

Odontocete Cetaceans Around the Main Hawaiian Islands: Habitat Use and Relative Abundance from Small-Boat Sighting Surveys

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Abstract

Knowledge of the distribution and relative abundance of odontocete cetaceans is important for helping to understand and potentially mitigate impacts of anthropogenic activities. We present small-boat survey and sighting data from 13 y (2000 through 2012) of field studies around the main Hawaiian Islands. We surveyed 84,758 km of trackline, with effort ranging from 3 to 11 y off each of the four different island areas. We had 2,018 sightings of odontocetes representing all 18 species known to exist in Hawai'i. Analyses indicated that sighting rates varied with depth for most species, with some found at their highest rates in shallow (< 1,000 m) water (e.g., common bottlenose and spinner dolphins), some in slope (500 to 2,500 m) water (e.g., dwarf sperm whales and short-finned pilot whales), and some in very deep (> 3,000 m) water (e.g., sperm whales, striped dolphins, Risso's dolphins, and rough-toothed dolphins). Most species (14 of 18) were recorded in all oceanographic seasons. Restricting effort data by depth indicates that in depths > 3,000 m, the most commonly encountered species are rough-toothed dolphins, pantropical spotted dolphins, striped dolphins, and sperm whales. In depths < 2,000 m, the most commonly sighted species were short-finned pilot whales, pantropical spotted dolphins, common bottlenose dolphins, and rough-toothed dolphins. Sighting rates for some species varied among islands, apparently unrelated to differences in effort in different areas. Off Kaua'i and Ni'ihau rough-toothed dolphins were seen more often than expected (25.9% of sightings) based on sighting rates of this species elsewhere in the islands, while pantropical spotted dolphins (3.9% of sightings) and short-finned pilot whales (6.5% of sightings) were seen less often than expected given that they are among the most common species off the other island areas.

Such patterns are relevant to interpreting results of acoustic and aerial survey methods in which species identifications are inferred from classification methods or limited by brief sighting opportunities, respectively.

Key Words: Hawai'i, dwarf sperm whale, melon-headed whale, pantropical spotted dolphin, Risso's dolphin, rough-toothed dolphin, short-finned pilot whale, striped dolphin, acoustic methods, habitat use

Introduction

Hawaiian waters are home to a diverse community of cetaceans, with 18 species of odontocetes and seven species of mysticetes documented (Barlow, 2006). Knowledge of the distribution and relative abundance of these species is important for environmental planning to help understand and potentially mitigate the impacts of anthropogenic activities such as commercial shipping, Navy training, ocean energy development, aquaculture operations, tourism, and fisheries. Such information is also relevant to interpreting the results from acoustic detection methods for cetaceans, including bottom- or glider-mounted hydrophones (McDonald et al., 2009; Klinck et al., 2012), and to help assess the efficacy of acoustic detection and classification systems.

While there have been a number of in-depth studies of individual odontocete species in Hawaiian waters (e.g., Norris et al., 1994; McSweeney et al., 2007, 2009; Baird et al., 2008a, 2009; Aschettino et al., 2011; Martien et al., 2011; Mahaffy, 2012), multispecies assessments have been relatively limited, and each is subject to a number of biases. In 2002, a large-scale multivessel line-transect survey was undertaken throughout the entire Hawaiian Exclusive Economic Zone (EEZ) covering some 17,000 km of trackline (Barlow, 2006). While all 18

species of odontocetes known to inhabit Hawaiian waters were documented, around the main Hawaiian Islands, there were no sightings of five species that are known to have island-associated resident populations, despite extensive effort (3,550 km of trackline covered; Barlow, 2006). In part, this reflects the low density of many species of odontocetes in the oligotrophic waters of the central tropical Pacific and the resultant large amount of effort necessary to effectively sample them. For example, one species not seen around the main Hawaiian Islands in the Barlow (2006) survey was false killer whales (*Pseudorca crassidens*); the main Hawaiian Islands insular population of this species is thought to number less than 200 individuals (Baird, unpub. data, 2000-2012). Although large vessels can survey in offshore waters and on the windward sides of the islands, the relatively poor sea conditions experienced in such areas limits the number of sightings, particularly of cryptic species. Three of the five species not seen around the main Hawaiian Islands in the Barlow (2006) survey were dwarf sperm whales (*Kogia sima*), Blainville's beaked whales (*Mesoplodon densirostris*), and Cuvier's beaked whales (*Ziphius cavirostris*); all three are difficult to detect in sighting surveys because they are cryptic and spend little time near the surface. While multi-species comparisons of stranded animals have been undertaken (Maldini et al., 2005), interpretation of stranding records are limited by factors which include the small proportion of carcasses found, the long distances that individuals may drift before reaching shore, and species-specific differences in the probability of stranding and persistence once beached (Williams et al., 2011). Multispecies aerial surveys have also been conducted around the main Hawaiian Islands (Mobley et al., 2000; Maldini, 2003). While aerial surveys can cover a broad area relatively quickly, in areas with high species diversity, including a number of cryptic species, the results from such surveys are limited by the difficulty in distinguishing between morphologically similar species during brief overflights, as well as by poor sea states typically found offshore and on the windward sides of the islands.

We have been conducting small-boat multi-species surveys of odontocetes around the main Hawaiian Islands each year since 2000, with survey effort in three or more years off four regions within the main Hawaiian Islands: from west to east, Kaua'i and Ni'ihau, O'ahu, the 4-island area (including Moloka'i, Lāna'i, Maui, and Kaho'olawe), and the island of Hawai'i (Figure 1). While these small boat surveys suffer from their own biases—in particular, having effort limited to relatively calm leeward areas and not following regular, randomized tracklines—the ability to closely approach groups allows for high certainty in species identification

and a relatively low proportion of encounters that are not identified to species. Additionally, small boat surveys are most suitable for collecting photographs and biological samples that may be relevant to interpreting population structure or demographic information from sightings, and for deploying tags to study diving behavior or movement patterns (e.g., Chivers et al., 2010; Baird et al., 2011). In the 13 y since the start of these surveys, we have covered almost 85,000 km of trackline and encountered more than 2,000 groups of odontocetes, representing all 18 species known to exist in Hawaiian waters.

Herein we use sighting and survey effort data to examine habitat use and relative abundance of odontocetes around the main Hawaiian Islands. These analyses use data from 2000 through 2012 to calculate sighting rates for each species and to assess how rates vary by depth and among islands. To help interpret differences in sighting rates among species and areas, we take into account potential factors that may influence species- or area-specific sighting rates, including sea state, detection distances, and survey coverage off different islands. Although some species-specific assessments have occurred using part of this same dataset (e.g., McSweeney et al., 2007, 2009; Baird et al., 2008a, 2009; Aschettino et al., 2011), our sample size of effort and sightings has increased substantially since these initial assessments. This is the first attempt to examine and compare habitat use and relative abundance of all species of odontocetes in the study area.

Methods

Field Methods

Field operations were undertaken using a variety of vessels ranging in size from 5.5 to 18 m, although 90% of survey effort was on vessels from 5.5 to 8.4 m in length. Surveys typically ranged from 1 to 6 wks off one island (or group of islands) at a time. On the majority of days (88.1%), a single vessel was operated. On the remaining days, two vessels were operated. To minimize overlap of survey coverage, the vessels operated at least several kilometers apart (and often in completely different parts of the study area). Within each field effort, areas of operation were primarily driven by sea conditions, with attempts made to remain in areas of Beaufort 3 or less and with relatively short swell. While taking sea conditions into account, we attempted to maximize the geographic scope and range of habitats of survey coverage while minimizing overlap of survey tracklines during each field effort. When conditions were particularly good, we would attempt to survey further offshore or as far outside our normal survey area

as the vessel range would allow. Survey vessels operated from approximately 15 to 30 km h⁻¹, with two to six observers scanning 360° around the vessel. A GPS logged locations every 5 min while on effort. The sea state was recorded (using the Beaufort scale) at the start of the day and as it changed throughout the day, taking into account the area 360° around the research vessel.

