SITE FIDELITY, ASSOCIATIONS, AND MOVEMENTS OF CUVIER'S (*ZIPHIUS CAVIROSTRIS*) AND BLAINVILLE'S (*MESOPLODON DENSIROSTRIS*) BEAKED WHALES OFF THE ISLAND OF HAWAI'I

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ABSTRACT

Although the Ziphiidae are the second-most speciose family of cetaceans, information on beaked whale species and populations has been limited by the difficulties in finding and approaching free-ranging individuals. Site fidelity, patterns of association, and movements of two species, Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales, were assessed using a 21-yr photographic data set from the west coast of the island of Hawai'i. Resightings of individuals of both species spanned 15 yr, suggesting long-term site fidelity to the area. Long-term resightings were documented primarily from adult females of both species. Group sizes for both species were small and most groups had only a single adult male present. For Blainville's beaked whales, repeated associations between adult females and adult males were documented for all resightings of adult males over periods from 1 to 154 d. Among adult females, although repeated associations occurred up to 9 yr apart, individuals were seen separately in intervening years. Individuals

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of both species seen on multiple occasions were typically documented in multiple months/seasons, suggesting they may use the study area throughout the year. Such long-term site fidelity has implications both for potential population structure and for susceptibility of beaked whale populations to anthropogenic impacts.

Key words: site fidelity, Ziphiidae, social organization, Hawai'i, association patterns.

Site fidelity is the tendency for individuals to return to the same area repeatedly or remain in an area for an extended period, and may occur at both breeding and feeding areas. High levels of site fidelity can have important implications for conservation and management of populations, potentially leading to an increase in population structure, as well as increasing vulnerability of individuals and populations to perturbations from localized anthropogenic influences (*e.g.*, Warkentin and Hernandez 1996, Brager *et al.* 2002). Site fidelity has been documented from numerous taxa (Switzer 1993), including a number of species of cetaceans. Returning to traditional feeding or breeding grounds has been documented for many species of migratory baleen whales (*e.g.*, Dorsey *et al.* 1990, Calambokidis *et al.* 2001), and restricted home ranges have been documented for many coastal populations of delphinids (*e.g.*, Shane *et al.* 1986, Gubbins 2002, Flores and Bazzalo 2004). Little is known regarding site fidelity for oceanic odontocetes, though the evidence that is available from photo-identification or tagging of sperm whales (*Physeter macrocephalus*) and offshore bottlenose dolphins (*Tursiops truncatus*) suggests that individuals roam over wide areas (Wells *et al.* 1999, Whitehead 2003). The beaked whales (Family Ziphiidae) are the second most speciose group of cetaceans, but relatively little is known about site fidelity in this group, due to the difficulties associated with finding and approaching individuals. High levels of site fidelity have been reported from one species of beaked whale, the northern bottlenose whale, *Hyperoodon ampullatus,* inhabiting submarine canyons offshore of the east coast of Canada (Hooker *et al.* 2002, Wimmer and Whitehead 2005). Site fidelity has also been reported in Blainville's beaked whales (*Mesoplodon densirostris*) off Great Abaco Island in the Bahamas (Durban *et al.* 2001, Claridge 2006) and Cuvier's beaked whales (*Ziphius cavirostris*) in the Ligurian Sea (Ballardini *et al.* 2005).

Understanding patterns of residency in beaked whales may be important both in terms of potential population structure and in assessing the impacts of anthropogenic activities. Although there are few samples available for genetic investigation of population structure in beaked whales, evidence of limited gene flow within ocean basins exists for the two species in which this has been studied (Dalebout *et al.* 2005, 2006). If populations are highly structured, anthropogenic activities may have a greater effect on them. Although beaked whales have rarely been the target of whaling operations (Reeves and Mitchell 1993, Reeves *et al.* 1993), they are recorded as occasional bycatch in drift gill net fisheries (Barlow *et al.* 1994, Henshaw *et al*. 1997). In addition, mortalities of beaked whales have been associated with high-intensity underwater sounds, particularly naval sonars, in several areas (Simmonds and Lopez-Jurado 1991, Frantzis 1998, Balcomb and Claridge 2001, U.S. Dept of Commerce and U.S. Navy 2001, Jepson *et al.* 2003, Fernandez *et al.* 2005).

In Hawaiian waters three species of beaked whales have been documented, Cuvier's beaked whales, Blainville's beaked whales, and Longman's beaked whales (*Indopacetus pacificus*), though the latter species has been positively identified from only one

sighting (Barlow 2006). One beaked whale has been reported killed in the offshore long-line fishery in Hawaiian waters (Forney and Kobayashi 2007), and extensive naval exercises occur in Hawaiian waters, with the potential to impact populations. In recent years, we have been studying the diving behavior and ecology of Cuvier's and Blainville's beaked whales off the west coast of the island of Hawai'i (Baird *et al.* 2006*a*), but we have also been photographing both species in the area since 1986. Individuals in these populations accumulate white oval scars from cookie cutter sharks (genus *Isistius*) that can be used both in identifying individuals and in broadly assessing age class. Adults of both species are sexually dimorphic in jaw and tooth morphology (Heyning 1989, Mead 1989) and sex of adults can also be determined using the number and extent of paired linear scars; thus, we are usually able to identify adult individuals to sex. Baird *et al.* (2006*a*) noted evidence of site fidelity of both species from a subset of photos (from 2002 to 2005), although the time frame was relatively limited and no detailed exploration of site fidelity was undertaken. Here we use the entire 21-yr set of photographs to assess long-term site fidelity and sex differences in site fidelity in these two species, as well as to examine association patterns and movements of individuals.

METHODS

Fieldwork was undertaken periodically off the west coast of the island of Hawai'i from May 1986 to December 2006 using survey vessels ranging in length from 6 to 15 m. The primary research vessels all had elevated viewing platforms with eye heights off the water of at least 3.9 m. Field efforts have been categorized as "opportunistic" or "directed." Opportunistic efforts were undertaken on a periodic basis year-round from 1986 to 2006 and were focused on studies of short-finned pilot whales, *Globicephala macrorhynchus* (see Shane and McSweeney 1990), though attempts were made to obtain photographs of all beaked whales observed. Several wildlife photographers also obtained additional opportunistic photos from encounters. Directed field efforts were undertaken from 2002 to 2006 as part of a multi species odontocete population assessment study, with quantification of effort and all odontocete sightings. Directed efforts since 2003 were focused primarily on beaked whales (see Baird *et al.* 2006*a*). These directed field efforts were undertaken during one or two shorter-term (10–40 d) periods each year, using two to six observers scanning 360 degrees around the survey vessel. For the purposes of examining sighting rates, information on all sightings (whether or not photographs for individual identification were obtained) of both species and of unidentified beaked whales are presented from directed efforts.

