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Population structure of melon-headed whales (*Peponocephala electra*) in the Hawaiian Archipelago: Evidence of multiple populations based on photo identification

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ABSTRACT

Despite the presence of melon-headed whales in tropical and subtropical waters worldwide, little is known about this species. To assess population structure in Hawai'i, dedicated field efforts were undertaken from 2000 to 2009. Using only good quality photographs, there were 1,433 unique photo-identified individuals, of which 1,046 were distinctive. Of these, 31.5% were seen more than once. Resighting data combined with social network analyses showed evidence of two populations—a smaller, resident population, seen exclusively off the northwest region of the island of Hawai'i, and a larger population, seen throughout all the main Hawaiian Islands (hereafter the "main Hawaiian Islands" population). A Bayesian analysis examining the probability of movements of individuals between populations provided a posterior median dispersal rate of 0.0009/yr (95% CI = 0–0.0041), indicating the populations are likely demographically independent. Depth of encounters with the Hawai'i Island resident population was significantly shallower (median = 381 m) than those with the main Hawaiian Islands population (median = 1,662 m). Resightings of individuals have occurred up to 22 yr apart for the Hawai'i Island resident population and up to 13 yr apart for the main Hawaiian Islands population, suggesting long-term residency to the islands for both populations.

Key words: melon-headed whale, *Peponocephala electra*, Hawai'i, site fidelity, population structure, movements.

Hawaiian waters are home to at least 18 species of odontocetes (Barlow 2006). Studies over the last decade have shown remarkable differences in population structure, habitat use, and movements among species and even between populations of the same species (*e.g.*, Andrews *et al*. 2006, 2010; Baird *et al*. 2008*a*, *b*, 2009; McSweeney *et al*. 2007, 2009). There are at least two genetically distinct populations of false killer whales (*Pseudorca crassidens*), for example, an insular population, closely associated with the main Hawaiian Islands, and an offshore population (Chivers *et al*. 2007, 2010; Baird *et al*. 2008*b*, 2010*c*). There are a number of distinct island-associated populations of common bottlenose dolphins (*Tursiops truncatus*), with limited movement between island regions (Baird *et al*. 2009, Martien *et al.* 2011). Spinner dolphins (*Stenella longirostris*) and pantropical spotted dolphins (*Stenella attenuata*) have been shown to have both offshore and multiple insular populations (Norris *et al*. 1994, Andrews *et al*. 2006, 2010; Courbis *et al*. 2010). As a result of these studies, the NOAA Fisheries Service now recognizes multiple stocks of several of these species within the Hawaiian Exclusive Economic Zone (EEZ) (Carretta *et al*. 2011).

Melon-headed whales (*Peponocephala electra*) are a poorly known odontocete found in tropical and subtropical waters worldwide (Perryman *et al*. 1994). Around the main Hawaiian Islands, Mobley *et al*. (2000) reported an abundance estimate of

154 individuals (CV = 0.88) based on aerial surveys over 3 yr in the 1990s, while a large-scale survey of the entire Hawaiian Islands EEZ in 2002 produced an abundance estimate of 2,950 (CV = 1.17) individuals (Barlow 2006). Currently only a single stock of this species is recognized in the Hawaiian EEZ (Carretta *et al*. 2011).

There is some evidence suggesting that this species is sensitive to high-intensity underwater sounds. In 2004, a group of 150–200 melon-headed whales entered the shallow waters of Hanalei Bay, Kaua‘i, coincident with mid-frequency sonar use during a naval training exercise (Southall *et al*. 2006). Although there has been some controversy as to whether sonar was truly to blame (*e.g.*, Fromm *et al*. 2006, Brownell *et al*. 2009), this event made transparent the lack of accurate information available on some of the basic biological parameters, including life history, range, and population size of this species in Hawaiian waters. This lack of scientific information is due in part to the fact that melon-headed whales are considered to be an oceanic species, found in offshore waters, which makes scientific study difficult. Recent studies of melon-headed whales at other island locations, including Mayotte in the Comoros Archipelago (Kiszka *et al.* 2011), Palmyra Atoll (Baumann-Pickering 2009), Nuku Hiva, and Mooréa in French Polynesia (Brownell *et al*. 2009) suggest that in addition to oceanic populations, there may also be island-associated populations of melon-headed whales. In this study, we examine photo identification and habitat use data of melon-headed whales in Hawai‘i in order to assess population structure and movements of this poorly known odontocete.

Methods

Field Methods

Dedicated surveys for odontocete cetaceans were undertaken around the main Hawaiian Islands (from Ni‘ihau in the west to Hawai‘i Island in the east) between February 2000 and December 2009 using small research vessels (generally under 9 m). Detailed field methods have previously been described by Baird *et al*. (2008*a*) and are therefore only summarized here. During dedicated surveys, locations were automatically logged every 5 min using a Global Positioning System (GPS), and two to five field observers scanned 360°. Fieldwork typically consisted of daily surveys based off one island at a time for durations of 2–6 wk. Although surveys were not systematic, they were also nonrandom in that they were designed to survey a broad area over a range of depths and minimize overlap in survey tracklines. When a group was encountered, species was identified and information was collected on the sighting cue, Beaufort sea state, initial behavior, and direction of travel. Photos were taken with film cameras through 2002 and with digital cameras from 2003 onward, by one to four photographers. Every effort was made to photo-identify all individuals within a group with no regard for how well marked an individual was. When possible, both left- and right-side photographs were taken, as well as multiple photographs of the same individuals. Depending on the priorities of a given survey, biopsy samples were sometimes collected for genetic analysis, and beginning in 2008, satellite tags were deployed on some individual melon-headed whales (see Woodworth *et al*. 2011). At the end of each encounter, additional information was recorded, including the estimated group size (minimum, maximum, and best), behavior, direction of travel, group envelope (an estimate of the maximum distance between the farthest apart individuals in the group in two dimensions), estimated percentage of the group observed closely, number of neonates and young of year, numbers of individuals with cookie cutter shark (*Isistius* spp.) wounds, the presence of other species of cetaceans, the reason for leaving, and, beginning in November 2006, the presence of fishing vessels. The distance from shore and start depth were determined in ArcGIS v. 9.2 (ESRI, Redlands, CA).

In addition to the dedicated survey efforts, opportunistic surveys took place off the island of Hawai'i starting in April 1985. Although photos were taken during these encounters, detailed sighting and effort information was not always recorded. A number of additional photos collected from other researchers between 2005 and 2010 underwent cursory examination to establish population identity by matching a minimum of two individuals to a known population. While the full photographic data from all years and sources were used in creating the catalog and determining resighting information, all other results, such as depth, distance from shore, and group size, were compiled using only the comprehensive data collected from the dedicated surveys through 2009.

Photo Identification

The photo-identification catalog was compiled following the same protocol used in other Hawaiian odontocete catalogs (*e.g.*, Baird *et al*. 2008*a*, *b*, 2009; McSweeney *et al*. 2009). Photo sorting and matching was performed in ACDSee Pro v. 2.0 and 2.5, without the use of any additional photo matching software. Individuals were sorted primarily through the use of unique notches along the trailing or leading edge of the dorsal fin (*cf.*, Wells and Scott 1990, Würsig and Jefferson 1990), as well as other features such as dorsal fin shape, pigmentation, or other scarring. When possible, individuals that had no unique markings or notches were also sorted by individual, using fin shape and temporary markings such as rakes or cookie cutter shark bite wounds.

