

Site fidelity and association patterns in a deep-water
dolphin: Rough-toothed dolphins (*Steno bredanensis*)
in the Hawaiian Archipelago

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ABSTRACT

In the Pacific, rough-toothed dolphins (*Steno bredanensis*) are typically found in the open ocean and in deep waters around oceanic islands. We examined habitat use, site fidelity, movements, and association patterns of this species in the main

Hawaiian Islands. Sighting rates were highest in depths >1,500 m. There were frequent within- and between-year resightings off the island of Hawai'i, indicating a small population size with high site fidelity. Resighting rates were lower off Kaua'i/Ni'ihau, indicating a larger population size, but with some site fidelity. Two individuals were documented moving from Kaua'i to Hawai'i, a distance of 480 km, but were not seen to associate with dolphins off Hawai'i. Observed movements were consistent with at most 2% dispersal per year between these two areas. Differences in group sizes, habitat use, and behavior imply that movements among the islands may be limited. Little is known about the diet of rough-toothed dolphins in Hawai'i, but they are thought to feed primarily on near-surface species. High fidelity to deep-water areas off the island of Hawai'i likely reflects an increase in the predictability of prey associated with upwelling due to the island mass effect, wind stress curl and cyclonic eddies that form off the island.

Key words: rough-toothed dolphin, *Steno bredanensis*, site fidelity, movements, islands, associations, Hawai'i.

Most studies of deep-water dolphin populations have involved large-vessel surveys, typically undertaken to estimate population sizes (*e.g.*, Wade and Gerrodette 1993). For deep-water species, studies of individuals using photo-identification have typically been limited to populations around oceanic islands (*e.g.*, Norris and Dohl 1980). Site fidelity, the tendency of an individual to return to an area previously occupied or remain in an area over an extended period, has been documented from a number of species of cetaceans, including humpback whales (*Megaptera novaeangliae*) returning to seasonal feeding and breeding grounds (Calambokidis *et al.* 2001), minke whales (*Balaenoptera acutorostrata*) returning to seasonal feeding grounds (Dorsey *et al.* 1990), and many populations of dolphins, including coastal, shallow-water common bottlenose dolphins (*Tursiops truncatus*), inhabiting small (<100 km²) and apparently permanent home ranges (Shane *et al.* 1986, Wells 1991, Gubbins 2002), as well as spinner dolphins (*Stenella longirostris*) using shallow-water areas for resting during the day (Norris and Dohl 1980, Norris *et al.* 1994). Coastal bottlenose dolphins typically feed on a diversity of benthic and schooling small fish, and in areas where local productivity is high enough to support a number of individuals, presumably they benefit from remaining within a small-home range by learning the location of spatially predictable food resources. There have been few studies of site fidelity in deep-water dolphins, due to the inherent difficulty of working with such populations. Exhibiting fidelity to a particular site would not be expected for an open-ocean species, as dolphins in deep waters are unlikely to be feeding on benthic prey, and most fish populations in open ocean waters that are suitable as prey for medium-sized dolphins are unlikely to be either spatially or temporally predictable. Evidence for bottlenose dolphins around two oceanic islands, Cocos Island off Costa Rica (Acevedo-Gutierrez 1999), and Bermuda (Klatsky *et al.* 2007), suggest individuals from such areas may have very large home ranges and show little fidelity to specific areas, although bottlenose dolphins in the Hawaiian Islands show considerable fidelity to specific areas (Baird *et al.* 2006a).

Opportunities for studying deep-water dolphins may be greatest around oceanic islands where deep-water populations may be found relatively close to shore, and the logistics of data collection may be relatively simple. In the Pacific Ocean, the rough-toothed dolphin (*Steno bredanensis*) is found primarily in open ocean areas and around oceanic islands in the tropics and subtropics (Jefferson 2002). This is a poorly known species, and most of what is known comes from stranded animals and those

caught in dolphin fisheries or from surveys that focus on distribution or abundance, rather than those that utilize information on individuals documented with photo-identification. There are no published studies on population structure for this species. As part of a long-term multi-species study of odontocete populations around the main Hawaiian Islands (see Baird 2005, Baird and Gorgone 2005, Baird *et al.* 2006a, 2008, McSweeney *et al.* 2007), we used photo-identification of distinctive individual rough-toothed dolphins to examine site fidelity and population structure.

There has been no previous directed research on rough-toothed dolphins in the Hawaiian Islands, though they have been well-documented from strandings in the main Hawaiian Islands (Mazzuca *et al.* 1999, Maldini *et al.* 2005) and from aerial and ship surveys, both around the main Hawaiian Islands and offshore (Mobley *et al.* 2000, Barlow 2006). Rough-toothed dolphins are one of the main species involved in fishery interactions in nearshore Hawaiian waters, stealing bait and hooked fish (Schlais 1984, Nitta and Henderson 1993). An estimate of abundance from aerial surveys around the main Hawaiian Islands (within 46 km of shore), an area of approximately 72,000 km², suggested the local population was small (123 individuals, CV = 0.63; Mobley *et al.* 2000). For the entire Hawaiian exclusive economic zone (EEZ), out to 380 km offshore and including the northwestern Hawaiian Islands (an area of approximately 2.4 million km²), there is a population estimate of 8,709 individuals (CV = 0.45; Barlow 2006) based on ship surveys.

METHODS

Surveys were undertaken around all of the main Hawaiian Islands between February 2000 and December 2006. A variety of dedicated research vessels were used, ranging in size from a 5.8-m outboard-powered rigid-hulled inflatable to an 18-m inboard-powered vessel, though the majority of surveys was undertaken from outboard-powered vessels between 6 and 8.2 m in length. Surveys around different islands were sometimes undertaken in different years. Survey effort was nonrandom and nonsystematic; tracklines followed were generally intended to maximize the likelihood of finding odontocetes, while covering as broad an area and as wide a depth range as possible given sea conditions and logistics (*e.g.*, distance from port). Attempts within field efforts were made to avoid overlap with previous survey lines. In most cases, we attempted to survey in areas where sea states were less than Beaufort 4, and almost all of the surveys were undertaken off the leeward sides of the islands to increase the likelihood of working in suitable sea conditions. Two to six observers were stationed to watch 360° around the survey vessels, which transited at speeds typically from 15 to 30 km/h, depending on sea state and vessel used. Effort data were logged automatically every 5 min with a global positioning system (GPS) on board survey vessels. Bottom depths at effort and sighting locations were derived by overlaying the point location data on a bathymetric raster surface in ArcGIS 9.1 (ESRI). Underlying depth values (in meters) were transferred to point locations using the "intersect point tool" in Hawth's analysis tools (Beyer 2004). We used gridded 3-arc s U.S. Coastal Relief Model bathymetry (~90 m × 90 m) from the National Geophysical Data Center.¹

During some of the periods in 2002 and 2003, two vessels were operated simultaneously, with vessels tending to travel 2–10 km apart to avoid overlap in survey coverage. On these days surveys were considered to have two "vessel days" of effort.

