STUDIES OF ODONTOCETE POPULATION STRUCTURE IN HAWAIIAN WATERS: RESULTS OF A SURVEY THROUGH THE MAIN HAWAIIAN ISLANDS IN MAY AND JUNE 2003

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Summary

We undertook a survey of the main (windward) Hawaiian Islands during May and June 2003 to examine odontocete population structure. Our goals were: 1) to collect genetic samples to be used for examination of inter- and intra-Hawaiian population structure; 2) to collect photo-identification data to examine movements of individuals between islands and as a basis for population assessment; and 3) to examine habitat use in relation to potential deep-water barriers to movement. A total of 521 hours were spent on-effort using two vessels, and 8,461 km of trackline were covered from Kaua'i and Ni'ihau east to Hawai'i in water depths to over 4,000 m. There were 140 sightings of 14 species of odontocetes. Species most commonly seen were bottlenose dolphins (41 groups), pantropical spotted dolphins (25 groups), spinner dolphins (19 groups), short-finned pilot whales (17 groups), rough-toothed dolphins (13 groups), and dwarf sperm whales (8 groups). A total of 116 bottlenose dolphins were photo-identified, and photographic identifications were compared to a catalog of bottlenose dolphins from 2000-2002 obtained from the islands of Hawaiʻi, Maui/Lana'i, and O'ahu. There were 13 between-year re-sightings, all to the area in which the individuals were first documented. The between-year re-sighting rate for bottlenose dolphins off Maui and Lana'i was approximately 70%. Using this rate of re-sightings, if movements between island areas were freely occurring, 70 of the 101 individuals documented off Kaua'i/Ni'ihau, O'ahu, and Hawai'i, should have been previously sighted off Maui/Lana'i. With no inter-island movements documented, it is clear that movements between island areas are rare, if not completely absent. While rough-toothed dolphins were the fifth-most common species overall, off Kaua'i/Ni'ihau they were the second-most encountered species (11 groups). Photo-identification efforts resulted in documentation of 94 distinctive individuals, with only eight individuals being re-sighted, suggesting a total population size much greater than 94. Other species sighted during this survey included dense-beaked whales (5 groups), melon-headed whales (3 groups), false killer whales (1 group), killer whales (1 group), pygmy sperm whales (1 group), pygmy killer whales (1 group), striped dolphins (1 group), and a single sperm whale. Genetic sampling resulted in a total of 346 samples from nine species. Combined with previously available samples this should allow for intra-Hawai'i assessment of genetic differentiation of four species, and assessment between Hawai'i and elsewhere of at least seven species.

Introduction

The Hawaiian Islands are the most isolated archipelago in the world. The closest major land mass is the North American continent, approximately 3,670 km to the north-east. The next closest island, Johnstone Atoll, is over 1,100 km south-west. While the islands rise steeply from the ocean floor, they create substantial shallow-water habitat (~7,500 km^2 of habitat <200 m in depth in the main islands) that may be used by some cetaceans for avoidance of predators (see e.g., Norris et al. 1994) or for feeding on benthic or slope associated prey (e.g., Benoit-Bird and Au 2003). In addition, the islands influence oceanographic conditions, resulting in increased nutrient levels in near-surface waters (Gilmartin and Revelante 1974) that may subsequently attract prey and associated predators (e.g., Palacios 2003).

Some 15 species of odontocete cetaceans may be regularly or occasionally found in Hawaiian waters (Shallenberger 1981; Mobley et al. 2000), including spinner dolphins (*Stenella longirostris*), bottlenose dolphins (*Tursiops truncatus),* pantropical spotted dolphins *(S. attenuata),* short-finned pilot whales (*Globicephala macrorhynchus*), false killer whales (*Pseudorca crassidens*), rough-toothed dolphins (*Steno bredanensis*), dwarf sperm whales (*Kogia sima*), dense-beaked whales *(Mesoplodon densirostris),* and melon-headed whales (*Peponocephala electra*). All of these species are broadly distributed across tropical and subtropical waters of the Pacific, and most have somewhat pelagic habits. Individuals of most open ocean species likely range over wide areas in search of ephemeral sources of prey. The presence of the Hawaiian Islands in an otherwise vast and somewhat unproductive expanse of deep open ocean may provide both a temporally and spatially predictable source of prey for a wide range of cetacean species, and as such may attract concentrations of these species. If such prey predictability is of enough value, it may have resulted in the evolution of insular populations of many species of odontocetes.

Management of cetacean populations requires knowledge of population structure (Wade and Angliss 1997). There has been considerable research on cetacean population structure in the waters of the eastern tropical Pacific, due primarily to the interaction between tuna-purse seine fisheries and a variety of dolphin species. Perhaps because of their isolation, and since such fisheries have not extended into Hawaiian waters, relatively little research on odontocete population structure has been undertaken in Hawaiian waters. In fact, within U.S. waters perhaps the largest gaps in knowledge of odontocete population structure are from Hawai'i, particularly given the large number of species regularly documented there. Considerable research has been undertaken on Hawaiian odontocetes but until recently it has focused primarily on just one species, the spinner dolphin (e.g., Norris et al. 1994; Benoit-Bird and Au 2003). In 2002 the Southwest Fisheries Science Center (SWFSC), National Marine Fisheries Service, undertook a large-scale survey for cetaceans in Hawaiian waters (the HICEAS survey, J. Barlow personal communication), but efforts for that survey were spread over the entire Hawaiian EEZ (to 200 miles offshore), with limited efforts in inshore areas.

During May and June 2003 we surveyed throughout all the main (windward) Hawaiian Islands with the purpose of examining population structure of Hawaiian odontocetes. Our goals were three-fold: 1) collection of skin samples to allow for assessment of genetic differentiation both within Hawaiian waters and between Hawai'i and elsewhere; 2) collection of photographic identifications of individual dolphins to allow for assessment of movements between islands, and as a basis for population assessment; and 3) collection of habitat use information (e.g., distribution relative to depth), to assess whether some species are restricted to shallow-water habitats such that movements across channels in Hawai'i might be limited or reduced.

Based on bathymetry and distance between islands, the main Hawaiian Islands can generally be broken down into four main groupings ("island areas"), each separated by channels ranging in depth from between 500 to about 2,000 m (Figure 1). These island areas are (from west to east): 1) Ni'ihau and Kaua'i; 2) O'ahu; 3) the "four-island area" (Moloka'i, Lana'i, Maui, Kaho'olawe); and 4) Hawai'i. Distances between islands within the four-islands range from 11-15 km, while Kaua'i and Ni'ihau are separated by about 28 km. By contrast, distance between island areas ranges from approximately 44 km (O'ahu – Moloka'i), to 112 km (Kaua'i – O'ahu). Given the known dispersal abilities of species like bottlenose dolphins (Wells et al. 1990, 1999), it seems unlikely that structure within a Hawaiian odontocete population would exist. However, preliminary work by Baird et al. (2002) documented an apparent lack of movement of bottlenose dolphins between the three eastern island areas, suggesting that differentiation of populations may even be occurring within the Hawaiian Island chain.

Methods

Surveys were undertaken from 4 May through 12 June 2003. Two vessels were used: a 7 m gasoline (outboard) powered Boston Whaler and an 18 m diesel (inboard) powered Striker. Weather permitting (i.e., Beaufort 3 or less), both vessels were operated simultaneously. When both vessels were operating, efforts were made to cover different areas (i.e., vessels generally remained greater than 4 km apart), though both vessels generally stayed within 30-50 km of each other. Between three and five observers would scan visually 360 degrees from each vessel. On the 18 m Striker 1-2 observers were approximately 7 m above sea level and remaining observers were stationed either at the bow (2 m above sea level) or the bridge (4 m above sea level). Search efforts were primarily concentrated in the morning and early afternoon, in order to take advantage of calmer seas prior to the onset of afternoon trade winds. Median time of departure from anchorage or docking site was 0601 hrs. Median time of return to anchorage or dockage site was 1441 hrs.

