

Chapter 14

Behavior and Ecology of Not-So-Social Odontocetes: Cuvier's and Blainville's Beaked Whales



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Abstract While beaked whales are the poorest-known family of cetaceans overall, the behavior and ecology of two species of beaked whales, Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*), have been studied extensively for more than 15 years in multiple areas around the world. This research was largely initiated as a result of the susceptibility of both species to react to high-intensity navy sonars, sometimes resulting in the death of individuals. In this chapter long-term studies of both species in Hawai'i are reviewed, informed by research on these species elsewhere. Both species have small populations that are resident to the island slopes, evidenced by a combination of long-term photo-identification and shorter-term satellite tag deployments. The two species coexist by partitioning their habitat in three dimensions, with Cuvier's beaked whales being found in deeper water, and diving deeper, than Blainville's beaked whales. Diving and acoustic behavior of the two species appears to be driven in part by predator avoidance. Both species echolocate only at depth, foraging deep in the water column during the day and at night, with less time spent near the surface during the day in between the deep foraging dives. Ascent rates are also slower than descent rates. All of these factors are likely ways of minimizing detection from near-surface visually or acoustically oriented predators such as large sharks and killer whales. There appears to be no strong selective pressure for grouping in these species. Both are often found alone and on average are found in very small groups (medians: Cuvier's = 2; Blainville's = 3). Groups that do form appear to function in part to avoid predators (for females with small calves) and allow for mating opportunities (for adult males seeking mates). Individuals of both species tend to have ephemeral social relations, although one pair of subadult Cuvier's have been documented together over an 11-year period. Blainville's beaked whale males exhibit female defense polygyny, while sperm competition may play a role in the mating system of Cuvier's beaked whales. Studies of these species in multiple areas spanning the tropics to temperate waters in two different oceans

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are beginning to earn them an important place in our overall understanding of cetacean ethology and behavioral ecology.

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Studies of the ethology and behavioral ecology of beaked whales (members of the family Ziphiidae) have lagged behind many other groups of cetaceans. The family Ziphiidae is the second-most speciose (after delphinids) taxonomic family of cetaceans, yet the poorest-known overall. There are 22 recognized species of beaked whales from 6 genera, as of 2018, and of those, 6 species (all from the genus *Mesoplodon*, with 15 recognized species) are known only from beach-cast specimens or skeletal remains. Such levels of obscurity reflect a combination of deepwater (usually open-ocean) habits, generally low abundance (at least for most species; Bradford et al. 2017), and very long dives, often exceeding 1 h (e.g., Hooker and Baird 1999; Minamikawa et al. 2007; Baird et al. 2008a; Schorr et al. 2014). Recent genetic studies have resulted in the recognition of new species (e.g., Perrin's beaked whale, *M. perrini*, Dalebout et al. 2002) and resurrection of long-lost species (e.g., Deraniyagala's beaked whale, *M. hotaula*, Dalebout et al. 2014) and revealed that there are undescribed species waiting to be recognized (e.g., a new species of *Berardius*, Morin et al. 2017). Of the 22 presently recognized species, only 2 have been studied based on large numbers of specimens (in both cases as they were targeted in whaling operations): the northern bottlenose whale (*Hyperoodon ampullatus*) and Baird's beaked whale (*B. bairdii*) (Benjaminsen and Christensen 1979; Kasuya 2017). Only four species, including the two above, have been the subject of long-term, in-depth studies in the wild, although two of those four have only been studied extensively in single localities: northern bottlenose whales in the Gully, off eastern Canada, and Baird's beaked whales off the Commander Islands, Russia (Whitehead et al. 1997; Gowans et al. 2000; Hooker et al. 2002; Fedutin et al. 2015).

Given their long dives and open-ocean habits, sightings of beaked whales tend to be infrequent and brief, limiting opportunities to study behavior and ecology with traditional observational methods.¹ Yet in recent years, our knowledge of behavior and ecology of beaked whales, in general, and of Cuvier's (*Ziphius cavirostris*) and Blainville's (*M. densirostris*) beaked whales, in particular (Fig. 14.1), has burgeoned. The impetus for most studies has been the evidence that at least some beaked whales are susceptible to effects of high-intensity sonar, occasionally stranding and dying as a result (Frantzis 1998; Balcomb and Claridge 2001; Fernández et al. 2005; Cox et al. 2006; Tyack et al. 2011). A wide range of research techniques includes traditional sighting

¹Some encounters with both Blainville's and Cuvier's beaked whales in Hawai'i primarily involve the animals floating motionless at the surface for a few minutes, before they disappear on a long dive, usually not seen again during the encounter.



Fig. 14.1 Top: While often considered cryptic, Cuvier's beaked whales, *Ziphius cavirostris*, in Hawai'i have been documented breaching in 11.6% of our encounters. We were able to identify the individual on the right as HIZc007, based on scarring patterns. Bottom: A juvenile Blainville's beaked whale, *Mesoplodon densirostris*, with a suction-cup attached time-depth recorder. Photos by (top) Annie B. Douglas and (bottom) Robin W. Baird

surveys, photo-identification, tagging to examine movements and behavior, analysis of acoustic behavior from animal-borne tags or towed or fixed hydrophone systems, controlled exposure experiments to document reactions to sonar and the sounds of potential predators, and genetic analyses of biopsy samples. We now have in-depth multi-year studies of Cuvier's beaked whales around oceanic islands (i.e., Hawai'i, the Canary Islands) and on continental slopes (i.e., off southern California, North Carolina, and in the Ligurian Sea). For Blainville's beaked whales, studies have been undertaken around a number of oceanic islands, in Hawai'i and the western (Bahamas) and eastern (Macaronesia) North Atlantic. Studies in multiple ocean basins and diverse habitats, from the tropics to temperate areas, can provide valuable opportunities for comparisons.

My work with Cuvier's and Blainville's beaked whales in Hawai'i began in April 2002 as part of a collaboration with Dan McSweeney, who had been working along the west coast of Hawai'i Island since the early 1980s, taking photos of beaked whales whenever encountered. The work in Hawai'i is a multi-species study² of odontocetes that includes efforts with a dozen species that range from nearshore to over 4000 m depth. Our studies are from small 6–9 m vessels on the leeward (west and southwest) sides of the islands, ranging from Ni'ihau in the northwest to Hawai'i Island in the southeast. Working conditions in typical deepwater beaked whale habitat (i.e., >500 m depth for Blainville's beaked whales and >800 m for Cuvier's beaked whales) are best off Hawai'i Island. In addition to our encounters (Cuvier's $n = 78$; Blainville's $n = 58$), we have photographs from other researchers (primarily Dan McSweeney) and from citizen science contributors (Cuvier's $n = 45$ encounters; Blainville's $n = 105$ encounters).