All identifications were compared with one another and unique identifications were assigned catalog identifications in the form of "HIPe####." The best photograph of each individual was assigned a photo quality rating, ranging from 1 to 4 where 1 = *poor*, 2 = *fair*, 3 = *good*, and 4 = *excellent quality*. This rating was based on a number of photo qualities, such as focus of the image, distance, and the angle of the dorsal fin relative to the frame. Use of the term "well-photographed" will refer to individuals with photo quality ratings of 3 or 4. Notches along the trailing edge of the dorsal fin were noted for each individual, as was the presence of leading edge dents (LED), leading edge notches (LEN), top notches (TN), or peduncle notches (PN). Identifications were then assigned a distinctiveness rating, also ranging from 1 to 4 where 1 = *nondistinctive*, 2 = *slightly distinctive*, 3 = *distinctive*, and 4 = *very distinctive*. Very distinctive dorsal fins typically had multiple notches along the trailing edge and/or disfigurements along the top or leading edge of the dorsal fin. Distinctive dorsal fins had similar types of markings but to a lesser extent. Slightly distinctive dorsal fins had few notches along the trailing edge. Nondistinctive dorsal fins usually had no notches along the trailing or leading edge; while these individuals could sometimes be sorted within a single encounter based on fin shape and temporary markings, they could not reliably be matched between encounters, and therefore were not included in the catalog. When calculating the ratio of distinctive to nondistinctive or slightly distinctive individuals, only encounters with 20 or more individuals were used in order to reduce variance due to small sample sizes.

Each dorsal fin match was confirmed by at least two experienced matchers. Over time, it is possible for dorsal fin markings to change, either with the addition of new

Table 1. Number of unique individuals identified and cumulative catalog sizes for each year of the study used in analyses of dispersal rates between populations.

	Hawai'i Island resident population		Main Hawaiian Islands population	
Year	No. of individual IDs	Total catalog size	No. of individual IDs	Total catalog size
2003	0	0	221	211
2004	0	0	200	401
2005	77	77	47	435
2006	110	142	22	454
2007	0	142	10	463
2008	75	180	593	866

nicks and/or notches or the smoothing out and eventual loss of nicks and/or notches. In order to estimate the rate of mark change, the time between the first and last sighting for all individuals seen on more than one occasion was summed and divided by the minimum and maximum number of mark changes that occurred. In order to determine a "missed-match rate," approximately 5% of cataloged individuals were taken through the full catalog again by an additional experienced matcher.

Association Analyses

Population structure was assessed based on associations of individuals between groups. Netdraw (Borgatti 2002) was used to illustrate association patterns. Resighting information was used in order to evaluate site fidelity. Resightings from individuals seen off a different island from where they were initially photographed were used to determine interisland movements. The analysis of the prestudy photographs (those photos taken between 1986 and 2000) was used in order to assess the long-term residency of melon-headed whales in Hawai'i.

We used the Bayesian method described by Baird *et al*. (2009) to determine what rates of dispersal between populations are consistent with our data. Baird *et al*.'s (2009) method uses the catalog size and number of individuals identified in each population in each year of the study (Table 1), along with estimates, drawn from prior distributions, of the abundance of each population (N_j) and the dispersal rate (d) between them, to calculate the likelihood of failing to detect any immigrant individuals. The Sample-Importance Resample (SIR) algorithm (Rubin 1988) is then used to estimate the posterior distributions of N_j and d. For d, we used a uniform prior between 0% and 1.5% per year. Prior distributions for abundances were normal distributions calculated from the POPAN analyses undertaken in MARK (see Aschettino 2010) and truncated at the lower end of the distribution by the catalog size for each island group. We estimated the likelihood for 500,000 sets of parameters drawn from these prior distributions and then resampled the resulting parameter sets, weighted by their likelihood, 5,000 times to generate posterior distributions. The sampling parameters were chosen to yield smooth posterior distributions.

From the dedicated survey efforts, straight-line distance (*i.e.*, not taking into account intervening land masses) between all combinations of encounter locations was calculated using the Microsoft Excel add-in, *geofunc* (http://www.afsc.noaa.gov/nmml/software/excelgeo.php). Based on photo identification and social network results, we determined overall sighting rates off the island of Hawai'i north and south

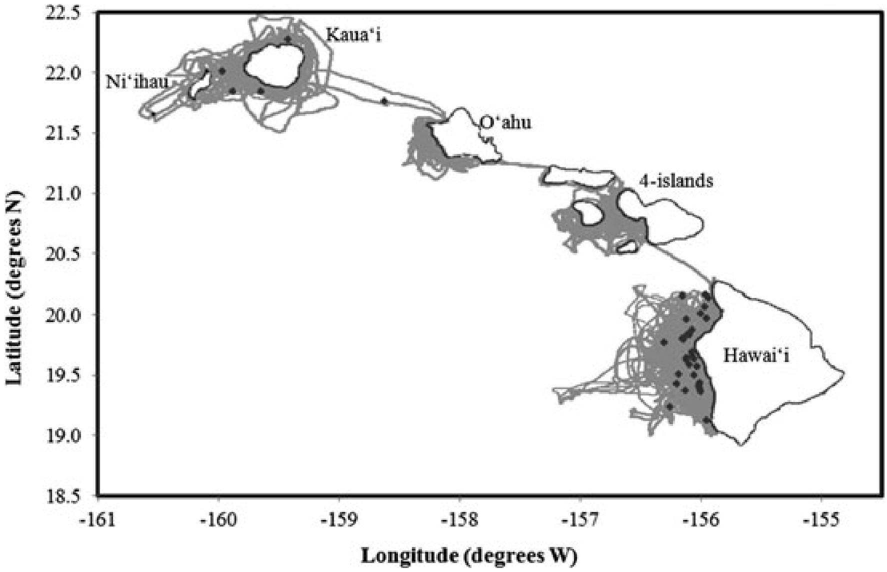

Figure 1. Survey effort trackline and sighting locations of melon-headed whales around the main Hawaiian Islands: 2000–2009.

of Keahole Point, using the number of sightings in each region divided by the sum of total effort hours for each region.