Field efforts began off the island of Hawai'i and progressed to the west-northwest, ending off the islands of Kaua'i and Ni'ihau, a linear distance of approximately 580 km (Figure 1). A WNW direction of travel allowed for calmer crossings between islands, not having to travel against the prevailing ENE winds. The total area covered was approximately 16,000 km^2, with search effort extending as far offshore as 42 km in some areas (Figure 2). Distribution of search effort was limited primarily by sea conditions, with the vessels generally attempting to remain in areas with sea states less than Beaufort 4. Within these constraints, efforts were made to cover as wide an area as possible, extending as far alongshore each of the islands, and as far offshore as possible, given sea and fuel constraints. Research was generally concentrated along the leeward (SW) shores of the islands of Hawai'i, Maui, Lana'i, and O'ahu. Off the islands of Kaua'i and Ni'ihau sea conditions allowed for surveying in all areas around both islands (Figure 2). Crossings between islands were undertaken on-effort and with both boats as sea conditions allowed. Effort data were collected with automatic location information recorded on board each vessel's GPS every 5 minutes, and recording of sea state at the start of each survey day and as sea state changed throughout the day. Kriging was used to interpolate depths at 5-minute effort locations using *Surfer* Ver. 6.0 (Golden Software), though digital bathymetry data (obtained from NOAA) were only available for the eastern-most islands (O'ahu to Hawai'i). Survey speeds were generally 16-18 km/hr for the 18 m vessel and 25-30 km/hr for the 7 m vessel.

When odontocetes were sighted, groups were approached to confirm species identity. For difficult to identify species (e.g., beaked whales, *Peponocephala, Feresa, Kogia*) photographs were taken to confirm species identity when possible. For any groups approached closely, when lighting conditions and animal behavior allowed, individual dolphins were photographed using a Canon 10D digital camera (set on the highest level of resolution, six megapixels), using a 100-300 mm autofocus zoom lens. Information recorded for each group encountered included minimum, maximum and "best" estimates of group size, sighting cue, reasons for leaving, and presence of other species. For most species in the majority of areas, collection of skin biopsies was also undertaken, using crossbow deployed darts or a hand-held pole-spear. Skin samples obtained were sub-sampled and stored in a DMSO/salt solution. Species sampling priorities for photo-identification and skin biopsying varied between islands depending on the number of samples previously available through collections at the SWFSC (La Jolla, CA). Greater sampling efforts were planned for Kaua'i and Ni'ihau, as these islands had not been sampled in the previous efforts of Baird et al. (2001a, 2002).

For photo-identification, only good quality photographs (in focus, un-obscured, with the dorsal fin relatively perpendicular to the plane of the photograph, and with the image of the dorsal fin large enough to identify small notches, if present) were used. Individual dolphins/whales were identified from photographs based primarily on the size, location and pattern of notches on the trailing edge of the dorsal fin and on the back directly behind the dorsal fin (cf. Wells and Scott 1990; Wursig and Jefferson 1990). Those individuals with dorsal fin or back notches, or distinctive pigmentation patterns, are hereafter referred to as "marked" animals.

Results and Discussion

Field operations were undertaken on 37 days during the study period. Both vessels operated simultaneously on 31 days, giving a total of 68 "vessel-days". A total of 521 hours were spent on effort, and vessels covered 8,461 km of trackline on-effort. In general, sea conditions during the survey were extremely good (>60% in Beaufort 2 or less). Distribution of effort was not equal between islands (Table 1), with greater effort spent off Kaua'i and Ni'ihau than any other island area. Overall sea conditions were best off Kaua'i/Ni'ihau and worst off Maui/Lanai (Table 1). For areas where detailed depth data are available (O'ahu to Hawai'i), depths at 5-minute effort locations indicated approximately 50% of total effort was spent in depths from 0-500 m, with some effort extending to over 4,000 m depth (Figure 3).

As expected, sighting rates were inversely related to sea state (Table 2). Sighting rates were high for sea states 0-2 but decreased substantially (<1/3) for sea states 3 or greater. In total there were 140 sightings of odontocetes (including three sightings of unidentified dolphins), representing 14 identified species (Table 3). A total of approximately 7,100 photographic frames were taken either for confirmation of species identity or to identify individuals (Table 3). There was substantial variation in group sizes and depths utilized among species (Table 4). Comparisons of depth distributions of effort (Figure 3) and of species regularly observed (10 or more sightings) between O'ahu and Hawai'i showed significant differences for all four species (Table 5). Overall sighting rates differed among islands (Table 6). A total of 346 genetic samples from nine species were collected (Table 7).

In comparison to the large vessel HICEAS survey (J. Barlow unpublished), overall sighting rates in our survey in the near-shore (generally <30 km) waters of the main Hawaiian Islands were high (mean = 1.66 sightings/100 km; Table 2). However, overall sighting rates by sea state were lower during this survey than the HICEAS efforts (J. Barlow unpublished), not surprisingly, given the lower platform height of the two vessels used in this study. The higher average sighting rates from this survey were thus likely due to substantially better sea states (91% of effort in Beaufort 3 or less, Table 1), compared with those experienced in the HICEAS survey (17% of effort in Beaufort 3 or less for HICEAS; J. Barlow unpublished). Sighting rates varied among island areas (Table 6), with Kaua'i/Ni'ihau having the highest sighting rate, and Hawai'i having the lowest. It is possible that differences in sighting rates between islands are not statistically significant, or the differences may be due to sea state differences (Table 1). Sea conditions were best off Kaua'i and Ni'ihau, however sea conditions were worst off Maui and Lana'i, which had the second highest overall sighting rate (Table 6).

Baird et al. 2003

Bottlenose dolphins

Baird et al. (2002) examined potential movements of bottlenose dolphins between island areas in the eastern-most islands, using a single year of data from O'ahu and Hawai'i and two years of data from the Maui/Lana'i area. Our study added additional samples from all three of these island areas, as well as the first bottlenose dolphin photo-identification efforts from Kaua'i and Ni'ihau, allowing an assessment of movements between all four of these areas.

From photographic efforts a total of 116 individuals were documented: 2 from Hawai'i, 15 from Maui/Lana'i, 50 from O'ahu, and 49 from Kaua'i/Ni'ihau. There were a total of 13 between-season (year) re-sightings and 14 within-season re-sightings. All of the within- and between-season resightings were from the same island area that the individuals had first been documented, that is, there was no evidence of movements between island areas.

Combining 2003 data with data presented by Baird et al. (2002), we have documented a total of 219 distinctive individual bottlenose dolphins from the main Hawaiian Islands since February 2000. Off Maui/Lana'i, 68 individuals were documented in 2000-2001. Of those documented in 2002 and 2003 (18 and 15 individuals, respectively), 11 and 12 had been documented in a previous year, suggesting that individuals are likely resident to that area. Given an average of an approximately 70% between-year re-sighting rate, we would expect about 70 of the 101 individuals documented off Hawai'i, O'ahu and Kaua'i/Ni'ihau in 2003 to have been previously documented off Maui/Lana'i, if individuals were freely mixing between islands. As noted by Baird et al. (2002) for a subset of these islands and with only a single season of data for O'ahu and Hawai'i, it is clear that bottlenose dolphins are not mixing freely between islands. Sample sizes for this comparison are reasonable for O'ahu (79 individuals in 2002/2003) and Kaua'i/Ni'ihau (49 individuals in 2003), though less so for Hawai'i (13 individuals in 2002/2003), thus additional effort off the island of Hawai'i is warranted.

Of the 13 between-season re-sightings, only one occurred off O'ahu, with 12 occurring off Maui/Lana'i. As 50 individuals were photo-identified off O'ahu in 2002, this rate (2%) suggests that the O'ahu population is not resident to the same extent as is the Maui/Lana'i population (with a 70% between-season re-sighting rate). The population size off Maui/Lana'i was estimated at approximately 134 individuals (Baird et al. 2001). Given the relative infrequency of within- and between-season re-sightings, the population off O'ahu must be much larger than that off Maui/Lana'i.