Our ability to understand beaked whale behavioral ecology in Hawai'i is enhanced by a broad suite of methods to study and compare two sympatric species, both of which travel in small groups. As well as photo-identification and some biopsy sampling, during our encounters we've obtained short-term information on diving and surfacing behavior from 13 suction-cup attached time-depth recorders (Baird et al. 2006, 2008a) and longer-term information on movements (and some dive behavior) from 27 LIMPET satellite tag deployments (Schorr et al. 2009; Baird 2016). In Hawai'i, it is helpful for photo-identification that both species are regularly bitten by cookie-cutter sharks (*Isistius* spp.), and the white oval scars that accumulate over time (McSweeney et al. 2007) can be used to identify individuals and assess age class of individuals. The scars can remain visible for up to 20 years (Baird 2016), and they allow individual identification from various angles, similar to the use of pigmentation patterns to identify blue whales (*Balaenoptera musculus*) or rough-toothed dolphins (*Steno bredanensis*), rather than just perpendicular photos of the dorsal fin. With good photos we are able to sex adults, because only adult males have erupted teeth (a single pair erupting from the lower jaw, at the tip in Cuvier's beaked whales

²The methods of this work have been published in detail so are not repeated fully here. Readers wishing more information on methods for surveys and during encounters should see Baird et al. (2013) and Baird (2016); on photo-identification and association analyses, see McSweeney et al. (2007); and on satellite tagging, see Schorr et al. (2009), Baird et al. (2011), and Baird (2016).

and approximately mid-jaw in Blainville's beaked whales), visible even when the mouth is closed. For adult and subadult Blainville's beaked whales, jaw morphology also differs dramatically between the sexes; as a male begins to mature, the arch of the lower jaw enlarges well before the teeth erupt, so we are also able to identify subadult males even before teeth erupt. Even if no photo of the head is available to assess whether teeth are present (or absent), the extensive linear scarring on adult males, and other pigmentation patterns, can be used to sex adult individuals (McSweeney et al. 2007; Baird 2016; Coomber et al. 2016).

This review uses published and unpublished results from our Hawai'i work, as well as insights from studies of beaked whales elsewhere, to help elucidate what factors influence the behavior and ecology of Cuvier's and Blainville's beaked whales. First, I set the stage by laying out the evidence for small resident populations of both species. Second, using satellite tag data, I show that the two species coexist on the island slopes by partitioning their habitat horizontally as well as vertically and also show how their range extends offshore and among the islands, outside our study area. Third, I use information on diving and vocal behavior to show that predation risk seems to drive not only where they spend their time in the water column but what they do while diving. Lastly, using information on group composition and association patterns, I draw insights into social organization—how grouping patterns reflect: (a) solitary foraging, (b) minimizing the risk of predation to calves, and (c) males seeking out, or sequestering, females for the opportunity to mate.

14.1 Evidence for Small Resident Populations

There are three species of beaked whales in Hawaiian waters (Cuvier's, Blainville's, and Longman's (*Indopacetus pacificus*) beaked whales), and another two (Ginkgo-toothed beaked whales, *M. ginkgodens*, and Hubbs' beaked whales, *M. carlhubbsi*) that are suspected to occur based on acoustics (Baumann-Pickering et al. 2014) but that have not been seen (Baird 2016). Beaked whale density is low in Hawai'i, even in suitable habitats. Off west Hawai'i Island, through early 2018, we have 4126 h of search effort in beaked whale habitats (i.e., depths >500 m) and have sighted Cuvier's only once every 52.9 h and Blainville's once every 71.1 h.³ Overall, there are 3.5 beaked whale sightings per 100 h of effort, but the study area is home to small resident populations of Cuvier's and Blainville's beaked whales, similar to what has been found for both species around other islands (e.g., Claridge 2013; Reyes 2017).

Photo-identifications allowed for estimating abundance of Cuvier's and Blainville's beaked whales from a Petersen capture–recapture model, with pooled data from 2003 to 2004 versus 2005–2006, two pairs of years where the sample sizes of identifications were high. For Cuvier's, abundance of marked (distinctive)

³As well as one sighting of Longman's beaked whales and eight sightings of unidentified beaked whales that were likely either Cuvier's or Blainville's.

individuals was estimated at only 55 ($CV = 0.26$), with 98.5% of individuals considered marked, while for Blainville's abundance of marked individuals was estimated at 125 ($CV = 0.30$), with 89.0% of individuals considered marked (Baird et al. 2009). Discovery curves, representing the rate at which new individuals are identified relative to the accumulation of identifications (i.e., not excluding re-sightings), also suggest that the populations of both species off Hawai'i Island are relatively small (Fig. 14.2). For Blainville's, this abundance estimate includes both a resident, island-associated population and some members of a pelagic, open-ocean population (Baird et al. 2011).

Long-term photo-identification data indicate a high level of site fidelity for Cuvier's and Blainville's beaked whales off west Hawai'i Island. For Cuvier's beaked whales, of the 40 individuals identified with excellent quality photos (thus maximizing the chances of being able to recognize them after even very long periods), 28 (70%) have been seen on more than one occasion, and 25 of those (89.3%) have been seen in more than 1 year. Over one-half (13 of 25) of those have been seen over spans of greater than 10 years, including females ($n = 6$) and males ($n = 5$). The longest span that an individual has been documented is 24.47 years, for a female first identified as a probable adult when seen in 1990. The adult sex ratio for Cuvier's beaked whales in Hawai'i appears to be close to 1:1 (54% female/46% male). Of the 37 known-sex distinctive adult individuals from Hawai'i Island, 20 are female and 17 male. Social network analyses show that the majority of individuals (59.7%) documented off Hawai'i Island are linked by association in the main cluster of the social network, indicating they are all part of the same island-associated population (Fig. 14.3).⁴ It is likely that many of the individuals in isolated clusters are also part of the island-associated population, but given the small group sizes (median = 2, range = 1–5), the likelihood of individuals being linked by association is relatively small for those individuals seen on only one occasion.

For Blainville's beaked whales photo-identified off the island of Hawai'i, the situation is similar: of 75 individuals with excellent quality photos, 44 (58.7%) have been seen more than once, and of those 36 (81.8%) have been seen in more than 1 year. Eleven of the 36 (30.5%) have been seen for over 10 years (maximum = 21.02 years). This includes eight adult females and three adult males. The adult sex ratio for distinctive Blainville's beaked whales also appears to be approximately 1:1 (52% female/48% male). Thus, the predominance of adult females among those seen over spans of 10 years or more suggests higher site fidelity for females. One female Blainville's that has been repeatedly photo-identified off Hawai'i Island (HIMd133, over a 10-year span) has been recently documented off O'ahu associated with a group there, suggesting that there may be links among communities off different islands. Social network analyses for Blainville's beaked whales off Hawai'i and O'ahu show that the majority of individuals (73.3%) are linked by association in

⁴This analysis was undertaken with individuals considered at least slightly distinctive and with fair- or better-quality photos; see McSweeney et al. (2007) for definitions. This result is particularly surprising given the high proportion of sightings of lone individuals and a median group size of two.