RESULTS

Sighting and Encounter Summary

In dedicated surveys between February 2000 and December 2009, a total of 55,810 km of trackline (Fig. 1) was covered during 504 d on the water (3,650 h on effort). The majority of fieldwork (69.4%) occurred off the leeward side of the island of Hawai'i, where depth, weather, and sea conditions make survey work most favorable. Although attempts were made to distribute survey effort as widely as possible during each field project, during winter months (November through mid-April) survey areas were often more restricted, with less coverage in areas that were more exposed to trade winds (*e.g.*, north of Keahole Point on the island of Hawai'i). In total, there were 1,291 sightings of 18 species of odontocetes, and melon-headed whales were the eighth most frequently encountered species, representing only 2.6% of all sightings, and occurring on average once every 14 d on the water. During this dedicated survey effort there were 36 encounters with melon-headed whales that occurred on 31 different days around the main Hawaiian Islands (Fig. 1). Thirty-one sightings were cued by the observation of an animal at the surface (splash, blow, or fin), four were cued from radio calls, and one was cued from another vessel. Four encounters occurred off the islands of Kaua'i and Ni'ihau, one encounter occurred off the island of O'ahu, and the remaining 31 encounters occurred off the island of Hawai'i (Fig. 1). Despite 8,178 km (682 h) of effort off the four-island area (Maui, Lana'i, Moloka'i, and Kaho'olawe) and sightings of 107 odontocete groups, there were no sightings of melon-headed whales in this area. Sightings took place between the hours of 0733 and 1758. Encounter duration ranged from 9 min to 4 h, 41 min (median = 1 h, 19 min) and initial Beaufort sea state for sightings ranged from 0 to 3 (median = 1). Twenty-six encounters (72.2%) either began or ended with the group traveling. Most often travel was slow, and on only two occasions was it fast (one of the two occasions was when killer whales (*Orcinus orca*) were also present). In 20 encounters (55.5%), start and/or end behavior involved milling, logging, resting, or socializing (with behaviors being nonmutually exclusive). Fishing vessels were seen in 3 of 13 (23.1%) encounters since 2006 and anecdotally recorded on one occasion prior. At least four fishing boats were seen trolling through groups of animals. Group size ranged from a single animal to a best estimate of 800 individuals (median = 275). The one encounter with a single individual involved an animal that was in poor body condition, both in terms of probable emaciation and skin condition. The animal was heavily marked with open cookie cutter shark wounds (at least seven were visible dorsally) and also had areas of discoloration covering its body, indicative of poor survival likelihood. The next two smallest groups (4 and 17 individuals) were both followed shortly thereafter by encounters with larger groups of animals (275 and 350, respectively, 5.8 and 11.2 km apart), suggesting the animals may have branched off from a main group.

In addition to the 36 encounters from the directed surveys, between 2005 and 2009, photographs from seven additional opportunistic encounters off the island of Hawai‘i on six additional days, and four encounters off the island of O‘ahu on four different days were also made available from other researchers. A total of 31,411 photographs from 40 encounters between 2002 and 2008 were available, as well as 9,380 photographs from seven encounters in 2009, and an additional 2,062 prestudy photographs taken from the island of Hawai‘i between 1986 and 2001. Photos taken in 2009 (which included the four encounters off O‘ahu) were examined only briefly to determine whether the photographed groups of melon-headed whales contained matches to individuals already in the catalog. Usable photographs were collected in all but one encounter. From the photographs collected between 2002 and 2008, 28 encounters were fully processed (*i.e.*, sorted and matched to the catalog in their entirety). The remaining 12 encounters from 2002 to 2008, along with the seven encounters in 2009, were partially processed, but were all examined at some level to ensure that there were individuals within the encounter that matched back to the catalog and to identify what group they matched to. Quantitative analyses of photo-identification data use only those encounters that were fully processed unless otherwise noted.

The photo-identification catalog included 1,640 individuals of which 1,433 individuals had a photo quality rating of good or excellent and 1,046 of these were rated distinctive or very distinctive in addition to being well photographed. These 1,046 individuals were based on 1,356 identifications across all fully processed encounters. From these fully sorted encounters, there were 310 resightings of 250 individuals, representing an overall resighting rate of 23.9% (Table 2). From both the fully and partially sorted encounters, there were 716 individuals seen only one time and 330 individuals seen on two or more occasions. The maximum number of times an individual was seen was eight. The number of photographs taken of each individual during an encounter varied (range 1–164; median = 4).

We assessed what percentage of individuals within groups were documented on more than one occasion (either before or after) using only fully processed encounters taking into account only well-photographed distinctive and very distinctive

Table 2. Number of well-photographed (rated 3 or 4), distinctive (rated 3 or 4) melon-headed whale identifications and individuals by area inclusive of only fully sorted encounters.

Island area	No. of IDs of marked individuals	No. of individuals (excluding within area resightings)	No. of (%) individuals seen more than once	No. of (%) documented at other islands	No. of within-area within-year resightings	No. of within-area between-year resightings	No. of between-area resightings
Kaua'i/Ni'ihau	426	316	96 (30.4)	21 (21.9)	87	0	26
O'ahu	18	18	0	0	n/a	n/a	n/a
Hawai'i	912	712	154 (21.6)	21 (13.6)	85	112	26
Hawai'i (residents only)	263	180	64 (35.6)	0	23	60	0
Hawai'i (excluding residents)	649	532	90 (16.9)	21 (23.3)	62	52	26
All areas	1,356	1,046[a]	250 (23.9)	21 (8.4)	172	112	26

[a]Excludes between-area resightings.

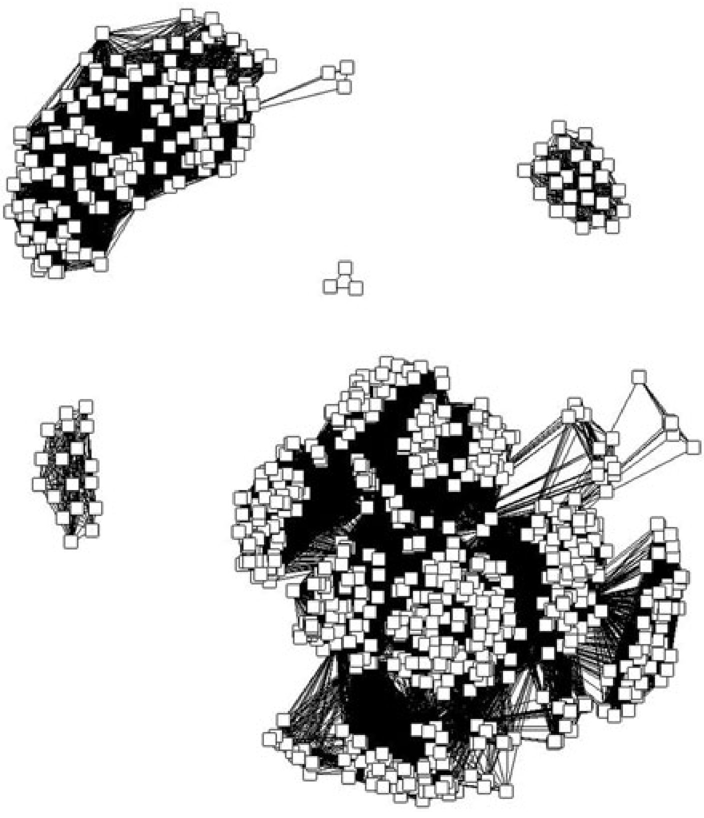

Figure 2. Social network diagram showing associations of all well-photographed (rated 3 or 4) distinctive (rated 3 or 4) individual melon-headed whales. Nodes correspond to individual melon-headed whales, and lines between nodes represent presence within the same group. The majority of individuals (820, 78.4%) are linked to the main cluster (main Hawaiian Islands population), 180 (17.2%) are part of a second large cluster (Hawai'i Island resident population), and the remaining 46 (4.4%) are part of three small clusters not linked to either of the main clusters (a cluster of three seen off Hawai'i, a cluster of 18 seen off O'ahu, and a cluster of 25 seen off Hawai'i).

individuals. The percentage of individuals within groups that were documented on more than one occasion ranged from 0% to 92.9% (median = 30.4%, n = 26). Excluding those encounters with fewer than 10 identifications, the median number of individuals within groups seen on more than one occasion was 48.0% (range = 0%–92.9%, n = 21).