¹ Available from <http://www.ngdc.noaa.gov/mgg/coastal/coastal.html>.

All groups of odontocetes encountered were approached to confirm species, determine location, and to estimate group size. Photo-identification of individual dolphins was undertaken by one to three photographers attempting to obtain photographs of all individuals present, using film (through 2002) or digital (from 2003 to 2006) SLR cameras with 100–300-mm zoom lenses. In addition we attempted to obtain skin biopsies (using a crossbow or pole spear) from most groups for genetic studies (to be reported elsewhere). Associations with other species, evidence of feeding behaviors, and avoidance of the research vessel (and the estimated distance of avoidance, if it occurred) were recorded. Primary observers were trained in distance estimation using laser range finders (Bushnell Yardage Pro 800s and 1000s, Bushnell Corporation, Overland Park, KS) during each field effort. Training involved repeatedly estimating distances to a variety of targets on the water (ranging in size from seabirds to small vessels), at distances of approximately 8–400 m, with feedback given to observers on measured distances to the targets.

Photographs from 15 opportunistic encounters with this species around the main Hawaiian Islands were also provided by other researchers. Photographs were sorted within encounters by individual, using distinguishing characteristics such as notches on the trailing and leading edge of the dorsal fin, pigmentation patterns, scarring, and dorsal fin shape. In the case of poorly marked small calves, body size relative to adult individuals and the identity of associated adults was sometimes used to discriminate individuals within an encounter. The best quality photograph of each individual was assigned a photo quality (excellent, good, fair, poor) based on the focus, the angle of the dorsal fin relative to the frame, the size of the fin relative to frame size, and whether the fin was obscured in any way by water or other dolphins. Each individual was also assigned a distinctiveness rating (very distinctive, distinctive, slightly distinctive, not distinctive) based on the number, size, and configuration of dorsal fin notches. Individuals with no or only very small dorsal fin notches were considered to be not distinctive, although they could still be sorted within and sometimes between encounters based on pigmentation patterns, scarring, dorsal fin shape, and relative body size. The proportion of individuals in the population that was considered to be “marked” (*i.e.*, having long-term (multi-year) distinctive features that could be recognized with either left- or right-side photographs) was estimated by dividing the number of individuals considered distinctive or very distinctive by the total number of individuals within each encounter using photographs of good or excellent quality, and calculating an average over all encounters. Photographs of all qualities and distinctiveness ratings were compared to examine movements among areas, although for resighting statistics, only good and excellent quality photographs of distinctive and very distinctive individuals were used.

For the purposes of examining depth distribution of effort, inter-island movements, and resightings within- and among-areas, we considered four “island areas”: (1) Kaua’i and Ni’ihau (2) O’ahu; (3) the “4-island area” (including Maui, Lana’i, Kaho’olawe, and Moloka’i); and (4) the island of Hawai’i (Fig. 1). Sighting rates in relation to effort by depth were calculated using 500-m depth bins (*e.g.*, 1–500 m, 501–1,000 m, *etc.*). The average straight-line distance between locations of sightings where individuals were resighted was calculated using the Posdist² add-in in Excel (Version 2000 Microsoft, Redmond, WA). For comparison, the average straight-line distance between all possible pairs of sightings within an area (*e.g.*, Kaua’i/Ni’ihau or

²Available from <http://nmml.afsc.noaa.gov/software/excelgeo.php>.