Off Kaua'i and Ni'ihau, 10 of 49 individuals documented in 2003 were seen on two occasions (in three different sightings). Movements of these individuals from their original sighting location were relatively small (8-18 km). Depth distribution of bottlenose dolphin sightings from Hawaii-O'ahu (Figure 4; Table 5) suggests a single population with a preference for shallower waters of the study area. While we were unable to quantify the depth distribution of our effort data off Kaua'i or Ni'ihau, the distribution of sighting depths for bottlenose dolphins off those islands (Figure 5, Figure 7) suggest the possibility of two populations, one with a preference for shallow (i.e., less than 200 m) waters, as is found off the other islands, and one with a preference for deeper (400-900 m) waters. While the sample size is small, sighting depths for the three sightings where individuals were re-sighted supports this suggestion. All three sightings were in deep (500-800 m) water, thus when individuals were re-sighted 2 or 10 days after they were first documented in deep water, they were also found in deep water. Our genetic sampling efforts could be used to address this possibility. Of the 45 bottlenose dolphin samples obtained off Kaua'i/Ni'ihau, approximately equal numbers were obtained from groups found in shallow (<200 m, n = 24) and deep (>300 m, n = 21) waters. Further photo-identification efforts off Kaua'i and Ni'ihau are also warranted to determine whether individuals in shallow and deep water are part of a single or separate populations.

Rough-toothed dolphins

Research efforts in 2000-2002 (Baird unpublished) off the easternmost islands (O'ahu – Hawai'i) have resulted in only one previous sighting of rough-toothed dolphins in 77 days (519 hours) of field effort. Combined with the sightings of this species in the same area from this survey, it appears rough-toothed dolphins are either rare in the near-shore (<25 km) waters from O'ahu to Hawai'i, or they actively avoid boats and are thus unlikely to be observed. Only one of the three groups of *Steno* we have observed on-effort in the easternmost islands since 2000 appeared to have avoided the research vessel, so this latter explanation is unlikely to be responsible for the low sighting rate. Based solely on 2003 efforts between O'ahu and Hawai'i, rough-toothed dolphins rank fifth in species observed, representing only 3.5% of the total number of sightings. Such sighting frequency is similar to most other areas where *Steno* has been documented: in the Marquesas they represent 4% of sightings (Gannier 1999); in the Solomans 5% (Shimada and Pastere 1995); and in the Sula Sea 2.9% (Dolar et al. 1997). In only one area, off the windward islands of French Polynesia, have they been recorded at much greater frequencies, representing 34% of the dolphin sightings (Gannier and West 2003); the second-most commonly observed delphinid.

Off Kaua'i and Ni'ihau, rough-toothed dolphin sightings represented 26% of the total odontocete sightings, and they were the second-most commonly observed cetacean (Table 3). The reason for such differences in sighting rates between islands (Table 6) is unclear. Rough-toothed dolphins have been implicated in interactions with fisheries in Hawai'i, particularly off the islands of Hawai'i and O'ahu (Schlais 1984; Nitta and Henderson 1993), and shooting of such "problem" dolphins has been reported. There has been an apparent decline in the frequency of sightings of rough-toothed dolphins off the island of Hawaii over the last 20 years (D. McSweeney personal observations). It is possible that this decline may be associated with shooting of animals in the areas where fishery interactions have been documented.

Group sizes in Hawaiian waters averaged 13 individuals, similar to group sizes reported off French Polynesia (average = 12.1; Gannier and West 2003), though substantially larger than the group sizes reported by Mobley et al. (2000) for Hawaiian waters (average = 3.3), based on aerial surveys. Whether the high abundance of *Steno* off Kaua'i and Ni'ihau during June 2003 represents a "resident" population to these islands is unknown, as no previous photo-identification efforts have been undertaken in that area. Photo-identification efforts with *Steno* resulted in a total of 103 dolphins identified (with good quality photos). The average number of notches per individual was 6.0 (SD=3.5), thus, on average, individuals should be easily re-recognized with good quality photographs. Of the 103, only nine (8.6%) identifications were of individuals that were unlikely to be re-identified if re-photographed, suggesting that the proportion of "marked" individuals in the population may be as high as 91%. Eight of the remaining 94 individuals were documented on two occasions each, thus 86 unique individuals were documented in this study. Re-sightings were only recorded off the islands of Kaua'i and Ni'ihau. The time period between the one sighting off O'ahu (where 12 marked individuals were identified with good quality photos) and the 11 sightings off Kaua'i and Ni'ihau (where 74 marked individuals were identified) was likely too short (8-18 days) to allow for re-distribution of individuals, if such movements occur. The rate of discovery of new individuals (Figure 6) shows no tendency of leveling off, and suggests that the actual number of individual rough-toothed dolphins in the area is likely much greater than the number we documented. In addition, while we attempted to photo-identify all dolphins present in each group, 4 of the 13 *Steno* groups were lost, one group was not approachable, and one group was encountered in Beaufort 4 sea conditions, thus we were unable to photo-identify all individuals present. Combining best estimates of group size from all *Steno* encounters, we were only able to photo-identify approximately 60% of the individuals encountered. Assuming the proportion of re-sightings and marked individuals were similar for those dolphins not photographed, our minimum estimate of population size would be 143 individuals. From aerial surveys Mobley et al (2000) produced an estimate of 123 rough-toothed dolphins (CV=0.63) from the main Hawaiian Islands.

Sea conditions during our efforts off Kaua'i and Ni'ihau were extremely good, and it is unlikely that any similar efforts of equal length will encounter similar sea conditions, allowing for work around all coastlines of the islands. However, a number of the rough-toothed dolphin encounters were in the lee of Kaua'i (Figure 8), thus future field efforts to determine whether the population is "resident", as well as to conduct a mark-recapture population estimate, could be undertaken.

Other species

Photo-identification data from other species were collected, and individual catalogs are being compiled for future inter-island comparisons. For examination of sighting distributions in relation to depth of survey effort, sample sizes are only sufficient for three additional species: pantropical spotted dolphins, short-finned pilot whales and spinner dolphins (Table 5).

Pantropical spotted dolphins and short-finned pilot whales were both found in deeper-portions of the study area (Table 4), and a comparison of depth distributions in relation to effort for the O'ahu-Hawai'i area were significant for both speices (Table 5). The four sightings of pantropical spotted dolphins off Kaua'i and Ni'ihau (Figure 7) were the four deepest recorded in the survey, and no sightings in relatively shallow (<2000 m) waters were made off those islands, despite substantial levels of effort in shallow water (Figure 2). Discussions with several local fishermen on Kaua'i also suggested that pantropical spotted dolphins may be less frequently sighted in that area compared to the other main Hawaiian Islands.

Spinner dolphins showed the shallowest depth distribution of any species (Table 4). On average, spinner dolphins were found in significantly shallower water than expected based on the distribution of effort (Table 5). This species is known to spend day-time hours in very shallow water (Norris et al. 1995), presumably to avoid predators. The only area where this species was sighted in deep-water was off Ni'ihau (Figure 9), where there were two sightings during mid-afternoon in waters from 400-800 m deep. Such deep-water mid-day sightings have been previously reported in Hawai'i (Mobley et al. 2000), but based on this survey and previous efforts by the authors, they appear to be extremely infrequent.

The sixth most frequently encountered cetacean was the dwarf sperm whale. This is a somewhat surprising result, given that this species was not recorded at all in the extensive aerial surveys by Mobley et al. (2000). However, seven of the eight dwarf sperm whale sightings were off Kaua'i and Ni'ihau (Figure 9) where almost 55% of survey efforts were in sea states of Beaufort 0 or 1. Due to their unobtrusive nature, *Kogia* are generally only seen in very calm sea conditions (Willis and Baird 1998). In fact, the average sea state for the nine *Kogia* sightings (including one pygmy sperm whale sighting) was Beaufort 0.55, while the average sea states for the four most frequently encountered species ranged from Beaufort 1.6 to 2.2. Of the species encountered on three or more occasions, dwarf sperm whales were found in the deepest water (mean = 2,004 m; Table 4), and also showed among the least variability in depths encountered (CV = 0.54).

