Movements of satellite-tagged Blainville's beaked whales off the island of Hawai'i

**Gregory S. Schorr[1],*, Robin W. Baird[1], M. Bradley Hanson[2], Daniel L. Webster[1],
Daniel J. McSweeney[3], Russel D. Andrews[4, 5]**

[1]Cascadia Research Collective, 218 ½ W. 4th Avenue, Olympia, Washington 98501, USA
[2]NOAA, Northwest Fisheries Science Center, 2725 Montlake Blvd E., Seattle, Washington 98112, USA
[3]Wild Whale Research Foundation, Box 139, Holualoa, Hawai'i 96725, USA
[4]School of Fisheries and Ocean Sciences, University of Alaska Fairbanks, Fairbanks, Alaska 99709, USA
[5]Alaska SeaLife Center, 301 Railway Ave., Seward, Alaska 99664, USA

ABSTRACT: Studies of movement patterns and habitat use in cetaceans are often constrained by factors such as ship time, logistics, and the ability to follow individuals over time. Obtaining this information on beaked whales is especially difficult, yet the information is critical to their management and conservation, particularly in light of their susceptibility to naval sonar. To better understand the movements of beaked whales around Hawai'i, Argos-linked satellite tags were remotely applied to the dorsal fins of 8 Blainville's beaked whales *Mesoplodon densirostris* in 2006 and 2008, representing the first time that beaked whales have been tracked by satellite. Transmissions from the tags were received for 15 to 71 d (mean = 48 d). All 8 individuals were tagged west of the island of Hawai'i, and moved out of the small-boat survey area, also making forays into naval training areas. Despite cumulative straight-line distances moved of up to 2383 km, maximum displacement from tagging location for any individual was only 139 km. Individuals utilized slope waters (mean depth = 1156 m) and remained relatively close to the island (mean distance = 16.9 km). No movements to the east side of the island were documented, despite the availability of similar deep-water habitat. Overall movement patterns suggest that the population is island associated and that individuals exhibit strong site fidelity, both of which increase the susceptibility of this small population to local perturbations.

KEY WORDS: Beaked whale · *Mesoplodon densirostris* · Argos · Satellite tracking · Mid-frequency active sonar · Site fidelity

INTRODUCTION

Studies of marine mammals in open-ocean environments present numerous challenges. Inclement weather conditions, high sea states, and logistic constraints (e.g. access to deep water) can make visual surveys difficult. Some species, such as beaked whales (family Ziphiidae), are particularly difficult to study in such circumstances. Common factors making them difficult to detect visually include their long dive times (Baird et al. 2006, Tyack et al. 2006), inconspicuous surfacing profile (Barlow et al. 2006), preference for deep-water habitats (often far offshore), and low population densities (Barlow 2006). These characteristics contribute to making beaked whales some of the least understood marine mammals.

Several beaked whale strandings around the world have been linked to the use of naval sonar (e.g. Simmonds & Lopez-Jurado 1991, Balcomb & Claridge 2001, Jepson et al. 2003, Cox et al. 2006), leading to an increased interest in the susceptibility of these species to impacts from anthropogenic noise sources, particularly mid-frequency active (MFA) sonar. The main Hawaiian Islands lie within one of the most heavily used US Navy ranges, the Hawai'i Range Complex (Anonymous 2008). This range is used by both the United States and visiting countries for naval training exercises that include the use of MFA sonar. The HRC covers a broad

area (806 000 km^2), encompassing all the main Hawaiian Islands; the area of particular interest for this study is the Alenuihaha Channel, which separates Maui and the island of Hawai'i (Fig. 1). According to the Final Environmental Impact Statement for the HRC released by the navy, the Alenuihaha Channel is the site of frequent sonar activity and was to be the site of choke point exercises during the 2006 Rim of the Pacific exercise. To date, no mass strandings of beaked whales have been documented in relation to naval activities in Hawai'i. However, Faerber & Baird (2007) conducted a geographic information system (GIS) analysis of the region, incorporating factors such as population size, percentage of cliff versus beach shoreline, currents, and other factors, and found that dead or moribund beaked whales would be less likely to strand or be detected in Hawai'i compared to the Canary Islands, where previous beaked whale strandings have been associated with naval activity (Simmonds & Lopez-Jurado 1991, Fernández et al. 2005).

A high degree of site fidelity has been documented for Blainville's beaked whales *Mesoplodon densirostris*

Fig. 1. *Mesoplodon densirostris.* Satellite-derived locations of Blainville's beaked whales tagged in 2006 after processing through the Douglas Argos-Filter Ver. 7.06. White circles: HIMd118; ▲: HIMd120; ■: HIMd001. Lines joining consecutive points illustrate time series rather than actual travel routes. The approximate boundary of the small-boat survey area is shown with a heavy black dashed line. The Alenuihaha channel, an area of antisubmarine warfare training exercises is outlined by the black dashed box

off the west (leeward) side of the island of Hawai'i (McSweeney et al. 2007), with some individuals having been re-sighted over 15 yr, and repeated sightings of individuals occurring in all oceanographic seasons (as defined by sea surface temperature; Flament et al. 1996). Over a 4 yr period, only 125 Blainville's beaked whales were estimated to use the west coast of the island (Baird et al. 2009). Long-term studies of beaked whales on the leeward side of Hawai'i have allowed for assessment of habitat use, site fidelity, aspects of social organization, and diving patterns using suction-cup attached data logging tags (Baird et al. 2006, 2008a, McSweeney et al. 2007). While photo-identification data have enhanced many aspects of our knowledge of these populations, they provide only snapshots of associations and the movements of individuals over time. Most importantly, conclusions regarding the distribution of animals derived from photo-identification studies are limited by effort (constrained by logistics and sea conditions); thus, the range of these individuals remains unknown.

Information on the movements of individuals is required to understand population structure and delineate stock boundaries. Unbiased information on where animals spend their time can also be used to identify important foraging habitats and assess the likelihood of repeated exposure to potential anthropogenic impacts. In areas where conditions often limit visual survey coverage, collecting unbiased information on movements is problematic. When survey conditions do not allow for broad coverage of all potential habitats, one method to examine movements is to instrument individuals with satellite tags, allowing for remote determination of locations.