Opportunistic efforts were concentrated in areas immediately to the south and offshore of Honokohau Harbor and typically involved searching in depths between 800 and 1,800 m. Directed efforts involved nonrandom, nonsystematic surveys that attempted to cover as wide a survey area as possible given weather and fuel constraints. Within a particular field effort overlap of survey lines was kept to a minimum. In general, the research vessels surveyed areas with sea states less than Beaufort 4, and efforts were made to cover both shallow (<500 m) and deep (>2,000 m) areas, usually alternating between areas to the north, south, and offshore of Honokohau Harbor, weather permitting. The size of the study area was approximately 5,000 km^2.

Beaked whale species were identified in the field and from photographs based on body size, the size of the dorsal fin relative to the amount of body visible, the degree of arch to the back, pigmentation patterns, whether the rostrum was clearly seen, and if so, the shape of the head and rostrum. Compared to Blainville's beaked whales,

adult Cuvier's beaked whales are larger, show a greater extent of back when surfacing (and thus the dorsal fin is smaller relative to the amount of body visible; Fig. 1), typically have a higher arch to the back, and rarely show the rostrum when surfacing. Some adult Cuvier's beaked whales can also be distinguished by extensive white on the head and back extending to or almost to the dorsal fin (Heyning 1989). When the rostrum is visible, the two beaked whale species can be easily distinguished based on head shape.

To confirm species, biopsy samples were obtained using a Barnett RX-150 crossbow (Barnett International, Odessa, Florida, USA) and Ceta-Dart 25-mm tips (Ceta-Dart, Copenhagen, Denmark) from three encounters with Blainville's beaked whales and two encounters with Cuvier's beaked whales in 2002/2003. Molecular identification of the specimens was made by comparing a 400 base pair sequence of the 5′ end of the mitochondrial DNA control region, which was sequenced using standard protocols (Saiki *et al*. 1988, Palumbi *et al*. 1991), to a reference collection of sequences held at the Southwest Fisheries Science Center, La Jolla, California.

With both types of effort, we attempted to photograph all whales in each group, including both left- and right-hand sides and the head, to confirm species and sex (of adults). Location of most groups was recorded using a GPS when the research vessel was within 100 m of the whales. Information on locations of two Blainville's beaked whales tagged with suction-cup attached VHF tags (with time-depth recorders) and tracked over 3 d in 2006 was used to examine short-term movements (see Baird *et al.* 2006*a*).

Within each encounter, photographs were sorted by individual based on dorsal fin shape, notches in the trailing or leading edge of the dorsal fin or along the back, holes through the dorsal fin, scarring patterns (including scars caused by inter- and intraspecific interactions, including those from cookie-cutter sharks and other larger
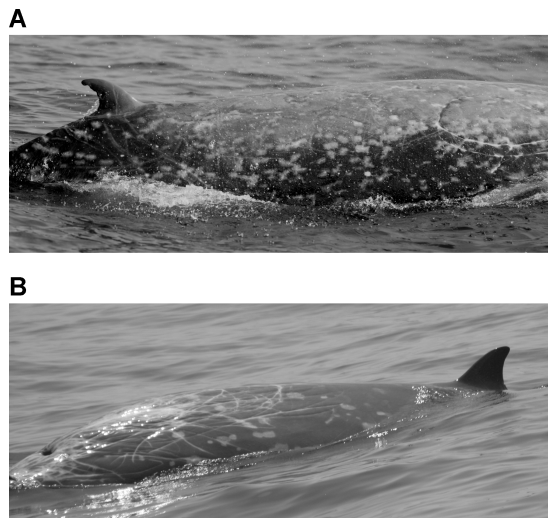
Figure 1. Features used in individual identification (dorsal fin notches, white oval scars from cookie-cutter sharks, linear scars from intraspecific interactions), and species identification (*e.g.*, relative size of dorsal fin to back showing). A. Adult male Cuvier's beaked whale (HIZc038) with shark bite scar near head. B. Adult male Blainville's beaked whale (HIMd110) with extensive linear scaring on anterior dorsal surface.

sharks; Fig. 1), and in the case of young whales, body size relative to other whales in photographic frames. Given the typically small group sizes (see Results), when sufficient photos were available it was usually possible to match left- and right-hand sides of each individual using features such as dorsal fin shape or overall pigmentation patterns, even in the absence of dorsal fin or back notches. For every individual within each encounter, the best photograph obtained was given a photo quality rating as poor, fair, good or excellent, based on the focus, size and angle of the body relative to the photographic frame, and proportion of the body visible. Each individual was given a distinctiveness rating of (1) not distinctive, (2) slightly distinctive, (3) distinctive, or (4) very distinctive. These ratings were based on the presence of one or more notches on the dorsal fin or back immediately in front of or behind the dorsal fin (which could be detected from either left- or right-hand side photographs), scars on the fin, or scars on the back immediately around the fin. For those resighted individuals whose distinctiveness classification changed between sightings, the greater (*i.e.*, more distinct) classification was used in calculating resighting statistics. Given that the probability of resighting individuals is lower for less distinctive individuals and with poor quality photographs, we restrict analyses of resighting rates to distinctive and very distinctive individuals with photographs of good or excellent quality only. For calculating resighting intervals and seasonal occurrence, photographs of all quality and distinctiveness ratings are used. The minimum catalog size for each species was determined by summing the number of individuals with both left- and right-hand side photos, the greater of the number of those individuals with only left- or only right-hand side photos, and the number of individuals with dorsal fin notches from the remaining category (*i.e.*, the lesser number of only left- or only right-hand side photos).

To quantify scar acquisition rates and to examine scar loss and fading in Blainville's beaked whales, we chose the individuals with the longest resighting histories that had high-quality photographs showing a large area of the body. We examined an area visible for most individuals photographed: the area immediately in front of, below, and behind the dorsal fin. To standardize the proportion of the body examined, we used an area equivalent to three times the length of the dorsal fin base centered below the dorsal fin, down as far as the equivalent of one length of the dorsal fin base, and counted the number of white oval scars (created by cookie-cutter sharks) on both the left- and right-hand sides of each individual. It was not possible to examine scar acquisition rates in Cuvier's beaked whales as photographs of sufficient quality and of the same side or area of the body for individuals with repeated sightings were not available over a long enough time span. The total number of white oval scars visible on one side of three adults of each species was counted from a series of photographs (taken during one surfacing) as a means of assessing the number of potential marks that can be used to identify individuals. Those individuals with a complete series of high-quality photographs from the head to the peduncle were chosen for assessing total scars.