Evidence of Multiple Populations—Social Network Analysis and Sighting Locations

A social network diagram including all well-photographed, distinctive individuals (Fig. 2) shows that most (820/1,046, 78.4%) individuals were linked by association in a single cluster (referred hereafter as the "main Hawaiian Islands population"). One hundred and eighty (17.2%) individuals were linked in a second large cluster (referred hereafter as the "Hawai'i Island resident population"), and there were three small clusters that included the remaining 46 (4.4%) individuals. These three small clusters included one encounter off the island of O'ahu (with 18 individuals) and two encounters off the island of Hawai'i (with 3 and 25 individuals). To assess whether associations between these clusters may actually occur but were missed because of the restriction of analyses to only the well-photographed distinctive individuals, a social network diagram was produced loosening the restrictions to also include fair photo quality images and slightly distinctive individuals (not shown). When doing so, the encounter with 18 individuals photo identified off the island of O'ahu linked to the main cluster, and slightly increases the percentage of individuals who link to the main Hawaiian Islands population (1,316/1,622, 81.1%). The percentage of animals in the second to largest cluster, the Hawai'i Island residents, decreased slightly (250/1,622, 15.4%) as did the remaining two smallest clusters (57/1,622, 3.5%). Individuals from the two smallest clusters were seen on only one occasion; therefore, it is not possible to infer whether or not they would be linked to the main cluster given additional sightings. The smallest cluster contained only five individuals (three when restricted to well-photographed, distinctive IDs), thus the likelihood of detecting links to other clusters is small. From the second smallest cluster, there were 52 individuals (26 when restricted to well-photographed, distinctive IDs) that were photographed off the island of Hawai'i; given the resighting rate, it is more surprising that none of these individuals would link to the main cluster.

The second to largest cluster (the Hawai'i Island resident population) contained 180 well-photographed, distinctive individuals from six encounters. Sixty-four of these individuals (35.6%) were seen on two or more occasions. Using information on estimated abundance for each population (from Aschettino 2010) and the number of identified individuals each year (Table 1), the posterior median dispersal rate between the main Hawaiian Islands population and the Hawai'i Island resident population from the Bayesian analysis was 0.0009 individuals per year (95% CI = 0–0.0041; Fig. 3). Calculated as the number of years per dispersal event, this equates to dispersal of one individual between the populations every 1,111 yr. This suggests that dispersal rates between these two populations are low enough that they are demographically independent. Posterior distributions for abundances of the populations were nearly identical to the prior distributions, indicating that the analysis was relatively insensitive to this parameter (Fig. 3). Subsequent results present certain information separately for the two identified populations.

Sighting locations for all encounters were off the leeward side of the islands being surveyed, with the exception of one encounter off Kaua'i that occurred to the north of the island (Fig. 4). When mapping sighting locations of melon-headed whales around the main Hawaiian Islands, the locations of the nine encounters from dedicated surveys with the Hawai'i Island resident population are clustered, occurring in the waters off the northwestern region of the island of Hawai'i (Fig. 4). Distance between locations for encounters off the Hawai'i Island resident population ranged from 1.5 to 36.1 km (median = 21.5, mean = 20.1, SD = 5.7, n = 32 combinations of 9 encounters). The Hawai'i Island resident population was seen in 8 of 12 mo (February, March, April, July, August, September, October, and December).

Of the other 21 encounters from the dedicated surveys that occurred off the island of Hawai'i, 20 of the sightings took place south of the region in which the resident population was found. While there were two encounters with groups of individuals that currently do not link by association to either the Hawai'i Island resident or the main Hawaiian Islands population, only one of these encounters was from dedicated survey effort (from 24 September 2004). This encounter was

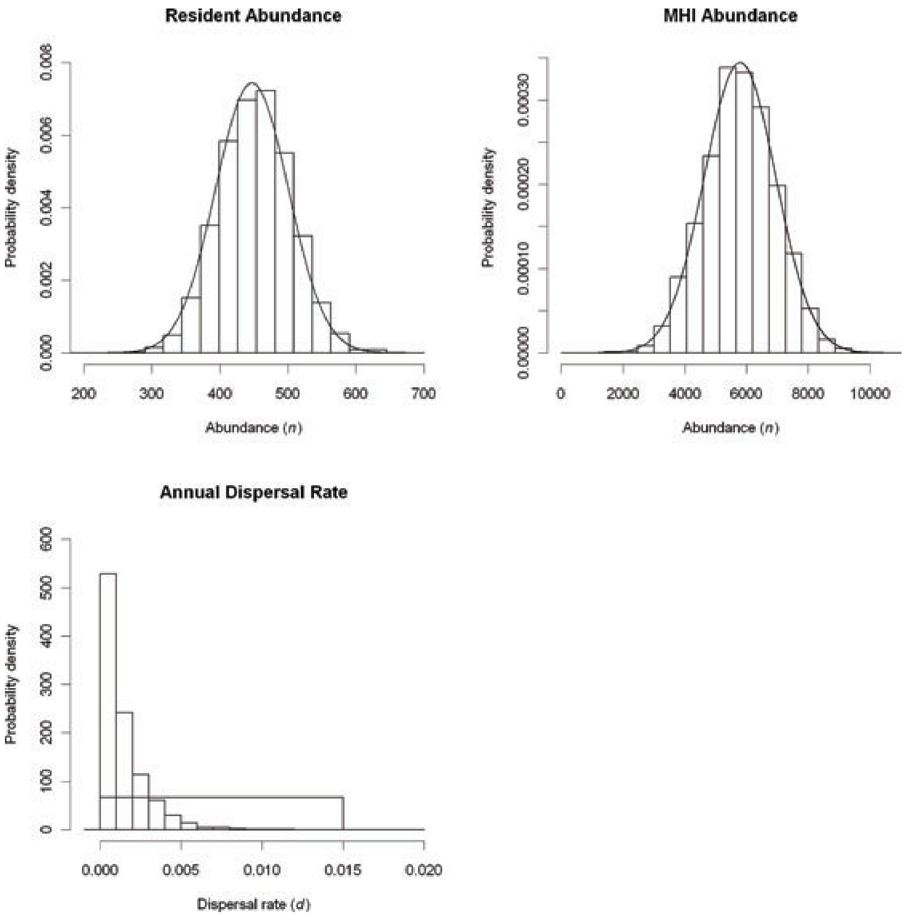

Figure 3. Posterior distributions (bars) of abundance of the Hawai'i Island resident and main Hawaiian Islands (MHI) populations and of the annual dispersal rate between them. Prior distributions are shown by solid lines.

the westernmost encounter off the island of Hawai'i. In total, there were 523 h of dedicated effort off the island of Hawai'i north of Keahole Point. In this area, there were nine sightings of the Hawai'i Island resident population, representing on average one sighting for every 58 h of effort. Only one sighting of the main Hawaiian Islands population occurred north of this same area, and one sighting with the group of animals that may or may not be part of the main Hawaiian Islands population. When including all surveyed areas, encounters with the main Hawaiian Islands population occurred on average once every 140 h of effort.