In order to assess movements of individuals over a larger scale than the existing small-boat survey area delineated by McSweeney et al. (2007)(Fig. 1), we tagged beaked whales using a modified version of a tag used previously on killer whales *Orcinus orca* (Andrews et al. 2008). In 2006, satellite tags were deployed on 3 Blainville's beaked whales, and, in 2008, we were able to deploy satellite tags on 5 additional Blainville's beaked whales off the island of Hawai'i. Here we report the movements of these individuals, the first beaked whales to have been satellite tagged, and provide an assessment of habitat use and the likelihood of exposure to anthropogenic impacts.
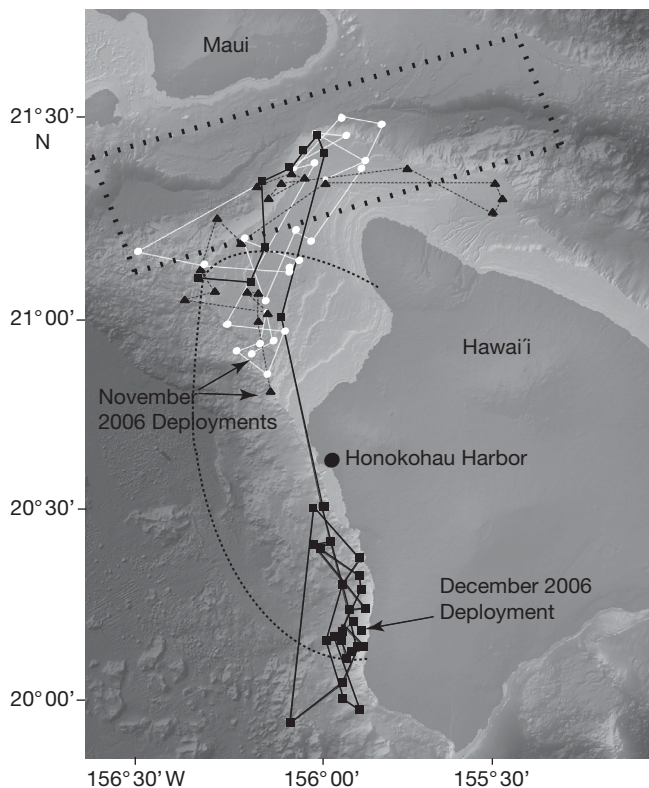
MATERIALS AND METHODS

Tags were constructed with a SPOT5 (Wildlife Computers), Argos-linked, location-only platform transmitter terminal (PTT), based on a design by Andrews et al. (2008). Tag dimensions were $65 \times 30 \times 22$ mm. Each tag

incorporated two 6.5 cm long medical-grade titanium darts that were screwed into 2 holes in the bottom of the tag. The darts were designed to penetrate the connective tissue in the dorsal fin and remain embedded with a series of backwards-facing 'barbs', which acted as anchors for the darts (see Andrews et al. 2008). The weight of the entire package was approximately 49 g. The transmitter electronics unit was designed to remain external to the body to minimize the invasiveness of the technique (Fig. 2). Tags were deployed using a Dan-Inject JM Special 25 pneumatic projector, with a modified arrow to hold the tag in flight at a range of 3 to 10 m.

Duty cycling of tags was modified throughout the study as additional information on the diving behavior of the whales became available (Baird et al. 2008a) and performance of tags in previous deployments was reviewed. Tags transmitted for either 5 or 10 h d^{-1} in 2006 and 18 h d^{-1} in 2008. Additionally, the repetition interval (minimum time between consecutive transmissions) was decreased from 45 s in 2006 to 15 s in 2008.

Field work was conducted off the west coast of the island of Hawai'i during November and December 2006 and July 2008. An 8.2 m Boston Whaler with a custom-built bowsprit was used for tagging. Searches were conducted in a non-random, non-systematic manner, with effort concentrated primarily in areas where conditions were conducive to spotting odontocetes and which could be reached by a small boat from Honokohau Harbor (Fig. 1).

Both the target whale and other individuals within the groups were photographed before and during tagging, and the sex of tagged whales was determined using the presence/absence of erupted teeth and scarring patterns. Photographs of tagged whales and companion animals were compared to a photo-identification catalog (McSweeney et al. 2007) to determine sighting history. Opportunistic efforts to re-sight tagged individuals were undertaken in the months following tagging, and individuals were photographed if possible.

Transmitter locations received from CLS Argos include a location class (LC), indicating the degree of accuracy in the reported position based on both the number of messages received in a single overpass and the temporal spacing of those messages (Argos User Manual, available at: www.argos-system.org/manual). LC 3, 2, and 1 locations each have a defined estimate of accuracy (defined by Argos as within 1 km of the individual's actual position); whereas LC 0, A, B, and Z transmissions do not include an estimate of accuracy. Therefore, all locations must be assessed for plausibility before being used to analyze an animal's movements (e.g. Argos User Manual; Harris et al. 1990, Mate et al. 1997, Vincent et al. 2002). We used the Douglas Argos-Filter, Ver. 7.06 (available at: http:// alaska.usgs.gov/science/biology/spatial/douglas.html), which assesses locations for plausibility using 2 independent methods: the distance between consecutive locations and the rate and bearings among consecutive movement vectors. The Douglas filter incorporates

Fig. 2. *Mesoplodon densirostris.* Adult male Blainville's beaked whale (HIMd118) with satellite tag attached to the dorsal fin. Photograph by R. W. Baird

several user-defined variables in the filtering process, including maximum-redundant distance (temporally near-consecutive points within a defined distance are kept by the filter), maximum sustainable rate of movement, which position should be kept based on location class, and the rate coefficient (Ratecoef) for assessing the angle created by 3 consecutive points. The algorithm for Ratecoef is based on the concept that the further an animal travels between position fixes, the less likely it is to return near the original location without any intervening location fixes, thereby creating an acute angle characteristic of typical Argos error. Larger angles become suspect (i.e. the filter becomes more conservative) as Ratecoef increases.