We observed one group of killer whales, and were able to obtain a biopsy sample for genetic studies. Killer whale sightings are extremely infrequent in Hawaiian waters, and virtually all previously published sightings have been from winter months, suggesting that there is no "resident" population in Hawaii (Mobley et al. 2001). Most previous sightings have been either from aerial platforms or by members of the public, so few if any photographs of distinctive individuals are available for comparison. Our encounter was cued by high-speed and evasive behavior by a group of melon-headed whales, suggesting that the melon-headed whales considered the killer whales a threat, and that they may feed on other marine mammals in Hawaiian waters. While there is no clear genetic marker that can be used to identify whether a killer whale is a "fish-eating" or "mammal-eating" form on a global basis, in the eastern North Pacific fish-eating and mammal-eating forms are genetically distinct (Hoelzel et al. 2002). Genetic analysis of the sample we obtained by the Southwest Fisheries Science Center indicated that it was a mitochondrial haplotype only previously documented from one other killer whale (collected in Hawaiian waters by the HICEAS cruise in 2002), and was most closely related to mammal-eating killer whales from Alaskan waters (R. LeDuc, personal communication).

Genetic sampling

Overall genetic sampling efforts were extremely successful. Prior to this survey efforts by the SWFSC, and by the authors, had resulted in collection of 294 odontocete genetic samples (from 14 species) from Hawaiian waters (S. Chivers, unpublished). This survey more than doubled the available sample size of genetic samples, including the first melon-headed whale samples from Hawaiian waters, and substantially increased the number of samples available for eight of the nine species sampled (Table 7). Sample sizes are likely now sufficient for intra-Hawai'i genetic analyses for pantropical spotted dolphins, bottlenose dolphins, spinner dolphins, and short-finned pilot whales. Photo-identification and scar/wound pattern evidence suggests that population differentiation within Hawai'i may exist for at least two species, bottlenose dolphins (Baird et al. 2002; this study) and pantropical spotted dolphins (Baird et al. 2001b). Sample sizes for inter-Hawai'i comparisons (e.g., between Hawai'i and eastern tropical Pacific populations) are likely now sufficient for robust comparisons for at least seven species of odontocetes (Table 7). Existing comparisons with relatively small sample sizes have already indicated high levels of genetic differentiation between Hawaiian and other populations for two species, false killer whales and short-finned pilot whales (Chivers et al. 2003). This suggests that island-associated populations may also exist for other species in Hawaiian waters.

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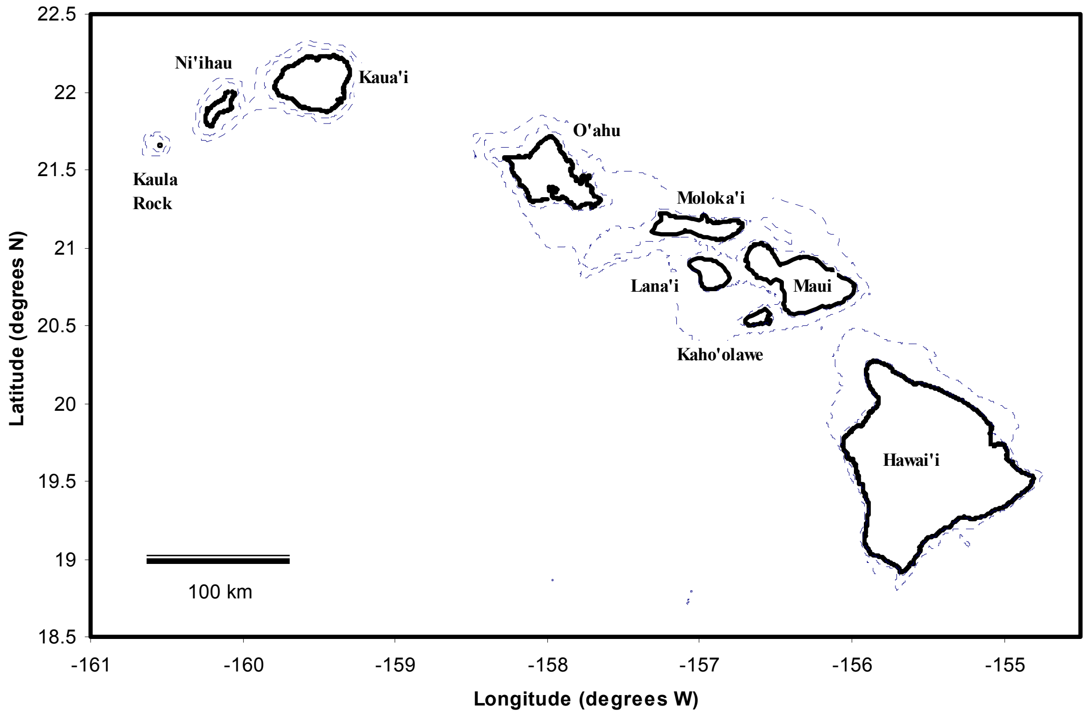


Figure 1. Map of the main (windward) Hawaiian Islands showing the 100 and 1,000 m depth contours.

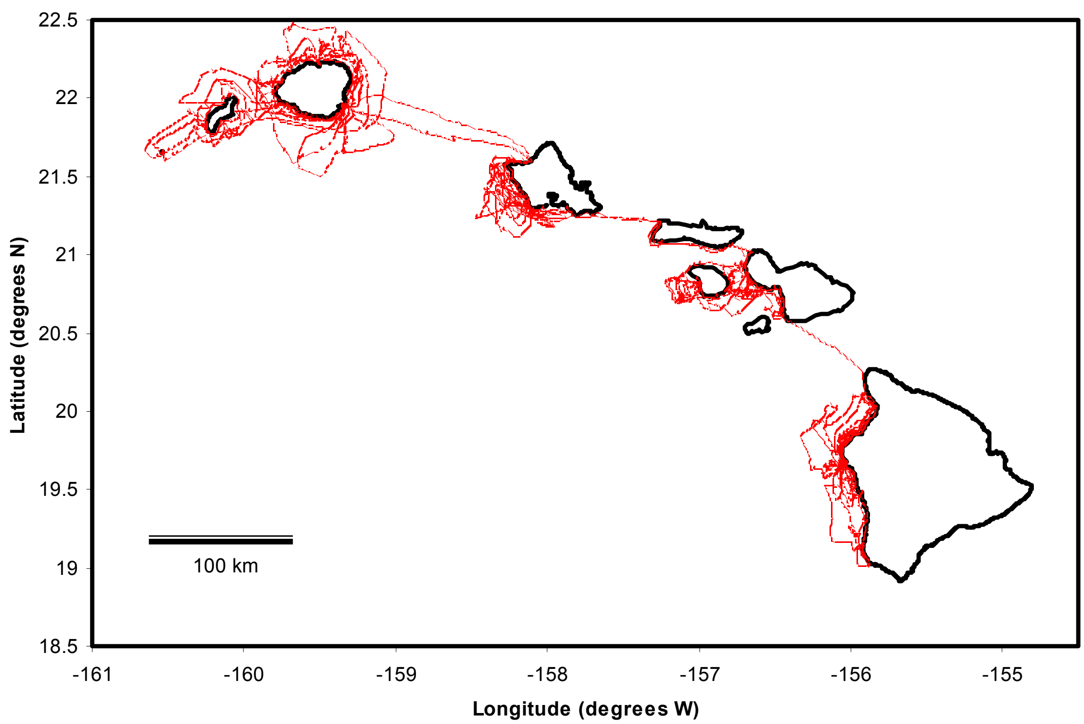


Figure 2. Map of the main Hawaiian Islands showing tracklines from effort during May and June 2003.