All groups of odontocetes detected were approached for species identification, to record location (obtained with a GPS), and to estimate group size. The sighting cue was also noted (e.g., splash, blow, or view of body; radio call from another vessel; detections from a radio tag deployed previously on an individual in the group, etc.). Photographs were taken of most groups encountered, and attempts were made to photograph species considered difficult to identify to species, including beaked whales, dwarf and pygmy (*Kogia breviceps*) sperm whales, melon-headed whales (*Peponocephala electra*), and pygmy killer whales (*Feresa attenuata*). Most encounters were detected using the naked eye, although some were first seen using binoculars. Beginning in 2005, efforts were made to record or estimate distance to the group when first seen, either from a GPS waypoint (to allow for measurement between it and the waypoint taken at the group), or estimated by the naked eye, although only measurements from pairs of waypoints were used in our analyses below.

Data Processing and Analysis

We quantify survey effort in two different ways: (1) the number of hours on effort each day and (2) the number of kilometers covered each day. For the purposes of calculating the amount of effort by sea state and within different depth ranges, we use time (the number of hours of survey effort in each sea state and depth range). To assess habitat use by species, all sighting and 5-min effort locations were processed with *ArcGIS* 10.0 (ESRI, Inc.) to determine depth and distance from shore for each location. A 50 m × 50 m bathymetry model from the Hawai'i Mapping Research Group was used, with depths transferred to point locations using the intersect point tool in Hawth's analysis tools. We calculated sighting rates (number of sightings per 100 h of effort) for each species within specific depth ranges (e.g., 1 to 500 m, 501 to 1,000 m, etc.). This was done using the number of sightings and the number of 5-min effort locations within each depth range. We also calculate average sea states corresponding to the same depth ranges to assess whether variability in sea state by depth may have influenced sighting rates by depth.

For analyses of sighting rates, group size, distance first seen, depth use, island, and sea state by

species, we reduced bias by excluding encounters that were initiated due to radio calls from other vessels (4.3%), by detections from radio or satellite tags that had been deployed in previous encounters (0.7%), by the presence of fishing vessels (2.0%), or through acoustic detections from a fixed hydrophone range off Kaua'i (2.5%). One species, spinner dolphins (*Stenella longirostris*), is known to regularly use specific bays as daytime resting areas (Norris et al., 1994). One of these resting areas is off the entrance to Honokohau Harbor, the harbor used for the majority of surveys conducted off Hawai'i Island. Of the sightings of spinner dolphins off Hawai'i Island, 68% were off the mouth of Honokohau Harbor (within 0.5 km of shore). To avoid this bias in assessing relative abundance, we excluded sightings of this species at Honokohau Harbor.

We calculated mean sea states for each species using sea states at the start of the encounter to help in assessment of relative sighting probabilities. To assess relative detection probabilities, we calculated the average distance to the group when first seen for species sighted on eight or more occasions, using GPS measurements. To assess potential seasonal use of the study area, we noted the number of months of the year each species was sighted. For those species seen in nine or less months of the year, we noted if they were recorded in all oceanographic seasons based on Flament et al. (1996): winter (February–April), spring (May–July), summer (August–October), and fall (November–January). For melon-headed whales and false killer whales, we assessed population identity by comparison of photographs of individuals from each sighting to photo-identification catalogs (see Baird et al., 2008b; Aschettino et al., 2011).

Results

Between January 2000 and December 2012, we had a total of 762 survey days, with 5,450 h on effort, covering 84,758 km of trackline (Figure 1; Table 1). Effort was distributed throughout the year, although there was relatively little effort in January through March (Figure 2). Between 68.7 and 70.4% of all effort was off Hawai'i Island when looking at the number of on-effort hours and number of kilometers surveyed, respectively. Over the entire study area, approximately 45% of survey effort was in water depths of < 1,000 m, although depth of survey efforts varied among islands (Figure 3). In the 4-island area, almost 99% of effort was in < 1,000 m depths; while off Hawai'i Island, only 27.3% of survey effort was in < 1,000 m depths. Distance from shore of survey effort was greater off Hawai'i Island (mean

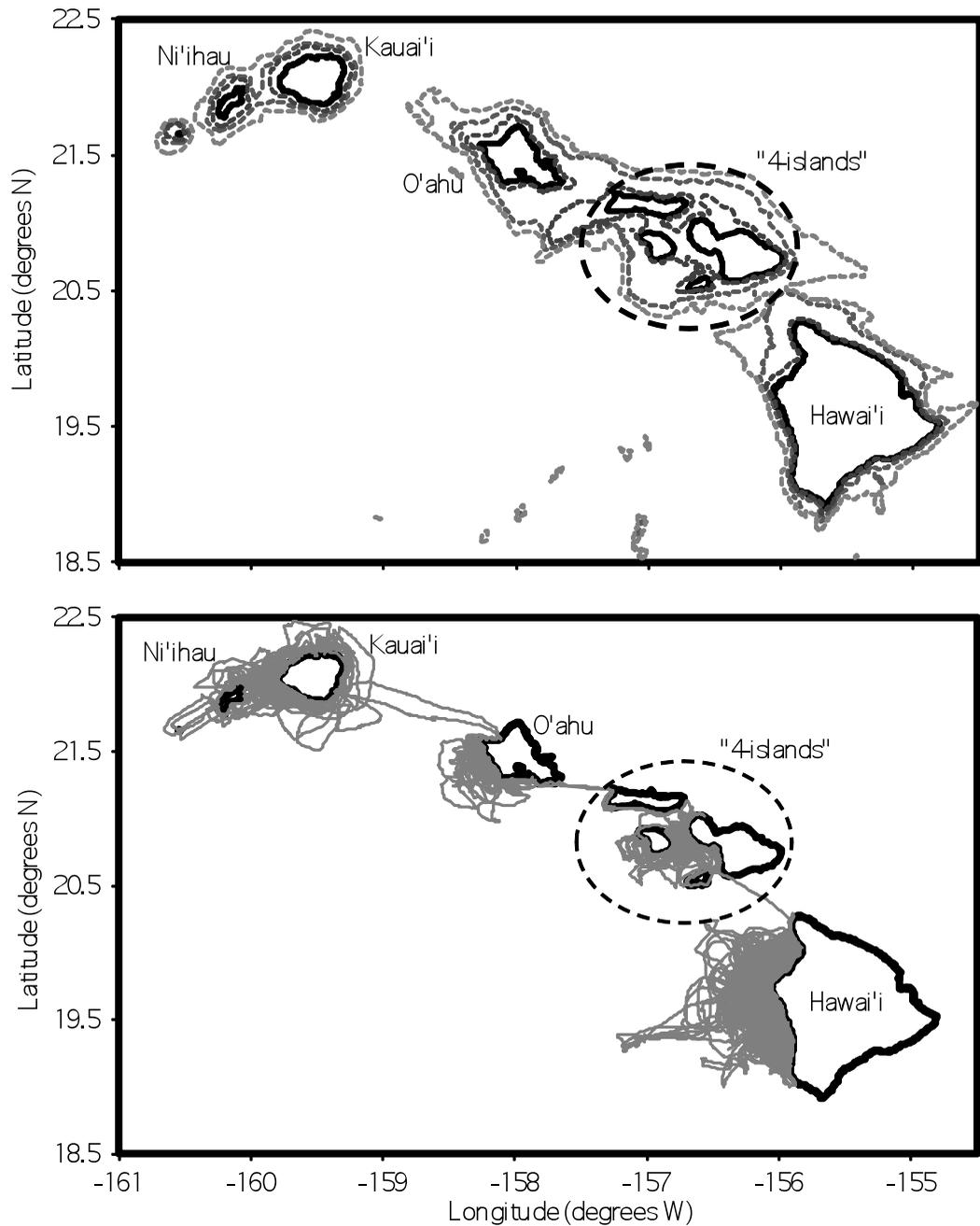


Figure 1. Top: The main Hawaiian Islands showing the 200 m, 1,000 m, and 2,000 m depth contours. Bottom: Tracklines showing all effort.

