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High site fidelity, strong associations, and long-term bonds: Short-finned pilot whales off the island of Hawai‘i

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ABSTRACT

Studies of short-finned pilot whales suggest they travel in stable mixed-sex groups composed of strongly associated individuals; however, temporal analyses of social structure are lacking. To examine site fidelity, association patterns, and temporal relationships, we analyzed data from 267 encounters of this species off the island of Hawai‘i from 2003 through 2007, identifying 448 distinctive individuals (68.1% seen more than once). About 72% of the whales were linked by association into a single social network, suggesting the possibility of multiple populations using the area. Sighting histories suggested that only some individuals exhibit high site fidelity. Individuals demonstrated preferential associations and community division was strongly supported by average-linkage hierarchical cluster analysis of the association data. Nine longitudinally stable social units composed of key individuals and their constant companions were identified. Qualitative assignment of age and sex classes of unit members indicated that some segregation between adult males and female/calf pairs may occur. Temporal analyses of individuals encountered on the same day indicate stable long-term associations. Differential patterns of residency and site fidelity were unexpected and may be indicative of multiple populations around the main Hawaiian Islands. The presence of a resident population demonstrating strong, long-term site fidelity and associations off Hawai‘i Island may warrant special management considerations.

Key words: short-finned pilot whale, *Globicephala macrorhynchus*, Hawai‘i Island, social structure, site fidelity, residency.

Social structure can influence the ecology, genetics, and population biology of a species (Wilson 1975, Whitehead 2008). Understanding social organization in cetaceans therefore has important implications for management and conservation. Bigg (1982) used associations of photo-identified individuals to define killer whale

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(*Orcinus orca*) populations in the coastal eastern North Pacific, and Wells (1986) used patterns of association among photo-identified common bottlenose dolphins (*Tursiops truncatus*) near Sarasota, Florida, to describe a discrete inshore community within the larger Florida population (see also Duffield and Wells 1991, Sellas *et al.* 2005), suggesting social analyses can be used to define biologically meaningful population units. Similarly, association patterns and genetic analysis revealed two demographically isolated populations of false killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands, resulting in the division of the Hawai'i stock into an open-ocean stock and a main Hawaiian Islands insular stock, each with specific management considerations (Chivers *et al.* 2007, Baird *et al.* 2008*a*, Carretta *et al.* 2014).

Pilot whales (*Globicephala* spp.) are thought to exhibit natal group philopatry (Heimlich-Boran 1993, Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008*a*, Alves *et al.* 2013), a type of social structure documented in killer whales in the coastal temperate waters of the eastern North Pacific (Bigg *et al.* 1990) and characterized by a lack of dispersal of male and female offspring from the natal group. The cohesive nature of this social structure has been suggested as a partial explanation for the frequency of pilot whale mass stranding events, which commonly involve groups of largely healthy individuals (Olson 2009). Indeed, these characteristic social bonds have been exploited by drive fisheries in the Faroe Islands as an efficient means of herding large groups, or grinds, of long-finned pilot whales (*G. melas)* to shore, where they are killed (Bloch *et al.* 1993). As with killer whales in the coastal eastern North Pacific, genetic analysis of relatedness within grinds has suggested a multigenerational matrilineal group structure composed of both sexes, with little evidence of breeding occurring within the group (Amos *et al.* 1993, Fullard *et al.* 2000); however, without knowledge of association patterns, limited inferences about long-term stability can be drawn.

Photo-identification studies on short-finned pilot whales (*G. macrorhynchus)* in the Madeiran archipelago (Alves *et al.* 2013) and off the island of Tenerife (Heimlich-Boran 1993) both identified year-round resident populations that demonstrate persistent preferential associations. Similarly, studies of long-finned pilot whales in the Strait of Gibraltar (de Stephanis *et al.* 2008*a*) and off Cape Breton Island, Nova Scotia (Ottensmeyer and Whitehead 2003), found subsets of the study group organized into stable, long-term groups, demonstrating preferential associations, although dyads disassociating over a period of a few days were also identified in the Nova Scotia population. Differing ecology or population size of the two study groups might account for slight differences in observed social structure; long-finned pilot whales in the Strait of Gibraltar represent a year-round resident population (de Stephanis *et al.* 2008*a*, *b*), while those studied off Nova Scotia are thought to be part of an offshore population with little residency (although some seasonal fidelity) to the area (Ottensmeyer and Whitehead 2003).