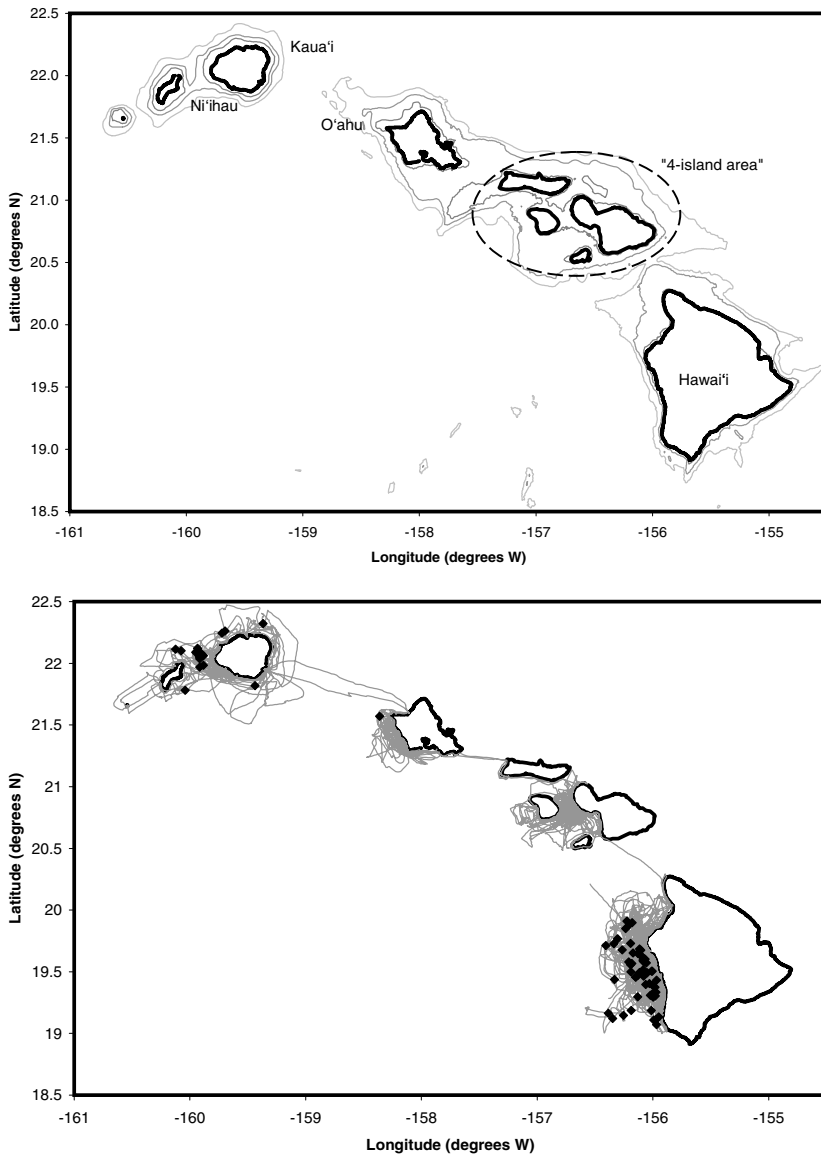


Figure 1. Top. Main Hawaiian islands showing 100 m, 1,000 m, and 2,000 m depth contours. Bottom. Survey tracklines and sighting locations of rough-toothed dolphins.

Hawai'i) were also calculated. For cases where two or more individuals were seen together in one sighting and resighted together at a later date, resighting distances were only calculated once. Statistical tests were undertaken with Minitab 13.2 (Minitab Inc., State College, Pennsylvania, PA).

To evaluate the significance of the between-area resighting rates, we used a simulation to estimate the probability of missing inter-island movements for different inter-island dispersal rates. In each year of the simulation (2000–2006), we randomly

sampled from each area the number of unique individuals (distinctive or very distinctive individuals with photo qualities of good or excellent) actually identified in that year. Following the sampling event, each individual had a probability d of dispersing from its current population. We kept track of the sighting histories of each simulated individual, noting in which area an animal was sighted for each sighting event.

The simulation required an estimate of the number of distinctive and very distinctive animals (hereafter "marked") for each area. We used the photo-identification data to generate crude capture-recapture estimates of the number of marked animals, using a Petersen estimator (Seber 1982). For Kaua'i/Ni'ihau we had photo-identification data primarily from 2003 and 2005, while for Hawai'i we pooled identifications from 2003/2004 as the first sample and from 2005/2006 as the second sample. The number of recaptures was the subset of individuals from the final year(s) that had been seen in the previous year(s). Because there is uncertainty around the estimates generated in this manner, we tested the sensitivity of our simulations to this parameter. The CVs of the estimates were used to generate upper and lower bounds on the estimates, using the 97.5th percentile and 2.5th percentile values, respectively. We simulated nine different potential inter-island dispersal rates, ranging from 0.2% to 5% per year, a spread that brackets levels of dispersal that should have demographic consequences. For each of the nine dispersal rates and three pairs of population estimates (2.5th percentile, best estimate, 97.5th percentile), we ran 500 replicate simulations and counted the number of replicates in which no inter-island resightings were observed. Estimates of population sizes (taking into account the proportion of marked individuals in the population and various biases that may influence population estimates) will be reported elsewhere.

Association levels were assessed with *Socprog* 2.3³, using a simple ratio index of association (Cairns and Schwager 1987, Ginsberg and Young 1992), with values ranging from 0 (for individuals that are never seen together) to 1 (for individuals that are always seen together). Calculations of mean and maximum association indices, and tests for preferred/avoided associations (following Bejder *et al.* 1998) included only individuals seen on three or more occasions. Tests for preferred/avoided associations compared the real association indices against 20,000 randomly permuted variations. P values were determined based on the proportion of the 20,000 permutations that had higher SDs of the association indices than the SD of the real association indices, thus P values that were large ($P > 0.95$) indicated a significant difference. The number of individuals linked by association off each island was assessed with Netdraw 2.043 (Analytic Technologies, Needham, MA).

RESULTS

Surveys were undertaken on 369 vessel days, covering 38,434 km of trackline in 2,634 h of effort. Overall surveys were undertaken in 11 different months of the year, with surveys off each island area in two to five different years (Table 1). Surveys were generally restricted to areas within 40 km of shore, although there was some effort off the island of Hawai'i out to 70 km from shore. For all islands except for Kaua'i, Ni'ihau, and Lana'i, surveys were restricted to the leeward (west and southwest) sides of the islands (Fig. 1) due to favorable sea conditions. Depth

³Dalhousie University, Halifax, Nova Scotia, Canada. Available from myweb.dal.ca/~hwhitehe/social.htm.

Table 1. Search effort and rough-toothed dolphin sightings by island area.

Island area	Dates	# km on effort	# d effort	# h on effort	# sightings
Hawai'i	April 2002	1,162	10	77	0
	September/October 2002	1,682	21	157	1
	May 2003	1,872	15	110	1
	October 2003	2,496	24	173	4
	September–December 2004	4,656	42	288	22
	January/February 2005	2,089	17	124	3
	March/April 2006	4,263	36	257	16
	July 2006	1,296	12	84	5
	November/December 2006	2,675	25	174	3
	Subtotal	22,191	202	1,444	55
Kaua'i/Ni'ihau	May/June 2003	3,222	24	195	11
	October/November 2005	2,194	24	145	5
	Subtotal	5,416	48	340	16
4-island area	February–April 2000	1,600	23	158	0
	November/December 2000	2,032	21	150	0
	January–March 2001	2,102	28	203	0
	April 2002	785	9	64	0
	May 2003	1,659	16	107	0
	Subtotal	8,178	97	682	0
O'ahu;	April/May 2002	860	9	57	0
	May 2003	1,789	13	111	1
	Subtotal	2,649	22	168	1
Total		38,434	369	2,634	72

of survey coverage varied greatly among the different island areas, with effort in shallowest water in the 4-island area and in deepest water off Hawai'i (Fig. 2). The overall size of the area surveyed (not including the major channels between the island areas) was approximately 17,000 km².