Filtering parameters applied to 2008 data were more stringent than those used for 2006, as improved programming provided a greater number of locations with better overall location classes associated with them. The maximum-redundant-distance was set at 3 km for both 2006 and 2008. The maximum sustainable rate of movement was set at 15 km h^{-1} for 2006 data and was reduced to 10 km h^{-1} for 2008. All Argos locations of classifications LC 2 and 3 were automatically retained. Bearings between locations (Ratecoef) were assessed using a rate of coefficient of 15 in 2006 and of 25 in 2008. All subsequent analyses were conducted using the resulting filtered dataset.

The cumulative distance covered during the signal contact period (period of time uplinks were received) and the straight-line distance from deployment were calculated using all locations that passed the filter. Rates of horizontal movement were calculated among consecutive locations with time intervals from 4 to 24 h; rates calculated from shorter and longer intervals were excluded to decrease the potential of spuriously low or high rates of movements being included. Times of sunrise and sunset were obtained for each day the tags transmitted in 2008, based on a central position of all filtered locations, and locations were classified as either day or night by transmission time to investigate diel patterns in movement rate and habitat use.

Depth, slope, and distance to shore were extracted for all filtered locations by overlaying point location data on a bathymetric raster surface in ArcGIS Ver. 9.2 (ESRI). Depth (in m) and slope values (in degrees) were transferred to point locations using the 'intersect point tool' in Hawth's analysis tools (Beyer 2004). A 50 × 50 m multibeam synthesis bathymetry model from the Hawai'i Mapping Research Group (available at: www.soest.hawaii.edu/HMRG/Multibeam/index.php) was used. The model had areas of missing data, so the grid was overlaid on a 3-arc second (90 × 90 m) US Coastal Relief Model bathymetry from the National Geophysical Data Center (available at: www.ngdc.noaa.gov/mgg/bathymetry/relief.html) to provide 90 m

resolution data where 50 m resolution data were absent. A combination of some low LC locations and the steep near-shore bathymetry sometimes resulted in locations that plotted on land. These locations were retained for the purposes of calculating rates of movement and distances covered, but were omitted for bathymetry calculations. We report the median values of our analyses to minimize the effect of outliers.

All whales tagged in 2008 were initially found in the same group; therefore, their locations were assessed to determine associations among group members over periods of days. Straight-line distances between pairs of whales were calculated using all pairs of locations received within single satellite overpasses (i.e. within <15 min of each other). Due to the error associated with satellite-derived positions, to assess whether individuals were together or apart, distance between pairs of locations were examined over consecutive sliding 2 d windows. Whales were considered associated if one or more pairs of locations (obtained within the same overpass) were within 8 km on either one of 2 consecutive days (e.g. distance apart could be 1.2 km on Day 1, 19.1 km on Day 2, and 5.6 km on Day 3, and the whales were considered associated for all 3 d). This comparison was undertaken simultaneously with a visual examination of the movement patterns of individuals in a time-lapse animation of locations, to confirm that movements of each individual were mirrored.

RESULTS

Three Blainville's beaked whales *Mesoplodon densirostris*, 2 adult males and 1 adult female, were tagged in 3 different encounters during November and December 2006, with tags functioning from 15 to 23 d (Fig. 1), resulting in a total of 83 locations (Table 1). Three Blainville's beaked whales, 1 adult male and 2 adult females were tagged during a single encounter of 10 whales on 10 July 2008. Only a single adult male (HIMd020) was present in the group. The same group was encountered 3 d later, and 2 additional adult females were tagged (Fig. 3). Locations from tags deployed in 2008 were obtained for a duration of 45 to 71 d (Table 1), with a total of 1714 locations after filtering. The LC varied for each individual, with LC 1 to 3 representing an average of 36% of all locations received (Table 2).

Comparisons of photographs of the tagged whales to our photo-identification catalog (McSweeney et al. 2007) indicate that 5 of the tagged whales (1 male and 4 females) had been previously identified in the study area (Table 3), and some had been previously associated with each other. HIMd001 and HIMd025 have the longest sighting histories of the tagged whales, having
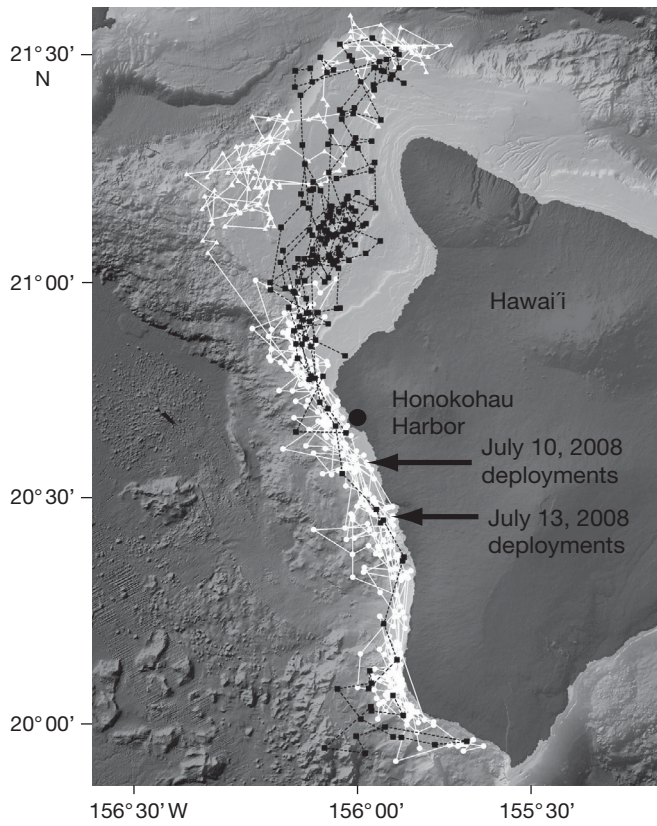
Fig. 3. *Mesoplodon densirostris.* Satellite-derived locations of Blainville's beaked whales tagged in 2008. HIMd007 (represented by the white circles and solid white line) is shown for the entire duration of signal contact, and because this whale traveled together with HIMd020 and HIMd036, its track is representative of movements by all 3 (see Fig. 4). HIMd025 (black squares and dashed black line) and HIMd148 (white triangles and solid white line, all north of 21° N) are shown for periods when they are separated from HIMd007 (see Fig. 4). HIMd025 and HIMd148 spent 41 and 31% of their time, respectively, mirroring the movements of HIMd007. Lines joining consecutive points illustrate time series rather than actual travel routes