Between-islands movements were documented only from individuals of the main Hawaiian Islands population. Several individuals were seen in April 2008 off the island of Hawai'i and were resighted 2 mo later in June 2008 off the island of Kaua'i. These two island regions represent the farthest two points of the main Hawaiian Islands and the areas that there are photos available. Several of the same individuals

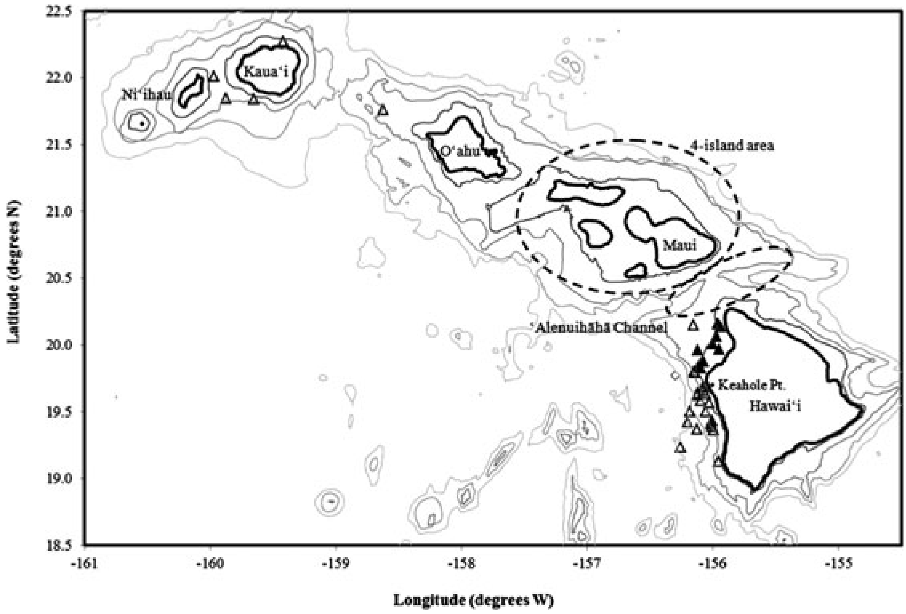

Figure 4. Map of melon-headed whale sightings from dedicated surveys between 2002 and 2009. Filled triangles show encounter locations with the Hawai'i Island resident population, unfilled triangles show encounter locations with the main Hawaiian Islands population, and the unfilled diamond represents the encounter with the group that did not link to either population. Depth contours are 500, 1,000, 3,000, and 4,000 m.

who were resighted off Kaua'i were also seen again in December 2008 off the island of Hawai'i. Distance among encounter locations for members of the main Hawaiian Islands population ranged from 1.03 to 526.6 km (median = 37.85, mean = 172.9, SD = 108.5, n = 276 combinations of 24 encounters). Sighting locations were significantly closer together for the Hawai'i Island resident population than for the main Hawaiian Islands population (Mann-Whitney U test, $P < 0.0001$). Individuals from the main Hawaiian Islands population were seen in 11 mo (all except March).

Sightings for all encounters from dedicated surveys occurred at depths ranging from 285 to 4,772 m (median = 1,460 m, n = 36) (Fig. 5) and between 3.1 and 43.0 km from shore (median = 9.9 km). Encounters with the Hawai'i Island residents occurred in substantially shallower waters, ranging from 285 to 905 m (median = 381 m, n = 9). When excluding these residents, overall depth of melon-headed whale sightings increased for all areas (median = 1,828 m, n = 27) and for those encounters just off the island of Hawai'i (median = 1,844 m, n = 22). Depths of groups known to be part of the main Hawaiian Islands population ranged from 968 to 4,014 m (median = 1,662 m, n = 25); for encounters with the main Hawaiian Islands population only off the island of Hawai'i, depths ranged from 1,111 to 4,014 m (median = 1,745 m, n = 20). The depths from dedicated survey encounters were significantly shallower for Hawai'i Island residents than for the main Hawaiian Islands population, whether considering sightings of the main Hawaiian Islands population off all islands or only off the island of Hawai'i (Mann-Whitney U test, $P < 0.0001$). Distance from shore was similar for the residents (median = 9.4 km) compared to all other encounters

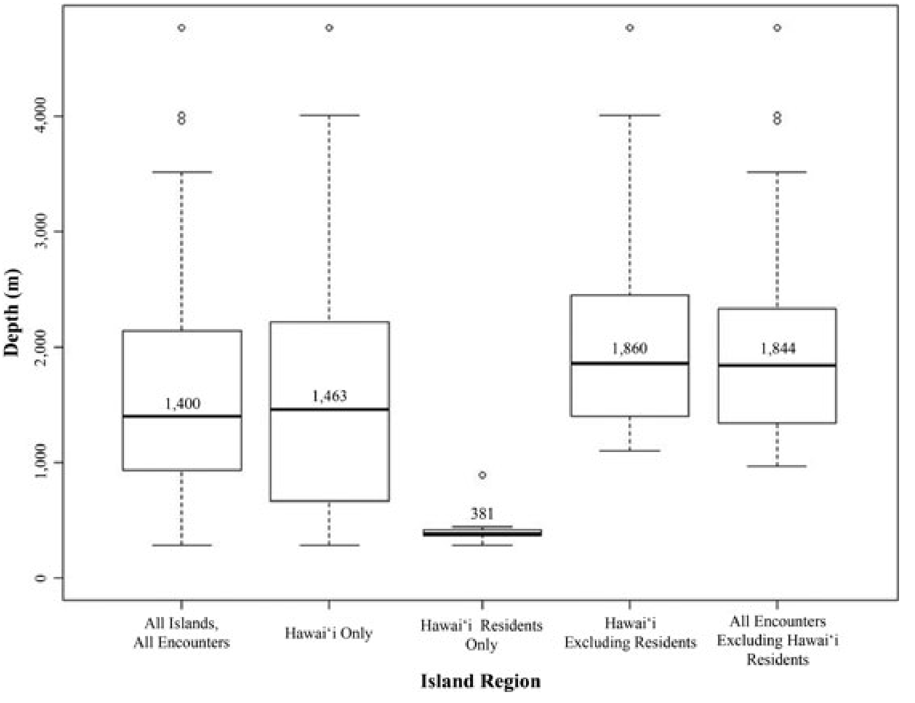

Figure 5. Box plots showing distribution of depths of melon-headed whale encounters by area and for Hawai'i residents and all others only. Middle bold lines show median values, upper and lower lines of boxes encompass the spread of data from the first to the third quartile, and upper and lower horizontal lines show minimum and maximum depth values unless outliers are present (○), in which the horizontal line is defined as the third quartile plus 1.5.

off the island of Hawai'i (median = 10.1 km). Survey efforts, and therefore distance from shore and depths, varied off each island region, and as a result, distance from shore and start depth are not comparable between islands.

Twelve of the 36 encounters (33.3%) were mixed encounters with one or more additional species. While both the main Hawaiian Islands population and the Hawai'i Island resident population were seen associating with other species, the residents were only seen associating with humpback whales (*Megaptera novaeangliae*) ($n = 2$),[1] whereas groups from the main Hawaiian Islands population were seen with five species, including rough-toothed dolphins (*Steno bredanensis*) ($n = 6$), short-finned pilot whales (*Globicephala macrorhynchus*) ($n = 3$), pantropical spotted dolphins ($n = 1$), killer whales ($n = 1$), and Fraser's dolphins (*Lagenodelphis hosei*) ($n = 1$).