There were 851 sightings of odontocetes, 72 of which were rough-toothed dolphins (8.5%), the fifth most frequently encountered species (out of 16 species of odontocetes documented). Rough-toothed dolphins were encountered in 10 of the 11 mo with survey coverage (all except February for which there was only ~18 h of search effort in depths >500 m), and were observed 55 times off the island of Hawai'i, once off O'ahu;, and 16 times off the islands of Kaua'i/Ni'ihau. Off the islands of Hawai'i and Kaua'i/Ni'ihau, they were the fourth and third most frequently encountered species, respectively (representing 9.5% of sightings off Hawai'i and 13.2% of sightings off Kaua'i/Ni'ihau). Despite substantial effort and 107 odontocete sightings in the 4-island area (Table 1), there were no sightings of rough-toothed dolphins there. Encounter duration ranged from approximately 1 min to 2 h and 52 min (median = 27 min).

Overall sightings of rough-toothed dolphins were more common in the deeper areas surveyed, although there was less effort in those areas (Fig. 3). Sighting rates of rough-toothed dolphins (measured as number of sightings per 100 h of effort) generally increased with depth (Fig. 4) and were particularly high in depths greater than 1,500 m. Distance from shore of sightings ranged from 3.29 km to 49.17 km (median = 12.58 km). Median distance from shore for effort data was 6.51 km.

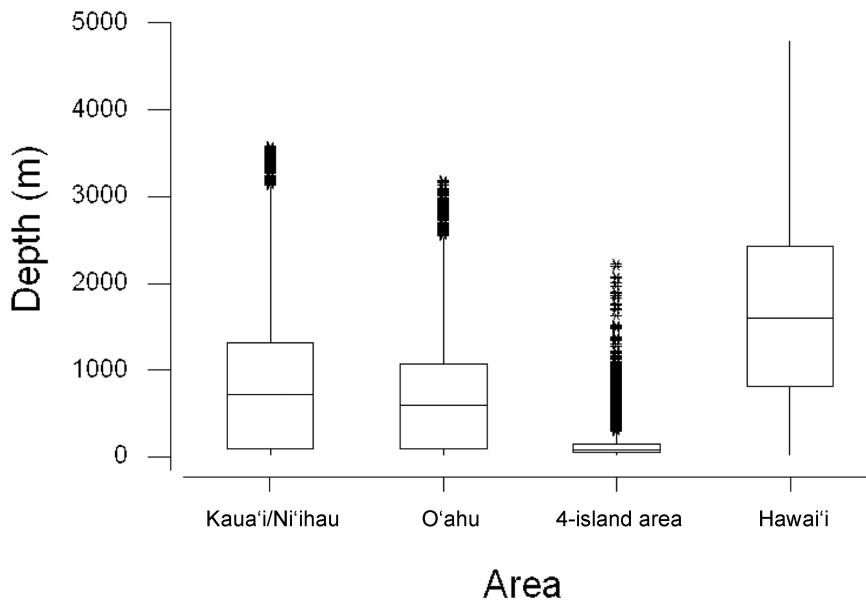


Figure 2. Box-plot showing depth distribution of effort around the different island areas. Middle line shows median value, upper and lower lines of box show 75th and 25th percentile, respectively. The ends of the upper and lower vertical lines indicate the minimum and maximum data values, unless outliers are present (*) in which case the vertical lines extend to a maximum of 1.5 times the inter-quartile range.

Associations with melon-headed whales (*Peponocephala electra*) were frequent (four encounters), particularly given that melon-headed whales were only encountered on 21 occasions during the study. Associations were also recorded with false killer whales, *Pseudorca crassidens* (one encounter out of 18 with false killer whales), and as with melon-headed whales both species were intermingled. They were also seen near short-finned pilot whales, *Globicephala macrorhynchus* (two encounters), common bottlenose dolphins (one encounter), Blainville's beaked whales, *Mesoplodon densirostris* (one encounter), and pantropical spotted dolphins, *Stenella attenuata* (two encounters), but the two species were not seen to interact. Associations were also recorded with six species of seabirds: great frigate birds, *Fregata minor* (four encounters), white-tailed tropicbirds, *Phaethon lepturus* (two encounters), brown boobies, *Sula leucogaster* (two encounters), dark-rumped petrel, *Pterodroma phaeopygia* (one encounter), sooty terns, *Onychoprion fuscatus* (one encounter), and wedge-tailed shearwaters, *Puffinus pacificus* (three encounters), typically with these species feeding in association with rough-toothed dolphins. Feeding behaviors (actively chasing or circling fish, or holding prey in the mouth) were documented in 18 encounters, including individual dolphins chasing unidentified species of flying fish and needlefish, circling schools of small (e.g., 5–15 cm long) fish, and holding squid parts in the mouth.

Group size estimates ranged from 2 to 90 individuals (median = 7). The largest group based on the number of identified individuals within the group was 109. It is likely that some group size estimates were negatively biased, due to short encounter duration or unfavorable sea conditions. Larger groups were often made up of subgroups of 2–10 individuals separated from other subgroups by tens or even

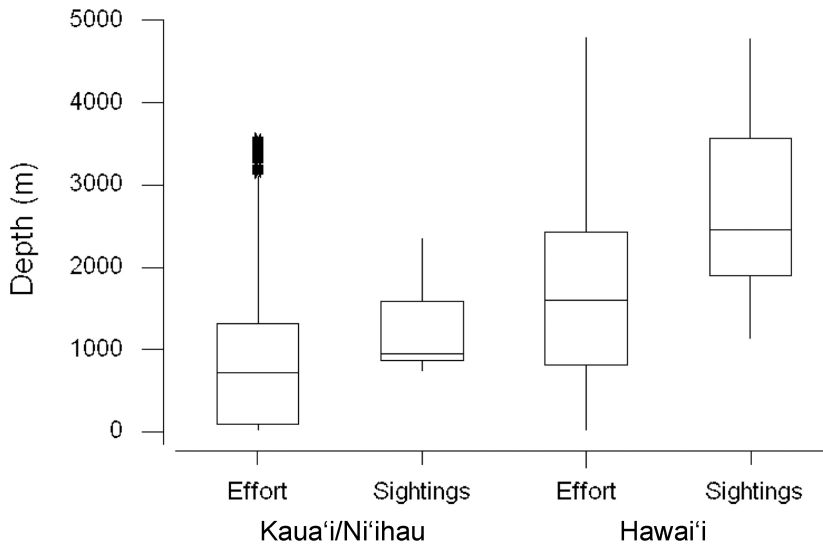


Figure 3. Box plot of depth distribution of rough-toothed dolphin sightings off Kaua'i/Ni'ihau and the island of Hawai'i in comparison to depth distribution of effort off those islands. Middle line shows median value, upper and lower lines of box show 75th and 25th percentile, respectively. The ends of the upper and lower vertical lines indicate the minimum and maximum data values, unless outliers are present (*), in which case the vertical lines extend to a maximum of 1.5 times the inter-quartile range.