We categorized individuals as adults or nonadults based on (1) the presence of erupted teeth and extensive linear scarring on the head (for adult males), (2) the number and extent of visible oval scars caused by cookie-cutter sharks, and (3) relative body size (when photos were available of two whales close to each other in the same frame, showing the area from the dorsal fin to the blowhole). Assigning tentative age ranges to these categories is not possible given the paucity of information on growth or age at sexual maturity for either species (Mead 1984). Individuals were categorized as adult males if erupted teeth were visible. For Cuvier's beaked whales where the tip of the rostrum was not visible, individuals were also categorized as

adult males if they had extensive single or paired linear scars on the head and back (presumably caused by conspecifics) and had extensive white pigmentation extending posterior from the head on the dorsal surface, to at least one-third of the way back towards the dorsal fin. Individual Blainville's beaked whales were also considered adult males if no head photographs were available but they had extensive linear scarring on the back presumably caused by conspecifics. All individuals of both species with erupted teeth had such extensive linear scarring (and white pigmentation for Cuvier's beaked whales), but individuals who were known or thought to be adult females based on jaw morphology typically only had scattered linear scars. Individuals were categorized as adult females if they had extensive scarring caused by cookie-cutter sharks (see below) but not extensive linear scars. When photographs of the rostrum were available for individuals that had extensive cookie-cutter scars but lacked extensive linear scars, no erupted teeth were visible. Some of these individuals were also accompanied by a small calf (an individual approximately <50% of the body length of the other individual in the photograph; these individuals had at most one or two cookie-cutter shark scars visible). For assessing cookie-cutter shark scars for age class categorization, repeated photographs of the same area of the body between sightings were not required. Thus we used an area of the back equivalent to about four times the length of the dorsal fin base extending from the dorsal surface to the waterline and covering any part of the body (thus including an area greater than that used for quantifying scar acquisition). Although the position of the waterline relative to the back varied between photographs, when available we used multiple photographs of each individual to assess scarring, and in doing so could choose those photos showing the largest amount of back. If only a small amount of the back (relative to the size of the dorsal fin) was visible, we prorated the number of scars relative to amount of area visible. Individuals were considered adults if they had >10 such scars visible, based on the number of scars visible on known adults (*i.e.*, individuals with erupted teeth or with small calves in close attendance). For Blainville's beaked whales, individuals were considered subadult males if teeth were barely erupted and if the jaw line was relatively straight.

Association levels were assessed with Socprog 2.3[2] (Dalhousie University, Halifax, Nova Scotia, Canada), using a simple ratio index of association (Cairns and Schwager 1987), with values ranging from 0 (for individuals that are never seen together) to 1 (for individuals that are always seen together). Average association indices were calculated using individuals seen on more than one occasion, restricting analyses to distinctive and very distinctive individuals with photo quality ratings of good or excellent. Network diagrams were produced with Netdraw 2.043 (Analytic Technologies, Needham, Massachusetts, USA). When locations were available, distances between locations were calculated using the Posdist[3] function in Excel (Microsoft, Redmond, Washington, USA), and calculations of horizontal displacement (in km/h) were speed over ground not speed through the water. For cases where all sighting locations of more than one individual were the same, distance among sighting locations was only calculated once. For individuals with more than two sighting locations, a mean of the distances among all sighting locations was calculated and used in examining movements. Calculations of distances among locations and seasonality of occurrence included individuals of all distinctiveness ratings and with no restrictions on photo quality. Statistical analyses were undertaken in Minitab 13.2 (Minitab, Inc., State College, Pennsylvania, USA).

[2] Available from myweb.dal.ca/∼hwhitehe/social.htm.
[3] Available from nmml.afsc.noaa.gov/Software/ExcelGeoFunctions/excelgeofunc.htm.

RESULTS

During directed field efforts (since 2002), we spent a total of 202 d on the water, covering 22,093 km of trackline in 1,439 h of field effort (Fig. 2). Directed field efforts were spread over 10 months of the year (all except June and August), with a peak in effort in September/October. On the directed surveys we encountered nineteen groups of Blainville's beaked whales, twenty-eight groups of Cuvier's beaked whales, and had three sightings of beaked whales that we were not able to identify to species (based on body size and group size they were most likely one of these two species, rather than Longman's beaked whales). Encounter duration (for both species combined) averaged 1.45 h (SD = 1.65 h), and were similar for the two species (Blainville's beaked whales mean = 1.48 h, SD = 1.53 h; Cuvier's beaked whales mean = 1.43 h, SD = 1.75 h). Encounter durations were prolonged (mean = 3.08 h, SD = 2.06 h, n = 13,
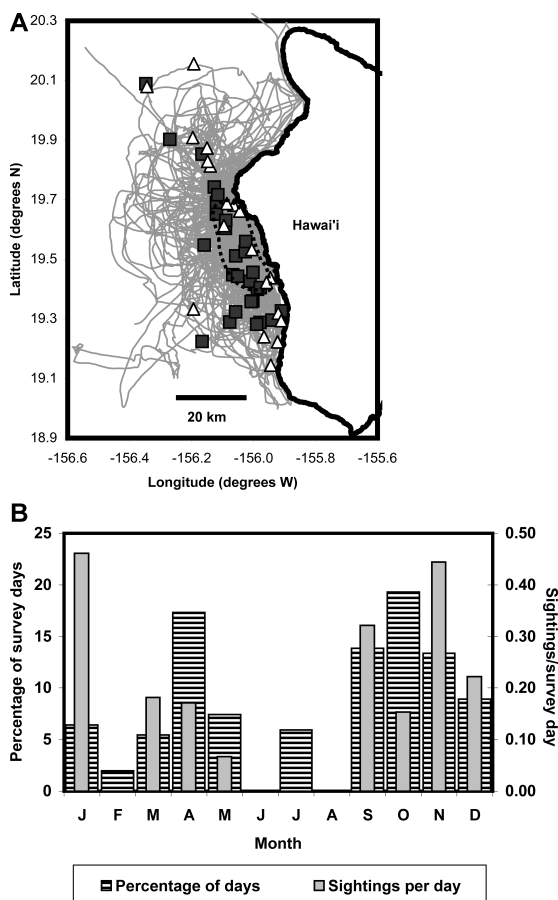

Figure 2. A. Map showing track lines from directed survey effort (solid lines), approximate limits of opportunistic survey effort (dotted line), and sightings of Cuvier's (squares) and Blainville's (triangles) beaked whales from directed survey effort. B. Seasonal distribution of survey effort and beaked whale sightings per survey day during directed survey efforts.

max. = 8.3 h) when individuals in the group were tagged with suction-cup attached radio tags (see Baird *et al.* 2006*a*), although groups were often out of sight during long (>50 min) periods when whales were diving. When relocated after such long dives, we know that the whales were from the same group based on photographs or signals from VHF radio tags, and we treated these as only single sightings or encounters. No group splitting was observed during encounters. Two of the nineteen encounters with Blainville's beaked whales (on consecutive days) were initiated due to the presence of a suction-cup attached radio tag on one of the individuals in the group (tagged on the first of the three days), and these individuals would likely not have been detected without the presence of the VHF signals. Group composition was the same on the second day of the three days of encounters with these radio-tagged individuals, though on the third day only two of the original three group members were present. Group size for Blainville's beaked whales was generally larger (median = 3, mean = 3.53, SD = 2.37, range 1–9, *n* = 19) than for Cuvier's beaked whales (median = 2, mean = 2.57, SD = 1.26, range 1–5, *n* = 28), though group sizes were not significantly different (Mann-Whitney *U*-test, *P* = 0.24), and modal group size for both species was two individuals. No Longman's beaked whales were seen in directed efforts, though one distant sighting (with no photographs) from opportunistic efforts (from 4 November 2000) was of a group of 40–50 beaked whales with distinctive blows and were likely this species (*cf*. Pitman *et al*. 1999).