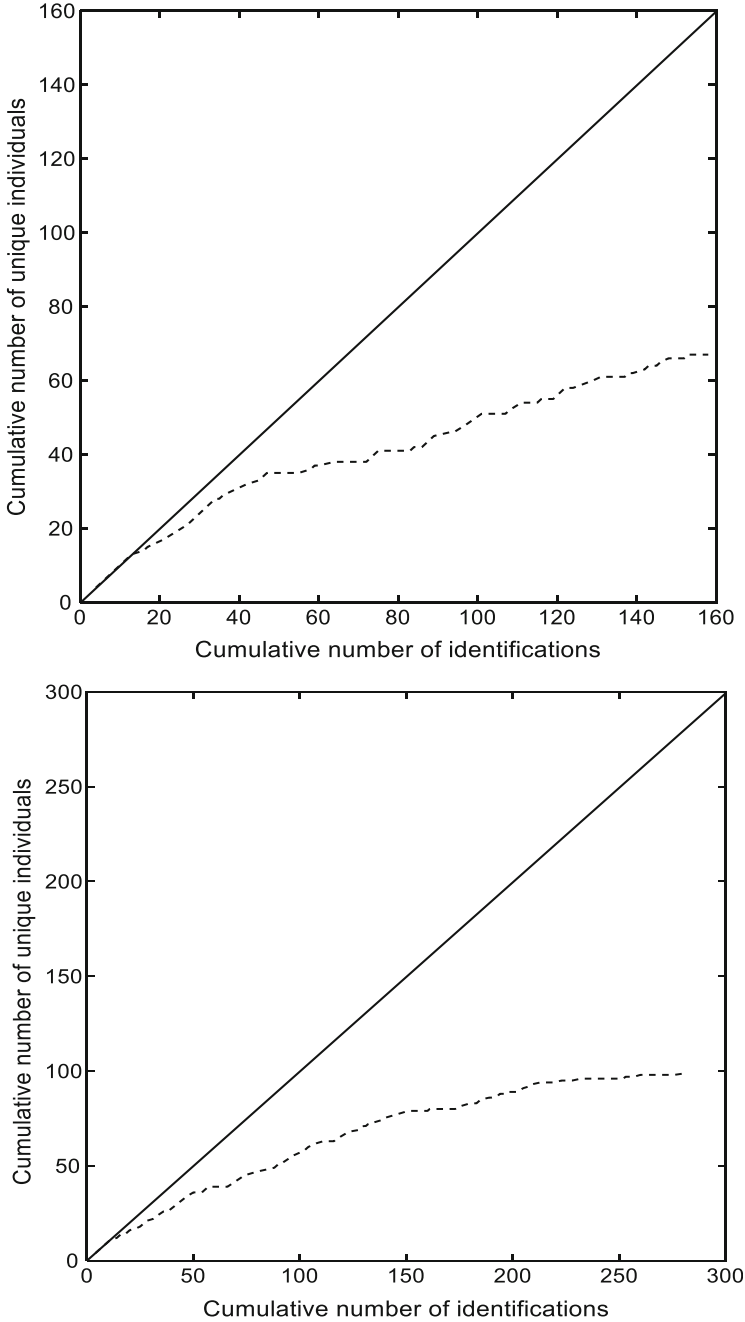


Fig. 14.2 Discovery curves for Cuvier's beaked whales, *Ziphius cavirostris* (top), and Blainville's beaked whales, *Mesoplodon densirostris* (bottom) off Hawai'i Island. Distinctive individuals with fair or better photo qualities are included, and a 1:1 line is shown. Time periods: Cuvier's photos 2002–2017; Blainville's 1986–2018, including individuals found in <3000 m only

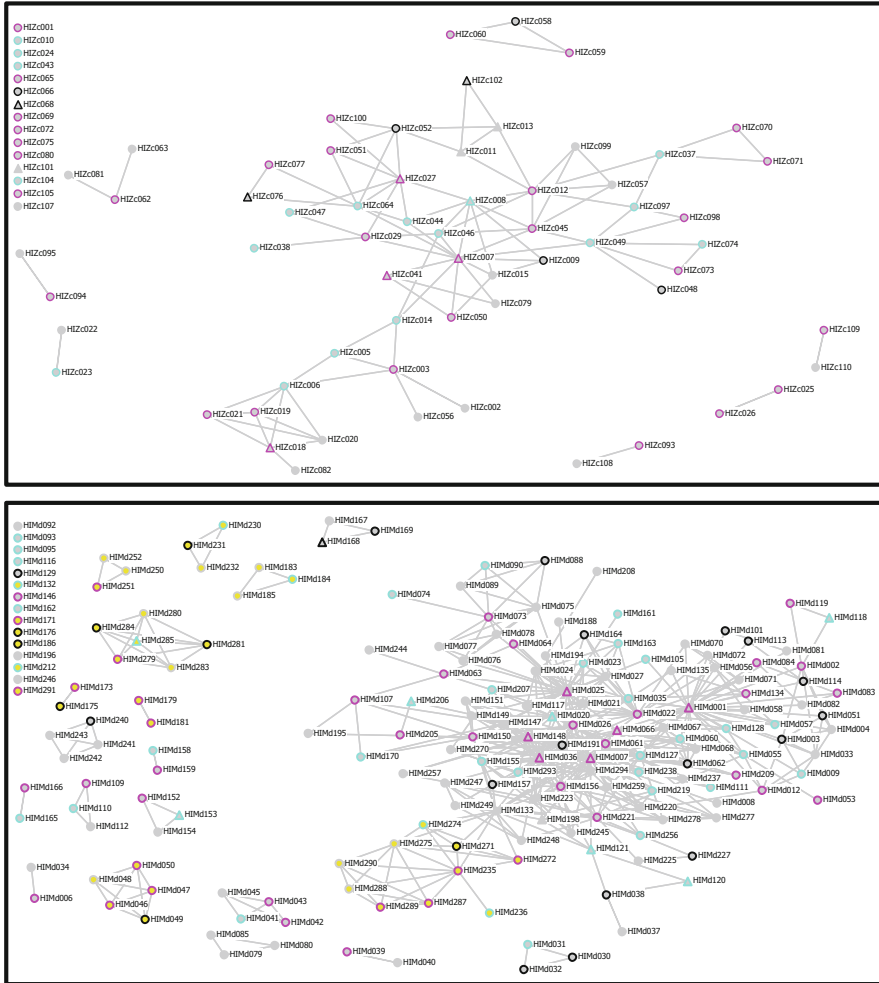


Fig. 14.3 Social networks for Cuvier’s beaked whales, *Ziphius cavirostris* (top), and Blainville’s beaked whales, *Mesoplodon densirostris* (bottom). For Cuvier’s beaked whales, only individuals photo-identified off the island of Hawai’i are shown, while for Blainville’s beaked whales, individuals from Hawai’i Island (gray centroid) and O’ahu (yellow centroid) are shown. Individuals that have been satellite tagged are indicated with triangles. Adult females are in pink, adult males in blue, unknown sex adults in black, and subadults, juveniles, and calves in gray

the main cluster of the social network (Fig. 14.3). The greater proportion of individual Blainville’s linked by association reflects their larger average group sizes (median = 3, range = 1–11) in comparison to Cuvier’s beaked whales, although there is also evidence for individuals from an open-ocean population of Blainville’s occasionally using the study area (see below and Baird et al. 2011).

14.2 Evidence for Niche Partitioning and Residency from Satellite Tag Data

Location data from satellite tags provides evidence of population identity (e.g., insular or open-ocean), habitat use, and niche partitioning between the two species. Tag data are available from ten individual Cuvier's (seven adult females, two adult males, and one subadult) tagged off Hawai'i Island between 2006 and 2015, for periods ranging from 7.2 to 49.5 days. While there is a combined 237 days of movement data, two pairs of individuals were tagged in the same group and remained associated for part of the period of overlap, so we effectively have 209 days of location and movement data. For Blainville's beaked whales, locations from satellite tags are available from 15 individuals tagged off Hawai'i Island between 2006 and 2015, for periods ranging from 10.4 to 169.2 days. Of these, three individuals tagged in the same group remained associated (Schorr et al. 2009), and two others were thought to be from an open-ocean population (see below). This leaves us with 456 days of location and movement data from the insular population, from adult females (six) and males (four).

Satellite tag data provide a more complete picture than do sighting surveys of how the species spend their time. On average, Cuvier's beaked whales stayed relatively close to the area where they were tagged (grand median = 51.4 km). All individuals remained largely associated with Hawai'i Island and nearby islands to the north, using our study area off the west side of the island and also off the south, east, and north sides—the latter three areas we have never surveyed (Fig. 14.4). For Cuvier's, the greatest distance moved from where they were tagged was only 203 km, by an adult female. This individual moved to off the north side of Moloka'i (via the east side of Maui). Of the ten tagged individual Cuvier's beaked whales, eight were in the main cluster of the social network (Fig. 14.3), indicating they are part of the resident, island-associated population, and both of those that were not in the main cluster remained close to the island regardless and were thus also probably part of the insular population.