hundreds of meters, and longer encounter durations often resulted in the detection of one or more scattered subgroups. There was a significant positive relationship between encounter duration and group size (regression, $P < 0.001$, $r^2 = 0.52$). Group size for encounters < 1 h ranged from 1 to 35 (median = 6), while for encounters > 1 h group size ranged from 2 to 90 (median = 26.5). Group sizes were significantly larger off Kaua'i/Ni'ihau (median = 11) than off Hawai'i (median = 6, Mann-Whitney U test, $P = 0.0212$; Fig. 5); however, encounter durations were also significantly longer off Kaua'i/Ni'ihau (median = 0.67 h) than off Hawai'i (median = 0.42 h; Mann-Whitney U test, $P = 0.0378$). There were behavioral differences between rough-toothed dolphins off Kaua'i/Ni'ihau and those off the island of Hawai'i. When approached for the purposes of photo-identification or biopsy sampling, avoidance of the research vessel was recorded half as frequently off Kaua'i/Ni'ihau (3 of 16 encounters, 18.75%) as off Hawai'i (21 of 55 encounters, 38.2%). The estimated distance between the research vessel and the dolphins when avoidance was noted was significantly lower (Mann-Whitney U test, $P = 0.0362$) off Kaua'i/Ni'ihau (range 5–10 m, median = 10 m) than off Hawai'i (range 10–80 m, median = 20 m). While it was not quantified, bowriding on the research boat occurred more frequently and for longer durations off Kaua'i/Ni'ihau than off Hawai'i. Biopsy samples were collected in 75% (12 of 16) of the encounters off Kaua'i/Ni'ihau, but in only 30.9% (17 of 55) of the encounters off Hawai'i, thus greater avoidance off of Hawai'i was not likely due to reactions from biopsy sampling. Dolphin associations with commercial or sports fishing vessels or fish aggregating devices were recorded on three occasions off the island of Hawai'i.

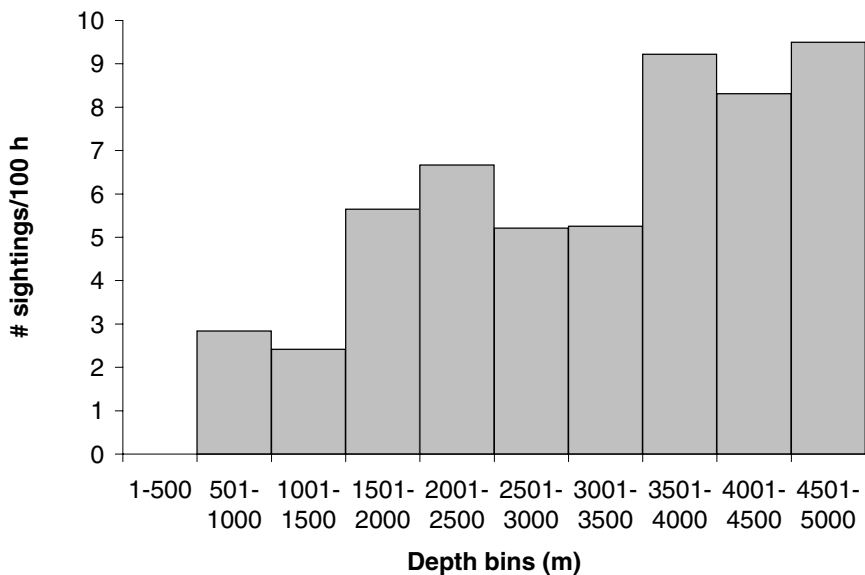


Figure 4. Sightings per unit effort (# sightings/100 h) of rough-toothed dolphins for various depth ranges (depths shown in 500 m bins) including all areas.

Photographs were obtained from 65 of the 72 encounters. Photographs of distinctive and very distinctive individuals of good or excellent photo quality were available from 60 of these encounters. Additional identification photographs were available from 15 opportunistic encounters by other researchers, although distinctive and very distinctive individuals with good or excellent photo qualities were available only from 10 of these. From all encounters combined there were 792 identifications of rough-toothed dolphins, not discounting individuals seen on multiple occasions or individuals that were poorly marked or with poor photo quality. Excluding individual identifications where photo quality was poor or fair resulted in 508 identifications. Of these, 440 were considered to be distinctive or very distinctive. The number of identifications per group (distinctive or very distinctive with photo quality of good or excellent) ranged from 1 to 91 (median = 3). Distinctiveness rating increased with the number of dorsal fin notches per individual: not distinctive, range 0–1, median = 0; slightly distinctive, range 1–7, median = 2; distinctive, range 2–14, median = 7; very distinctive, range 2–17, median = 9. Those considered distinctive or very distinctive were thought to have enough long-term recognizable markings to be reidentified both within- and among-years with any photo quality greater than poor or fair. The rate of mark change and mark acquisition was assessed by summing all the intervals between resightings for individuals seen on more than one occasion, and examining all resightings of individuals for new notches or changes in notch shape. Of the 70 individuals that were seen more than once, 17 were documented with a total of 30 mark changes and/or new marks (2 changes in notch shape, 26 new notches, and two losing notches). The sum of time intervals between resightings of all 70 individuals was 26,497 d (approximately 72.5 yr), thus changes in marks (new notches, changes in notch shape, or loss of notches) were estimated to occur