first been identified in 1991. The adult male HIMd020 was first documented in 2003 and was in association with HIMd025 at the time, but had not been documented with any of the other tagged individuals. All previously identified adult females had been identified in groups with other individual males prior to tagging. Of the 3 tagged whales not previously identified, all were associated with individuals that had been previously identified at the time of tagging, and all individuals could be linked together as part of the same island-associated social network. Seven of the tagged whales were re-sighted post-tagging, with the most recent sightings ranging from 46 to 497 d after tag deployment.

Initial tag deployments occurred across the full extent of our small-boat survey area; HIMd118 and HIMd120 were tagged in the northern portion of the survey area, HIMd001 was tagged in the southern portion of our sur-

Table 2. *Mesoplodon densirostris.* Percentage of all locations for each individual which passed the Douglas Argos-Filter Ver. 7.06, by location class (LC). LCs of 1, 2, and 3 have an estimated error from Argos of <1 km, while LCs 0, A, B, and Z do not have an estimation of error associated with them and are presumed to be less accurate

Individual catalog no.	LC 3	LC 2	LC 1	LC 0	LC A	LC B	LC Z
HIMd118	4.0	8.0	12.0	16.0	36.0	16.0	8.0
HIMd120	0.0	10.5	5.3	15.8	31.6	31.6	5.3
HIMd001	0.0	11.1	16.7	19.4	22.2	30.6	0.0
HIMd025	1.1	11.3	30.6	41.0	6.4	8.8	0.8
HIMd020	3.3	12.7	34.0	41.7	3.8	4.1	0.3
HIMd007	2.0	15.8	35.9	30.2	0.6	9.6	5.9
HIMd148	1.5	12.1	30.9	44.4	4.2	6.7	0.2
HIMd036	0.8	7.8	20.9	38.9	11.1	19.3	1.2
Mean of all locations	1.6	11.2	23.3	30.9	14.5	15.8	2.7

Table 1. *Mesoplodon densirostris.* Details of Blainville's beaked whale satellite tag deployments. Photographs of tagged whales were compared to an existing individual photo-identification catalog to determine individual catalog number. Sex (M: male; F: female) of tagged whales was determined based on the presence of erupted teeth and scarring patterns (see McSweeney et al. 2007). Total number of locations was determined after processing data through the Douglas Argos-Filter Ver. 7.06, taking into account distance between consecutive locations and rate and bearings among consecutive movement vectors (see 'Materials and methods' for details)

Individual catalog no.	Sex	Deployment date	Date of last location obtained	Duration of signal contact (d)	No. of days locations were obtained	Total no. of locations after filtering
HIMd118	M	22 Nov 2006	15 Dec 2006	23	15	26
HIMd120	M	22 Nov 2006	8 Dec 2006	16	15	20
HIMd001	F	4 Dec 2006	19 Dec 2006	15	15	37
HIMd025	F	10 Jul 2008	10 Sep 2008	63	60	373
HIMd020	M	10 Jul 2008	30 Aug 2008	51	51	338
HIMd007	F	10 Jul 2008	11 Sep 2008	63	62	354
HIMd148	F	13 Jul 2008	22 Sep 2008	71	67	405
HIMd036	F	13 Jul 2008	27 Aug 2008	45	45	244

Table 3. *Mesoplodon densirostris.* Sighting history of tagged individuals, including previous associations with other tagged individuals. Adult males are noted in bold. All adult females tagged have previously been associated with non-tagged adult males. N/A: not applicable

Individual catalog no.	Year first documented	No. of times previously identified	Previous association with other tagged individuals prior to tagging (no. of times)
HIMd118	2006	0	N/A
HIMd120	2006	0	N/A
HIMd001	1991	14	HIMd007 (1), HIMd025 (2)
HIMd025	1991	7	HIMd001 (2), HIMd036 (1), HIMd020 (1)
HIMd020	2003	2	HIMd025 (1)
HIMd007	1997	11	HIMd001 (1)
HIMd148	2008	1	N/A
HIMd036	2008	1	N/A

vey area (Fig. 1), and the 5 individuals tagged in 2008 were tagged in the central portion of our survey area (Fig. 3). Locations of tagged individuals spanned from the south end of the west side of Hawai'i, north into the Alenuihaha Channel, which separates Maui and Hawai'i. HIMd120 was the only individual to move to the northeast side of the island, spending 3 d there before moving back to the west (Fig. 1). There were no movements of individuals to the east side of the island.

Straight-line distances between individuals tagged in 2008 indicate that some individuals stayed together for extended periods, while others disassociated and reassociated over time (Fig. 4). The median distance between HIMd007 and HIMd020 was 2.2 km (0.0 to 18.2 km, 89 pairs of locations) and between HIMd007 and HIMd036 it was 2.8 km (0.1 to 39.2 km, 56 pairs of locations), indicating that these whales were closely associated for the majority of transmission duration (bearing in mind the level of error associated with poor location qualities [55.8% of the locations received from 2008 deployments]; Table 2). Reviewing the locations of these 3 individuals in a time-lapse sequence (Supplement 1, available at: www.int-res.com/articles/suppl/esr00229_app/) also shows similar movement patterns. As HIMd007 had the longest transmission duration of these 3 individuals (Table 1) and the highest percentage of LCs between 1 and 3 (Table 2), rates of movements, distance traveled, and analysis of GIS data from this individual are used to represent all whales from the group while they were together.