The short-finned pilot whale has a ubiquitous presence around the main Hawaiian Islands; a 2002 ship line-transect survey found pilot whales to be one of the most abundant and frequently encountered cetaceans within the Exclusive Economic Zone (EEZ) (Barlow 2006), and this species is consistently the most commonly encountered cetacean during small boat surveys (Baird *et al.* 2013). Despite year-round presence and relative accessibility from shore, little research has been published on this species in the Hawaiian archipelago. Preliminary studies suggest short-finned pilot whales off Hawai'i Island may be a genetically isolated island-associated population[2,3] demonstrating a high degree of site fidelity and group cohesiveness (Shane and McSweeney 1990); however, there is no knowledge of whether social or genetic isolation exists among islands or island regions within the archipelago. Research off Hawai'i Island has demonstrated the existence of small resident populations of several other typically deep-water odontocetes, including pygmy killer whales (*Feresa attenuata*), rough-toothed dolphins (*Steno bredanensis*), and two species of beaked whales (McSweeney *et al.* 2007, 2009; Baird *et al.* 2008*b*), suggesting that the isolation of the islands and specific features off the island of Hawai'i may be ecologically important to deep-water odontocetes and potentially favorable for the development of resident populations.

In this study, we used repeated observations of photographically identified individual short-finned pilot whales off Hawai'i Island to describe association patterns among individuals, following the framework developed by Hinde (1976) in which individual interactions are used to describe the "nature, quality and patterning of relationships" among individuals within a population. This study uses long-term photographic data sets from both directed research surveys and opportunistic encounters to assess levels of site fidelity, residency, and association patterns of short-finned pilot whales, focusing particularly off the island of Hawai'i. Only a single stock of this species is currently recognized in the Hawaiian archipelago (Carretta *et al.* 2014); the demonstration of population substructure could greatly influence future management decisions.

METHODS

Directed Research

Research was conducted off the west coast of the island of Hawai'i (an area of approximately 2,500 km^2) from 2003 through 2007, as part of a long-term, multispecies study of odontocete stock structure and behavior (Fig. 1; see Baird *et al.* 2013). Research vessels ranged in length from 5.8 to 18 m; the majority of surveys were conducted using outboard-powered vessels from 6 to 8.2 m in length. Surveys were typically undertaken several times a year with daily effort extending for periods ranging from about 2 to 6 wk. Within each survey period, effort typically covered the majority of the west coast of the island, with efforts made to cover as broad a range of depths as possible, from near-shore to approximately 5,000 m deep and to minimize overlap of survey tracklines within each survey period. Surveys were nonrandom and nonsystematic, but were meant to maximize the geographic and depth range of survey coverage while remaining in areas with good working conditions for sighting cetaceans. Surveys undertaken off Lāna'i, O'ahu and Kaua'i in 2003 and off

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[3] Chivers, S. J. 2005. An update on molecular genetic analyses of population structure for false killer whales and short-finned pilot whales. Draft document PSRG-2005-10 presented to the Pacific Scientific Review Group, 4–6 January 2005, Santa Cruz, CA. Available from NOAA, Southwest Fisheries Science Center, 8901 La Jolla Shores Dr., La Jolla, CA 92037.

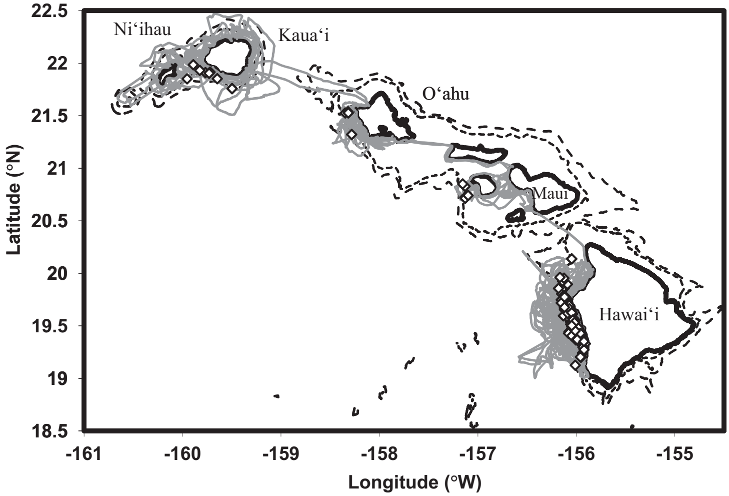

Figure 1. Directed research effort around the main Hawaiian Islands from 2003 through 2007. Short-finned pilot whale sightings are represented by black and white diamonds and survey tracklines are shown in gray; the 1,000 m and 2,000 m depth contours are represented as broken lines.