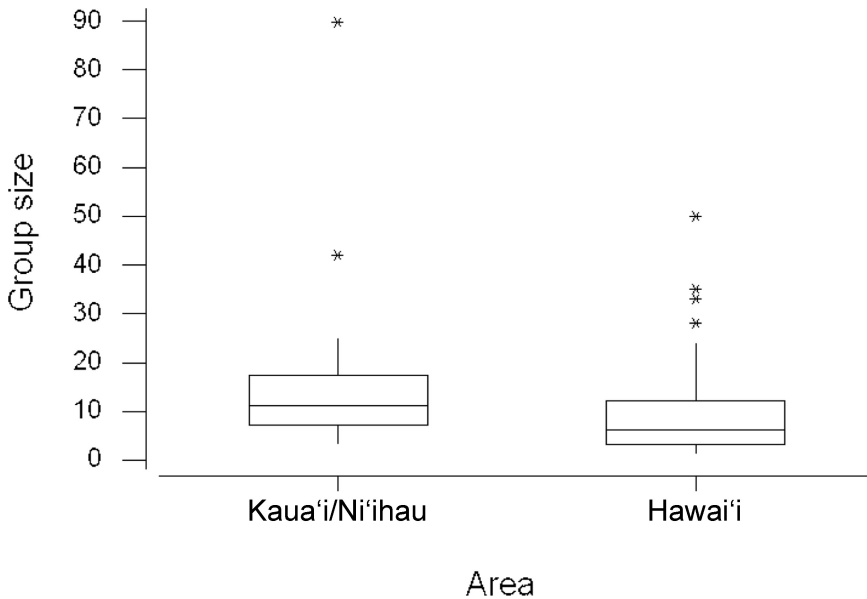


Figure 5. Box plot of distribution of group sizes of rough-toothed dolphins off Kaua'i/Ni'ihau and the island of Hawai'i. Middle line shows median value, upper and lower lines of box show 75th and 25th percentile, respectively. The ends of the upper and lower vertical lines indicate the minimum and maximum data values, unless outliers are present (*), in which case the vertical lines extend to a maximum of 1.5 times the inter-quartile range.

at the rate of approximately one change every 2.42 yr (72.5 yr divided by 30 mark changes/new marks).

The percentage of dolphins within each group that were distinctive or very distinctive ranged from 33 to 100% (median = 100%). Of the distinctive and very distinctive individuals, 209 were documented off Kaua'i/Ni'ihau, 6 off O'ahu, and 124 off the island of Hawai'i (Table 2). The percentage of distinctive and very distinctive individuals within groups seen on more than one occasion ranged from 0 to 100% (median = 67%). The percentage of individuals within groups seen on more than one occasion was significantly greater off Hawai'i (median = 75%) than off Kaua'i/Ni'ihau (median = 8%, Mann-Whitney U test $P = 0.0013$). There were both within-year and between-year resightings for animals off Kaua'i/Ni'ihau (5 between- and 11 within-year resightings of 16 individuals) and for animals off Hawai'i (43 between-year and 42 within-year resightings of 52 individuals). Time intervals between resightings ranged from 1 to 896 d (2.45 yr) off Kaua'i/Ni'ihau (median = 10 d, $n = 16$), and from 1 to 920 d (2.52 yr) off Hawai'i (median = 111 d, 0.3 yr, $n = 85$). Time intervals from when an individual was first seen to when it was last seen ranged from 1 to 1,011 d (median = 435 d, $n = 52$) off Hawai'i. Two individuals were found to move from Kaua'i to Hawai'i after an interval of 309 d, with a straight-line distance of 480 km between sighting locations. There was no significant relationship between the time interval and distance between resightings off Hawai'i (regression, $P = 0.73$, $r^2 = 0.0027$) or off Kaua'i/Ni'ihau (regression, $P = 0.74$, $r^2 = 0.03$). Distance between all possible pairs of sightings ranged from

Table 2. Rough-toothed dolphin photo-identification results by area.

Island area	# IDs of marked individuals	# individuals (excluding within-area resightings)	# (%) seen more than once	# within-area within year resightings	# within-area among year resightings	# individuals seen at other islands
Kaua'i/Ni'ihau	225	209	18 (8.6%)	11	5	2
O'ahu;	6	6	0	N/A	0	0
Hawai'i	209	124	54 (43.5%)	42	43	2
Overall	440	337	70 (20.8%)	53	48	2

Only distinctive and very distinctive individuals with photo qualities of good or excellent are considered.

1.7 to 91.6 km (median = 27.7 km, $n = 120$) off Kaua'i/Ni'ihau, and from 0.3 to 96.9 km (median = 29.4 km, $n = 1,711$) off Hawai'i. Distances between resightings of individuals off Kaua'i/Ni'ihau (median = 31.8 km, range 3.94–56.02 km, $n = 8$) and off Hawai'i (median = 23.0 km, range = 3.01–59.43, $n = 41$), were not statistically different (Mann-Whitney U test, $P = 0.5792$).

The mean association index for those individuals seen on three or more occasions ($n = 21$) was 0.08 (SD = 0.04), and the mean of the maximum association indices for these individuals was 0.58 (SD = 0.31). Tests for preferred/avoided associations were significant ($P = 0.9936$). Analyses of associations indicated that 97 of the 124 individuals (78.2%) documented off the island of Hawai'i were linked by association in a single social network (not shown). Off Kaua'i/Ni'ihau, 162 of 209 individuals (77.5%) were linked by association in a single social network. The two individuals documented off both Kaua'i/Ni'ihau and the island of Hawai'i were members of the large social network documented off Kaua'i/Ni'ihau, but were not recorded associating with any other individuals off the island of Hawai'i.

Petersen mark-recapture estimates (for the number of "marked" individuals in the population) for Hawai'i were 198 (CV = 0.12) for a comparison of 2003/2004 vs. 2005/2006 identifications, and for Kaua'i/Ni'ihau were 1,665 (CV = 0.33) for the 2003/2005 comparison. The 2.5th and 97.5th percentiles calculated from these estimates were 156 and 250 for Hawai'i, respectively, and 855 and 3,241 for Kaua'i/Ni'ihau, respectively. A simulation to determine the probability of failing to detect more than two movements between Kaua'i/Ni'ihau and Hawai'i, given the sampling in each area and using multiple population estimates, indicated that sampling was consistent with, at most, a 2%/yr dispersal rate between the two areas (Table 3).