= 11.2 km, max = 128.7 km) than other islands (O'ahu mean = 7.3 km, max = 59.7 km; 4-island area mean = 6.1 km, max = 58.2 km; Kaua'i/Ni'i'hau mean = 8.1 km, max = 59.7 km). Over the entire study area, 92.0% of survey effort was in

areas with reasonable sea conditions (Beaufort 3 or less), with 73.0% of effort in excellent (Beaufort 0 or 1) or good (Beaufort 2) conditions (Figure 2). Sea state did vary by island area (Table 2), with the best conditions off Hawai'i Island and the worst

Table 1. Summary of survey effort by island area and by year

Year	Islands	# vessel d	# h on effort	# km on effort	Primary vessel used
2003	Kaua'i/Ni'ihau	24	195	3,222	6.4 m Whaler
2005	Kaua'i/Ni'ihau	24	145	2,194	6.4 m Whaler
2008	Kaua'i/Ni'ihau	7	54	819	6.7 m Sea Cat
2011	Kaua'i/Ni'ihau	23	152	2,411	8.2 m Whaler
2012	Kaua'i/Ni'ihau	29	158	2,763	7.3 m RHIB
Total Kaua'i/Ni'ihau		107	704	11,409	
2002	O'ahu	9	57	860	6.4 m Whaler
2003	O'ahu	13	111	1,789	6.4 m Whaler
2010	O'ahu	14	96	1,385	8.2 m Whaler
Total O'ahu		36	264	4,034	
2000	4-islands	44	308	3,632	6.4 m RHIB
2001	4-islands	28	203	2,102	6.4 m RHIB
2002	4-islands	9	64	785	5.5 m RHIB
2003	4-islands	16	107	1,659	6.4 m Whaler
2012	4-islands	15	77	1,415	7.3 m RHIB
Total 4-islands		112	759	9,593	
2002	Hawai'i	31	234	2,844	6.4 m Whaler
2003	Hawai'i	39	281	4,368	6.4 m Whaler
2004	Hawai'i	42	290	4,656	8.2 m Whaler
2005	Hawai'i	17	124	2,089	8.2 m Whaler
2006	Hawai'i	73	515	8,234	8.2 m Whaler
2007	Hawai'i	17	130	2,275	6.4 m Whaler
2008	Hawai'i	65	500	8,379	8.2 m Whaler
2009	Hawai'i	46	331	5,903	8.2 m Whaler
2010	Hawai'i	58	414	7,048	8.2 m Whaler
2011	Hawai'i	63	463	7,164	8.2 m Whaler
2012	Hawai'i	56	441	6,762	8.2 m Whaler
Total Hawai'i		507	3,723	59,722	
Total all islands		762	5,450	84,758	

Table 2. Percentage of effort by sea conditions for each island area

Sea conditions (Beaufort scale)	Kaua'i and Ni'ihau	O'ahu	4-islands	Hawai'i
Excellent (0-1)	23.3	22.0	31.0	35.8
Good (2)	36.6	40.7	36.3	41.4
Fair (3)	23.4	24.2	22.8	17.2
Poor (4-6)	16.7	13.0	9.9	5.6

conditions off Kaua'i and Ni'ihau. Mean Beaufort scale overall was 1.99 (SD = 1.01); and for different depth bins, it ranged from 1.7 (3,501 to 4,000 m) to 2.2 (1 to 500 m). Highest average sea states were in < 501 m (mean = 2.2, SD = 1.09) and between 501 to 1,000 m (mean = 2.08, SD = 1.02).

In total, there were 2,018 sightings of odontocetes (Table 3). After excluding biased data, including sightings reported from other vessels, groups located using radio tags or acoustic detections, and spinner dolphin sightings immediately adjacent to the mouth of Honokohau

Harbor, there were 1,758 sightings. Of these, all but 46 (2.6%) were identified to species. Average distance first seen ranged from 401 to 1,739 m depending on the species (Table 3; mean = 918.6 m). Three species—pygmy killer whales, dwarf sperm whales, and Blainville's beaked whales—were seen at average distances of from 401 to 582 m (43 to 63% of the grand mean). All are fairly cryptic in their surfacing profile. Four species, pantropical spotted dolphins (*Stenella attenuata*), Cuvier's beaked whales, sperm whales (*Physeter macrocephalus*), and striped dolphins

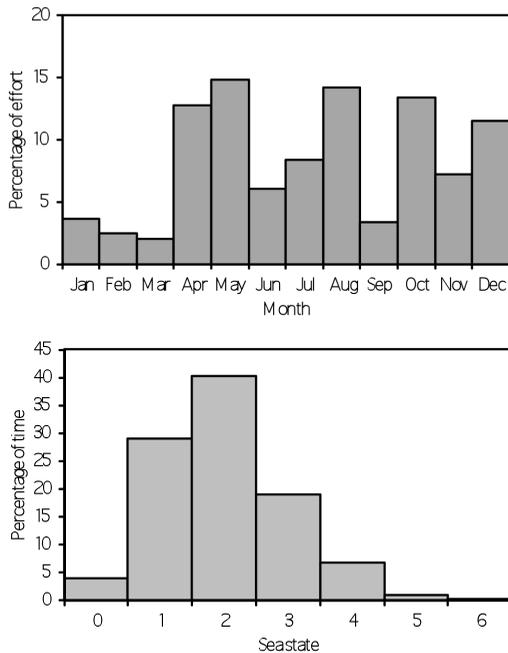


Figure 2. Top: Distribution of effort by month over all islands based on the number of survey days. Bottom: Distribution of effort by sea state for all islands based on the number of hours.

(*Stenella coeruleoalba*), were seen at average distances of from 1,116 to 1,739 m (121 to 189% of the grand mean distance). Although not quantified, pantropical spotted dolphins and striped dolphins were frequently observed leaping out of the water, and Cuvier's beaked whales were occasionally observed breaching, both behaviors visible from a great distance, likely increasing sighting distances for these species. For sperm whales and Cuvier's beaked whales, their large size and visible blows also increased sighting distance. It should be noted that measurements of distances first seen calculated from waypoints will be less accurate for faster moving species (e.g., striped dolphins, pantropical spotted dolphins, and Cuvier's beaked whales) as individuals may have moved either toward or away from the research vessel during the period from when the group was first sighted and when it was actually approached. Pantropical spotted dolphins showed no obvious avoidance of the research vessel, so distances are likely to be less biased; but striped dolphins and Cuvier's beaked whales were documented showing avoidance, so estimates for those species may be positively biased (i.e., the groups may have been closer to the research vessel when first seen than the distance measurements obtained).