For Blainville's beaked whales, we used three different factors to assess whether individuals are part of the resident insular population or part of an open-ocean population: (1) sighting history or association with known-resident individuals, (2) depth where the group was first encountered, and (3) spatial use after tagging. Of the 15 individuals tagged off Hawai'i Island, 12 are part of the main cluster of the social network, indicating they are part of the resident insular population. These individuals were encountered at depths ranging from 636 to 1492 m (median = 1024 m) when tagged. One other tagged individual, not part of the main cluster, was encountered in 737 m depth, and during the 20 days of tag data, this whale remained in relatively shallow waters (median = 1114 m). In general, individuals remained relatively close to where they were tagged (grand median = 55.1 km). Within their range, areas of highest density tend to have relatively weak surface currents and a high density of mid-water micronekton (Abecassis et al. 2015). Of the known or suspected resident individuals, the greatest distances moved were by two adult males, with one moving to north of

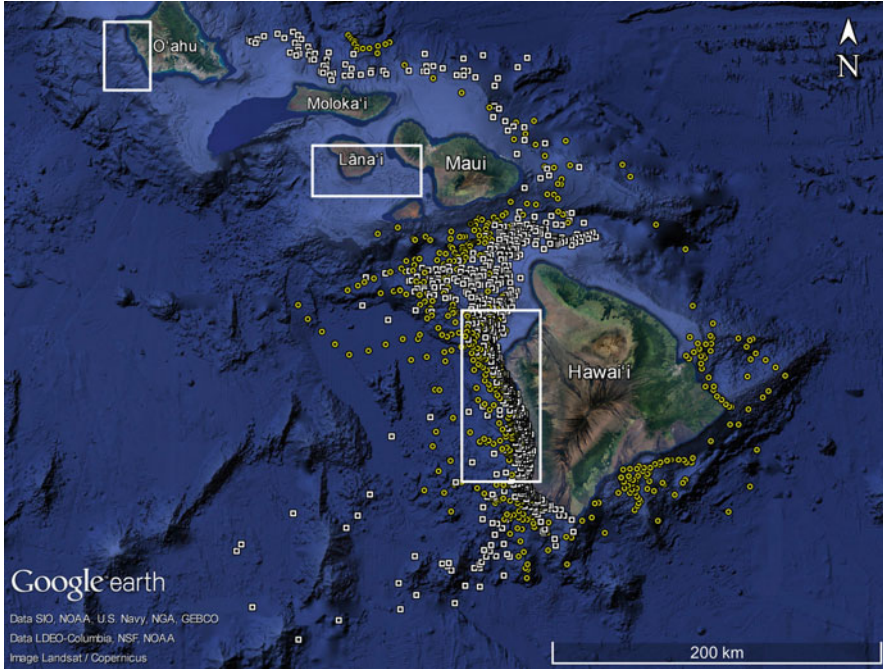


Fig. 14.4 Locations (produced using a switching state space model with 12-h time steps) from satellite tagged Cuvier's beaked whales, *Ziphius cavirostris* (yellow circles), and Blainville's beaked whales, *Mesoplodon densirostris* (white squares) including individuals known or thought to be from the island-associated populations and excluding individuals known to be acting in concert with others. The primary study areas are in white boxes

Maui, and the other as far as the east side of O'ahu (Fig. 14.4), a distance of 291 km from where it was tagged.⁵ Even individuals that are known to be part of the resident, island-associated population can move quite far offshore on occasion. One adult female (HIMd066), part of the resident social network and first documented off the island in 1997, moved as far as 192 km offshore, visiting several seamounts to the southwest of the island, before returning back to the island. By contrast, two other individuals that were not part of the main social cluster were encountered in deep water (3800 and 4000 m) and spent their time in very deep water (medians of 4702 and 4424 m, respectively), suggesting they are part of an open-ocean population. One individual in particular, tagged in 3800 m depth, moved about 1000 km west of the island in the first 20 days after tagging, remaining in deep water over the 39 days of tag data (Baird et al. 2011).

Although the two species broadly overlap along the slopes of the islands, spatial use data suggest they are able to coexist by partitioning the habitat between

⁵This individual, HIMd206 in our catalog, was our longest duration track (169 days). HIMd206 also moved offshore of the island for a short period, as far as 72.9 km from shore.

them.⁶ On average, Cuvier's beaked whales use depths more twice that of the island-associated Blainville's beaked whales (grand median of 2333 and 1155 m, respectively), and this difference is statistically significant (Mann–Whitney *U*-test, $p = 0.0035$, $n = 10$ Cuvier's, $n = 11$ Blainville's). By contrast, Cuvier's beaked whales may be found closer to shore (grand median = 15.0 km) than Blainville's beaked whales (grand median = 21.2 km), although this difference was not significant (Mann–Whitney *U*-test, $p = 0.45$). This potentially somewhat contradictory finding, with Cuvier's being in deeper water but closer to shore, is perhaps explained by differences in area use. For example, Cuvier's beaked whales used nearshore deepwater areas off the east side of the island of Hawai'i and off the south side of Maui, areas that Blainville's beaked whales did not use. Similarly, Blainville's beaked whales extensively used a relatively shallow area far from shore off the northwestern part of Hawai'i Island, and this area was less frequently used by Cuvier's (Fig. 14.4).

14.3 Diving and Surfacing Behavior: Foraging at Depth and Predator Avoidance Near the Surface

Whalers knew that at least some species of beaked whales could remain underwater for extended periods, with a report of a harpooned northern bottlenose whale remaining submerged for 2 h (Irving 1939). Application of suction-cup attached data logging tags (Hooker and Baird 1999; Baird et al. 2006; Tyack et al. 2006), harpoon-attached data loggers (Minamikawa et al. 2007), and most recently depth-transmitting satellite tags (Schorr et al. 2014; Baird 2016; Joyce et al. 2017) confirmed such long dives and demonstrated that, as noted by Tyack et al. (2006), beaked whales are “extreme” divers, both in terms of durations and depths. In Hawai'i, we have dive data from Cuvier's and Blainville's beaked whales, with short-term high-resolution dive data available from suction-cup attached data loggers (Cuvier's $n = 2$, Blainville's $n = 7$; Baird et al. 2006, 2008a) and longer-term lower-resolution information (i.e., depths and durations of dives and lengths of “surface” periods) from depth-transmitting satellite tags (Cuvier's $n = 4$, Blainville's $n = 2$). Combined, this represents 766 h (~32 days) of dive data for Cuvier's beaked whales (332 dives > 800 m) and 559 h (~23 days) of dive data for Blainville's beaked whales (205 dives > 800 m).

Cuvier's and Blainville's beaked whales typically perform at least three different types of dives: short and shallow dives during surfacing series that function primarily for gas exchange, very long and deep foraging dives, and intermediate dives that appear to serve some other purpose than either respiration or foraging. Between longer dives, in Hawai'i Cuvier's typically perform a series of 20–30 short dives (3–15 s in duration) that are only to 2–3 m in depth. For Blainville's beaked whales,

⁶Dive data from the two species also suggest niche partitioning; see the diving behavior section below.

these inter-ventilation dives are also only to 2–4 m deep, and the inter-breath intervals range from 5 to 42 s. It is during these relatively short surface periods that we have the opportunity to observe social behaviors, such as they are, and identify individuals as well as record information on the proximity of individuals at the surface.