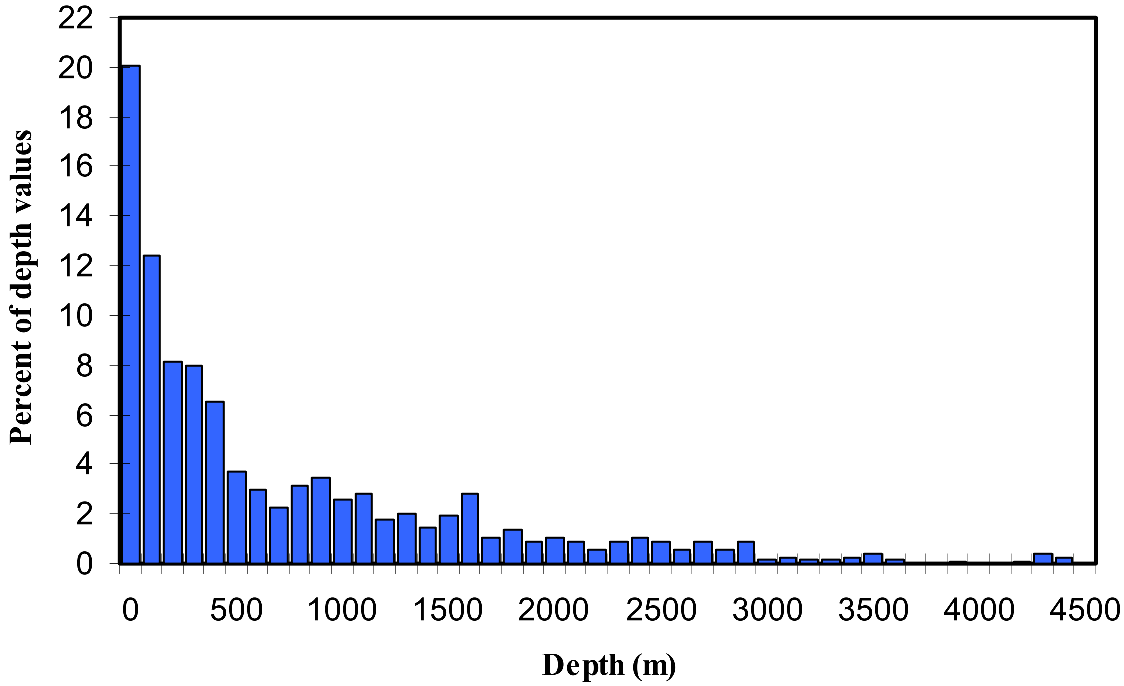


Figure 3. Distribution of depth values from locations recorded on GPS at 5-minute intervals (n=2,944), for the area between O'ahu and the island of Hawai'i. Each mark on the x-axis indicates a 100-m depth bin (e.g., 1-100, 101-200, etc). Values shown include on-effort data only, with the first value included for each encounter. Approximately 55% of search effort was spent in depths from 0-500 m for these areas. Median depth = 420 m.

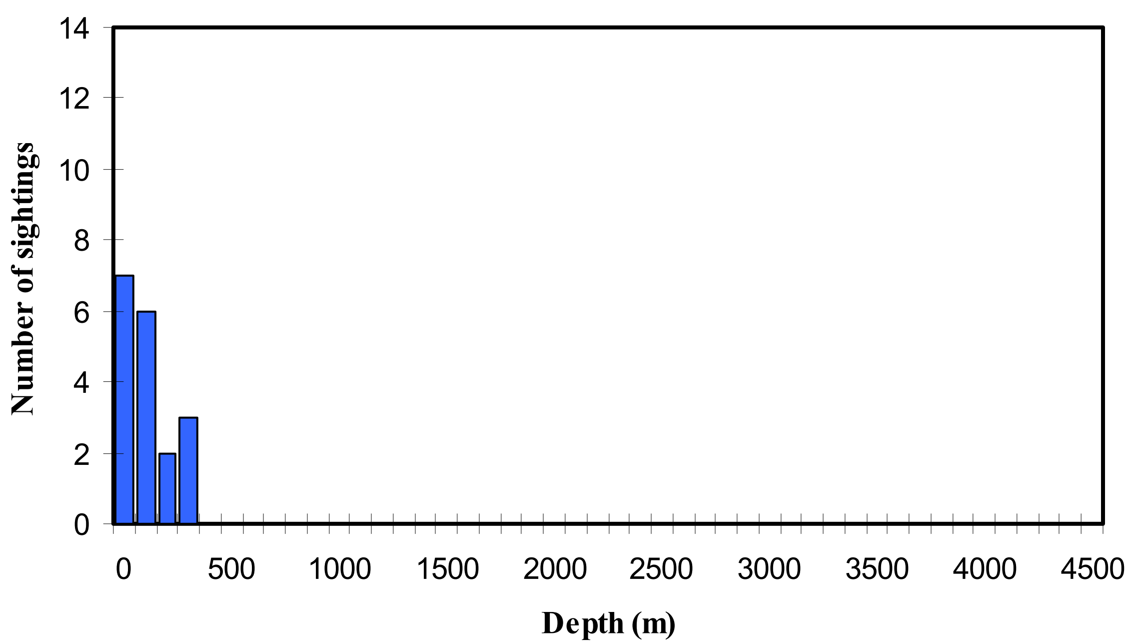


Figure 4. Distribution of bottlenose dolphin sightings (n=18) in relation to depth for the area between O'ahu and the island of Hawai'i. Each mark on the x-axis indicates a 100-m depth bin (e.g., 1-100, 101-200, etc).

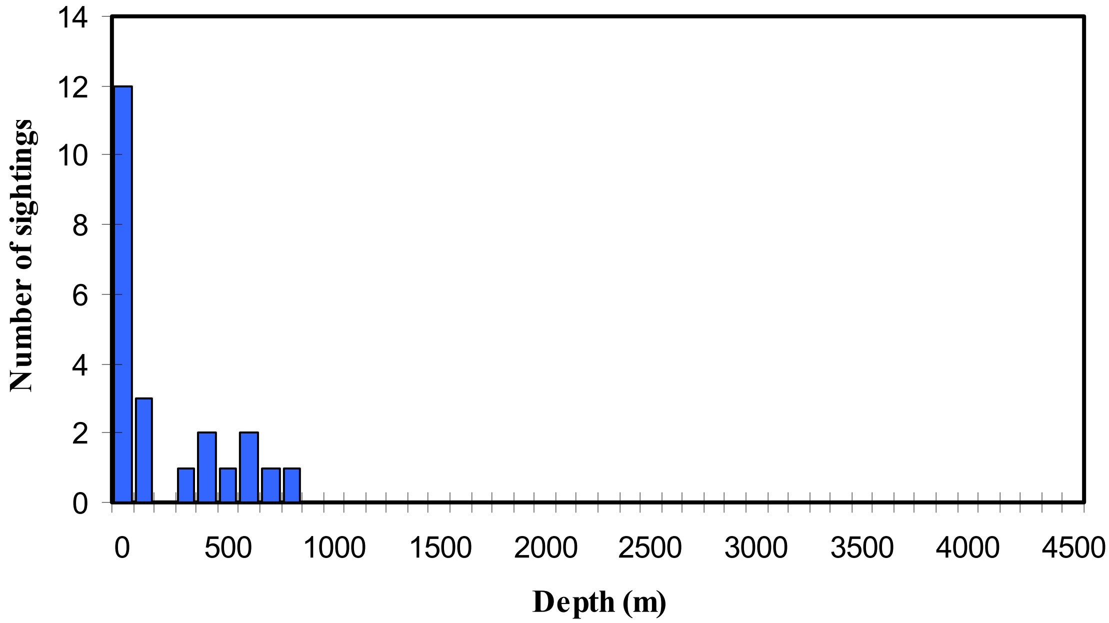


Figure 5. Distribution of bottlenose dolphin sightings (n=23) in relation to depth off the islands of Kaua'i and Ni'ihau, showing a bi-modal distribution of depth values. Each mark on the x-axis indicates a 100 m depth bin (e.g., 1-100, 101-200, etc). The shallowest value in the right-hand mode was 400 m, while the deepest value was 900 m.

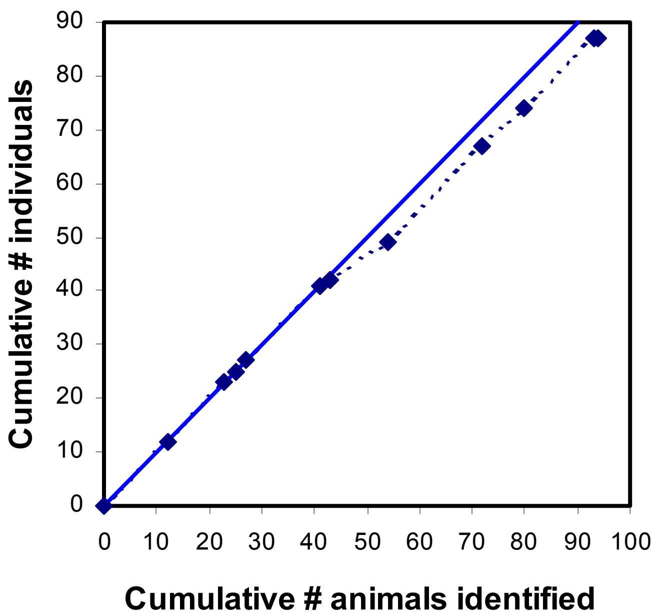


Figure 6. Rate of discovery of new individual rough-toothed dolphins (dashed line with closed diamonds). The one-to-one line is shown (solid), indicating the slope if all individuals documented were new.