HIMd148 left the group 3 d after tagging, separating as far as 164.0 km over 29 d before re-joining the other tagged whales (Fig. 4). HIMd025 left the group 10 d after tagging, separating as far as 129.6 km. Twenty-seven days post-tagging, these 2 individuals re-associated for 7 d (median distance between them of 1.9 km, range = 0.3 to 19.6 km, 23 pairs of locations) before re-associating with the other 3 tagged individuals. The adult male (HIMd020) remained associated with HIMd036 for the entire transmission duration and with HIMd007 for all but 3 d (Fig. 4). During times when HIMd148 and HIMd025 were separated from the rest of the group, they both spent more time in the northern portion of the study area, an area where the other 3 individuals were not tracked (Fig. 3). Cumulative straight-line distances between consecutive locations for entire tag durations ranged from 284.8 to 2383.0 km (median = 1303.0 km), but the maximum distance displaced from the tagging location was only 139.1 km (Table 4).

All tagged whales utilized similar depths (grand mean depth = 1156 m, range = 880 to 1455 m, n = 6) and remained closely associated with the island of Hawai'i (Table 5). Although the degree of bathymetric slope over which the whales spent their time differed
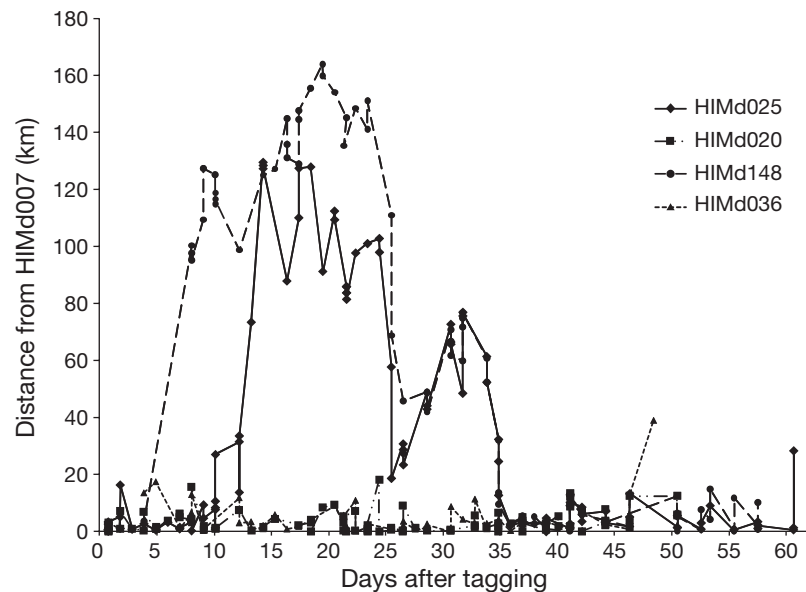

Fig. 4. *Mesoplodon densirostris.* Pair-wise distances of 4 individuals tagged in the same group in 2008 to HIMd007, using locations obtained within 15 min of each other (during a single overpass). HIMd020 and HIMd036 remained closely associated with HIMd007 for all but 3 d of the duration of signal contact (median distance = 0.9 km, range = 0.0 to 18.5 km and median = 1.2 km, range = 0.1 to 21.2 km, respectively)

Table 4. *Mesoplodon densirostris.* Information on movements of individual Blainville's beaked whales determined using locations from satellite tags after processing through the Douglas Argos-Filter Ver. 7.06. Cumulative horizontal distance moved was calculated using straight-line distances between all filtered locations. Rates of horizontal movement were calculated among consecutive pairs of locations with time intervals from 4 to 24 h; thus, sample sizes differ from those in Table 1. These values represent minimum rates, as movements between locations were likely not always in a straight line and do not take into account vertical movement (diving)

Individual catalog no.	Cumulative distance moved(km)	Distance from tagging location (km)		Rate of horizontal movement (km h^{-1})		
		Median	Max.	Median	Range	n
HIMd118	410.4	32.0	74.1	1.31	0.50–3.25	15
HIMd120	284.8	53.9	85.3	0.84	0.20–2.83	14
HIMd001	495.6	19.9	139.1	1.22	0.33–8.06	28
HIMd025[a]	2383.3	55.1	100.4	1.53	0.13–4.03	61
HIMd007[b]	2110.3	28.1	72.7	1.02	0.04–5.14	118
HIMd148[a]	2312.7	91.8	117.4	1.06	0.14–4.85	48
Grand mean	1332	46.8		1.16		

[a]Rate of horizontal movement data represent times when these whales were separate from HIMd007 (see Fig. 4)
[b]Data are representative for individuals HIMd020 and HIMd036

significantly among individuals (Kruskal-Wallis 1-way ANOVA, p < 0.001), plots of the positions overlaid on bathymetric data indicated that all whales remained associated with the slope of Hawai'i, with >96% of all locations plotting closer to the island of Hawai'i than to any of the other islands (Figs. 1 & 3, Table 5). A significant difference (Kruskal-Wallis 1-way ANOVA, p = 0.01) was found in diel depth utilization by the 2008 individuals. For all 3 individuals, slightly deeper depths were utilized at night, though the difference was only significant for HIMd025 (Mann-Whitney *U*-test, p = 0.005). However, the median difference in depth between day and night was only 97 m, likely not biologically significant.

Median rates of horizontal movement between consecutive locations from 4 to 24 h apart ranged from 0.84 to 1.5 km h^{-1}, with a maximum rate of 8.1 km h^{-1} (Table 4). Overall, rates of movement were slightly faster during the day (median = 1.33 km h^{-1}) than during the night (median = 1.15 km h^{-1}), but were not significantly different (Mann-Whitney *U*-test, p = 0.41). HIMd007 was the only individual to show a significant difference in diel rates of movement, with a rate of 1.4 km h^{-1} during the day and 0.9 km h^{-1} at night (Mann-Whitney *U*-test, p = 0.02, n = 73).