Blainville's Beaked Whales

A total of 5,885 photographs were obtained from 50 encounters with Blainville's beaked whales (17 directed, 33 opportunistic) taken in 16 different years spanning the period from 1986 to 2006 (Table 1). Using photographs of all quality ratings we documented 98 individuals. The number of photographs per identification ranged from 1 to 672 (median = 7). Restricting analyses to only good and excellent quality photographs, a total of 59 distinctive or very distinctive individuals were documented (Table 2), though not all individuals were documented with both left- and right-hand side photos or with dorsal fin notches (so they could be identified from either side). The minimum catalog size (as defined in Methods) of distinctive and very distinctive individuals with good or excellent quality photographs was 55 individuals (20 very distinctive, 34 distinctive). Of the 59 individuals, 47 were categorized as definite or probable adults (21 as females, 19 as males, 7 as unknown adults). Twenty individuals (33.9%) were seen on two or more occasions, for a total of 24 between-year resightings and 24 within-year resightings.

Mean association index values for all those individuals seen more than once (*n* = 20) was 0.07 (SD = 0.05). Over 60% of the Blainville's beaked whales (36 of 59) could be linked by shared associations (Fig. 3). The remaining individuals, most seen only on a single occasion each, were spread among ten different clusters (individuals linked by shared associations), the largest with only six individuals (and four not linked to any other individuals). The relative lack of links for these individuals is most likely due to the small number of times these individuals were documented.

Including photographs of all quality ratings and "slightly distinctive" individuals, but excluding resightings due to radio tracking, 10 adult females were seen on more than one occasion, for a total of 35 resightings. Four of the ten adult females were first documented as subadults/juveniles, based on size and scarring when first seen. The interval between resightings ranged from 12 to 3,539 d (median = 348,

Table 1. Summary of encounters and identifications for Blainville's and Cuvier's beaked whales by year. For years with overlapping opportunistic and dedicated field effort, the number of encounters for each is designated as (no. of opportunistic/no. of dedicated). Identifications listed include all photo qualities and all distinctiveness ratings. Identification photographs were not obtained in all encounters

	Blainville's beaked whales		Cuvier's beaked whales	
Year	No. of encounters	No. of identifications/ no. of new identifications	No. of encounters	No. of identifications/ no. of new identifications
1986	1	5	0	0
1987	1	1	0	0
1988	1	3/2	0	0
1989	0	0	0	0
1990	0	0	1	3/3
1991	7	23/19	3	5/5
1992	1	3/1	0	0
1993	1	2/0	0	0
1994	3	8/5	2	4/3
1995	4	9/5	1	3/2
1996	0	0	0	0
1997	4	16/11	2	3/0
1998	0	0	0	0
1999	3	11/3	0	0
2000	1	1/0	0	0
2001	0	0	0	0
2002	2 (0/2)	10/7	4 (0/4)	9/9
2003	5 (3/2)	17/6	5 (0/5)	4/4
2004	5 (1/4)	17/13	7 (2/5)	16/10
2005	3 (1/2)	7/7	4 (0/4)	4/3
2006	10 (1/9)	27/13	11 (1/10)	27/10
Total	52 (33/19)	160/98	40 (12/28)	78/49

$n = 35$), and there were between-year resightings for all 10 individuals. The interval from when an individual was first seen to when it was last seen ranged from 225 to 5,762 d (median = 2,958 d, $n = 10$). One adult female was seen fourteen times in seven different years (spanning 1991–2006), one was seen seven times in six different years (spanning 1997–2006, with two of the seven sightings on consecutive days with the group being relocated on the second day using radio-tracking), two were seen six times (one in four years spanning 1999–2006, and one in five years spanning 1991–2003), and one was seen five times in two different years (from 1997 and 2006, though three of the five sightings for this individual were on three consecutive days with the individual being relocated on the last two days using radio tracking).

Excluding resightings due to radio tracking, five adult males were resighted for a total of eight resightings. The interval between resightings ranged from 9 to 1,192 d (median = 398 d, $n = 8$), and there were between-year resightings for four of the five adult males resighted. One of the individuals was categorized as a subadult male when first seen (*i.e.*, teeth barely visible, no linear scars on head) and was resighted

Table 2. Information on number of individuals and resightings by distinctiveness for Blainville's beaked whales, restricting analyses to "distinctive" and "very distinctive" individuals with photo quality ratings of good or excellent

	Distinctive	Very distinctive	Total
No. of individuals	39	20	59
No. of (%) seen more than once	15 (38.5)	5 (25)	20 (33.9)
No. of resightings total	26	22	48
No. of within-year resightings	14	10	24
No. of between-year resightings	12	12	24
No. of (%) photos both sides	25 (64.1)	17 (85.0)	42 (71.2)
No. of (%) photos left-hand only	9 (23.1)	2 (10.0)	11 (18.6)
No. of (%) photos right-hand side only	5 (12.8)	1 (5.0)	6 (10.2)
No. of (%) with dorsal fin notches	19 (48.7)	17 (85.0)	36 (61.0)
No. of (%) adults	30 (76.9)	17 (85.0)	47 (79.6)