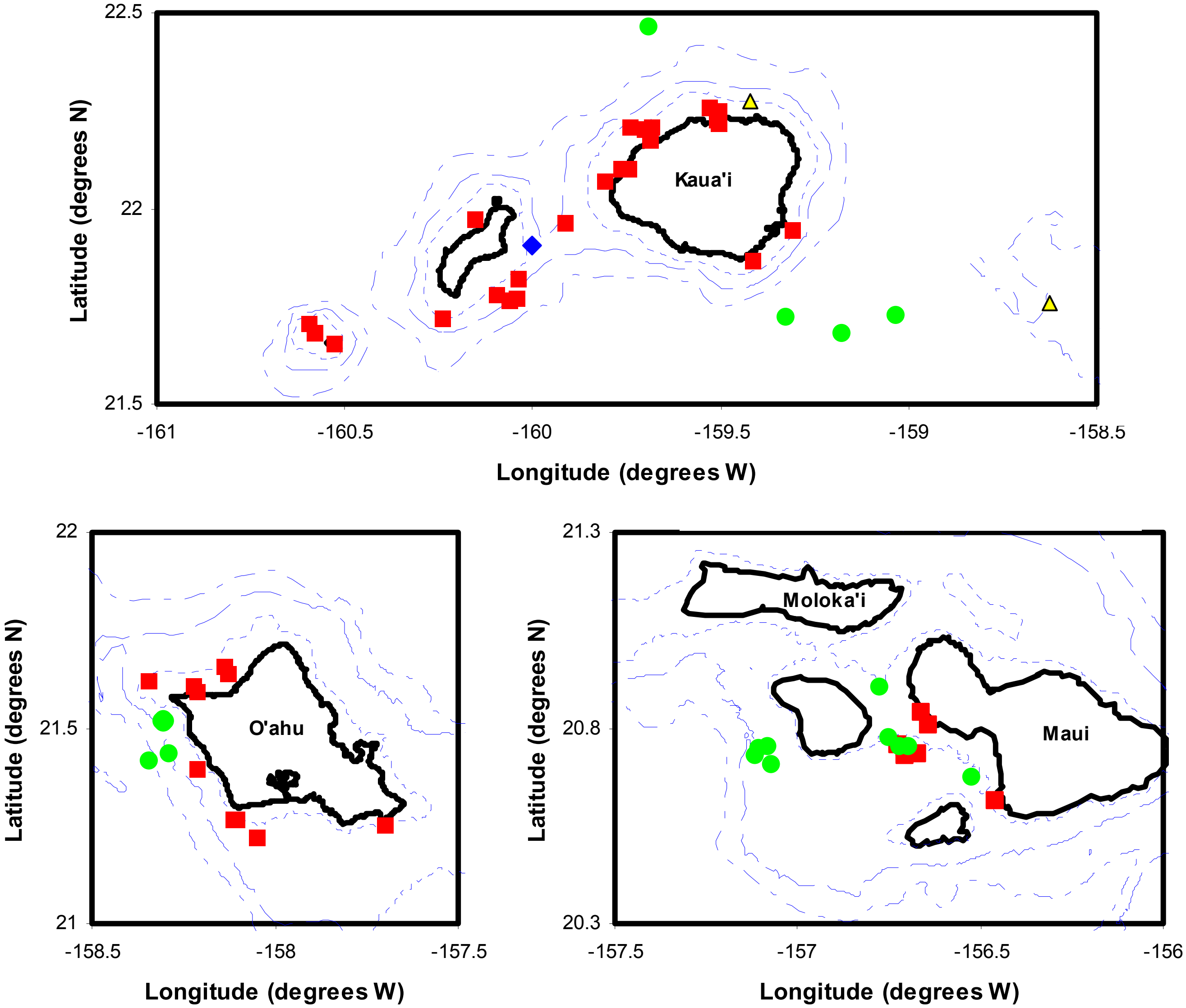
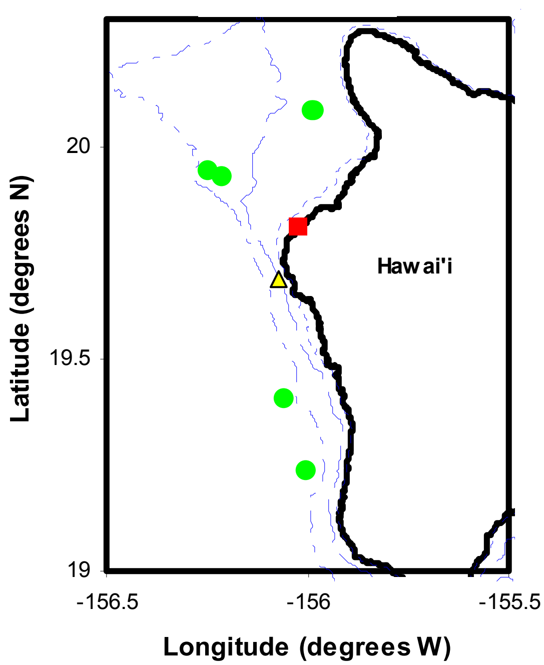
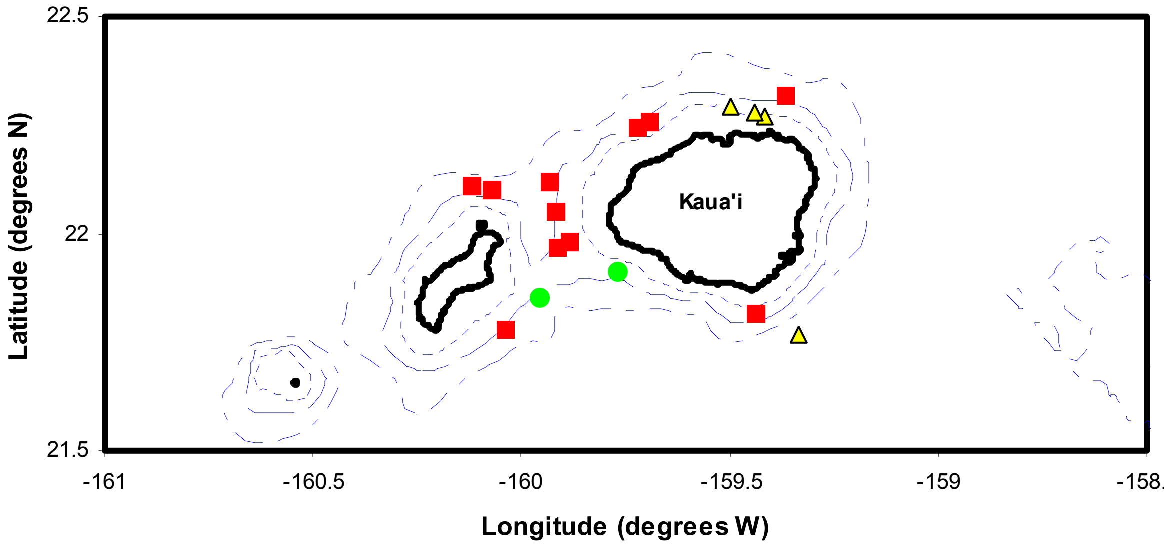


Figure 7. Sighting locations of bottlenose dolphins, pantropical spotted dolphins, melon-headed whales and pygmy sperm whales (see key below). Sighting depths of bottlenose dolphins averaged 222 m (SD=232 m), pantropical spotted dolphins averaged 1,254 m (SD=1,034 m), and melon-headed whales averaged 1,113 m (SD=537 m). Depth contours are shown for 100 m, 1,000 m, and 2,000 m.