DISCUSSION

Despite some relatively short durations of signal contact, 1797 locations were obtained over 119 d from individual Blainville's beaked whales *Mesoplodon densirostris* tagged in 4 different groups, providing more information on the movements, habitat use, and associative patterns of individuals in this population than has been obtained with any other method. By comparison, in 202 d of field effort over 5 yr, McSweeney et al. (2007) documented just 19 sightings of Blainville's beaked whales in the same survey area and a median re-sighting interval for identified individuals of 348 d. This disparity is likely due to both the difficulty of detecting this species even in good sea conditions and to their low density in the survey area. Movements revealed by the satellite tag data, in combination with the sighting history of some tagged individuals (Table 3), support the supposition that these

Table 5. *Mesoplodon densirostris.* Details of habitat use by individual beaked whales based on a bathymetry analysis of filtered satellite location data using ArcGIS. The numbers of locations may be lower than those in Table 1, due to a small number of locations plotting on land. See 'Materials and methods' for details of analysis

Individual catalog no.	No. of locations	Depth (m)		Distance to shore (km)		Slope (°)	
		Median	Range	Median	Range	Median	Range
HIMd118	25	1108	777–2635	21.2	13.5–43.9	2	0–18
HIMd120	20	1218	802–2721	27.7	11.3–46.7	4	1–20
HIMd001	36	1455	49–3430	7.1	0.04–46.0	11	1–29
HIMd025[a]	187	880	111–2997	16.4	1.4–29.5	3	0–37
HIMd007[b]	335	1098	14–3268	4.4	0.1–28.1	13	0–41
HIMd148[a]	399	1179	392–2661	25.3	7.9–46.8	3	0–37
Grand mean		1156		16.9		6	

[a]Data represent times when these whales were separate from HIMd007 (see Fig. 4)
[b]Data are representative for individuals HIMd020 and HIMd036

individuals are part of an island-associated population and help extend our knowledge of habitat use and distribution of this population outside our small-boat survey area. Movement rates were low (Table 4), and despite cumulative distances covered over the duration of the tag transmissions of several 1000s of kilometers, the individuals remained relatively close to the original sites of tagging over periods of up to 71 d. While HIMd148 moved furthest from the island (Table 5), the median distance from shore for this individual was only 15.5 km (range = 0.1 to 46.8 km). Throughout the study, the whales showed a distinct association with the slope of the island of Hawai'i (Figs. 1 & 3).

While a small number of locations (3.3%) were closer to the islands of Kaho'olawe or Maui, the whales did not move away from the slope of the island of Hawai'i or towards other nearby bathymetric features. The association with the island of Hawai'i may be due to a local increase in productivity, resulting from island-associated upwelling caused by strong local trade winds and island topography (Seki et al. 2001). Similar associations with the main Hawaiian Islands have been documented for cetacean species that feed in near-surface waters, presumably taking advantage of increased availability or predictability of prey (Benoit-Bird & Au 2003, Baird et al. 2008b,c).

Despite the association with the island of Hawai'i, there is a clear lack of movements to the east side of the island. With the exception of 3 d spent by HIMd120 off the northeastern coast in the Alenuihaha Channel, there was no utilization of the habitat on the eastern side of the island by any individual. This disparity in use may relate to a combination of oceanic and atmospheric conditions that lead to an intense eddy field on the leeward side (i.e. to the west) of the islands (e.g. Seki et al. 2001, Calil et al. 2008). These mesoscale cyclonic eddies help bring nutrient-rich waters at depth to the euphotic zone, which helps increase biological activity and primary productivity (e.g. Seki et al. 2001, Nencioli et al. 2008), a phenomenon that does not occur to the same extent on the eastern side of the island where such eddies do not form. What little is known about diet indicates that Blainville's beaked whales in other regions primarily consume deep-water squid and small fish (MacLeod et al. 2003). Reduced prey availability on the east side of the island may explain the lack of movements, though more information is needed on prey types and prey availability to assess this supposition. Given the lack of survey effort and difficulty in studying this species on the windward (eastern) side of the island, it is also possible that a separate population of whales with a similar level of site fidelity occupies this part of the range and precludes eastward movements by individuals from the west.

However, no Blainville's beaked whales were sighted off the east side of the island during aerial surveys from 1993 to 1998 (Mobley et al. 2000).

Habitat use revealed by the satellite tag data fits well with that found by visual surveys. The grand mean depth of satellite-derived locations for tagged Blainville's beaked whales (1 156 m, n = 6) was similar to the mean sighting depths (922 m) reported for this species in previous studies (Baird et al. 2006). The greater depths documented from satellite-tagged individuals likely reflect the bias from sighting surveys towards the shallower waters of the study area. A large flat shelf north of Honokohau Harbor accounts for the difference in slope use between individuals (Figs. 1 & 3). Six of the tagged whales spent time both on the shelf and in areas of steep bathymetry, with the range of slopes varying between 0 and 41° (Table 4). Dive data from individuals tagged with time-depth recorder tags indicate that foraging dives occur over the shelf and further south, where a steeper bathymetry prevails (Baird et al. 2006, 2008a). This fact, coupled with the significant variability in slope use among tagged individuals, suggests that a specific slope angle does not influence foraging strategies or prey availability for this population. This result is in contrast with the findings of MacLeod & Zuur (2005) for Blainville's beaked whales off the coast of Great Abaco in the northern Bahamas, where slope, aspect, and depth were all correlated with the occurrence of the species. However, MacLeod & Zuur (2005) hypothesize that the relationship between seabed topography and the occurrence of Blainville's beaked whales may be influenced more by the distribution of prey due to localized upwelling, which the data also suggest for this population.

The lack of significant diel variation in location depths of the satellite-tagged whales reflects what is known of the diving behavior of this species from time-depth recording tags (Baird et al. 2008a). Baird et al. (2008a) demonstrated that Blainville's beaked whales spent more time at depths <100 m between foraging dives at night than during the day; however, rates and depths of foraging dives were similar. The significant difference in diel rates of movement of HIMd007 suggests a slower rate of travel at night, which could be a reflection of spending more time at the surface logging. However, the lack of significant difference in diel rates of movement in the other tagged individuals suggests this may be an artifact of overall low rates of movement and the quality of satellite locations, combined with our small sample size.