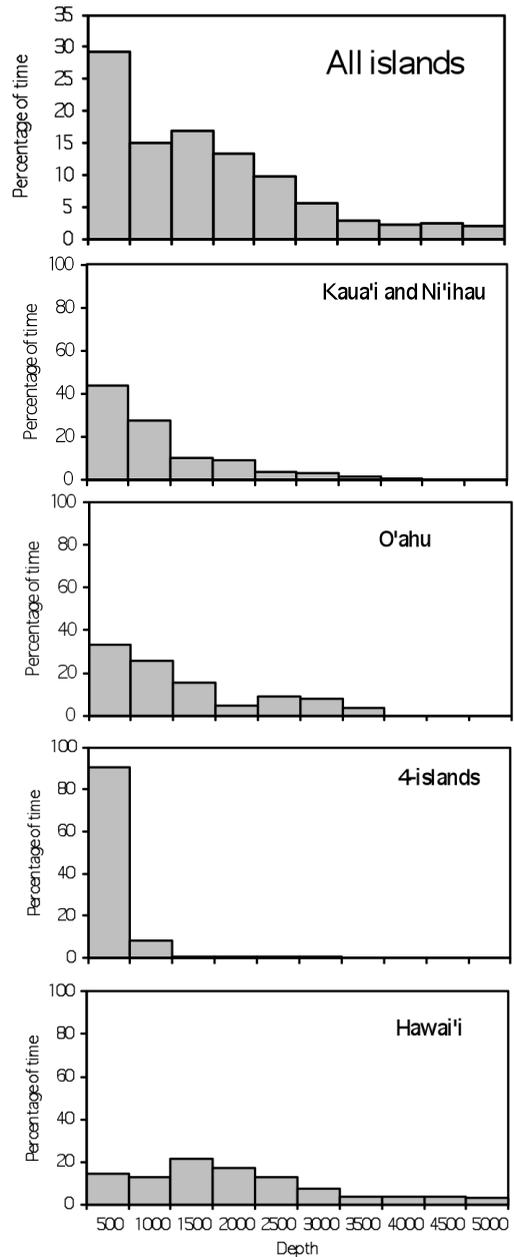


Figure 3. Distribution of effort by depth overall (top) and for each island area; note the depth bin values shown are the end value for each bin (e.g., 500 includes effort from 1 to 500 m, 1,000 includes effort from 501 to 1,000 m, etc.).

Analyses of sighting rates corrected for the amount of effort in different depth ranges (Figures 4 & 5) indicated that sighting rates for individual species varied considerably by depth, with some species found at the highest rates in very shallow

Table 3. Sightings characteristics by species for all island areas

Species	Number/% of sightings			Sightings per 100 h	Distance first seen (m) mean	Beaufort scale mean
	# all	# subset*	% subset			
Short-finned pilot whale	502	454	25.82	8.33	890	1.8
Pantropical spotted dolphin	398	359	20.42	6.59	1,116	1.7
Rough-toothed dolphin	248	202	11.49	3.71	818	1.7
Common bottlenose dolphin	227	211	12.00	3.87	864	2.0
Spinner dolphin	198	119	6.77	2.18	684	2.0
Dwarf sperm whale	74	74	4.21	1.36	465	1.3
Cuvier's beaked whale	64	64	3.64	1.17	1,315	1.4
Melon-headed whale	53	46	2.62	0.84	881	1.7
False killer whale	47	35	1.99	0.64	952	2.0
Blainville's beaked whale	45	41	2.33	0.75	582	1.3
Pygmy killer whale	37	30	1.71	0.55	401	1.8
Sperm whale	32	32	1.82	0.59	1,352	1.9
Striped dolphin	29	29	1.65	0.53	1,739	1.6
Unidentified odontocete	19	19	1.08	0.35	N/A	--
Unidentified small delphinid	17	17	0.97	0.31	N/A	--
Risso's dolphin	8	7	0.40	0.13	802	2.1
Unidentified beaked whale	5	5	0.28	0.09	N/A	--
Pygmy sperm whale	5	5	0.28	0.09	N/A	0.6
<i>Kogia</i> sp.	5	5	0.28	0.09	N/A	--
Killer whale	2	2	0.11	0.04	N/A	--
Fraser's dolphin	2	2	0.11	0.04	N/A	1.5
Longman's beaked whale	1	0	0.00	0.00	N/A	--

*The subset of sightings excludes sightings initiated from radio calls from other vessels, acoustic detections from the hydrophone range off Kaua'i, groups detected through the use of radio tags, groups approached because they were with other vessels (including fishing vessels), and spinner dolphins off the mouth of Honokohau Harbor, Hawai'i Island.

(< 500 m) water (e.g., common bottlenose dolphins [*Tursiops truncatus*], hereafter bottlenose dolphins, and spinner dolphins). For spinner dolphins, of the eight sightings in depths > 1,000 m, seven were very small groups (1 to 3 individuals) of spinners mixed in with large groups (> 30 individuals) of pantropical spotted dolphins (the eighth sighting was a group of seven individuals in 1,790 m depth moving offshore in mid-afternoon), while median group sizes for spinner dolphins in less than 1,000 m depth was 28 individuals (range 2 to 185). Some species were found at the highest rates in very deep (> 3,500 m) water (e.g., Risso's dolphins [*Grampus griseus*], striped dolphins, and sperm whales). Two species showed strong unimodal peaks in slope waters (dwarf sperm whales and short-finned pilot whales [*Globicephala macrorhynchus*]). Melon-headed whales showed no clear pattern in depth use; of the 53 sightings of this species, based on matches to a photo-identification catalog (Aschettino et al., 2011), 32 sightings were of the main Hawaiian Islands population, 18 were of the Hawai'i Island resident population, and three could not be attributed to one or the other population.

Off the island of Hawai'i, all 18 species of odontocetes were documented (Tables 3 & 5), although one species, Longman's beaked whale (*Indopacetus pacificus*), was only documented with a single sighting initiated from a radio call from another vessel. From 8 to 14 species were recorded off each of the other island areas (Table 5). While the least diversity (8 species) was documented in the 4-island area, this reflects both the relatively shallow depths in the area and limited amount of effort there (Figure 3), given that the species not recorded there were either all relatively deep-water species (e.g., sperm whales, Risso's dolphins, striped dolphins, and beaked whales) or relatively rare (e.g., pygmy killer whales, killer whales [*Orcinus orca*], Fraser's dolphins [*Lagenodelphis hosei*], and pygmy sperm whales). Overall, pantropical spotted dolphins represented more than 20% of all sightings (Table 3), and when considering the average group size (Table 4), appeared to be the most abundant species of cetacean around the main Hawaiian Islands. They represented from 22.9 to 26.5% of all sightings for three of four study areas (O'ahu, the 4-islands, and Hawai'i Island; Table 5), yet