KEY

Bottlenose dolphins ■
Pantropical spotted dolphins ●
Melon-headed whales △
Pygmy sperm whales ◆



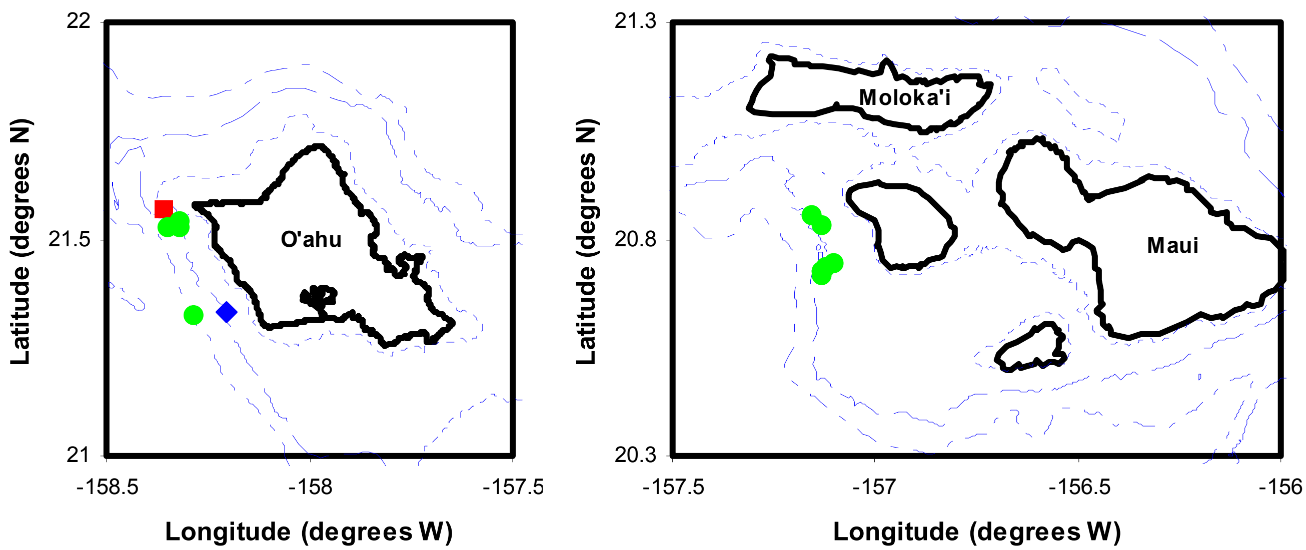
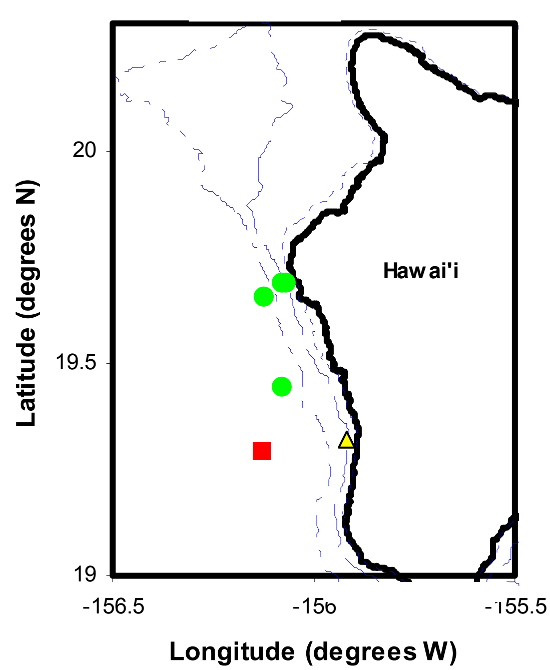


Figure 8. Sighting locations of rough-toothed dolphins, short-finned pilot whales, dense-beaked whales, and a single sighting of false killer whales (see key below). Sighting depths of rough-toothed dolphins averaged 1,339 m (SD=793 m), short-finned pilot whales averaged 1,142 m (SD=670 m), and dense-beaked whales averaged 1,304 m (SD=882 m). Depth contours are shown for 100 m, 1,000 m, and 2,000 m.

KEY

Rough-toothed dolphins ■
Short-finned pilot whales ●
Dense-beaked whales △
False killer whales ◆



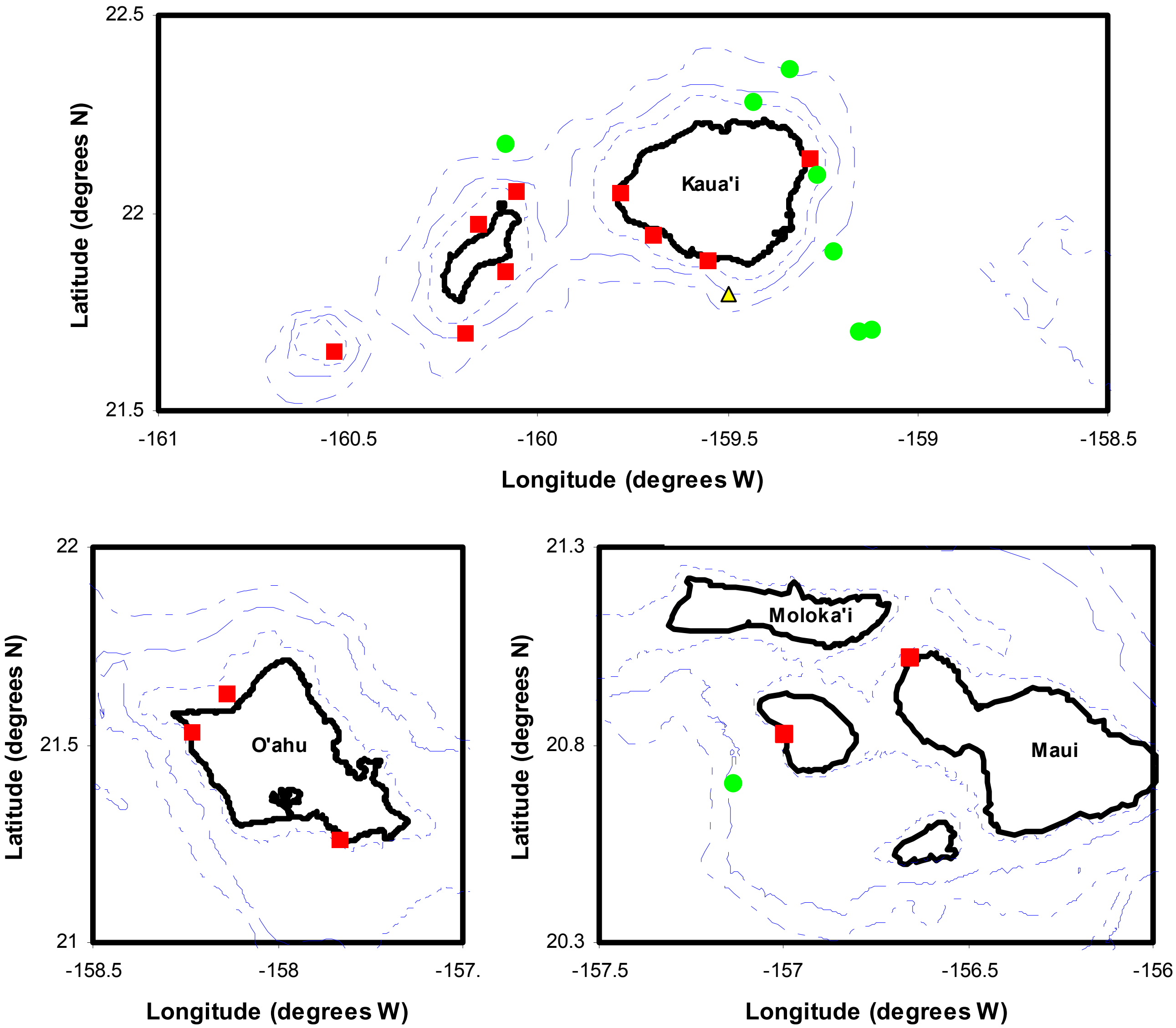


Figure 9. Sighting locations of spinner dolphins, dwarf sperm whales, a single sperm whale, and a single group of killer whales (see key below). Sighting depths of spinner dolphins averaged 95 m (SD=196 m), and dwarf sperm whales averaged 2,004 m (SD=1,092 m). Depth contours are shown for 100 m, 1,000 m, and 2,000 m.