Tagging multiple individuals in a single group allowed us to gain insight into association patterns and social structure on a much finer scale than previously documented. Claridge (2006) and McSweeney et al. (2007) have discussed the reproductive strategy of

female defense polygyny in Blainville's beaked whales, and association patterns documented by individual movements in 2008 provide further evidence for this. Association of the adult male and HIMd036 across all paired locations (45 d) and with HIMd007 for all but 3 d indicates at least short-term close association between adult males and groups of females. While females HIMd025 and HIMd148 separated from the male for periods of from 26 to 29 d and for distances of up to 164.0 km, their locations indicated an association with the adult male for 41 and 31%, respectively, of his transmission duration (51 d). Both HIMd020 and HIMd036 were photo-documented on 4 September 2008 (after their tags stopped transmitting) in association with HIMd025 (D. J. McSweeney unpubl. data).

Documentation of HIMd020 with HIMd025 over 5 yr indicates that there may be some long-term associations between males and females; however, the previous documentation of HIMd001, HIMd025, and HIMd036 in groups with other males (McSweeney et al. 2007) suggests that these are not exclusive to individual males over the years. The identity of the adult male escorting a group of females likely changes with competition between males, evidenced by the long linear tooth scars on their bodies (Heyning 1984). Lack of continual associations between all animals in the group suggests that either males do not exert great influence over the behavior of females, or there is a high rate of competition between males.

McSweeney et al. (2007) documented a lower resighting rate of adult males compared with females, and the maximum number of years between re-sightings of adult males was 5, compared with 15 yr for adult females. This might suggest that males tend to move in and out of the area over time, though the time scale of such movements would appear to be longer than the weeks to months represented here.

The application of small dorsal-fin-attached satellite tags allowed us to extend our knowledge of the range and movement patterns of Blainville's beaked whales around the island of Hawai'i. Previous boat-based studies of beaked whales have not been conducted in the Alenuihaha Channel, due to the logistical challenges associated with small-boat surveys. Prevailing weather conditions in the Alenuihaha Channel are generally very windy, with high seas that increase in steepness as they are funneled between the islands of Maui and Hawai'i. Aerial surveys conducted in the channel during the 2006 RIMPAC exercises reported the mean sea state to be 4 to 5 on the Beaufort scale (Mobley 2006). Barlow et al. (2006) demonstrated a low encounter rate for *Mesoplodon* spp. as sea states increase above Beaufort 3, with a >10-fold reduction in encounter rates between Beaufort 0 to 1 and Beaufort 5. For these reasons, neither boat-based nor aerial

visual observations (a primary marine mammal mitigation measure used in conjunction with navy training exercises; Anonymous 2008) are likely to detect beaked whales in this area.

Movements revealed by satellite tracking indicate that the range of this population extends outside our small-boat survey area, both to the south and to the north into the Alenuihaha Channel, with 4 individuals spending much of their time in or adjacent to the channel (Figs. 1 & 3). As part of the HRC, all of the waters around the Hawaiian Islands may be used by naval forces for training exercises, and antisubmarine warfare exercises are known to be carried out in the Alenuihaha Channel (Anonymous 2008). These exercises include the use of MFA sonar and, in the case of choke-point exercises, may include several simultaneous sources of MFA sonar. While no MFA activity is known to have occurred in the area during the time of signal contact of tags in 2008, the technique demonstrates promise for monitoring movements of whales before, during, and after naval exercises.

The evidence of site fidelity, associations of individuals over time, and a small population estimate (Baird et al. 2009) from this and previous studies all suggest that this population consists of a distinct group of island-associated individuals. Small, isolated populations are generally at greater risk of population-level effects as a result of anthropogenic impacts (Bräger et al. 2002, Weilgart 2007). While these impacts may include fisheries interactions, environmental degradation (oil or chemical spill, depletion of primary food source), ship strikes, and anthropogenic noise sources, the potential impact of MFA sonar is likely high relative to these, given the overlap in naval training areas and whale movement patterns, and the sensitivity to sonar seen in this species elsewhere. The Hawai'i-based longline fishery operates in waters >45 km from shore, and a single mortality of Blainville's beaked whale has been reported associated with the fishery (Forney & Kobayashi 2007). Within the observed range of these populations there are no large-scale longline fisheries, although there are a number of troll fisheries that may interact with cetacean populations (Nitta & Henderson 1993). No major shipping lanes are routed through this area, though large cruise ships do routinely visit the island and local tug and barge traffic uses the channel for transit. Thus, a risk may be present from ship strikes, petroleum spills, or other waste, though this risk should be mitigated by the limited amount of time spent by Blainville's beaked whales at or near the surface compared to other species.

Application of this type of satellite tag shows promise for the study of small- to medium-sized cetaceans for which movement patterns, habitat use, and social structure are difficult to assess by traditional means.

Understanding these movements is critical for discerning stock structure and home ranges, particularly for species that may be at greater population-level risk from anthropogenic sources due to population size, distribution, and ecology.

LITERATURE CITED

Andrews RD, Pitman RL, Balance LT (2008) Satellite tracking reveals distinct movement patterns for Type B and Type C killer whales in the southern Ross Sea, Antarctica. Polar Biol 31:1461–1468

Anonymous (2008) Hawai'i Range Complex Final Environmental Impact Statement/Overseas Environmental Impact Statement (May 2008). United States Navy, Kekaha, HI. Available at: www.govsupport.us/navynepahawaii/FEIS.aspx (accessed in January 2009)

Baird RW, Webster DL, McSweeney DJ, Ligon AD, Schorr GS, Barlow J (2006) Diving behaviour of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales in Hawai'i. Can J Zool 84:1120–1128

Baird RW, Webster DL, McSweeney DJ, Schorr GS, Barlow J (2008a) Diel variation in beaked whale diving behavior. Mar Mamm Sci 24:630–642

Baird RW, Webster DL, Mahaffy SD, McSweeney DJ, Schorr GS, Ligon AD (2008b) Site fidelity and association patterns in a deep-water dolphin: rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. Mar Mamm Sci 24:535–553

Baird RW, Gorgone AM, McSweeney DJ, Webster DL and others (2008c) False killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands: long-term site fidelity, inter-island movements, and association patterns. Mar Mamm Sci 24:591–612