Photo Identification

From all melon-headed whale photographs, the number of notches on the trailing edge of the dorsal fin for nondistinctive individuals was 0–1 (median = 0). Slightly

[1]In August 2010, after the cutoff for analyses for this study, we did document one occasion of individuals from the Hawai'i Island resident population associating with common bottlenose dolphins.

distinctive individuals had 0–9 notches (median = 2.5), distinctive individuals had 0–15 notches (median = 5), and very distinctive individuals had 0–12 notches (median = 5). The one very distinctive individual with no notches had a unique fin-shape, which allowed classification into this category. While the median number of notches for both distinctive and very distinctive individuals was the same, notches for the very distinctive individuals tended to be larger or more prominent than those of the distinctive animals. Thirty-seven percent of slightly distinctive individuals, 63% of distinctive individuals, and 90% of very distinctive individuals had at least one LED, LEN, TN, or PN. The percentage of distinctive or very distinctive individuals varied by encounter, ranging from 53.4% to 64.0% (median = 61.8%, CV = 0.06, $n = 6$). In order to compare the distinctiveness results for the Hawai'i populations with melon-headed whales elsewhere, the proportion distinct was recalculated to also include individuals considered to be slightly distinctive, which produced a median "identifiable" percentage of 85.3% (range 79.8–87.0, $n = 6$) for melon-headed whales in Hawai'i.

Matches to either the main Hawaiian Islands population or the Hawai'i Island resident cluster were found in all of the partially processed encounters. The number of resightings off Hawai'i shows a high number of between-year resightings, reflective of the increased survey efforts off this island region (Table 2). With only one encounter from dedicated survey effort off O'ahu, the number of identifications is very low in comparison to other island regions. There are photos from four additional encounters from October 2009 off the island of O'ahu. Though these encounters have not been fully analyzed, cursory examination of the photos confirms that there are several matches from each encounter to the main Hawaiian Islands population.

From encounters with the Hawai'i Island resident population, the median proportion within groups seen on more than one occasion was 62.2% (range 48.1–75.0; $n = 6$), while for the main Hawaiian Islands population (excluding the two small groups that do not link to either population), the median percentage of individuals within groups documented on more than one occasion was 31.8% (range = 0–92.9; $n = 15$). The Hawai'i Island residents showed the highest overall percentage of individuals resighted (35.6%), with 72.3% of resightings occurring between years. Excluding the Hawai'i Island residents, the proportion of individuals resighted off the island of Hawai'i was only 16.9% (23.4% when including the partially sorted encounters) (Table 2), and is indicative of a larger population than the residents.

Comparisons of photos from 1986 to 2000 with more recent photos did produce eight resightings, one of an individual first seen in 1986, suggesting long-term residency in Hawaiian waters. Two were from the main Hawaiian Islands population, and six were from the Hawai'i Island resident population. The longest resighting for an individual from the main Hawaiian Islands population was 13 yr, from an individual seen in 1995, 2004, and 2008. The longest resighting from the Hawai'i Island resident population was over a 22 yr span, an individual seen in 1986, 1996, 2005, 2006, and 2008. Two additional individuals from an April 1986 encounter match to individuals that were most recently sighted in 2008. For all melon-headed whales, the length of time between the initial and final sighting of an animal therefore ranged from 1 to 8,277 d (22.6 yr) (median = 124 d) when including animals seen prior to 2002. For individuals from the resident population, the time span was the same; however, the median number of days between the first and last sighting of an animal was 990 (2.7 yr) (both when including and excluding the prestudy resightings). For individuals of the main Hawaiian Islands population, the time between the initial and final sighting of an animal ranged from 1 to 4,792 d (13.1 yr) (median = 5 d).

The median value reflects the high number of resightings that occurred during the same trip (*i.e.*, over the course of several days or weeks). When these within-trip sightings were excluded, the median value of time between the first and last sighting of an animal increased to 691 d (1.9 yr) (median = 664 d (1.6 yr) when excluding prestudy resightings).

Of the 330 well-photographed, distinctive individuals who were resighted, 36 incurred changes to either the number or shape of dorsal fin notches, representing approximately 10.9% of all well-photographed, distinctive resightings. This included four individuals who underwent multiple independent mark changes. Of the 36 individuals, 23 were from the Hawai'i Island resident population, and 13 were from the main Hawaiian Islands population. Taking into consideration that multiple mark changes between resightings could have occurred on either a single or multiple occasions, of 60 documented mark changes, the minimum number of mark change events was 40. The cumulative time between the first and last sighting for all individuals seen on more than one occasion was 201,524 d (552.1 yr), therefore mark changes were calculated to occur every 9.2–13.8 yr. However, based on the differences in the number and percent of individuals with mark changes between the two populations, the occurrence of mark changes was recalculated to assess the two populations independently. For the resident population, a mark change is estimated to occur every 6.7–10.3 yr, and once every 15.2–21.0 yr for the main Hawaiian Islands population. Two individuals from the main Hawaiian Islands population who underwent minor mark changes due to tagging attempts were excluded from these calculations since the changes were considered to occur artificially.

Discussion

Despite the presence of melon-headed whales in tropical and subtropical waters worldwide, very little dedicated research has been carried out on this species. The creation of the Hawai'i catalog was the first photo-identification catalog for this species anywhere in the world and provided a means to closely examine the species' biology in Hawai'i. More than 1,600 unique individual melon-headed whales were included in this catalog; associations, resightings, and encounter locations were fundamental in providing evidence that there are at least two populations of this species within Hawaiian waters. The Hawai'i Island resident and main Hawaiian Islands populations showed a number of important differences in terms of their sighting locations, movements, water depth preferences, and apparent population sizes. The resident population was only ever found in shallow waters off the northwest side of the island of Hawai'i (Fig. 4, 5). In contrast, the main Hawaiian Islands population was found to move throughout the range of the main Hawaiian Islands and was most often encountered in deep water (Fig. 4, 5). These findings greatly improve our understanding of melon-headed whales in Hawai'i and offer valuable information to further our knowledge of the species elsewhere in the world.

Site Fidelity, Movements, and Behavior

Initial analyses showing evidence of between-island movements throughout the main Hawaiian Islands indicated that behavior of melon-headed whales in Hawai'i more closely resembled the offshore deep water preference of the species described by some (*e.g.*, Mullin 1994), rather than the behavior of the populations described at some oceanic islands (*e.g.*, Brownell *et al.* 2009). Evidence of multiple populations in Hawai'i, however, suggests that both types of patterns are found within one region, with the main Hawaiian Islands population moving greater distances between islands, and the resident population remaining within a limited range off the northwestern region of the island of Hawai'i. Shallenberger (1981) noted that 75–100 melon-headed whales were consistently seen off the North Kohala Coast, Hawai'i. It seems plausible that these sightings were of individuals comprising the resident population and may suggest the presence of this population for nearly three decades or more. That multiple populations of the same species can occur in adjacent, and even overlapping waters, suggests that each population is taking advantage of different foraging niches and perhaps also exhibiting dissimilar social organization and behavior. In Brownell *et al.*'s (2009) review of melon-headed whale occurrences and behavior near oceanic islands, they note a possible resident community off the island of Mooréa in French Polynesia, based on photo identification of more than 100 individuals in the area. Preliminary photo-identification results for melon-headed whales off Palmyra Atoll also suggest at least some degree of site fidelity based on resightings (Baird *et al.* 2010*a*). Diurnal resting behavior was typical at several island locations; for instance, melon-headed whales near Palmyra Atoll remained in the shallower waters (about 400 m) close to the reef line during the day and moved offshore to deeper waters (up to 1,300 m) in the late afternoon (Brownell *et al.* 2009). Similar observations also occurred at Nuku Hiva in French Polynesia (Brownell *et al.* 2009).