only once, as an adult male, after 1,192 d. Including this individual, the interval from when an individual adult male was first seen to when it was last seen ranged from 46 to 1,192 d (median = 644 d, *n* = 5). Adult or probable adult males were documented in twenty-eight groups, three of which had two adult males (a group of eight containing three female/juvenile pairs, a group of three containing one adult female, and a group of five containing three adult females). In all three groups one of the two males had substantially more tooth rake scars on the head than the other, and in two the degree of tooth eruption differed greatly between the two males). In each group, the two adult males generally remained separated by other whales in the group.
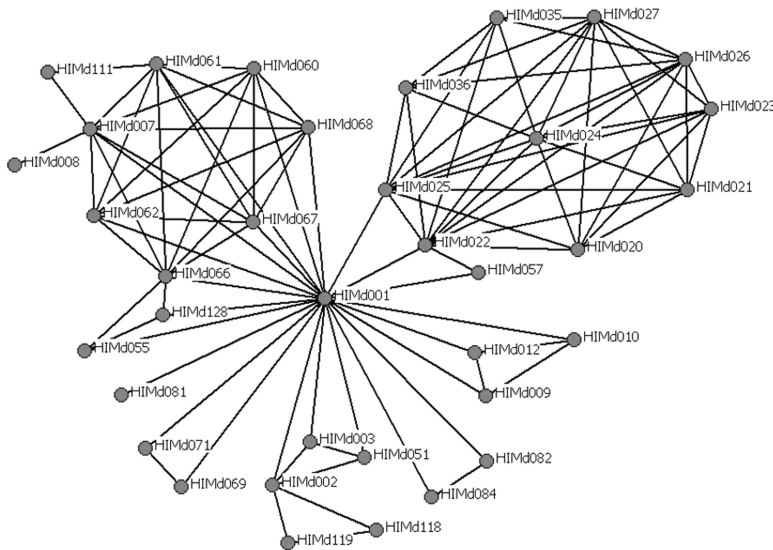

Figure 3. Network diagram of Blainville's beaked whales showing largest cluster (36 of 59) of individuals linked by associations. Line length and placement of individuals is for display purposes only and does not imply strength of association.

Table 3. Information on number of individuals and resightings by distinctiveness for Cuvier's beaked whales, restricting analyses to "distinctive" and "very distinctive" individuals with photo quality ratings of good or excellent

	Distinctive	Very distinctive	Total
No. of individuals	14	21	35
No. of (%) seen more than once	6 (42.9)	8 (38.1)	14 (40)
No. of resightings total	8	13	21
No. of within-year resightings	4	9	13
No. of between-year resightings	4	4	8
No. of (%) photos both sides	8 (57.1)	17 (80.9)	25 (71.4)
No. of (%) photos left-hand only	3 (21.4)	2 (9.5)	5 (14.3)
No. of (%) photos right-hand side only	3 (21.4)	2 (9.5)	5 (14.3)
No. of (%) with dorsal fin notches	4 (28.6)	14 (66.7)	18 (51.4)
No. of (%) adults	10 (71.4)	20 (95.2)	30 (85.7)

All four within-year resightings of adult males (three individuals) involved repeated associations with individual adult females, with time periods between repeated associations of 1, 1, 15, and 46 d (the two 1-d intervals were of radio-tagged individuals). One of the five between-year resightings of an adult male involved a repeated association with an adult female (after 154 d, the shortest of the between-year resighting intervals for adult males). Six of thirteen within-year resightings of adult females involved repeated associations with other adult females (1, 14, and 61 d apart, the 1-d interval was of radio-tagged individuals). Nine of twenty-five between-year resightings of adult females involved repeated associations with other adult females (125, 164, 164, 2,821, and 3,539 d apart). In both cases for the two repeated associations >7 yr and >9 yr apart, the individuals were seen in the intervening periods without the other individuals present, suggesting that despite reassociations between adult females, they are not stable over long periods.

Three of the four individuals seen most often (6, 6, and 14 times) were seen in all four of Hawaii's oceanographic seasons (defined based on sea surface temperature, see Flament 1996), whereas the third (seen seven times) was seen in three of the four oceanographic seasons. For those individuals seen on more than one occasion, there was a strong positive relationship between the number of times an individual was seen and the number of months it was recorded (regression $r^2 = 0.79$, $P < 0.001$, $n = 26$). Restricting analyses to those seen three to seven times shows the same trend (regression $r^2 = 0.64$, $P = 0.003$, $n = 11$). Individuals seen three or more times (seen an average of 5.1 times, SD = 3.3, $n = 11$) were seen in an average of 3.54 mo (SD = 1.8 mo). Combined this suggests individuals use the study area year-round rather than in one particular season.

The total number of oval scars counted on one side of three adult female individuals was 103, 115, and 120. All adult individuals also had linear scars from intraspecific interactions; one individual had scars from an attack by a large shark, and one individual had five to six parallel tooth rakes on both sides of the dorsal fin from an unidentified odontocete (probably a false killer whale, *Pseudorca crassidens,* or killer whale, *Orcinus orca*, based on spacing of the tooth rakes). Combined this suggests that adults and subadults from this population are likely to have sufficient numbers of marks for all individuals to be identifiable (*e.g.*, Fig. 1). Scar acquisition rate was quantified in three individuals with time periods between resightings (where all marks within the

specified range could be noted) of 8, 9, and 11 yr. It was possible to quantify scar acquisitions on both the left- and right-hand side for one individual (over 11 yr) but only for one side each of the other two individuals. Mean scar acquisition rate was 0.68 scars/yr (SD = 0.16) for the area immediately in front of, below, and behind the dorsal fin, equivalent to three times the length of the dorsal fin base in length and the length of the dorsal fin base in depth. Scar loss due to fading was assessed in the same three individuals over the same time intervals. In addition, scar loss was examined in one of the three over a 15-yr period, although the photographs available for the 15-yr interval did not cover the entire area examined for scar acquisition and could not be used for that purpose. All scars visible in the earliest encounters were still visible in the last encounters (over 8, 9, and 15 yr), though over 15 yr they had faded from white to skin color and were only recognizable in good quality photographs as disfigurement of the skin. Scars were known to remain unchanged in color over 9-yr time spans, though some had faded from white to gray over 11 yr, with just a few white flecks in the center of the scars. For scars that did change color (over 15 yr) they were seen to fade from the edges inward.

Precise coordinates were available for twenty-nine sighting locations (all sightings from directed effort and ten sightings from opportunistic effort). Mean horizontal distance among all combinations of sighting locations was 33.3 km (SD = 24.0, n = 406). Coordinates were available for sighting locations of fifteen different individuals or pairs of individuals seen on more than occasion. The number of sighting locations per individual ranged from two to eleven (mean = 3.53). There was no relationship between the number of sightings per individual and the mean horizontal distances among sighting locations (regression, $P = 0.56$, $r^2 = 0.02$), although the maximum horizontal distance among sighting locations for each individual increased with the number of locations available (regression, $P = 0.01$, $r^2 = 0.41$). Mean horizontal distances among resighting locations for each individual ranged from 2.85 to 42.34 km (mean = 23.22 km, SD = 11.65 km). Maximum horizontal distances among resighting locations for each individual ranged from 2.85 to 69.45 km (mean = 36.02 km, SD = 18.8 km). The average distance among sighting locations for each individual increased with the proportion of those locations from dedicated survey effort (regression, $P = 0.04$, $r^2 = 0.29$).