Baird RW, McSweeney DJ, Schorr GS, Mahaffy SD and others (2009) Studies of beaked whales in Hawaii: population size, movements, trophic ecology, social organization and behaviour. ECS Spec Publ 51:23–25. Available at: www.cascadiaresearch.org/robin/hawaii.htm#pubs

Balcomb KC, Claridge DE (2001) A mass stranding of cetaceans caused by naval sonar in the Bahamas. Bahamas J Sci 5:1–12

Barlow J (2006) Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. Mar Mamm Sci 22:446–464

Barlow J, Ferguson MC, Perrin WF, Ballance L and others (2006) Abundance and densities of beaked and bottlenose whales (family Ziphiidae). J Cetacean Res Manag 7:263–270

Benoit-Bird KJ, Au WWL (2003) Prey dynamics affect foraging by a pelagic predator (*Stenella longirostris*) over a range of spatial and temporal scales. Behav Ecol Sociobiol 53:364–373

Beyer HL (2004) Hawth's analysis tools for ArcGIS®, Vers. 3.21 [computer program]. Available at: www.spatialecology.com/htools (accessed in September 2008)

Bräger S, Dawson SM, Slooten E, Smith S, Stone GS, Yoshinaga A (2002) Site fidelity and along-shore range in Hector's dolphin, an endangered marine dolphin from New Zealand. Biol Conserv 108:281–287

Calil PHR, Richards K, Jia Y, Bidigare RR (2008) Eddy activity in the lee of the Hawaiian Islands. Deep-Sea Res II 55:1179–1194

Claridge DE (2006) Fine-scale distribution and habitat selection of beaked whales. MSc thesis, University of Aberdeen

Cox TM, Ragen TJ, Read AJ, Vos E and others (2006) Understanding the impacts of anthropogenic sound on beaked whales. J Cetacean Res Manag 7:177–187

Faerber MM, Baird RW (2007) Does a lack of beaked whale strandings in relation to military exercises mean no impacts have occurred? A comparison of stranding and detection probabilities in the Canary and Hawaiian Islands. In: Abstracts of the 17th Biennial Conference on the Biology of Marine Mammals, 29 Nov–3 Dec 2007. Society for Marine Mammalogy, Cape Town

Fernández A, Edwards JF, Rodríguez F, Espinosa De Las Monteros A and others (2005) 'Gas and fat embolic syndrome' involving a mass stranding of beaked whales (family Ziphiidae) exposed to anthropogenic sonar signals. Vet Pathol 42:446–457

Flament P, Kennan S, Lumpkin R, Sawyer M, Stroup ED (1996) Ocean atlas of Hawaii. University of Hawaii, Manoa. Available at: www.soest.hawaii.edu/hioos/oceanatlas/index.htm (accessed 15 March 2009)

Forney KA, Kobayashi DR (2007) Updated estimates of mortality and injury of cetaceans in the Hawai'i-based longline fishery, 1994–2005. NOAA Tech Mem 412:1–30

Harris RB, Fancy SG, Douglas DC, Garner GW, Amstrup SC, McCabe TR, Pank LF (1990) Tracking wildlife by satellite: current systems and performance. US Fish Wildl Tech Rep 30:1–60

Heyning JE (1984) Functional morphology involved in intraspecific fighting of the beaked whale, *Mesoplodon carlhubbsi*. Can J Zool 62:1645–1654

Jepson PD, Arbelo M, Deaville R, Patterson IAP and others (2003) Gas-bubble lesions in stranded cetaceans: Was sonar responsible for a spate of whale deaths after an Atlantic military exercise? Nature 425:575–576

MacLeod CD, Zuur AF (2005) Habitat utilization by Blainville's beaked whales off Great Abaco, northern Bahamas, in relation to seabed topography. Mar Biol 147:1–11

MacLeod CD, Santos MB, Pierce GJ (2003) Review of data on diets of beaked whales: evidence of niche separation and

geographic segregation. J Mar Biol Assoc UK 83:651–665

Mate BR, Nieukirk SL, Kraus SD (1997) Satellite-monitored movements of the northern right whale (*Eubalaena glacialis*). J Wildl Manag 61:1393–1405

McSweeney DJ, Baird RW, Mahaffy SD (2007) Site fidelity, associations and movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales off the island of Hawai'i. Mar Mamm Sci 23:666–687

Mobley JR (2006) Results of 2006 RIMPAC surveys of marine mammals in Kaulakahi and Alenuihaha Channels. In: Hawaii Range Complex Final Environmental Impact Statement/Overseas Environmental Impact Statement (Final EIS/OEIS), Vol 5 of 5. United States Navy, Kekaha, HI, p F53–F64. Available at: www.govsupport.us/navynepahawaii/FEIS.aspx (accessed in January 2009)

Mobley JR, Spitz SS, Forney KA, Grotefendt R, Forestell PH (2000) Distribution and abundance of odontocete species in Hawaiian waters: preliminary results of 1993–98 aerial surveys. SWFSC administrative report LJ-00-14C, Southwest Fisheries Science Center, La Jolla, CA

Nencioli F, Kuwahara VS, Dickey TD, Rii YM, Bidigare RR (2008) Physical dynamics and biological implications of a mesoscale eddy in the lee of Hawaii: cyclone *Opal* observations during E-Flux II. Deep-Sea Res II 55:1252–1274

Nitta ET, Henderson JR (1993) A review of interactions between Hawaii's fisheries and protected species. Mar Fish Rev 55:83–92

Seki PM, Polovina JJ, Brainard RE, Bidigare RR, Leonard CL, Foley DG (2001) Biological enhancement at cyclonic eddies tracked with GEOS thermal imagery in Hawaiian waters. Geophys Res Lett 28:1583–1586

Simmonds MP, Lopez-Jurado LF (1991) Whales and the military. Nature 351:448

Tyack PL, Johnson M, Soto NA, Sturlese A, Madsen PT (2006) Extreme diving of beaked whales. J Exp Biol 209:4238–4253

Vincent C, McConnell BJ, Ridoux V, Fedak MA (2002) Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. Mar Mamm Sci 18:156–166

Weilgart LS (2007) The impacts of anthropogenic ocean noise on cetaceans and implications for management. Can J Zool 85:1091–1116