Maximum dive depths and durations in Hawai‘i were 2800 m and 117 min for Cuvier’s beaked whales and 1599 m and 83.4 min for Blainville’s beaked whales, and both species dive deeper than 800 m about ten times per 24 h. Based on studies of diving behavior in other sympatric odontocetes in Hawai‘i, both species of beaked whales are regularly diving deeper than any other odontocetes (Baird 2016). Cuvier’s beaked whales do not appear to prepare for such long dives or recover from them at the surface (Baird et al. 2006), while Blainville’s beaked whales do both. From our observations with suction-cup attached time-depth recorders, Blainville’s increase the number of breaths prior to long dives (we recorded 38 and 41 breaths; Baird et al. 2006) and also recover from long dives, with 15 or more breaths.

These deep dives are known to be foraging dives, based on studies with acoustic tags. Neither species echolocates near the surface; instead echolocation, including buzzes associated with prey captures, occurs at depths greater than about 200 m (Johnson et al. 2004; Tyack et al. 2006). Echolocation starts shallower on the descent of dives and ends deeper on the ascent, suggesting that the whales begin foraging during the descent and stop shortly after they begin to ascend toward the surface. Although they often forage in groups, results from such studies have shown that Blainville’s beaked whales are individually catching multiple small prey (an average of about 25) on each foraging dive (Arranz et al. 2011; Madsen et al. 2013). There is limited information on what they are feeding on at such depths, but these deep foraging dives allow the whales to exploit a variety of deepwater cephalopods and fishes that rarely come close to the surface (West et al. 2017).⁷ Such long and deep foraging dives occur at similar rates and to similar depths during day and night (Baird et al. 2008a), suggesting that their prey do not vertically migrate, at least on short time scales (but see below for lunar cycle-related movements).

The number of ≥ 800 m dives per hour is similar between species (grand mean = 0.44 dives per hour for Cuvier’s and 0.41 dives per hour for Blainville’s). There is significant evidence of niche partitioning in dive depths: the grand mean dive depths and durations for Cuvier’s are 1284 m and 61.3 min, versus 1050 m and 49.9 m for Blainville’s (Mann–Whitney *U*-tests, depth $p = 0.008$, duration $p = 0.01$). Given the water depths where they are typically found in Hawai‘i (see above), Cuvier’s are likely feeding primarily in mid-water, while Blainville’s may feed at least occasionally on or near the bottom (see also Arranz et al. 2011). Lunar

⁷Beaked whales are suction feeders, retracting their tongue and using throat grooves to expand their gular region, creating suction (Heyning and Mead 1996). We documented one adult female Cuvier’s completely missing her rostrum and two adult female Blainville’s with rostrum deformities that might influence their ability to completely close the mouth (Dinis et al. 2017); but even with such deformities, the individuals appeared healthy and obviously able to feed.

cycles may influence the diving behavior of at least some species of beaked whales. One of the depth-transmitting satellite tags deployed on a Blainville's beaked whale in Hawai'i produced 11.8 days of dive and surfacing data over a 15.5-day span of time. From this, we found a significant positive relationship between deep-dive (i.e., dives > 500 m) depth and moon illuminated fraction, both overall (regression, $r^2 = 0.21$, $p = 0.0002$) and, more strongly, for nighttime dives when the moon was above the horizon ($r^2 = 0.366$, $p = 0.0017$), indicating that some vertical migration of prey occurs over longer time scales.

For species that feed at such depths, one obvious question is what happens when a female is accompanied by a small calf. In 2004 we deployed a suction-cup attached time-depth recorder/VHF radio tag on a female Blainville's that was accompanied by a calf estimated to be less than 2 months old. Using VHF radio tracking, we followed the group for over 5 h, and the calf was never seen at the surface while the female was down on any of her long dives, including dives of 48.0 and 47.5 min (to 1408 and 1380 m, respectively). Conditions were good during the period we followed the pair, suggesting we were unlikely to have missed surfacings by the calf (Baird et al. 2006). While it is hard to imagine such a young calf remaining beneath the surface for such periods, beaked whale calves are extremely precocious, even for cetaceans, with very high oxygen storage capabilities in the muscles (Velten 2012). Dunn et al. (2016) note that in 155 encounters with Blainville's beaked whale groups in the Bahamas with calves present, the calves were never seen at the surface alone. This is quite unlike the situation for sperm whales (*Physeter macrocephalus*), where calves of deep-diving mothers are often left with other subadults and adults in female-based matriarchies (Whitehead 1996).

While the very short and shallow dives are intervals between breaths when the whales are near the surface, and the long and deep dives function for foraging, what is the purpose of intermediate dives, typically to depths of 100–600 m for Cuvier's and 30–300 m for Blainville's? Unlike foraging dives, there is a diel pattern in the frequency of these intermediate dives, with an almost complete absence of them during the night (Baird et al. 2008a; see Fig. 14.5). This suggests that these intermediate dives are tied in some way to light levels; during the day, when they are not foraging and not breathing, they avoid near-surface waters. The silence of Blainville's beaked whales when near the surface, and during their long ascents toward the surface, has been suggested as a way of minimizing detection by near-surface predators (Aguilar de Soto et al. 2011). Predators such as killer whales (*Orcinus orca*) detect potential prey through passive listening and, like large sharks, also use vision. Beaked whales in Hawai'i are subject to predation pressure from both killer whales and large sharks (McSweeney et al. 2007; Baird 2016). Such a diel difference in occurrence of intermediate dives suggests that these dives represent avoidance of near-surface waters during the day to minimize detection by visually oriented predators (Baird et al. 2008a). Beaked whale descent rates are much faster than ascent rates (Baird et al. 2006; Tyack et al. 2006). It was originally thought that the slow ascents might function in reducing the likelihood of suffering decompression sickness (Hooker et al. 2009), but more recent models of blood and gas exchange (García-Párraga et al. 2018) suggest that slow ascents might not be physiologically needed.