A total of sixteen locations for two whales (HIMd061 and HIMd111) tagged in the same group were obtained over a 3-d period in 2006 (Fig. 5). Time intervals between consecutive locations ranged from 0.18 to 24.33 h (mean = 3.39 h, SD = 7.17 h, $n = 15$), though thirteen of these intervals were within-days (mean interval = 0.73 h, SD = 0.65 h, $n = 13$). Distances between locations within-days averaged 1.49 km (SD = 1.74 km), representing a minimum rate of horizontal movements of 1.94 km/h (SD = 0.94). Minimum distances moved between the two pairs of days were 2.05 km (in 16.9 h) and 30.54 km (in 24.3 h).

Cuvier's Beaked Whales

A total of 4,611 photographs of Cuvier's beaked whales were obtained from 35 encounters (23 directed, 12 opportunistic) in 10 yr spanning the period from 1990 to 2006 (Table 1). Using photographs of all quality ratings we documented 49 individuals, with the number of photographs per identification ranging from 1 to 295 (median = 21). Restricting analyses by photo quality and distinctiveness resulted in a catalog of thirty-five individuals. The minimum catalog size (taking into account

those with left-/right-hand side photos and dorsal fin notches) was 33 individuals: 21 "very distinctive" and 12 "distinctive." Of the individuals classified as adults, 13 were considered adult males (all 10 with rostrum photos showing erupted teeth, and 3 with no rostrum photos based on heavy linear scarring and extensive white pigmentation), 15 were considered adult females (all 10 with rostrum photos showed no erupted teeth, and all had no or light linear scarring), and 2 were not classifiable to sex due to photo quality. The presence of extensive white pigmentation extending backwards from the head was not by itself diagnostic for an adult male; two of the ten individuals confirmed to be adult females based on no erupted teeth and extensive white oval scars had white pigmentation on the back extending posterior up to half way to the dorsal fin. Of the 35 distinctive and very distinctive individuals, 21 were seen on only a single occasion and 14 (40%) were seen on two or more occasions, with 8 between-year resightings and 13 within-year resightings. All but one of the resighted individuals were classified as adults (the exception was a calf seen on two occasions in association with an adult female). Mean association index values for those individuals seen more than once ($n = 14$) was 0.08 (SD $= 0.07$).

For analyses of resighting intervals additional resightings using lower-quality photographs were used, adding one sighting of an adult male and six sightings of adult females, including one new individual seen on three occasions. Five adult males were resighted eight times, with resighting intervals ranging from 3 to 728 d (median $= 11$ d). The interval from when an adult male was first seen until it was last seen ranged from 3 to 744 d (median $= 71$ d, $n = 5$). Nine adult females were resighted nineteen times, with resighting intervals ranging from 5 to 3,774 d (median $= 432$ d). The interval from when an adult female was first seen until it was last seen ranged from 16 to 5,676 d (median $= 737$ d, $n = 9$). Resighting intervals were significantly longer for adult females than for adult males (Mann-Whitney U-test, $P = 0.0487$). One adult female was seen on five occasions in four different years, spanning the period from 1991 to 2006, and one was seen on three occasions in 3 yr spanning 1990 to 2005.

Using all quality photographs, there were five repeat associations, one between an adult female and an adult male 71 d apart, two of a group of four individuals (two adult females, two adult males) seen on three occasions with intervals between sightings of 11 and 5 d, and two the above-noted mother-calf pair seen on three occasions, with intervals between sightings of 82 and 747 d. Adult males were documented in twenty-one encounters. In five of these, two confirmed adult males were present (one to two adult females were also present in each group). In one of these five encounters, the two males remained separated by approximately 30–100 m for the duration of the encounter. Information on the relative spatial positions was not recorded for the other encounters when two adult males were present.

The total number of oval scars visible on one side of three adults (one female and two males) was 211, 275, and 290. All adults and subadults also had linear scars, and one individual had a healed scar from a large shark bite (Fig. 1). Combined this suggests that all adult and likely all subadult individuals from this population probably have enough distinctive features to be considered individually recognizable. Photo quality (*e.g.*, backlighting) restricted examination of scar loss to one individual photographed over an 11-yr span (1995–2006). All white oval scars visible in 1995 remained unchanged in color in 2006.

Precise coordinates were available for thirty-six sighting locations (all of those from directed effort and eight from opportunistic effort). Mean horizontal distance among all combinations of sighting locations was 25.7 km (SD $= 20.3$, $n = 630$). Coordinates

were available for sighting locations of eleven different individuals or pairs of individuals seen on more than occasion. The number of sighting locations per individual ranged from two to five (mean = 2.9). There was no relationship between the number of sightings per individual and the mean (regression, $P = 0.78$, $r^2 = 0.0093$) or maximum (regression, $P = 0.56$, $r^2 = 0.039$) horizontal distances among sighting locations. Mean horizontal distances among resighting locations ranged from 2.88 km to 88.73 km (mean = 23.9 km, SD = 23.7 km). Maximum horizontal distances among resighting locations for each individual also ranged from 2.88 to 88.73 km (mean of maximum distances = 31.1 km, SD = 25.3 km), as the individuals with the smallest and greatest distance values were both calculated from only two locations.

Individuals seen more than once were usually (13 of 15 individuals, and all 9 seen more than twice) seen in multiple months. For those individuals seen on more than one occasion, there was a positive relationship between the number of times an individual was seen and the number of months in which it was recorded (regression $r^2 = 0.42$, $P = 0.01$, $n = 14$). The individual seen most often (HIZc029, $n = 5$) was seen in four different months (April, October, November, December) in three of Hawaii's oceanographic seasons. Combined this suggests individual Cuvier's beaked whales use the study area year round, rather than in one particular season.

DISCUSSION

Beaked whales were only infrequently encountered off the west coast of the island of Hawai'i, with ninety-six encounters spanning a 21-yr period. We suspect the low sighting rates reflect a combination of low density (Barlow 2006), extremely long dive times (Baird *et al.* 2006*a*, Tyack *et al.* 2006), and the cryptic nature of these species, rather than an absence of individuals from the area for extended periods. Our experience with trying to relocate individual Blainville's beaked whales that were radio tagged supports the cryptic nature of their surfacing patterns—even in the best scenario, with excellent sea conditions (Beaufort 0 and 1), knowing exactly when individuals were at the surface (from radio signals) and which direction those individuals were relative to the boat, and with five observers scanning in the appropriate direction (three from an elevated viewing platform), tagged whales were not visually detected until they were within approximately 300 m of the research vessel (Baird, personal observations). Visual detection of Cuvier's beaked whales occurred at much greater distances than Blainville's beaked whales, so fewer animals that are at the surface are likely missed. However, dive times of up to 87 minutes were documented for tagged Cuvier's beaked whales (Baird *et al.* 2006*a*), and many are likely missed due to extended dive durations (see Barlow 1999).