KEY
Spinner dolphins
Dwarf sperm whales
Sperm whale
Killer whale

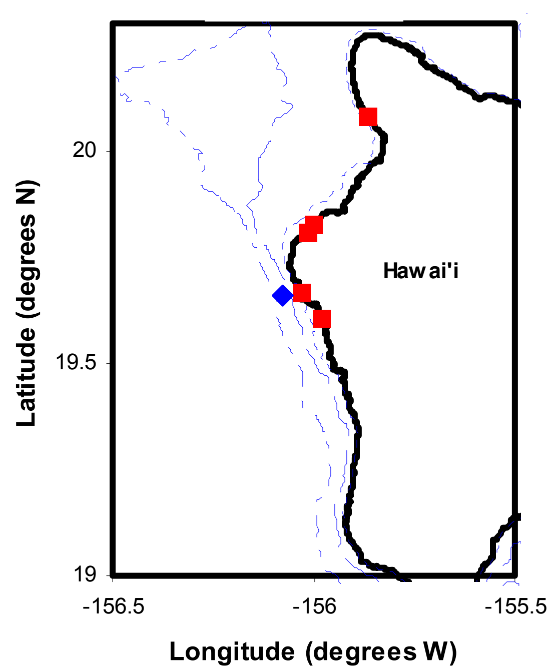


Table 1. On-effort hours and kilometers spent off each island area in relation to sea state. Similar levels of effort were expended off Hawai'i, Maui/Lana'i (which also includes some time off Moloka'i), and O'ahu, while greater levels of effort, with better sea conditions, were expended off Kaua'i and Ni'ihau.

Island area	**Study Area Size (km^2)**	**# hrs**	**# km**	**% km Bft[1] 0**	**% km Bft 1**	**% km Bft 2**	**% km Bft 3**	**% km Bft 4+**
Hawai'i	3,830	108	1,791	1.9	23.5	34.0	34.1	6.4
Maui/Lana'i	1,765	107	1,659	1.6	9.5	34.1	35.7	19.2
O'ahu	1,470	111	1,789	3.1	21.9	38.2	28.2	8.6
Kaua'i/Ni'ihau	8,305	195	3,222	20.3	34.6	19.2	20.8	4.2
Sum	**15,370[2]**	**521**	**8,461**	**9.1**	**24.7**	**29.2**	**28.1**	**8.6**

[1]Bft = Beaufort sea state.[2]Study area size for each island area calculated using polygon around distribution of search effort (area covered when moving between island areas not included).

Table 2. Sighting rate in relation to sea state. As expected, sighting rates generally decreased with an increase in sea state.

Sea state	**# Sightings**	**# km**	**Sightings /1,000 km**
Beaufort 0	24	770	31.17
Beaufort 1	41	2,087	19.65
Beaufort 2	54	2,475	21.82
Beaufort 3	15	2,379	6.31
Beaufort 4+	6	724	8.29
Total	**140**	**8,435**	**16.60**

Table 3. Number of sightings by species and island area, and photographs obtained.

Species	Number of sightings by island area: Hawai'i	Maui & Lana'i	O'ahu	Kaua'i & Ni'ihau	Total	# photographic frames taken
Bottlenose dolphin	1	7	10	23	41	1,262
Pantropical spotted dolphin	6	9	6	4	25	921
Spinner dolphin	5	2	3	9	19	503
Short-finned pilot whale	4	7	4	2	17	1,783
Rough-toothed dolphin	1	0	1	11	13	1,312
Dwarf sperm whale	0	1	0	7	8	147
Dense-beaked whale	1	0	0	4	5	561
Melon-headed whale	1	0	1	1	3	130
Unidentified dolphin	2	0	1	0	3	0
False killer whale	0	0	1	0	1	355
Killer whale	1	0	0	0	1	43
Sperm whale	0	0	0	1	1	0
Pygmy killer whale	0	0	0	1	1	53
Pygmy sperm whale	0	0	0	1	1	0
Striped dolphin	0	0	0	1	1	58
Total	**21**	**19**	**17**	**42**	**140**	**7,128**

Table 4. Group size and depth information by species.

Species	N	Group size (mean)	Group size SD	Mean depth (m)	Depth SD (m)
Bottlenose dolphin	41	5.2	4.9	222	232
Pantropical spotted dolphin	25	77.1	29.6	1,254	1,054
Spinner dolphin	19	47.4	41.2	95	196
Short-finned pilot whale	17	15.6	9.4	1,142	670
Rough-toothed dolphin	13	13.1	9.7	1,339	793
Dwarf sperm whale	8	2.0	1.2	2,004	1,092
Dense-beaked whale	5	4.0	2.8	1,304	882
Melon-headed whale	3	146.7	83.9	1,113	537
False killer whale	1	35	NA	1,000	NA
Killer whale	1	4	NA	773	NA
Sperm whale	1	1	NA	1,400	NA
Pygmy killer whale	1	13	NA	613	NA
Pygmy sperm whale	1	2	NA	700	NA
Striped dolphin	1	45	NA	2,800	NA

Table 5. Comparisons of depths (for species with 10 or more sightings between O'ahu and Hawai'i) with effort data (Figure 3, median depth = 420 m). Pair-wise statistical comparisons using two-sample Kolmogorov-Smirnov tests.

Species	**Mean depth (m)**	**Depth SD**	**Median depth (m)**	**n**	**p-value**
Bottlenose dolphin	72.2	121.2	155.0	18	<0.001
Pantropical spotted dolphin	902.8	718.4	731.0	21	0.040
Spinner dolphin	28.5	43.1	18.0	10	<0.001
Short-finned pilot whale	1,163.9	710.5	900.0	15	0.001

Table 6. Sightings per unit effort by island. See Table 1 for details of effort and Table 3 for details of sightings.

	Sightings per unit effort (#/100 km)				
Species	**Hawai'i**	**Maui & Lana'i**	**O'ahu**	**Kaua'i & Ni'ihau**	**Overall**
Bottlenose dolphin	0.06	0.42	0.56	0.71	0.48
Pantropical spotted dolphin	0.34	0.54	0.34	0.12	0.30
Spinner dolphin	0.28	0.12	0.17	0.28	0.22
Short-finned pilot whale	0.22	0.42	0.22	0.06	0.20
Rough-toothed dolphin	0.06	0.00	0.06	0.34	0.15
Dwarf sperm whale	0.00	0.06	0.00	0.22	0.09
Dense-beaked whale	0.06	0.00	0.00	0.12	0.06
Melon-headed whale	0.06	0.00	0.06	0.03	0.04
False killer whale	0.00	0.00	0.06	0.00	0.01
Killer whale	0.06	0.00	0.00	0.00	0.01
Sperm whale	0.00	0.00	0.00	0.03	0.01
Pygmy killer whale	0.00	0.00	0.00	0.03	0.01
Striped dolphin	0.00	0.00	0.00	0.03	0.01
Pygmy sperm whale	0.00	0.00	0.00	0.03	0.01
Overall	**1.12**	**1.57**	**1.45**	**2.02**	**1.62**
Number of species	**8**	**5**	**7**	**12**	**14**

Table 7. Number of genetic samples obtained, by species and island area.

Species	Island area				Total	# previously available[1]
	Hawai'i	**Maui &Lana'i**	**O'ahu**	**Kaua'i &Ni'ihau**		
Pantropical spotted dolphin	29	28	22	8	87	26
Bottlenose dolphin	1	9	27	45	82	43
Short-finned pilot whale	0	15	19	14	48	78
Spinner dolphin	7	10	3	19	39	52
Rough-toothed dolphin	0	0	2	36	38	6
Melon-headed whale	0	0	7	17	24	0
False killer whale	0	0	22	0	22	28
Dense-beaked whale	4	0	0	1	5	3
Killer whale	1	0	0	0	1	5
Total	**42**	**62**	**102**	**140**	**346**	**241**

[1]Number of previously available samples from Hawaiian waters in the collection of the SWFSC, La Jolla (information courtesy S. Chivers, SWFSC).