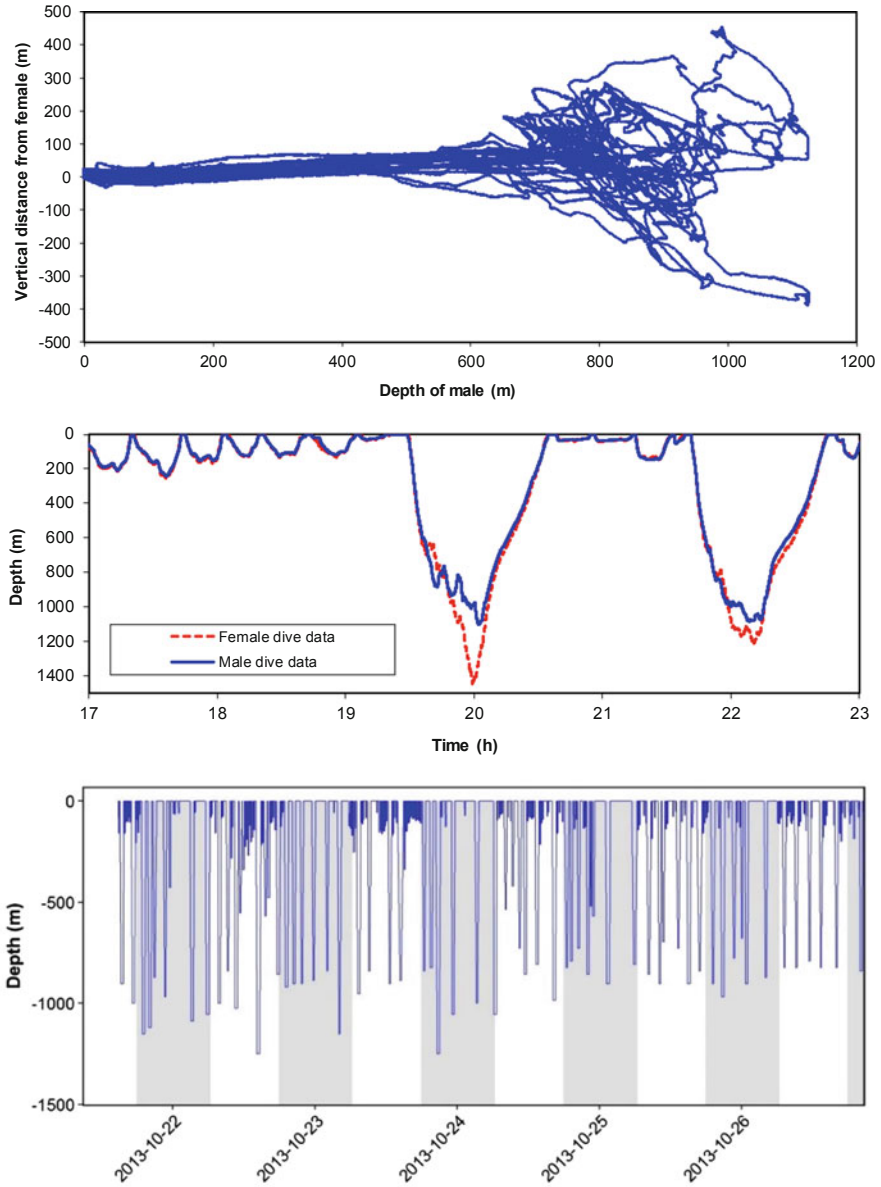


Fig. 14.5 Top: Dive data from a pair of Blainville’s beaked whales, *Mesoplodon densirostris*, showing the depth of the adult male in relation to its vertical distance from the adult female. Middle: A 6-h time series of dive data from both individuals, showing intermediate dives (~50–200 m) and two deep foraging dives. Bottom: A ~5.5 day series of dive data from a juvenile Blainville’s beaked whale (HIMd198), with nighttime periods indicated by shading. Note the relative lack of intermediate dives during nighttime periods

Slow and quiet ascents would, however, provide an opportunity for visual and potential acoustic detection of predators that might be closer to the surface while not advertising their presence to acoustically astute killer whales.

Based on observations at the surface, individuals tend to dive in synchrony, but less is known about what happens at depth. In Hawai'i we have dive data from two Blainville's beaked whales tagged in the same group, an adult male and female. In this case (Fig. 14.5), until the whales were about 500–600 m deep, they remained at similar depths (within ~30 m), but after that they diverged, the male foraged deeper than or shallower than the female. While we were not able to assess horizontal distances between the two, this is consistent with the whales remaining close to each other prior to the start of foraging (i.e., when they began echolocating), after which they were likely able to keep track of each other by listening to echolocation clicks. They were coordinating behavior, or, more likely, the male was following the female, given the mating system of this species (see below), rejoining on ascents. From tracking individuals through multiple long dives with the aid of VHF tags, individuals would always surface within 10–20 m of each other after the end of long dives. Work by Aguilar de Soto et al. (2018) also demonstrates that when foraging in a group, Cuvier's and Blainville's coordinate their dives and their vocal activity, in such a way that would minimize detection by potential predators such as killer whales while generally foraging on small individual prey several hundred meters apart.

14.4 Social Organization: Insights from Group Composition, Association Patterns, and Social Behavior

Knowing sex and approximate age of many individuals makes it possible to understand social organization. One limiting factor in interpreting association patterns is that we do not yet know precisely the age of sexual maturity for Cuvier's beaked whales. Few calves have been documented, and only one female has been known to have two calves (7 years apart). Therefore, it is unlikely that Cuvier's become pregnant when still nursing a calf, which helps in the interpretation of association patterns. Blainville's beaked whales are thought to give birth to their first calf when between 10 and 15 years of age (Claridge 2013).

14.4.1 Cuvier's Beaked Whales

Cuvier's beaked whales are not particularly social. Of the 18 species of odontocetes in Hawaiian waters, only pygmy sperm whales are found in smaller groups, on average (Baird 2016). In Hawai'i, the most frequently encountered groups are of

lone individuals, representing 34.2% of all sightings, and the median group size is two (mean = 2.2, maximum = 5). Group sizes in the Canary Islands are similar (mode = 1, median = 2, max = 7, $n = 357$; C. Reyes and N. Aguilar de Soto, personal communication). Off Cape Hatteras, North Carolina, in an area with much higher density of Cuvier's beaked whales (McLellan et al. 2018), two is the most frequently encountered group size (Fig. 14.6), and lone individuals are uncommon (14.5% of sightings). While median group size off Cape Hatteras is only three, the maximum group size documented was eight (A.J. Read, unpublished), with a similar sample size (Hawai'i $n = 79$; North Carolina $n = 83$). Group sizes in the Ligurian Sea are somewhat in between (mode = 2, median = 2, max = 8, $n = 100$; Moulins et al. 2007; Tepsich et al. 2014; CIMA Foundation unpublished data). Such differences in group size likely reflect ecological differences among the areas. Although our understanding of deepwater ecology is limited, the area surrounding the Hawaiian Islands is generally oligotrophic, with only small increases in productivity associated with the islands, while the area off Cape Hatteras is highly productive. Whether such productivity extends into the bathypelagic ecosystem is unclear, but I suspect it does, allowing for the formation of slightly larger groups (Fig. 14.6).

Group size, as well as age and sex of the group members, can be used to help interpret the function or purpose of grouping or in this case lack of grouping. In Hawai'i, of 22 lone individuals for which we were able to determine age class, 8 were adult males, 8 adult females, and 6 subadults of unknown sex. Such a high presence of lone adults suggests that, at least in an area with relatively low abundance, there is no strong selective pressure for grouping, in terms of either potential benefits of group foraging (evidence from acoustic studies suggest the whales forage on small individual prey, even when in a group) or avoidance of predation (at least for lone adults). For pairs of individuals, of the 13 cases when we were able to confirm age class, there was only one single pair comprised of an adult male and adult female; other groups were an adult female with a juvenile or small calf (seven groups), pairs of subadults (two groups) or unknown adults with a subadult (two groups), and one adult female–adult female pair. Of 18 groups of 3 or more where all individuals were identified and sex of all adults was known, only 3 calves less than 1 year of age were documented, and all were in groups of 4 or 5 individuals that contained 2 adult females and 1 adult male (3 of 7 groups, ~43%). This suggests that females with small calves may be more likely to associate with other adults. One possible explanation is reduced predation risk—a female nursing a small calf that may not have completely developed its diving capabilities might be more likely to associate with other adults as a way of diluting the risk of predation to her calf or to benefit from the increased ability of the group to detect predators (Mann et al. 2000; Creel et al. 2014).