DISCUSSION

While they are widely distributed throughout tropical and warm-temperate waters worldwide, little is known about rough-toothed dolphins anywhere in their range. Rough-toothed dolphins were found in deep-water areas throughout the main Hawaiian Islands and were found at higher rates in the deepest portions of the study

Table 3. Estimated probability of failing to detect more than two movements between Kaua'i/Ni'ihau and Hawai'i, as a function of annual dispersal rate and the estimated number of marked animals in each population, using three different pairs of population estimates for each area (best estimate as well as the upper and lower 97.5% confidence intervals on the estimate).

Dispersal rate (%/yr)	Estimates of number of marked animals		
	Best estimates	2.5 th percentile estimates	97.5 th percentile estimates
0.2	0.996	0.986	1.0
0.4	0.924	0.90	0.968
0.6	0.752	0.616	0.83
0.8	0.47	0.304	0.616
1.0	0.228	0.106	0.364
2.0	0.038	0.008	0.16
3.0	0.002	<0.001	0.032
4.0	<0.001	<0.001	0.004
5.0	<0.001	<0.001	<0.001

area (Fig. 4), similar to reports from elsewhere in the Pacific (*e.g.*, Gannier and West 2005), and in contrast to some reports from the Atlantic (*e.g.*, Kuczaj and Yeater 2007). Due to weather and vessel limitations, surveys were generally restricted to relatively nearshore areas (within approximately 40 km of shore), and thus the offshore limits of the island-associated population have not been determined. In our study, rough-toothed dolphins were found primarily in two separate parts of the study area, off Kaua'i/Ni'ihau in the northwest and off the island of Hawai'i in the southeast, but we had little effort in the deep-water channels between the islands (Fig. 1). And while there were no sightings in the 4-island area and only one sighting off O'ahu;, most of the effort off those islands was in relatively shallow areas (Fig. 2) where rough-toothed dolphins are unlikely to be found.

We were able to photo-identify distinctive individuals in three areas, 124 off the island of Hawai'i, 6 off O'ahu;, and 209 off Kaua'i/Ni'ihau. Two of the individuals documented off Kaua'i/Ni'ihau were also documented off Hawai'i, resulting in a total of 337 distinctive individuals cataloged. These two individuals were not documented associating with rough-toothed dolphins off the island of Hawai'i, thus it is not known if such movements represent immigration into that subpopulation, or reflect temporary movement of individuals. Given our sampling off the different islands, the movement of two individuals is consistent with an annual dispersal rate of up to 2%, but not greater (Table 3).

Despite their preference for deep waters (>1,500 m), resighting rates were high off the island of Hawai'i, with 75% of the distinctive and very distinctive individuals within groups being seen on two or more occasions, suggesting both high site fidelity and a relatively small population size. More individuals were identified off Kaua'i/Ni'ihau than off Hawai'i, although in less than a third the number of encounters, due to larger group sizes. The lower resighting rates off Kaua'i/Ni'ihau are likely due, in part, to the relatively small number of encounters from only two field efforts (Table 1), as well as greater abundance off those islands. In Barlow's (2006) survey of the entire Hawaiian EEZ, rough-toothed dolphin density was approximately 2.5 times higher in the "Main Island Stratum" (within 140 km of the main islands)

compared to the "Outer EEZ Stratum," possibly reflecting these island-associated populations.

Evidence of high site fidelity was not expected for rough-toothed dolphins, given their deep-water distribution around the main Hawaiian islands. While central tropical Pacific waters are generally oligotrophic, there is increased productivity around the Hawaiian Islands for a variety of reasons, including upwelling due to the "island mass effect," input of nutrients from freshwater runoff, and wind stress curl induced upwelling (Doty and Oguri 1956, Gilmartin and Revelante 1974). In addition, cyclonic eddies that form in the lee of the island of Hawai'i cause upwelling and substantially increased productivity (Seki *et al.* 2001, 2002, Bidigare *et al.* 2003). It is likely that such increased productivity and thus increased spatial and temporal predictability of prey have led to the high site fidelity documented off the island of Hawai'i. Upwelling due to the island mass effect and wind stress curl should be lower off Kaua'i and Ni'ihau, and cyclonic eddies tend not to form off those islands. The effects of cyclonic eddies that occur in the lee of the island of Hawai'i often extend tens to hundreds of kilometers offshore (Seki *et al.* 2001, 2002, Bidigare *et al.* 2003), which may also explain the deeper water distribution found off that island in comparison to Kaua'i/Ni'ihau (Fig. 3).

Mayr and Ritter (2005) have noted that individual rough-toothed dolphins may be "resident" off the Canary Islands, also based on resightings of photo-identified individuals. Like Hawai'i, productivity is greater around the Canary Islands, due to a variety of oceanographic processes (Aristegui *et al.* 1997, Ritter 2001), possibly encouraging high site fidelity. High site fidelity has been previously documented for several other deep-water cetaceans, the northern bottlenose whale (*Hyperoodon ampullatus*) inhabiting deep-water canyons off the east coast of Canada (Hooker *et al.* 2002, Wimmer and Whitehead 2005), both Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales off the island of Hawai'i (McSweeney *et al.* 2007), and both spinner dolphins (Norris *et al.* 1994, Marten and Psarakos 1999) and false killer whales (*Pseudorca crassidens*) around the Hawaiian Islands (Baird *et al.* 2008). All three species of beaked whales are deep divers, typically feeding at depths of greater than 1,000 m (Hooker and Baird 1999, Baird *et al.* 2006b). Spinner dolphins feed on mesopelagic fish and squid that become available to the dolphins at night due to a combination of vertical and horizontal (toward shore) diel migrations (Benoit-Bird and Au 2003). False killer whales around Hawai'i appear to feed primarily on large pelagic fish (Baird *et al.* 2008) that typically are found near the surface. Little is known of the diving behavior of rough-toothed dolphins, though dive data from two animals tagged and released after stranding and rehabilitation in the Atlantic suggest they remain primarily in near-surface waters (Wells and Gannon 2005). Based on observations of predation and stomach contents (Miyazaki and Perrin 1994, Pitman and Stinchcomb 2002), as well as our observations of regular feeding on near-surface prey (flying fish, needlefish, and unidentified small schooling fish), there is little evidence of predation on deep-water species.