Despite relatively small catalog sizes (a minimum of 33 Cuvier's and 55 Blainville's beaked whales) and a limited number of individuals photo-identified in the early years of our sampling (Table 1), there were high resighting rates for both species, with 40% of the Cuvier's and 33.9% of the Blainville's being seen on more than one occasion. There are several reasons why these resighting rates should be negatively biased, that is, that they underestimate true site fidelity. Given the 21-yr span of this study there were probably a number of births and deaths in both populations, thus not all individuals may have been available for resighting throughout the duration of the study. It is also possible that the broad survey coverage (over an area of about 5,000 km^2) out to depths of over 4,000 m (see Baird *et al.* 2006a) may have resulted in encounters both with island-associated "resident" individuals and individuals from

a more open ocean population (Ferguson *et al.* 2006). Blainville's beaked whales in our study area typically have a much shallower (and thus inshore) distribution (*e.g.*, Fig. 3; Baird *et al.* 2006*a*), suggesting an island-associated population, though several of the groups encountered here were found in deep (>2,000 m) water. There is some evidence to support this suggestion; there are no resightings of any individuals from the three groups encountered in the deepest waters in our directed efforts, whereas there was at least one individual resighted out of all the remaining fourteen shallower groups photo-identified in directed efforts (Baird, unpublished). It is also possible that there may be some seasonal component to individual use of the area, although sightings of known individuals in multiple seasons suggests this is unlikely.

Given the few sightings each year and thus the long time-intervals between potential resightings (particularly for Cuvier's beaked whales), changes in marks may also have occurred to such an extent that some resightings may have been missed, though our restriction of resighting rate calculations to distinctive and very distinctive individuals, and to higher photo quality ratings, should reduce this bias. Although the large number of white oval scars on adult individuals mean that probably all adults (and most subadults) can be individually identified with sufficient quality photographs, the white scars do fade (over periods >10 yr), thus long time-intervals between encounters could result in some missed matches. Of the eight Cuvier's identified in 1990/1991, only three were considered "very distinctive," and two of those three were the individuals resighted up to 15 yr later (the third very distinctive whale was a probable adult male, and males may exhibit lower site fidelity, see below). Such a high resighting rate reflects a very high degree of site fidelity for this population. High resighting rates have been previously reported for Blainville's beaked whales in the Bahamas (Durban *et al.* 2001, Claridge 2006), though over a shorter time span than in the current study.

For both species of beaked whales, long-term resightings were documented much more frequently for adult females than for adult males, despite relatively similar numbers of known adult males and females in our catalogs (Cuvier's: adult males = 13, adult females = 15; Blainville's: adult males = 19, adult females = 21). We can think of no reasons why adult females should be easier to observe or photograph than adult males; in fact the opposite is likely true for Cuvier's beaked whales, where the extensive white pigmentation on adult males makes them easier to spot from a distance (personal observations). Simultaneous dive data from an adult male and an adult female Blainville's beaked whale tagged over a 30-h period indicate that dive durations of the two sexes are similar (Baird *et al*. 2006*b*). Similar findings of sex difference in resightings were reported for northern bottlenose whales (Wimmer and Whitehead 2005) and for Blainville's beaked whales in the Bahamas (Durban *et al.* 2001), where long-term resightings were higher for adult females than for adult males. In theory, depending on the mating system, the degree of site fidelity to foraging areas should vary by sex (Clutton-Brock 1989). Cetaceans rarely exhibit territorial behavioral (Miller 2002). For species where the females are either solitary or live in small groups, Clutton-Brock (1989) notes that males may search widely for females. For females, remaining in an area or returning to an area repeatedly may occur if prey are particularly abundant or reliably concentrated, whereas for males, females are the "resource," so individuals should move between concentrations of females for mating opportunities. How far individuals move away from this area is unknown however. Distances among resighting locations of known individuals (Fig. 4), as well as short-term movements of individuals tagged with suction-cup attached tags (Fig. 5), suggest that our study area does not represent the full range
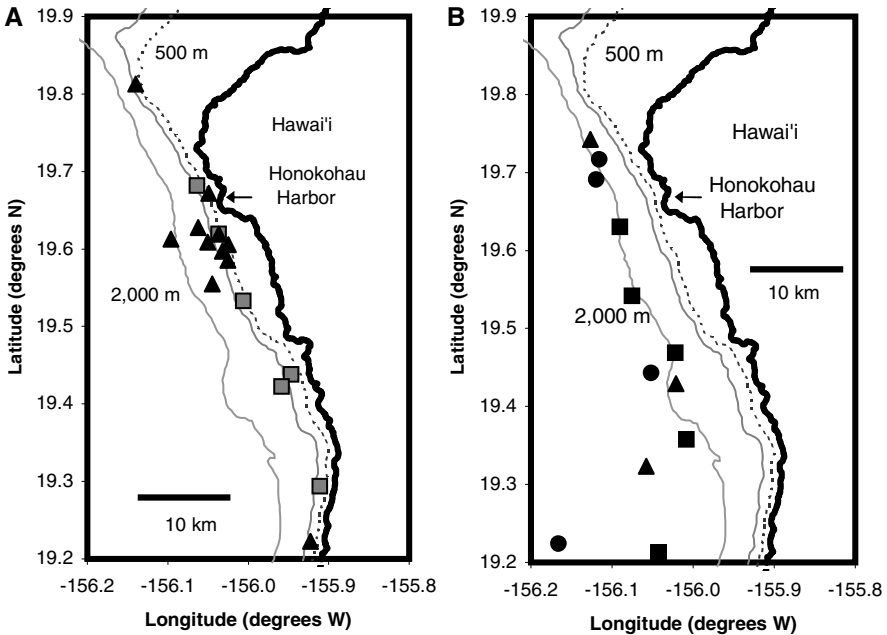
Figure 4. A. Resighting locations of two adult female Blainville's beaked whales (HIMd001, triangles *n* = 11 locations from 6 yr spanning 1994–2006, mean distance among locations 16.17 km [SD = 17.02 km]; HIMd007, squares *n* = 6 locations from 5 yr spanning 1997–2006, mean distance among locations 20.91 km [SD = 12.03 km]). B. Resighting locations of three adult female Cuvier's beaked whales (HIZc003, triangles, *n* = 3 locations from 2 yr spanning 2003–2004, mean distance among locations 32.02 km (SD = 17.79 km); HIZc029, squares, *n* = 5 locations from 4 yr spanning 1991–2006, mean distance among locations 23.35 km [SD = 12.33 km]; HIZc012, circles, *n* = 4 locations from 2 yr spanning 2004–2006, mean distance among locations 32.8 km [SD = 19.06 km]). The 500 m, 1,000 m, and 2,000 m depth contours are shown.

of individuals. Although we do have photographs of a small number of individual Blainville's beaked whales from elsewhere in the main Hawaiian Islands (seven, with no inter-island matches), we know of no photographs available of Cuvier's beaked whales from elsewhere in the main Hawaiian Islands. Field efforts elsewhere in the Hawaiian Islands where these two species may be found, or deployment of long-term satellite tags, are needed to address questions regarding movements. Given the site fidelity documented for both species, there is a potential for limited gene flow within the Hawaiian Islands, and genetic studies of population structure are warranted.