Five of the groups of three or more individuals had no adult males present; in each case there was a pair of adult females with one or two additional juvenile or subadult individuals. By contrast, there were seven groups with two adult males and one or two adult females, with no juveniles or subadults, presumably reflecting that females are

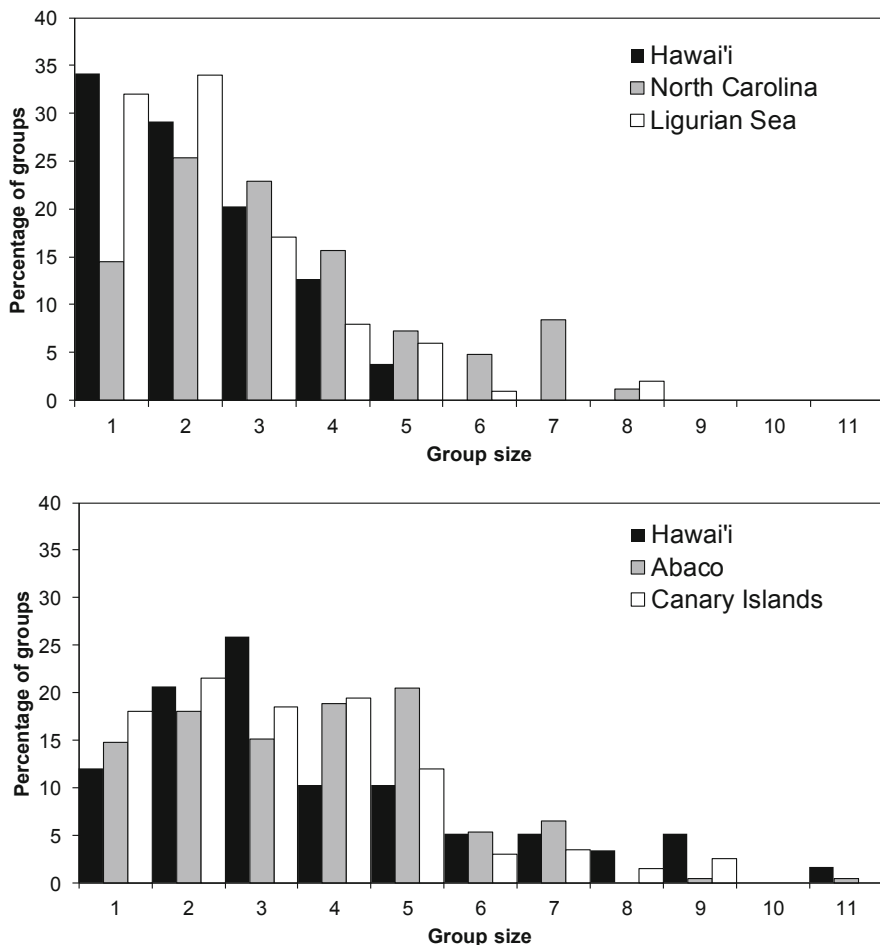


Fig. 14.6 Comparison of group sizes for Cuvier's beaked whales, *Ziphius cavirostris* (top), and Blainville's beaked whales, *Mesoplodon densirostris* (bottom) encountered during small-boat effort, each in three different study areas. North Carolina data provided by A. J. Read; Abaco, Bahamas, data provided by D.E. Claridge; Canary Islands data provided by C. Reyes and N. Aguilar de Soto; and Ligurian Sea data provided by M. Rosso. The x- and y-axis scales are the same for comparative purposes

more likely to come into estrus once their earlier calf has weaned and dispersed.⁸ Association analyses provide a basis for understanding the details and nature of these groupings. Using a half-weight association index with all individuals in our larger dataset (i.e., including citizen science contributions) seen three or more times, the

⁸Much of this is speculative of course, since so little is known about the reproductive cycles of beaked whales.

mean association index is 0.05 (SD = 0.03), while the mean of the maximum association index is 0.40 (SD = 0.25). Not surprisingly, values are lower than for three other social odontocetes that are sympatric, all of which have mean maximum values of >0.50 (rough-toothed dolphins max = 0.58 (SD = 0.31), Baird et al. 2008b; short-finned pilot whales max = 0.91 (SD = 0.31), Mahaffy et al. 2015; false killer whale max = 0.64 (SD = 0.24), Baird et al. 2008c).

There is one pair of individuals though that provides some evidence of long-term associations, even if such associations are rare. In November 2004, we encountered a group of five Cuvier's, including two juveniles, HIZc011 and HIZc013. In December 2010, in a group of three individuals, both individuals were again present. During that encounter, we deployed LIMPET satellite tags on both and obtained a biopsy of one (HIZc013, confirmed genetically to be a male). Based on scarring and the lack of erupted teeth, HIZc013 was considered to be a subadult at that time. Tag data for the two individuals overlapped for 16 days; during that period the pair separated and rejoined four times, with the longest time apart about 6 days (separating as much as 90 km). In October 2011, we encountered the pair again, with no others present, and most recently, in November 2015, we encountered them together again, this time with one other adult individual. These two individuals have not been seen on other occasions; thus their association index value is 1. Interestingly, while we do not have photos of two of the individuals seen with them in November 2004, all other individuals with which they were documented were adult females or individuals thought to be adult females based on scarring and the lack of erupted teeth. In November 2015, HIZc013, the known male, still did not have erupted teeth so was considered a subadult, although it was likely a minimum of about 13 years old at that time, and the sex of HIZc011 is unknown. Head photos of HIZc011 were available in 2015, and no erupted teeth were visible. Given the apparent lack of bonds between adult females and adult males, based on the sex composition of groups encountered and the number of cases with two males present in the same group, I suspect that HIZc011 may also be a male. If so, this example may represent a bonded male/male pair, similar to those seen in some bottlenose dolphin populations (Connor et al. 2000). When we have seen two adult males together in the same group, there has always been at least one (and often two) adult female(s) present, and the males have always remained apart, typically on either side of the female(s). In the past I interpreted such separation as evidence of competition between the two males over access to the females, effectively some sort of prolonged posturing, while the individuals were sorting out who was dominant (or the female was trying to choose with whom to mate). The large number of linear scars in adult male Cuvier's beaked whales clearly indicates that direct male-male competition occurs, but there is also a suggestion that sperm competition may be important for this species (MacLeod 2010). It is possible that pairs of adult males at times cooperate to sequester a female from other competing males, and if both get to mate with the female, they thus have an increased likelihood of siring offspring.

Surprisingly, this type of time series is the best indicator of the age of sexual maturity for Cuvier's beaked whales—we are awaiting our next encounter of these two, with the hopes of documenting tooth eruption in HIZc013, to confirm the sex of HIZc011 and to see if they are still together. If they are still together, knowing the sex

of HIZc011 should help confirm or refute the idea that males may occasionally form long-term bonds. Obtaining a genetic sample of HIZc011 to examine relatedness between the pair would also help elucidate the potential reasons for such apparently enduring bonds. We had one other case with two Cuvier's satellites tagged in the same group, an adult female and adult male tagged in the same group in May 2008. In this case, the pair remained together for the first 8 days before separating. Although they have been seen a combined 13 times (6 times for the adult male and 7 times for the adult female), this is the only encounter where the two were documented together, so associations over those 8 days likely represented a relatively rare association, rather than an enduring bond between them.

