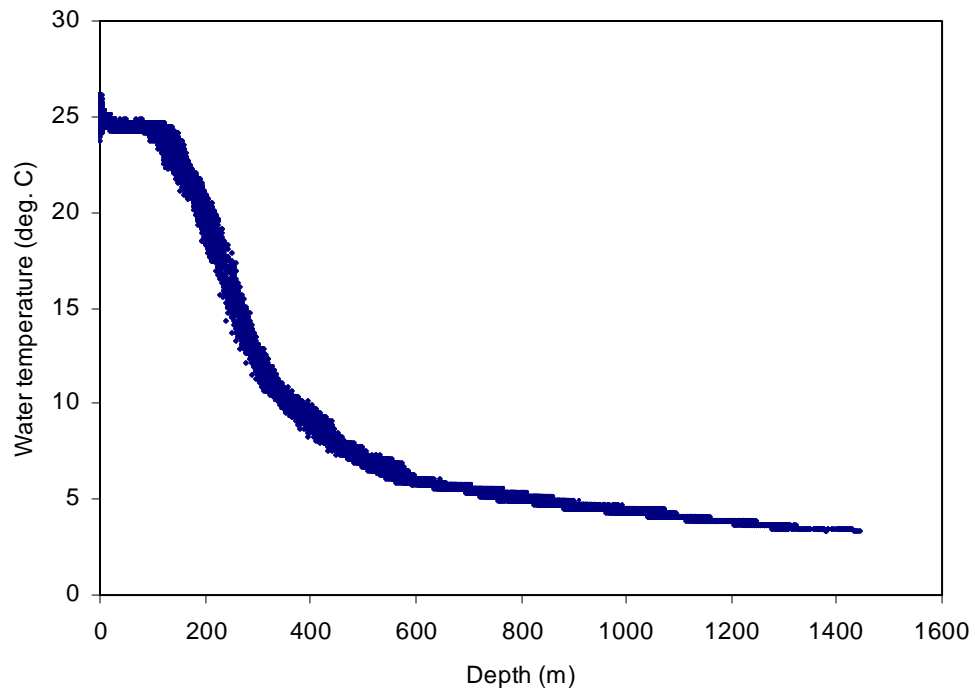
Table 1. Information on odontocete encounters by species (in decreasing order based on number of encounters) including group size, number of genetic samples obtained and number of photographs taken for species and/or individual identification. Comments note number of encounters cued in by other sources/methods, or in the case of spinner dolphins the number of groups detected at the mouth of the departure harbor.

Species	# encounters	Group size (mean, range)	# genetic samples	# photos	Comments
Short-finned pilot whale	48	18.0 (2-53)	38	12,088	
Pantropical spotted dolphin	32	58.1 (3-158)	43	2,224	
Spinner dolphin	17*	26.7 (6-50)	0	44	*16 at harbor mouth
Rough-toothed dolphin	16	9.9 (1-35)	0	3,453	
Dwarf sperm whale	10	3.5 (1-5)	0	1,890	
Blainville's beaked whale	6*	2.8 (1-5)	3	2,691	*2 from radio tracking
Sperm whale	6*	3.2 (1-5)	6	484	*clustered on 4 days over 5-day span
Bottlenose dolphin	5	10.2 (2-22)	11	1,322	
False killer whale	4*	8.5 (1-28)	0	1,483	*3 on same day
Melon-headed whale	4*	141 (1-350)	16	1,722	*2 from radio call
Striped dolphin	4	20.5 (7-40)	0	270	
Cuvier's beaked whale	2	1.5 (1-2)	0	728	
Un-identified odontocete	2	1	0	0	
Pygmy killer whale	1*	33	3	905	*From radio call

Table 2. Details of tag attachments on Blainville's beaked whales off the island of Hawaiʻi in 2006. Group size when tagged for all = 3 individuals