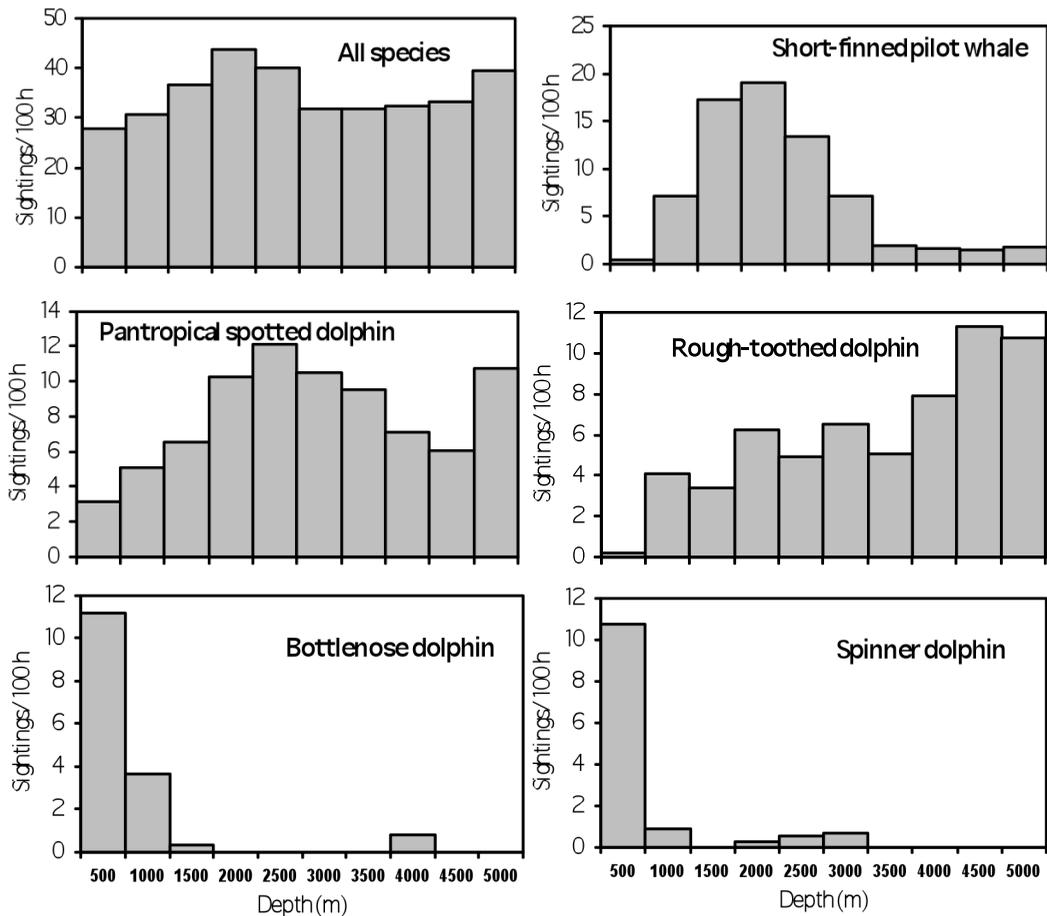


Figure 4. Sighting rates by depth for all species (top left) and the five most frequently encountered species of odontocetes including all effort; the x-axis is the same for all graphs, although the y-axis scale varies by species. Note the depth bin values shown are the end value for each bin (e.g., 500 includes sightings from 1 to 500 m, 1,000 includes sightings from 501 to 1,000 m, etc.).

only 3.9% of sightings off Kaua'i and Ni'ihau. Furthermore, of the nine sightings off Kaua'i and Ni'ihau, four were represented by just a single individual seen with a group of spinner dolphins in shallow water, and four of the five remaining sightings were of groups in very deep (> 3,000 m) water. Comparisons of the photographs of the single individual seen on four occasions with spinner dolphins in two different years (2005 and 2011) indicated that it was the same spotted dolphin on all four occasions.

A comparison of the percentage of sightings for each species (of the total number of sightings) within different depth ranges demonstrated that the relative sighting rates varied considerably between deep and shallow water (Table 6). For example, in waters deeper than 3,000 m, the most frequently encountered species (in decreasing order) were

rough-toothed dolphins (*Steno bredanensis*), pantropical spotted dolphins, striped dolphins, and sperm whales; while in waters < 2,000 m, the most frequently encountered species were short-finned pilot whales, pantropical spotted dolphins, bottlenose dolphins, and rough-toothed dolphins (Table 6). Distribution maps of selected species off the island of Hawai'i are illustrated in Figure 6. Fourteen of the 18 species documented (all those with more than five sightings) were seen in all oceanographic seasons, seven of which were seen in all months of the year (Table 4).

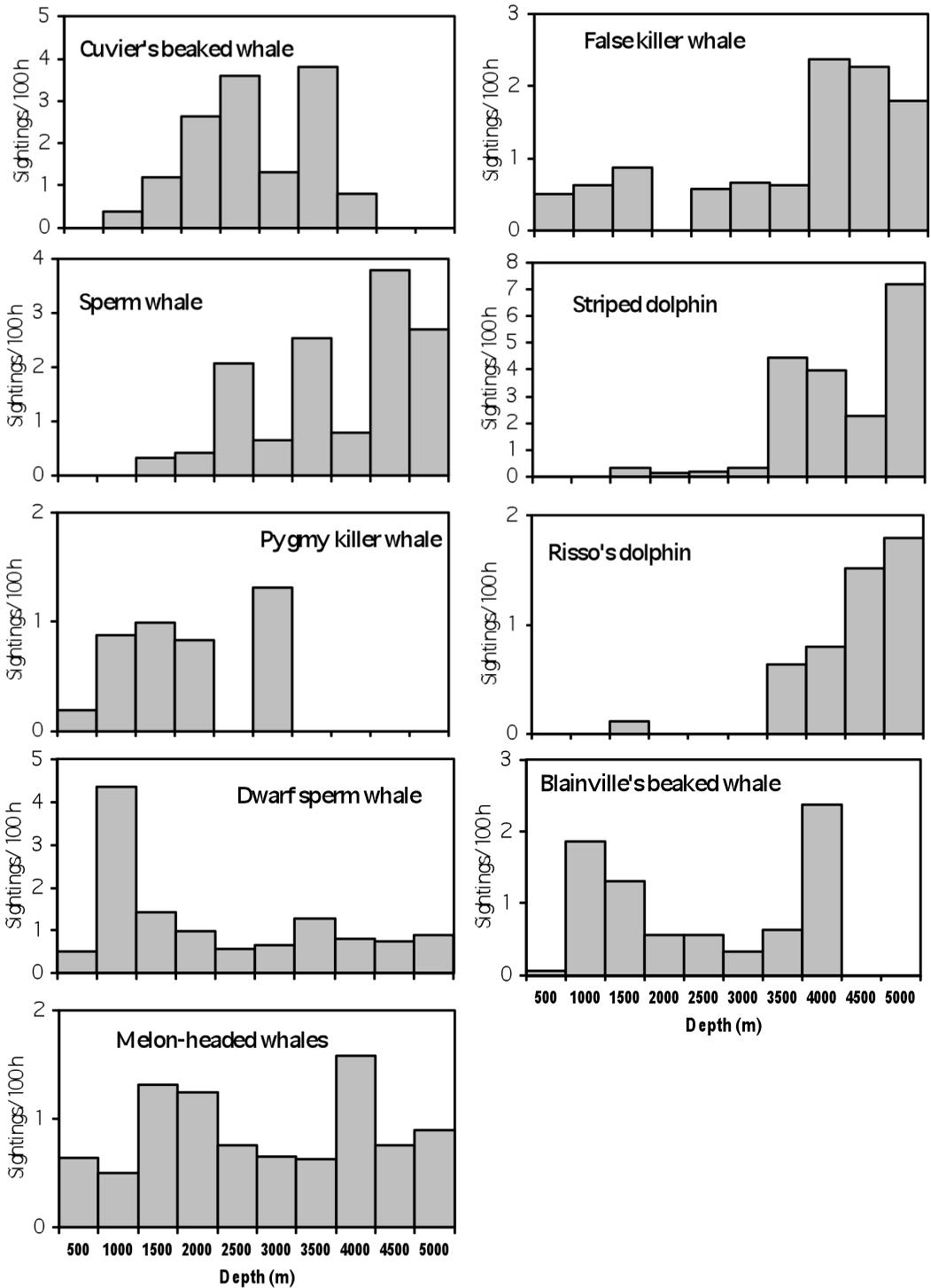


Figure 5. Sighting rates by depth for different species; the x-axis is the same for all graphs, although the y-axis scale varies by species. The depth bin values shown are the end value for each bin (e.g., 500 includes sightings from 1 to 500 m, 1,000 includes sightings from 501 to 1,000 m, etc.).

Table 4. Group size and seasonality by species

Species	Group size*					# months/ seasons** documented
	Mean	SD	Min	Max	Median	
Short-finned pilot whale	20.0	15.6	1	195	18	12/All
Pantropical spotted dolphin	65.4	49.6	1	350	55	12/All
Rough-toothed dolphin	11.1	12.1	1	90	7	12/All
Common bottlenose dolphin	9.3	15.9	1	200	5	12/All
Spinner dolphin	38.7	35.1	1	185	27.5	12/All
Dwarf sperm whale	2.7	1.8	1	8	2	10/All
Cuvier's beaked whale	2.1	1.2	1	5	2	9/All
Melon-headed whale	251.8	167.6	1	800	240	12/All
False killer whale	15.6	8.8	1	35	16	12/All
Blainville's beaked whale	3.7	2.4	1	11	3	11/All
Pygmy killer whale	10.2	7.0	2	25	9.5	10/All
Sperm whale	6.2	6.0	1	25	4	8/All
Striped dolphin	28.3	23.4	2	110	25	8/All
Unidentified odontocete	1.3	0.8	1	4	1	9/All
Unidentified small delphinid	3.4	6.9	1	30	1	8/All
Risso's dolphin	8.1	8.2	1	25	4	6/All
Unidentified beaked whale	1.8	0.8	1	3	2	5/W, Su, Fa
Pygmy sperm whale	1.4	0.6	1	2	1	4/W, Sp, Su
<i>Kogia</i> sp.	1.8	0.8	1	3	2	3/W, Su, Fa
Killer whale	4.0	0.0	4	4	4	2/Sp
Fraser's dolphin	80.0	7.1	75	85	80	2/W, Sp
Longman's beaked whale	35.0		35	35	35	1/Su

*Sample sizes from "Subset" column in Table 3.