Little is known regarding the social organization of either species of beaked whale studied here. Claridge (2006) noted that Blainville's beaked whales in the Bahamas appear to exhibit female defense polygyny, with a social group of females accompanied by one male who denies access of other males to the group. Three groups encountered in our study had two adult males present, although the males remained spatially separated during the encounters. Our observations of the sex composition of Blainville's beaked whale groups and the repeated associations among adult males and adult
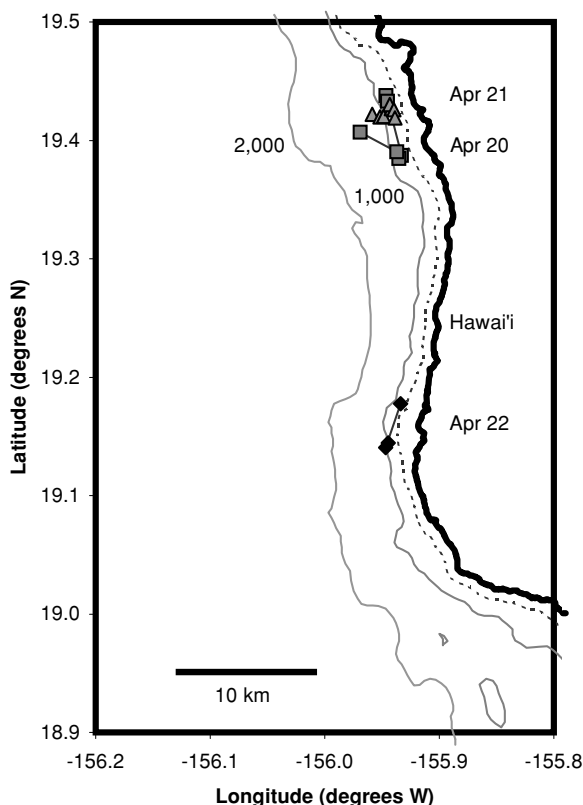
Figure 5. Resighting locations within- and between-days for two tagged Blainville's beaked whales (one adult male, one adult female) together in the same group. The 500, 1,000, and 2,000 m depth contours are shown.

females in all of the short-term resightings (1–154 d) tend to support the suggestion that Blainville's beaked whales exhibit female defense polygyny, very different to the social organization of northern bottlenose whales (Gowans *et al.* 2001) and likely social organization of Sowerby's beaked whales (*M. bidens*), where multi-male groups are regularly documented (Hooker and Baird 1999). Associations between both Cuvier's and Blainville's beaked whales encountered in this study were relatively fluid (mean association index of 0.08 and 0.06, respectively). For Blainville's beaked whales, individuals seen most frequently had numerous social partners (Fig. 3), and associations among adult females also appeared to be relatively short duration (weeks to months). For Cuvier's beaked whales our sample size of identifications is smaller (both fewer encounters and smaller average group sizes), and there were only five cases of repeated association between individuals. Repeated associations over several years were documented for a female and her calf, though other repeated associations were over short periods, thus we can say little about social organization of this species. Despite smaller group sizes and just over 70% as many groups of Cuvier's than Blainville's beaked whales, we did find two adult male Cuvier's beaked whales together on five

occasions, all with one or two adult females present in the group. In one of these cases, we observed percussive behavior by one of the males, which we interpret as potentially indicative of agonistic or competitive behavior between the two males present. Based on heavy linear scarring seen on adult males of both species (Fig. 1), agonistic interactions must occur regularly between adult males (Heyning 1984).

Although the high rates of resightings suggest considerable fidelity to the area for both Cuvier's and Blainville's beaked whales, information on resighting locations of individuals of both species suggest that individual ranges in this area are broad (Fig. 4, 5). Although the somewhat clustered locations for one individual Blainville's beaked whale (HIMd001 in Fig. 4) suggest a restricted home range, the majority of those locations came from the opportunistic field work, which was much more restricted in spatial coverage than the dedicated field work. Sighting locations from another individual Blainville's (HIMd007 in Fig. 4) obtained primarily from the more spatially diffuse directed effort were spread much more broadly over our study area (an average distance among sighting pairs of 20.9 km). With Cuvier's beaked whales, the average distance among sighting locations for eleven individuals (23.9 km) was similar to the average distance among all sighting locations (25.7 km), suggesting that individuals move throughout our study area. Information obtained over shorter-time periods of hours to days from a group of Blainville's beaked whales also indicated considerable movements (Fig. 4), suggesting that there is no single feature that individuals particularly associate with in our study area (*cf*. MacLeod and Zuur 2005). Short-term rates of movement were substantially slower than is typically documented for sperm whales (Whitehead 2003), though were similar to movement rates documented for northern bottlenose whales (Hooker *et al.* 2002).

There are several possible reasons for such long-term site fidelity of both species off the west coast of the island of Hawai'i. In theory, this area could be a refuge from predators, although photographs of one individual of both species show evidence of unsuccessful attacks from large sharks (Fig. 1), and killer whales have been documented in the area (Baird *et al.* 2006c). More likely, we suspect the high level of site fidelity relates to relatively high abundance or predictability of prey resources in the area. Unfortunately, virtually nothing is known regarding diet of either species within our study area, although Cuvier's are known to feed on deep-water squid and Blainville's are known to feed on deep-water squid and fish elsewhere (MacLeod *et al.* 2003). From tagging data, we know both species appear to dive as deep at night as they do during the day (Baird *et al.* 2006a, b), so it is unlikely the prey of either species are vertical migrating species associated with the deep-scattering layer. Productivity in the central tropical Pacific is very low, and densities of cetaceans in offshore waters of the Hawaiian 370-km Exclusive Economic Zone is relatively low compared to the more productive waters of the eastern tropical Pacific (Barlow 2006). The islands themselves result in a localized increase in both productivity (in surface waters) and predictability of prey resources, through nutrient input from freshwater runoff and upwelling driven by the "island mass effect" and wind stress curl (Doty and Oguri 1956, Gilmartin and Revelante 1974), as well as upwelling associated with cyclonic eddies that are generated in the lee (to the west) of the island of Hawai'i (Seki *et al.* 2001, 2002; Bidigare *et al.* 2003). What role these forces have in increasing density or predictability of deep-water (>800 m) cephalopods or fish is unknown, however, as little is known regarding deep-water currents or oceanography in the area. Studies of deep-water currents and their potential role in increasing deep-water productivity may help shed light on the high site fidelity of beaked whales reported here.

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