Kaua'i in 2005 are included here only to examine interisland movements (see Baird *et al.* 2013 for details).

A sighting (synonymous with encounter) was defined using a 1,000 m chain-rule, as a group of individuals separated by 1,000 m or less. Given the typical spatial spread of pilot whale groups off Hawai'i Island (RWB, unpublished data), this definition would likely capture virtually all individuals that were potentially interacting and avoid artificially subdividing large groups with widely spaced individuals (*e.g.*, those that were foraging). Effort and sighting data were recorded including estimated group size and the spatial spread of the group (m × m). We attempted to photograph the right and left sides of all individuals present equally using SLR digital cameras with 100–400 mm lenses, with one to four photographers.

Opportunistic Encounters

Photographs from opportunistic encounters were also available from the Wild Whale Research Foundation (WWRF) from the same study area off the west coast of Hawai'i Island from 2003 through 2007. No location data for effort or precise sighting locations were available from WWRF data. Additional opportunistic photographs were contributed from the same areas surveyed off Kaua'i and O'ahu from 2003 through 2007 and were used only to examine interisland movements.

Photo-identification Protocol

Photo-identification protocol followed Baird *et al.* (2008*a*) and is summarized here. Encounters were sorted visually by individual using the unique pattern of markings on the leading and the trailing edge of the dorsal fin. Sorted individuals were compared against an existing photo-identification catalog, with new individuals assigned a sequential alphanumeric ID (*e.g.,* HIGm####), and resightings incorporated under their existing ID. The best photo for each individual in an encounter was assigned a photo quality (PQ) on a scale of 1–4 (1 = poor, 2 = fair, 3 = good, 4 = excellent), and the distinctiveness (Dist) was also rated on a scale of 1–4 (1 = not distinctive, 2 = slightly distinctive, 3 = distinctive, 4 = very distinctive), following Baird *et al.* (2008*a*). Photograph quality and individual distinctiveness ratings were determined independently. Changes to the leading and trailing edge of the dorsal (such as the addition of new nicks or notches) were recorded for an individual each time they were observed, and these mark changes were then verified by another experienced matcher.

The proportion of individuals that could be reliably identified between years using good- or excellent-quality photographs was estimated within each encounter and averaged over all encounters as the ratio of distinct and very distinct individuals to all individuals regardless of distinctiveness (see Baird *et al.* 2008*a*, *b*; McSweeney *et al.* 2009; Aschettino *et al.* 2011). All analyses were restricted to distinctive or very distinctive individuals with good- or excellent-quality photographs.

Age/Sex Classification

Inferences about the age and sex of certain individuals were made based on several factors following Heimlich-Boran (1993). Pilot whales are sexually dimorphic, with adult males obtaining a maximum length of up to 1 m greater than adult females. Very large individuals exhibiting a substantial thickening of the dorsal fin were considered adult males (Heimlich-Boran 1993). Adults that were in close, consistent association with a calf were considered females, although it should be noted other adult females may have been present but were either postreproductive (Marsh and Kasuya 1984) or with no small calves in close association. Individuals approximately the size of adult females, but without juveniles or calves in close association or a characteristic thickening of the leading edge of the dorsal fin, were classified as unknowns (Heimlich-Boran 1993) and may have been either females or males. Sex of 36 individuals was determined genetically by the Southwest Fisheries Science Center using a Real-Time PCR (Stratagene) assay of the zinc finger genes, as described in Morin *et al.* (2005). In all cases sex determinations matched determinations based on size/association from photographs.

Encounters and Sampling Period

In an effort to reduce the probability that an individual present during an encounter was not photographed, a coverage rating was assigned to each encounter. Using the protocol developed by Ottensmeyer and Whitehead (2003), encounters were assigned a coverage index based on the ratio of the number of photos taken during an encounter to group size (see Table 1 for encounter coverage ratings). Restricting association analyses to encounters with a coverage index of two provides a more representative view of the individuals present within a group, and also allows for comparison between this study and other studies using the same parameters (see Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008*a*). When group size information was not available (*e.g.,* certain WWRF and opportunistic encounters), the number of individuals identified was used as a proxy for group size in the calculation of coverage, scaled from 0 to 3, with only those encounters with a coverage = 3 included in the analysis (Mahaffy 2012). In order to minimize confusion surrounding two separate

Table 1. Coverage ratings for directed research and opportunistic encounters off the island of Hawai'i from 2003 through 2007. Coverage ratings were assigned to provide a metric of how completely groups were sampled (Ottensmeyer and Whitehead 2003).