While we produced mark-recapture estimates of the number of "marked" individuals (*i.e.*, not corrected to take into account the proportion of marked *vs.* unmarked individuals) off both areas, they should be viewed with caution for several reasons. While the low rate of inter-island resightings implies some degree of population structure, the biases in survey coverage suggest that we have not covered the entire range of the population(s). In addition, we have not taken into account a variety of sources of heterogeneity of capture probabilities that could bias estimates. In

particular, the estimate for Kaua'i/Ni'ihau is likely positively biased, as it is over a 2.5-yr period, and thus likely violates the assumption of population closure. Mark acquisition/mark change is relatively low (an average of one change every 2.4 yr), and individuals have large numbers of marks, thus the likelihood of missing matches due to mark change is relatively small. We present these estimates purely to indicate that the population is likely relatively small off the island of Hawai'i (apparently in the low hundreds of individuals) and likely much higher off Kaua'i/Ni'ihau (in the low thousands of individuals). Despite the uncertainty associated with these estimates, combined they are considerably larger than the estimate (123 individuals, $CV = 0.63$) available from aerial surveys covering a 72,000 km² area around the main Hawaiian Islands (Mobley *et al.* 2000). A larger population estimate off Kaua'i and Ni'ihau seems counter-intuitive if productivity (and presumably thus prey availability) is lower there. However, the lower resighting rates may reflect greater movements of individuals if home ranges must be larger to account for the reduction in predictability of resources. While straight-line distances between resighting locations of individuals off Kaua'i/Ni'ihau (median = 31.8 km) were not statistically greater than straight-line distances between resighting locations off Hawai'i (median = 23.4 km), the sample size for resightings off Kaua'i/Ni'ihau was small ($n = 8$), thus the power of the test was relatively low. In addition, due to the geographic distribution of sightings around the islands, such straight-line distances underestimate the true distances of sighting locations off Kaua'i/Ni'ihau, but not off Hawai'i (Fig. 1). The situation off Kaua'i and Ni'ihau seems similar to that found with bottlenose dolphins off Cocos Island, Costa Rica, where large numbers of individuals were documented with very few resightings (Acevedo-Gutierrez 1999), presumably reflecting that the island is only one stop-over in a larger range for that population. From an oceanographic standpoint, there is little in the way of island-induced phenomena (*e.g.*, wakes, eddies) caused by Cocos Island that would result in enhanced local production.⁴ In addition, the island sits within a highly productive region in the eastern tropical Pacific (*e.g.*, Palacios *et al.* 2006). Thus, there is likely little benefit associated with fidelity to the island for dolphin populations there.

Approximately 38% of the groups of rough-toothed dolphins around the island of Hawai'i exhibited avoidance of our research vessel, at an estimated median distance of 20 m, while such avoidance behavior was much less frequent off Kaua'i and Ni'ihau (18.7%) and occurred at a closer distance (median = 10 m). More biopsy sampling was undertaken off Kaua'i and Ni'ihau than off the island of Hawai'i, thus avoidance of the research vessel due to reactions to biopsy sampling is unlikely to explain this difference. Ritter (2002) reported no such avoidance of rough-toothed dolphins around the Canary Islands. We suspect such avoidance may be a response to occasional shooting of this species in the area; they are known to steal bait and hooked fish, and shooting has been reported as a method of deterrence, albeit illegal, in Hawai'i (Kuljis 1983). Furthermore, fishing effort is lower off Kaua'i and Ni'ihau (Hawai'i Department of Land and Natural Resources, unpublished data), and fisheries interactions are thought to be much less frequent there (Kuljis 1983), thus it is less likely that individuals in that area may be shot at. There were several differences

⁴Personal communication from D. M. Palacios, Environmental Research Division, NOAA Fisheries, 1352 Lighthouse Avenue, Pacific Grove, CA 93950, 6 March 2006.

in habitat use/group structure between the two areas where rough-toothed dolphins were regularly found (Hawai'i and Kaua'i/Ni'ihau) which support the supposition of population structure. Off Kaua'i/Ni'ihau, rough-toothed dolphins were found in significantly larger groups, and despite differences in the depth distribution of survey effort between these two areas, they were found in much shallower water off Kaua'i/Ni'ihau than off the island of Hawai'i (Fig. 3). Similarly, differences in their reactions to vessels suggest that movements of individuals between these island areas may be infrequent.

Evidence of population structure within the Hawaiian Islands has also been suggested for bottlenose dolphins and spinner dolphins, based both on genetic analyses (Andrews *et al.* 2006, Martien and Baird 2006), and in the case of bottlenose dolphins a lack of movements of photo-identified individuals among islands (Baird *et al.* 2006a). Both species around the main Hawaiian Islands inhabit much shallower water than rough-toothed dolphins do, however. Stranded rough-toothed dolphins that have been rehabilitated, then radio-tagged and released in the Gulf of Mexico and the western Atlantic, have traveled distances ranging from several hundred kilometers, with relatively localized movements over a period of 5 mo (Wells *et al.* 1999), to more than 1,500 km (Wells and Gannon 2005), thus the distance between the two clusters of sightings in our study are well within the range of individual dolphins. Clearly, more survey effort in the deep-water areas between Kaua'i/Ni'ihau and the island of Hawai'i is needed, as well as survey coverage off the windward sides of islands and in areas further offshore, to better understand population structure for this species in the Hawaiian Islands. However, such evidence implies that impacts from localized fisheries interactions may have a greater effect on the population of rough-toothed dolphins off the island of Hawai'i than if individuals were moving regularly among islands. NOAA Fisheries, the agency responsible for the management of rough-toothed dolphins in U.S. waters, currently considers there to be a single stock of rough-toothed dolphins within the Hawaiian EEZ (Carretta *et al.* 2006). Our evidence of site fidelity and potential population structure within the main Hawaiian Islands suggests that there is likely more than one stock within the Hawaiian EEZ.

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