**W = Winter, Sp = Spring, Su = Summer, Fa = Fall

Table 5. Sightings of each species by island area (number/%) based on a subset of sightings*

Species	Kaua'i-Ni'ihau	O'ahu	4-islands	Hawai'i
Common bottlenose dolphin	61/26.3	14/20.6	56/45.5	77/5.8
Rough-toothed dolphin	60/25.9	4/5.9	1/0.8	138/10.3
Spinner dolphin	60/25.9	13/19.1	14/11.4	32/2.4
Short-finned pilot whale	15/6.5	8/11.8	17/13.8	420/31.4
Pantropical spotted dolphin	9/3.9	18/26.5	31/25.2	306/22.9
Dwarf sperm whale	7/3.0	1/1.5	1/0.8	64/4.8
Blainville's beaked whale	5/2.2	2/2.9	0/0	33/2.5
Melon-headed whale	3/1.3	2/2.9	1/0.8	40/3.0
Unidentified odontocete	3/1.3	0/0	0/0	15/1.1
Unidentified small delphinid	3/1.3	1/1.5	0/0	13/1.0
False killer whale	1/0.4	3/4.4	2/1.6	29/2.2
Pygmy killer whale	1/0.4	2/2.9	0/0	26/1.9
Sperm whale	1/0.4	0/0	0/0	31/2.3
Striped dolphin	1/0.4	0/0	0/0	28/2.1
Pygmy sperm whale	1/0.4	0/0	0/0	3/0.2
Killer whale	1/0.4	0/0	0/0	1/0.1
Cuvier's beaked whale	0/0	0/0	0/0	63/4.7
Risso's dolphin	0/0	0/0	0/0	7/0.5
Unidentified beaked whale	0/0	0/0	0/0	5/0.4
<i>Kogia</i> sp.	0/0	0/0	0/0	5/0.4
Fraser's dolphin	0/0	0/0	0/0	2/0.1
Total species	14	10	8	17

*See Table 3.

Table 6. The percentage of sightings of species for different depth ranges

Species	% < 1,000 m	% < 2,000 m	% > 3,000 m	% > 4,000 m
Common bottlenose dolphin	29.4	13.9	1.1	1.1
Spinner dolphin	17.7	8.4	0.0	0.0
Pantropical spotted dolphin	15.2	18.1	24.4	22.7
Short-finned pilot whale	10.9	29.4	5.0	4.5
Dwarf sperm whale	7.7	5.2	2.8	2.3
Rough-toothed dolphin	6.5	9.3	25.0	30.7
Blainville's beaked whale	2.7	2.6	2.2	0.0
Melon-headed whale	2.5	2.9	2.8	2.3
False killer whale	2.0	1.6	5.0	5.7
Pygmy killer whale	1.8	2.1	0.0	0.0
Unidentified small delphinid	1.4	1.0	1.1	1.1
Unidentified odontocete	0.9	1.2	1.1	1.1
Cuvier's beaked whale	0.5	2.7	3.9	0.0
<i>Kogia</i> sp.	0.5	0.2	0.0	0.0
Pygmy sperm whale	0.2	0.2	1.1	1.1
Striped dolphin	0.0	0.3	12.8	12.5
Sperm whale	0.0	0.4	7.2	9.1
Risso's dolphin	0.0	0.1	3.3	4.5
Unidentified beaked whale	0.0	0.2	1.1	1.1
Killer whale	0.0	0.2	0.0	0.0
Fraser's dolphin	0.0	0.1	0.0	0.0

Discussion

While our survey efforts were largely restricted to leeward waters (with the exception of Kaua'i and Ni'ihau; Figure 1), they do broadly cover all the islands from near-shore to about 5,000 m depth. Although relatively little time was spent in very deep-water areas off islands other than Hawai'i (Figure 3), sea states were similar across all depths, and, thus we believe our conclusions regarding differences in depth distribution by species (see below) are relatively robust. With almost 85,000 km of survey trackline over 13 y, this dataset is the largest and most comprehensive for odontocetes around the main Hawaiian Islands. During our efforts, we encountered all 18 species of odontocetes known in Hawaiian waters and were able to identify 97.4% of groups encountered to species. This high rate of species identification compares favorably to the 85.8% of groups identified to species in a large vessel survey in Hawai'i (Barlow, 2006), and the 76.8% identified to species in aerial surveys in Hawai'i (Mobley et al., 2000). Our high rate of species identification reflects in part our research goals, approaching all groups seen and attempting to work with them long enough to confirm species identity and obtain photos. With a lower sighting platform typical of small-boat surveys, we also sighted groups at reduced distances in comparison to large vessel or aerial surveys, and thus were usually able to approach a group closely before they dove to confirm species identity. Our

high rate of species identification suggests that our results are broadly representative of all species found off the leeward sides of the islands. The taxa with the greatest uncertainty of species identity are the kogiids (dwarf and pygmy sperm whales) and beaked whales, with 5.9% of groups of kogiids and 4.5% of groups of beaked whales encountered not identified to species. These taxa are known for being difficult to identify; in the Barlow (2006) survey, 50% of the beaked whale groups sighted were not identified to species. For *Kogia*, our sample of dwarf sperm whales is quite large (74). Even if all five *Kogia* sp. were dwarf sperm whales, it is unlikely to change any of our conclusions regarding this species (Table 3).

Our most important finding with relevance to interpreting patterns of species relative abundance and presence among the islands as well as potential overlap with anthropogenic activities were the strong depth preferences exhibited by some species (Figures 4 & 5). Some species were found at very high rates in very shallow water (e.g., bottlenose and spinner dolphins) and were frequently sighted off all islands (Table 5). Others primarily used slope waters (e.g., dwarf sperm and short-finned pilot whales), and some used primarily very deep waters (e.g., striped dolphins, sperm whales, and Risso's dolphins). Such results are relevant to assessing overlap between anthropogenic activities that are either fixed in location (e.g., ocean thermal energy development and moored net pens for aquaculture; Papastamatiou et al., 2010)