14.4.2 Blainville's Beaked Whales

Blainville's beaked whales are more social than Cuvier's, albeit only slightly; the mean group size in Hawai'i is 3.8, and both the median and modal group sizes are three (range = 1–11). Group sizes in other areas where this species has been studied are generally in the same range, although there is variability (Fig. 14.6). Lone individuals are much less common than for Cuvier's, representing just 12% of all sightings, and have included adult females (twice), an adult male (once), subadult male (once), and subadult of unknown sex (once). This lack of an obvious sex bias for lone individuals suggests they are not adult males moving between groups. For pairs of individuals, of the ten cases when we were able to confirm age class (and in most cases sex) of both individuals in the group, there were two pairs comprised of an adult male and an adult female; other groups were of an adult female with a juvenile or small calf (five groups), an adult female–adult female pair (one group), a subadult and a juvenile (one group), or an unknown adult with a subadult (one group). Of 34 groups of 2 or more individuals for which the sex of all adults in the group was known, there were only 2 groups with more than 1 adult male present: a group of 8 including 3 adult female/juvenile pairs and a group of 5 containing 3 adult females. In both cases, the adult males remained separated from each other during the encounters. Calves less than 1 year old were documented in ten different groups, and the median group size of these was six individuals (maximum = 9), double the overall median group size. This suggests that females with small calves preferentially associate with other females, possibly due to some advantage in terms of detecting predators or minimizing predation risk on their calf, as mentioned for Cuvier's above. Adult males were present in only three of the ten groups, and in all three cases, there were multiple adult females present (2, 3, 3), suggesting that adult males only associate with such groups if there are adult females present that might be in, or may be about to come into, estrus. In those same ten groups, adult females were present in all groups, and more than one adult female was present in five groups.

Using a half-weight association index with all individuals in our larger dataset (i.e., including citizen science contributions) seen three or more times, the mean association index for Blainville's beaked whales is 0.08 (SD = 0.03), while the mean

of the maximum association index is 0.44 (SD = 0.22). Examining dyads illustrates the duration of bonds among different age/sex classes.⁹ For example, between adult females and juveniles or calves ($n = 36$ dyads), at least some of which are likely mothers with their calves, 16 (44.4%) were seen together over periods greater than 2 months, and the maximum span of time together has been about 2.5 years, suggesting that calves disperse between 2 and 3 years of age.¹⁰ For adult male–adult female dyads ($n = 23$), only three (13%) were longer than 2 months. Based on the number of intervening sightings of one or both individuals in the dyad without the other present, the three that were longer represented cases where the two individuals associated, disassociated for periods of from 1 to 11 years, and then reassociated, rather than reflecting a long-term association among them. Adult male dyads were only documented four times, and there were no repeated associations for them. Unlike the unusual example of the two subadult Cuvier’s beaked whales appearing to remain associated for more than 10 years, there were no long-term associations among subadults or juveniles. Of the five dyads between subadults and juveniles meeting our criteria,⁹ all were associated for less than 1 year. For Blainville’s, the only age/sex classes that appeared to reassociate on a semi-regular basis are adult females with other adult females. Of the 39 adult female dyads that were seen together on 2 more occasions, almost half of cases where they reassociated (17, 43.6%) were greater than 2 months apart, and 12 of those were greater than 1 year. In most cases there are numerous intervening sightings of one or both individuals in the dyad without the other present, suggesting that these associations are not constant. Individual females reassociated with each other over spans ranging up to 17 years. These types of associations are consistent with the larger group sizes documented when calves are present, again suggesting that females seek out other females when they have small calves.

Like Cuvier’s, Blainville’s beaked whale males clearly fight repeatedly with other males, with extensive scarring focused on the front half of the body. Injuries occasionally include removal of tissue around the base of one or both teeth and tissue loss on the head. As previously suggested by Claridge (2006) and McSweeney et al. (2007), Blainville’s beaked whales appear to exhibit female defense polygyny, where one male escorts one or more receptive females and denies access of other males to the group. Our sample size, adding 12 additional years to the study of McSweeney et al. (2007), supports this suggestion, based on the composition and stability of groups. The few examples we have of subadult males in Hawai’i suggest that they associate with adults of both sexes as well as younger animals. One subadult male, HIMd147, for which we have the longest sighting history, was initially found in

⁹There were 609 dyads documented, but these analyses, with the exception of adult male–adult male dyads, were restricted to cases where both members of the dyad have been seen at least three times (together or apart, $n = 167$ dyads).

¹⁰Note some of these were documented without the other individual present in intervening periods, but particularly for the citizen science contributions, we do not always have good identifications from all individuals of a group, so in some cases both members of a dyad may have been present and not documented.

larger groups composed of adult females occasionally with adult males present, but as a subadult has been seen either by itself or with one adult male. This individual lacks the linear scarring characteristic of adult males; however, other subadult males in Hawai'i exhibit some scarring consistent with occasional interactions with adult males, a likely indicator that they are close to reaching sexual maturity.

14.5 Conclusions

Our studies in Hawai'i and research elsewhere have provided evidence of small populations that show high site fidelity for Blainville's and Cuvier's beaked whales. Coexisting in the same bathypelagic ecosystem, the two species show clear signs of resource partitioning in three dimensions, both where they occur in relation to island slopes and in how deep they dive. Like most other animals, behavior is largely driven by competing demands to avoid predators, find food, and, at least for males, increase mating opportunities. Both species are somewhat asocial, and groups that form seem to do so for reasons other than cooperative foraging, in the case of females with small calves seemingly to reduce predation risk. Their vocal behavior, the depths they dive to when not foraging, and even their ascent rates from dives appear to be driven at least in part to minimize detection from predators. As research on these species has expanded in varied habitats worldwide, and with results coming in from multiple ongoing long-term studies, beaked whales are beginning to earn an important place in our overall understanding of cetacean ethology and behavioral ecology.

Let us not forget the conservation concerns that originally spurred on research on these species. Both Cuvier's and Blainville's, and at least some other species of beaked whales, show strong responses to anthropogenic sounds, at times resulting in the death of individuals (Balcomb and Claridge 2001; Aguilar Soto et al. 2006; Cox et al. 2006; Manzano-Roth et al. 2016; Cholewiak et al. 2017; Falcone et al. 2017). For those individuals repeatedly exposed to high-intensity anthropogenic sounds, cessation of foraging for periods of time has the potential to influence survival and reproduction (New et al. 2013). Even in areas where the species persist in spite of repeated exposure to sonar, such as around San Clemente Island off California (Falcone et al. 2009), it is possible such areas act as population sinks, with cryptic mortality (Faerber and Baird 2010), or reduced reproductive rates that could result in population declines (Moore and Barlow 2013). Given the low density of most beaked whale populations, and the evidence of population structure, detecting declines using abundance estimates from traditional line transect surveys will be difficult, if not impossible. For small populations, mark-recapture abundance estimates using photo-identification data will produce more precise estimates, potentially allowing for examining population trends. However, for assessing population-level effects of repeated disturbance, studies of age structure of populations (e.g., Claridge 2013) may be more useful. Combining such studies with satellite tagging and genetics to understand population structure and range may be necessary to help elucidate the details of beaked whale lives. Despite studies in multiple areas that

have been ongoing for 20 years or more, and tremendous advances in our understanding of 4 of the 22 recognized species of beaked whales, much remains to be learned, not only about the most well-known species of beaked whales but about the many others in this diverse family.

Acknowledgments Our work is a team effort, in the field and office. Dan McSweeney deserves special mention for systematically photographing beaked whales in Hawai'i since the mid-1980s and contributing them to this study, and I also thank Daniel Webster, Greg Schorr, and numerous staff and volunteers for their work in the field. Much of what we know about beaked whales in Hawai'i comes from citizen science and contributions of photographs by individuals who work or play on the water, and their efforts are greatly acknowledged as they play a major role in our understanding of these species. In the office, I particularly thank Sabre Mahaffy for her contributions both to understanding beaked whales in Hawai'i and to providing results from many of the analyses used in this chapter, as well as David Anderson for analyses of satellite tag data. I also thank a number of colleagues, Natacha Aguilar de Soto, Diane Claridge, Andy Read, Cris Reyes, Massimiliano Rosso, and Greg Schorr, for providing unpublished data and answering questions regarding their studies and Bernd Würsig and two anonymous reviewers for helpful comments on the manuscript.

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