Variability in both behavior and social structure has been shown for different populations of spinner dolphins in the Hawaiian Archipelago (*e.g.*, Norris *et al.* 1994, Karczmarski *et al.* 2005), and there is no reason to believe other species would not also exhibit such differences. Andrews *et al.* (2006, 2010) further showed genetic differentiation among populations of spinner dolphins off each of the main Hawaiian Islands and throughout areas of the Northwestern Hawaiian Islands. Photographic data on common bottlenose dolphins in Hawai'i showed high site fidelity to specific island regions, along with an absence of movement between islands (Baird *et al.* 2009). Rough-toothed dolphins off the island of Hawai'i also showed strong site fidelity documented through frequent resightings (Baird *et al.* 2008*a*). Resighting rates were lower for rough-toothed dolphins seen off the islands of Kaua'i/Ni'ihau, and only two instances of between-island movements were recorded from these individuals, suggesting the possibility for multiple stocks for this species in Hawai'i (Baird *et al.* 2008*a*). Off Kaua'i, rough-toothed dolphins were found in larger groups and in shallower waters (Baird *et al.* 2008*a*), so like melon-headed whales, differences between putative stocks were shown through multiple lines of evidence. Both genetic and photographic evidence has shown that multiple populations of false killer whales occur in Hawai'i: a near-shore insular stock and an offshore stock (Chivers *et al.* 2007, Baird *et al.* 2008*b*). With so much variability in range and movements of odontocetes—both on a global scale and in Hawai'i—it should come as no surprise that melon-headed whales are behaving differently than each of the other species in Hawai'i that have been studied in recent years.

The Hawai'i Island resident population exhibited high site fidelity over a relatively limited range (Fig. 4). The main Hawaiian Islands population exhibited some site fidelity (given the resighting information); however, animals from this population utilized a large range, encompassing at least the 600 km that stretch from Kaua'i/Ni'ihau to the island of Hawai'i (Fig. 4). Woodworth *et al.* (2011) showed a highly variable range of movements *via* satellite data for melon-headed whales tagged in Hawai'i. Further support for this resident population comes from satellite information of two individuals tagged during two separate encounters; both individuals, linked to the resident population, stayed within close proximity to their original tagging locations while most other individuals tagged from the main Hawaiian Islands population moved great distances (Schorr *et al.*, unpublished observations). The large-scale movements that were shown to occur over relatively short periods of time through the satellite data were also confirmed *via* photographic evidence. Clearly, movements seem to occur frequently, and often over a wide range, for individuals comprising the main Hawaiian Islands population. Such resightings suggest that both populations exhibit site fidelity—the residents to a limited range off the northwest side of the island of Hawai'i, and the main Hawaiian Islands population to the much larger 600 km linear range that encompasses the main Hawaiian Islands.

The discovery of the resident population of melon-headed whales using the shallower waters off the northwest side of the island of Hawai'i was not expected, considering the generally deep-water preference for this species. The existence of this resident population suggests that there may be other island-associated populations of melon-headed whales in Hawai'i, but field efforts have so far been unable to detect them. If there are, in fact, other small populations of melon-headed whales exclusively using island-specific niches, these animals may be at greater risk for a number of different localized threats, including fisheries interactions, high-intensity anthropogenic noise, and potentially coastal runoff, which can increase harmful disease-causing organisms in the marine environment and/or harmful chemicals that may bioaccumulate in higher trophic level species. Native Hawaiians hunted melon-headed whales in the shallow waters off Hilo on the windward side of the island of Hawai'i in the early 1840s (Wilkes 1845). These animals may or may not have been part of today's resident population that uses the northwestern side of the island.

Hawai'i Island Residents vs. Main Hawaiian Islands Population

When comparing and contrasting the Hawai'i Island resident population with the main Hawaiian Islands population, a number of differences were evident. While distance from shore off the island of Hawai'i did not vary between residents and the main Hawaiian Islands population (median 9.4 km compared to 10.1 km, respectively), depth of the encounters did (median 381 m compared to 1,844 m) (Fig. 5). All sightings of the resident population were clustered at the northern end of the range for sightings off the island of Hawai'i, north of Keahole Point. South of this point, water depths drop off quickly close to shore. Encounters with the main Hawaiian Islands population took place in much deeper water, whereas the habitat range for the resident population occurred over a shallow plateau (Fig. 4). Whether movements further offshore, toward the deeper 'Alenuihāhā Channel (maximum depth ~1,900 m) (Fig. 4) occurred at nighttime for individuals of the resident population would have to be assessed through satellite data because all sightings took place during the daytime hours. Spinner dolphins in Hawai'i have been shown to undergo nightly movements offshore to feed on a vertically migrating prey layer (Benoit-Bird and Au 2003) and diel acoustic patterns of melon-headed whales at Palmyra Atoll suggest that feeding is most likely occurring at night (Baumann-Pickering 2009).

While associations with other species occurred for both the Hawai'i Island resident and main Hawaiian Islands population, the species with which they were found associating were completely different. Residents were seen associating with humpback whales, and given that humpback whales only occupy Hawaiian waters during the winter months (typically December through April), this association was seen in two of the possible seven "winter" occasions. Humpback whales migrate to Hawai'i to utilize the warm, shallow waters as their breeding grounds, and some of the shallowest waters off the island of Hawai'i are in the same location as the resident population. In one of the two encounters with the humpback whales, several of the melon-headed whales were closely associating with the humpbacks.

The main Hawaiian Islands population of melon-headed whales was seen associating with or near a broader range of species, including rough-toothed dolphins, short-finned pilot whales, pantropical spotted dolphins, killer whales (albeit fleeing from them, see Baird *et al.* 2006), and Fraser's dolphins. Of 26 encounters with the main Hawaiian Islands population, 10 were mixed encounters with at least one other species present. Like the melon-headed whales, each of the associated species also shows some preference for a deep-water habitat (*e.g.*, Baird *et al.* 2003, 2008*a*; Reeves *et al.* 2002). It is possible that it may be more advantageous for the more oceanic species to aggregate for predator avoidance.

Distinctiveness is a measure of how easy it is to identify individuals. The overall percentage of distinctive and very distinctive melon-headed whales ranged from 53.4 to 64.0 (median = 61.8). This percentage of distinctiveness is less than other species in Hawai'i, such as pygmy killer whales (median = 73.2%) (McSweeney *et al.* 2009), false killer whales (mean = 73.7% (Baird *et al.* 2008*b*), common bottlenose dolphins (median = 80%) (Baird *et al.* 2009), and rough-toothed dolphins (median = 100%) (Baird *et al.* 2008*a*). Kiszka *et al.* (2008) reported that 81% of melon-headed whales around the Mozambique Channel Island of Mayotte were "identifiable" (*i.e.*, had any markings). A comparable calculation from Hawai'i, including those rated slightly distinctive, results in a median "identifiable" percentage of 85.3%, similar to the findings of Kiszka *et al.* (2008).