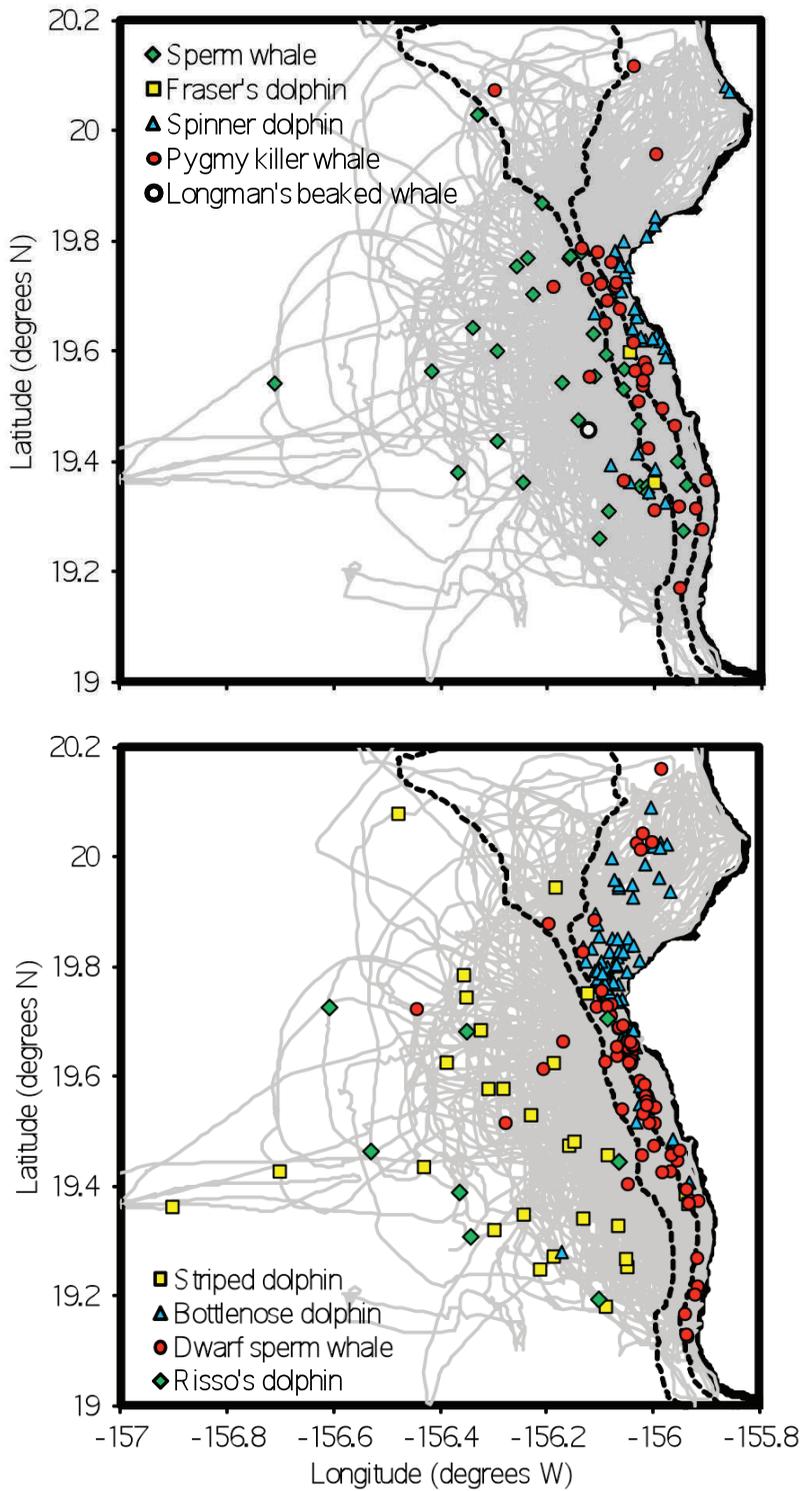


Figure 6. Distribution of selected species off the island of Hawai'i, with effort tracklines (gray solid lines) and the 1,000 and 2,000 m depth contours (black dashed lines) shown.

or those that move (e.g., Navy exercises, towed aquaculture operations, and most fishing; U.S. Department of Navy, 2012). Susceptibility to impacts from anthropogenic activities varies by species and the activity in question. Some species are more likely than others to deplete fish from fisheries or aquaculture operations, in particular bottlenose dolphins, rough-toothed dolphins, and false killer whales (Shallenberger, 1981; Kuljis, 1983; Nitta & Henderson, 1993). With bottlenose dolphins found primarily in shallow water, rough-toothed dolphins being found primarily in deep water, and false killer whales found over the entire range of depths (Figures 4 & 5), our results suggest that fisheries or aquaculture operations will likely overlap with one or more of these species, regardless of the depth they are undertaken or situated. Similarly, species known or suspected to be susceptible to impacts from high-intensity mid-frequency active sonar, including beaked whales, melon-headed whales, dwarf sperm whales, pygmy killer whales, and short-finned pilot whales (Cox et al., 2006; Hohn et al., 2006; Southall et al., 2006; Brownell et al., 2009), span the full range of depths off the main Hawaiian Islands. This indicates that there are likely no large areas within Hawaiian waters where overlap with at least one of these species could be avoided.

Of all the species of odontocetes in Hawaiian waters, only one, spinner dolphins, is known to show strong fidelity to small specific areas, their daytime shallow-water resting sites (Norris et al., 1994). After excluding sightings immediately adjacent to the mouth of Honokohau Harbor off Hawai'i Island, we were left with 119 sightings of this species from throughout the main Hawaiian Islands (Tables 3 & 5). In our assessment of sighting rates in relation to depth, this species showed the strongest preference for a narrow depth range, with sighting rates in < 500 m depth more than an order of magnitude higher than in any other depth range (Figure 4). We had only eight sightings of this species in > 1,000 m depth. Seven of the eight involved from one to three individuals mixed in with larger groups of pantropical spotted dolphins, unlike the much larger and typically single-species groups we found in shallow water. There are a number of recognized stocks of spinner dolphins in Hawaiian waters (Carretta et al., 2011), including three island-associated stocks around the main Hawaiian Islands, and a Hawai'i Pelagic stock. Our results on sighting rates in relation to depth (Figure 4) suggest that groups from the pelagic stock rarely approach near the main Hawaiian Islands, at least off the leeward sides of the islands. Our lack of sightings of typical single-species groups of spinner dolphins in deep (>1,000 m) water are also in contrast to sightings of this

species reported in deep waters during aerial surveys around the main Hawaiian Islands (Mobley et al., 2000). At least 7 of 50 spinner dolphin sightings (14%) from aerial surveys were in depths greater than 1,800 m. It was not reported whether these were unusually small groups (Mobley et al., 2000). There are a number of possible explanations for this discrepancy, including differences in survey years (the aerial surveys were undertaken in 1993, 1995, and 1998 vs our surveys beginning in offshore waters in 2002, and patterns may have changed in the time interval), differences in area covered (a large proportion of the aerial surveys were on the windward sides of the islands), the detection of small numbers of spinner dolphins mixed in with larger groups of spotted dolphins without confirming identity of all the individuals, as well as potential misidentification of species. It is unclear which of these possible explanations for the discrepancy between the aerial survey and our small-boat survey results is most likely.

Some of the bimodal or more unusual patterns of sighting rates by depth likely represent our sampling both of island-associated and offshore populations. For example, Blainville's beaked whales (Figure 5) showed a strong peak in encounter rates between ~500 and 1,500 m depth, and then another peak from ~3,500 to 4,000 m depth. Evidence from photo-identification (McSweeney et al., 2007) and satellite tagging (Schorr et al., 2009; Baird et al., 2011) indicate the existence of a resident population that inhabits primarily slope water, as well as an offshore population that uses open-ocean water. We suspect the bimodal distribution of sighting rates reflects sampling of both populations. The lack of sightings in depths > 4,000 m for this species (Figure 5) is primarily an artifact of the relatively limited sampling in such depths and the low typical encounter rates of this species. The strong peak in sighting rates of dwarf sperm whales between 500 and 1,000 m depth (Figure 5) suggest an island-associated population. Given this species was seen primarily in relatively calm sea states (mean Beaufort scale = 1.3), and sea states in depths between 500 and 1,000 m were the second-highest over all depth ranges (mean Beaufort = 2.08), the peak in sightings likely underrepresents their high use of those depths. Evidence for an island-associated population of dwarf sperm whales is also available from photo-identification, with repeated sightings of some individuals over several years (Mahaffy et al., 2009). For false killer whales, there are three populations that overlap in range within our study area: (1) a population resident to the main Hawaiian Islands that extends as far west as Ni'ihau, (2) a population resident to the northwestern Hawaiian Islands that extends as far

east as Kaua'i, and (3) an open-ocean population (Baird et al., 2010, 2012, 2013). Sighting rates for this species are relatively constant from < 500 m to 3,500 m depth, but then show an increase in > 3,500 m depths (Figure 5). We suspect the increase in sighting rates > 3,500 m depth likely reflects the overlap between the island-associated and open-ocean populations. It should also be noted that based on results from satellite tagging, that while individuals from the main Hawaiian Islands insular population use windward and leeward waters relatively equally, on the windward sides of the islands, false killer whales tend to concentrate in relatively shallow (< 1,500 m) areas (Baird et al., 2012), and it is possible such differences in use of windward sides of the islands may exist for other species. There are two populations of melon-headed whales around the main Hawaiian Islands, a population resident to relatively shallow waters off the northwest coast of the island of Hawai'i and another that moves offshore and among the islands (Aschettino et al., 2011); sighting rates by depth for this species showed no clear pattern (Figure 5), likely reflecting our sampling of both populations (see "Results").