Tag #	Date tagged	Time tag on (hh.hh)	Date tag off	Time tag off (hh.hh)	Tag duration (h.hh)	Duration followed after tagging (h.hh)	# hours day	# hours night	Age/sex/catalog ID
*Md*5	15 Apr	11.35	17 Apr	3.50	40.15	0.53	19.87	20.16	Adult female/HIMd112
*Md*6	20 Apr	11.93	23 Apr	4.47	64.53	9.52*	32.2	32.34	Adult female/HIMd061
*Md*7a	20 Apr	12.16	20 Apr	13.36	1.20	-*	1.20		Adult male/HIMd111
*Md*7b	20 Apr	14.55	21 Apr	20.0	29.45	-*	16.87	12.58	Adult male – re-tagged
Total					135.33	10.05	70.24	65.08	

*Whale *Md6* and *Md7* in same group and followed on 20 April 2006 (4.43 hours), 21 April 2006 (2.62 hours) and 22 April 2006 (2.47 hours).

Table 3. 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 beaked whales off the island of Hawaiʻi. Data for two taggings of *Md7* combined.

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)
*Md*5	3,200	3,200	1,520	14	0.35	173.5	68.2
*Md*6	835	1,100	1,443	28	0.43	78.4	83.4
*Md*7	835	1,100	1,126	13	0.42	58.5	65.7
Mean (SD)			1,365 (205)		0.40 (0.05)		

[1]Tag #s correspond to individuals listed in Table 2.

Table 4. Comparison of day- and night-time data including information from one tag attachment on a Blainville's beaked whale from 2004 (*Md3*, see Baird et al. 2006). All depths are in meters, all durations are in minutes.

Tag #[1]	# >800 m dives h[-1] (day)	# >800 m dives h[-1] (night)	Depth (dives>800m) day Mean (SD)	Depth (dives>800m) night Mean (SD)	Duration (dives>800 m) day Mean (SD)	Duration (dives>800 m) night Mean (SD)	# 100-600 m dives h[-1] (day)	# 100-600 m dives h[-1] (night)
Md3	0.47	0.33	1,085.0 (78.2)	1,159.2 (204.6)	48.7 (3.07)	48.6 (7.81)	1.32	0
Md5	0.30	0.40	1,408.8 (132.7)	1,181.5 (93.8)	60.2 (4.7)	53.2 (4.53)	1.40	0.35
Md6	0.31	0.56	1,016.3 (86.8)	1,070.7 (212.6)	53.3 (7.7)	55.3 (10.05)	2.02	0.53
Md7	0.33	0.56	911.3 (71.6)	1,045.6 (81.2)	56.2 (5.3)	57.5 (6.79)	2.21	0.40
Mean (SD)	0.35 (0.10)	0.46 (0.12)	1,105 (214.3)	1,113.7 (66.3)	54.6 (4.8)	53.6 (3.8)	1.74 (0.44)	0.32 (0.22)

[1]Tag #s correspond to individuals listed in Table 2.

Table 5. Rates of descent and ascent (in m/sec) from Blainville's beaked whales tagged in 2006. 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		
Md5	1.59 (0.17)	0.70 (0.28)	0.71 (0.53)	0.61 (0.30)	1.76 (0.50)	1.45 (0.39)	0.75 (0.61)	0.66 (0.32)	14	35
Md6	1.50 (0.23)	0.81 (0.29)	0.67 (0.33)	0.61 (0.31)	1.62 (0.32)	1.03 (0.50)	0.68 (0.38)	0.60 (0.26)	28	82
Md7	1.37 (0.23)	0.63 (0.18)	0.60 (0.32)	0.61 (0.22)	1.71 (0.28)	1.10 (0.47)	0.60 (0.36)	0.61 (0.27)	12	45
Average	1.49 (0.11)	0.71 (0.09)	0.66 (0.06)	0.61 (0.0)	1.7 (0.07)	1.19 (0.23)	0.68 (0.08)	0.62 (0.03)		

[1]Tag #s correspond to individuals listed in Table 2.