Mark changes were evident from individuals of both populations; however, the number of individuals with mark changes from the Hawai'i resident population was higher than that of the main Hawaiian Islands population. This could be a result of the more complete sighting histories for resident individuals (*i.e.*, it is more likely that mark changes were detected with the residents) or, alternatively, individuals of the main Hawaiian Islands population may be less likely to undergo mark changes. Nicks and notches along the dorsal fin are known to occur both naturally (*e.g.*, through conspecific interactions) as well as from anthropogenic sources (*e.g.*, line entanglements). Attributing the cause of any dorsal fin mark or injury will almost always carry with it a high degree of uncertainty; however, the source of some injuries may be more apparent than others. Dorsal fin disfigurements indicative of line injuries were present on individuals of both populations (Aschettino 2010), suggesting that fisheries interactions occur throughout both ranges.

For all individual melon-headed whales, mark changes were estimated to occur on average once every 9.2–13.8 yr; although, given the higher number of resightings for the Hawai'i Island resident population, the estimated occurrence of mark changes for the residents (once every 6.7–10.3 yr) may be more accurate than the overall rate of mark changes. For the main Hawaiian Island population there are likely more missed matches due to large mark changes given the larger population with fewer resightings. The rate in which mark changes occurred for other small odontocetes in Hawai'i was calculated in several studies similar to this one. For rough-toothed dolphins, mark changes occurred on average once every 2.42 yr (Baird *et al.* 2008*a*).

In pygmy killer whales, a mark change occurred every 3.9–6.1 yr (McSweeney *et al*. 2009), and false killer whales underwent a mark change every 6.9–8.8 yr (Baird *et al*. 2008*b*). In general, occurrence of mark change for melon-headed whales in Hawai‘i was less frequent than rough-toothed dolphins and pygmy killer whales, and was most similar to the frequency for false killer whales. These results would be anticipated based on the percentage distinctive for each species; the greater the percentage distinctive, the more frequently mark changes would be expected to occur.

Resident Population: Why so Shallow?

Why would one population of melon-headed whales choose to use a shallow water habitat while their conspecifics primarily utilize the adjacent deeper offshore waters? The answer may lie in the productive waters between the islands of Hawai‘i and Maui/Kaho‘olawe, an area separated by the ‘Alenuihāhā Channel (maximum depth ~1,900 m) (Fig. 4). In this area, northeasterly trade winds are accelerated and funneled between the islands due to their steep topography, and result in the formation of cyclonic eddies. Nowhere else in Hawai‘i are these highly productive mesoscale features more prominent than the ‘Alenuihāhā Channel (Seki *et al*. 2001). Cyclonic eddies, or cold ring eddies, cause upwelling of cool waters, and are hot spots for biological and physical activities. The rising of the cool waters creates physical gradients in the ocean that predators can use to locate accompanying aggregations of prey (Seki *et al*. 2001). Fishermen can also utilize these same cues to find fish, thereby increasing the likelihood of overlap and potential for interactions between humans and melon-headed whales (as well as other predators, such as birds, fish, or turtles, tracking these features). A 1995 study of cyclonic eddies occurring over the course of the Hawaiian International Billfish Tournament (HIBT) found that eddy location overlapped with areas of high tournament fish catches (Seki *et al*. 2001). A recent analysis of offshore movements of satellite tagged melon-headed whales in Hawai‘i (*i.e.*, nonresidents) showed that these animals were found in association with both the edges of cyclonic eddies and the centers of the warm anticyclonic eddies (Woodworth *et al*. 2011).

Brownell *et al*. (2009) noted that although quantitative data were lacking, reports of melon-headed whales near some oceanic islands were seasonal. The resident population off Hawai‘i was observed in 8 of 12 mo, but there was seasonal variation in effort, thus the lack of sightings from other months cannot be used to assess the likelihood of their occurrence during those months. Despite less prevalent trade winds driving eddy formation during the summer months (June–August), productive waters off the island of Hawai‘i are maintained year round through oceanographic influences driven by the presence of the islands themselves (*e.g.*, Doty and Oguri 1956, Gilmartin and Revalante 1974). We believe the Hawai‘i Island resident population is likely resident year round, given the presence of these oceanographic features.

Long-Term Fidelity

Although dedicated surveys did not begin until 2000, resightings of individual melon-headed whales from the island of Hawai‘i dated as far back as 1986, suggesting long-term use of this area. The longest and most comprehensive resighting spans more than 20 yr, and comes from a member of the Hawai‘i Island resident population, HIPe1579, who was seen in 1986, 1996, 2005, 2006, and 2008. As marks tend to accumulate with age, the distinctiveness of this individual in 1986 suggests that at the time it was a mature adult, and therefore, this animal is likely to be at least in its thirties. The oldest known melon-headed whale based on aging using dentinal growth layers was a 44.5 yr old female from a mass stranding in Japan (Miyazaki *et al.* 1998). From this same group, the oldest male was 38.5 ($n = 75$ males, $n = 44$ females). It is not uncommon for mammalian females to live longer than their male counterparts (Ralls *et al.* 1980). HIPe1579 was seen on five occasions between 1986 and 2008; in four of these occasions, the animal was swimming alongside other seemingly large, well-marked individuals, suggesting that these were male (Miyazaki *et al.* 1998) associates (the fifth occasion in 2008, the animal was photographed alone). There were never any calves or otherwise clean-finned individuals, which would be more suggestive of a female's associations; therefore, it can be hypothesized that this is, in fact, a long-lived male.

Implications for Management

While NOAA Fisheries currently only recognizes a single stock of melon-headed whales within the Hawaiian EEZ (Carretta *et al.* 2011), this study has shown strong evidence of at least two populations of melon-headed whales utilizing the main Hawaiian Islands—a smaller, resident population, which appears to exhibit minimal movements over a limited area off the island of Hawai‘i, and a larger, main Hawaiian Islands population, that shows extensive movements as evidenced from between-island resightings. While genetic analyses to assess the level of differentiation between these two populations are needed, our results suggest that stock designations need to be reconsidered. The existence of a resident population off the island of Hawai‘i suggests the possibility that there may be other resident populations off other islands in Hawai‘i, and dedicated field efforts are needed to determine whether such populations exist.

Small populations, such as the Hawai‘i Island residents, often have significant management concerns, especially when the population has a restricted habitat. The habitat for these individuals overlaps with popular recreational fishing grounds, increasing the possibility for fisheries interactions. The biennial RIMPAC naval sonar training exercises as well as other naval exercises may also occur in waters adjacent to or overlapping with the habitats of both the resident and main Hawaiian Islands populations (Anonymous 2006), and given the evidence of susceptibility to sound impacts (Southall *et al.* 2006, Brownell *et al.* 2009), this may pose additional concern. Given the difficulty in mitigating impacts from anthropogenic sounds, the area off the northwestern side of the island of Hawai‘i should be considered as an exclusion zone for mid-frequency sonar use for training purposes. There are other populations of potentially vulnerable species that also utilize this area, including Blainville's beaked whales (Schorr *et al.* 2009), Cuvier's beaked whales (Baird *et al.* 2010*b*), and pygmy killer whales (Baird *et al.* 2011) that would also receive protection from such an exclusion zone. Efforts to increase protection for spinner dolphins have been underway for several years in an attempt to alleviate the number of people swimming with and interacting with the species. One concern is that if regulations are put into place to protect only spinner dolphins, the problem of such human interactions will only be displaced to other species. Due to the shallower and more localized (and predictable) habitat in which the Hawai‘i Island resident population of melon-headed whales is found, they are one species that could be vulnerable to such interactions.

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