Comparisons of species presence and relative abundance among the four regions is complicated by three different factors: (1) differences in the total amount of effort among the study locations (e.g., ~70% of all effort was off Hawai'i Island, while only 4.7% was off O'ahu; Table 1), (2) differences in survey conditions (~40% of survey effort off Kaua'i and Ni'ihau was in marginal or poor conditions compared to ~23% off Hawai'i Island; Table 2), and (3) differences in the distribution of survey effort by depth (e.g., more than 90% of effort in the 4-island area was in less than 1,000 m depth, while off other islands this ranged from ~71 to 27% of survey effort). All 18 species of odontocetes were only documented off the island of Hawai'i, although this is not surprising given the relative amount of effort there, the broad depth range of survey efforts, and the high proportion of excellent or good survey conditions (Table 2). In general, the species not recorded from the other areas were largely deep-water (e.g., sperm whales, Risso's dolphins, striped dolphins, and Cuvier's beaked whales) and/or very rare species (e.g., Fraser's dolphins and Longman's beaked whales). We suspect that all species may be found off all islands at least occasionally, but that sampling off Kaua'i and Ni'ihau, O'ahu, and in the 4-island region was too limited (e.g., O'ahu) or in too shallow depths (e.g., 4-island area) to encounter all species.

For species that were relatively abundant in depths < 1,500 m, where we have a reasonable amount of effort off all islands (Figure 3), there

were some differences in species composition among the island areas that are not likely related primarily to differences in effort. For the main Hawaiian Islands as a whole, pantropical spotted dolphins were the most abundant species of odontocete when taking into account both sighting rates and average group sizes. Our surveys off different islands showed that this was likely the case in the central and eastern main Hawaiian Islands (O'ahu to Hawai'i Island), where they represent about a quarter of all sightings in each area, but not the case off of Kaua'i and Ni'ihau, where the species represented only 3.9% of sightings (Table 5). Furthermore, four of the nine sightings off Kaua'i and Ni'ihau were of the same single individual associating with spinner dolphins in multiple years. Genetic analyses of spotted dolphin samples collected among the islands indicate three genetically differentiated populations: (1) off O'ahu, (2) in the 4-islands, and (3) off Hawai'i Island (Courbis, 2011). Spotted dolphin samples collected off Kaua'i were more likely to be either from an open-ocean population or possibly a northwestern Hawaiian Islands population (Courbis, 2011). There are several other differences in relative abundance of species off Kaua'i/Ni'ihau vs the other island areas that are inconsistent with the overall patterns of depth use by species (Figures 4 & 5) and depth of survey effort (Figure 3). The distribution of survey effort in relation to depth off Kaua'i and Ni'ihau was similar to effort off O'ahu but shallower than effort off the island of Hawai'i and deeper than effort in the 4-islands (Figure 3). Given their overall preferences for deeper waters in general (Figure 4), it appeared that rough-toothed dolphins were seen more often than would be expected off Kaua'i and Ni'ihau than off the other islands (representing almost 30% of sightings vs 5.9% off O'ahu and 10.3% off Hawai'i). By contrast, short-finned pilot whales, which showed a preference for shallower water overall than rough-toothed dolphins and were the most frequently encountered species over all areas, were seen less often than expected off Kaua'i and Ni'ihau given their sighting rates off other islands (6.5% vs from 11.8 to 31.4% off other islands; Table 5). Although it is unclear what may cause such differences in relative abundance of these species among the islands, there are several possibilities. There are oceanographic differences among the islands caused by the island mass effect (Doty & Oguri, 1956) and by cyclonic eddies that form primarily in the lee of Hawai'i Island (Seki et al., 2001, 2002). How such differences might influence the relative abundance of the prey of these three different odontocete species is unknown, both because of uncertainty associated with diet of the species and

a poor understanding of the dynamics of many of the potential prey populations. Additionally, there are differences in anthropogenic activities among the islands. Commercial shipping traffic is concentrated around O'ahu, recreational and charter fishing activity is greatest around Maui and Hawai'i Island, and much of the major Navy training exercises occur off Kaua'i and Ni'ihau or in water further offshore.¹ The level of susceptibility to impacts from Navy activities or other types of disturbance for these species (i.e., pantropical spotted dolphins, rough-toothed dolphins, and short-finned pilot whales) is unknown. Based on resightings from photo-identification, for both rough-toothed dolphins and short-finned pilot whales, the high sighting rates in some areas at least partially reflects repeated sightings of individuals and groups that exhibit high site fidelity (Baird et al., 2008a; Mahaffy, 2012).

While our surveys did not use distance sampling and we do not estimate density, we were able to use information on the average distance first seen and the average sea states in which species were detected in order to qualify our results on encounter rates and relative abundance for some species. For example, Blainville's beaked whales and dwarf sperm whales were both seen primarily in relatively calm sea conditions (average Beaufort of 1.3) and at relatively close distances (average of 582 and 465 m, respectively), while pygmy killer whales were seen at the closest average distances (401 m), suggesting that our encounter rates with these species substantially underrepresent their true abundance in our study area. Conversely, some species were seen at distances substantially greater than the mean (e.g., pantropical spotted dolphins and striped dolphins) and thus are likely overrepresented in our sample. Given the typical sizes of groups for different species (Table 4) and the relative sighting rates in different depth ranges (Table 6), these considerations are unlikely to change the relative rankings of any of the species in different depth ranges by more than one position.

We did not attempt to look for trends among years due to relatively small sample sizes off any particular island in each year. While our assessment of seasonality was coarse, only looking for strong signals (i.e., complete absence during some oceanographic seasons), the fact that 14 of 18 species documented were seen in all oceanographic seasons suggests that there is no strong seasonal fluctuation in presence of odontocetes around the main Hawaiian Islands. Attempting to assess more subtle seasonal variability would be difficult at this stage given the relatively low density of most species, the seasonal limitations in our sampling (Figure 2), and the fact that sampling in offshore

areas is particularly limited during the winter months due to the increased swell height.

Comparisons of our results from visual surveys to information obtained from acoustic methods suggest some discrepancies. Au et al. (2013) reported that Risso's dolphins were the second-most frequently detected species of odontocete, after short-finned pilot whales, from recordings made with several bottom-mounted acoustic systems in 400 to 800 m of water off Ni'ihau and Kaua'i, followed by sperm whales and small delphinids. In our surveys, Risso's dolphins represented less than half of 1% of all odontocete sightings (Table 3) and were found primarily in water deeper than 3,500 m (Figure 5). With over 11,000 km of survey effort around Kaua'i and Ni'ihau (Table 1), with more than 50% in depths > 500 m (Figure 3), we had zero sightings of Risso's dolphins. We suggest that this discrepancy between visual and acoustic methods is most likely due to acoustic misclassification of another more common delphinid found off Kaua'i and Ni'ihau such as rough-toothed dolphins. Such differences suggest that interpretations of species composition or presence/absence based on acoustic methods, particularly those with fixed location sensors, be viewed with caution. Interpretation of results from acoustic detection methods is most powerful when undertaken in concert with visual survey results (e.g., Klinck et al., 2012).

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Endnote

¹ See annual monitoring reports for the Hawai'i Range Complex at <http://navymarinespecies-monitoring.us/reading-room>.

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