Coverage index (0–3)	Description (directed research)	Description (opportunistic)
0	No. photos < group size	No. photos < no. individuals
1	No. photos > 1 × group size < 2 × group size	No. photos > 1 × no. individuals < 2 × no. individuals
2	No. photos > 2 × group size	No. Photos > 2 × no. individuals <3 × no. individuals
3	–	No. photos > 3 × no. individuals

coverage indices, an overall coverage index ≥2 was used in all analyses to encompass encounters for both directed research with coverage ≥2 and opportunistic encounters with coverage = 3.

Residency to the Study Area

Potential residency to the study area was examined using individual sighting histories. For the purpose of this study, individuals demonstrating a high degree of fidelity to the study area were termed *core residents* and defined as those documented on at least five occasions in three or more years: individuals that fell below this threshold (but that were seen more than once) were termed *residents,* and individuals seen on a single occasion were termed *visitors* (Mahaffy 2012). While the criteria used to designate residency is somewhat arbitrary, it is meant to separate individuals that exhibited multiyear site fidelity to the area (*core residents*) from individuals with multiple sightings over a short temporal scale (*residents*). Due to the conservative nature of the residency criteria, individuals assigned *visitor* status may also demonstrate some degree of site fidelity; however, the size of the study area limited the inferences for residency that could be drawn because the potential for individuals to be present in a portion of the study area not being surveyed could alter the perception of habitat usage. Thus, the ability to detect fine-scale patterns of occurrence was beyond the scope of this study.

Association Analyses and Community Structure

Association analyses were undertaken in SOCPROG 2.4 (Whitehead 2008). A sampling period of a day was used; all individuals documented during an encounter at least once during that day were assumed to be associated for the day (Whitehead 2008). We used a half-weight index (HWI) of association to provide a quantitative measure of the frequency of cooccurrence of individuals, while controlling for effort (Whitehead 2008). The HWI is suggested in situations in which not all individuals within a sampling period are identified or when individuals are more likely to be identified when they are not in association (Cairns and Schwager 1987, Whitehead 2008). Permutation tests (which took into account the number of associations for a given individual within a sampling period) were used to determine whether preferential associations existed among individuals and to test for differences in gregariousness (Bejder *et al.* 1998; Whitehead 1999, 2009). Each test was repeated four times once the *P*-value had stabilized at 1,000 trial flips. Preferred associations among dyads were also determined by examining dyadic association indices relative to the mean association index of the study group; following Durrell *et al.* (2004) and Gero *et al.* (2005) "preferred associations" were those with an association index greater than or equal to twice the mean association index of the study group and "acquaintances" were those that fell below this threshold.

In order to determine whether realistic divisions existed within the study group, the modularity (Newman 2004) of the population was measured using association indices. Modularity (Q), defined as the difference between the proportion of the total association within clusters and the expected proportion, has a range from 0.0 (randomly formed clusters) to 1.0 (clusters with no shared associations). Newman (2004) indicates that acceptable cluster division occurs at $Q \geq 0.3$. Social clusters were created by maximizing modularity in both hierarchical cluster analysis and social network analysis, and the results were compared. Hierarchical cluster analyses, with the use of a cophenetic correlation coefficient (CCC), were used to identify dendrograms that are truly representative of complex social structure; values for the CCC range from 0.0 (no correlation) to 1.0 (complete correlation) with CCC $\geq$ 0.8 indicative of a well-represented population (Whitehead 2008, 2009). Clusters were also constructed following a method for maximizing modularity in weighted networks (Newman 2006) where the study group was divided based on the dominant eigenvector of the modularity matrix, such that cluster division was stopped when modularity was maximized. To examine whether substructure existed within clusters, the presence of meaningful subclusters was then investigated for each cluster using Newman's eigenvector-based method. A 1,000 permutation Mantel test was used to compare associations within and among clusters. Only individuals seen off the island of Hawai'i on more than four occasions (*i.e.,* core residents and residents that meet this criterion) were included in analyses of association and community structure.

Delineating Temporally Stable Units

Standardized lagged association rates (SLAR) were used to estimate the probability that two individuals would randomly associate over time (Whitehead 1995). Four models were fit to the SLAR curves using maximum likelihood and binomial loss, and the model with the best fit was determined as that with the lowest QAIC value. All individuals were included regardless of the number of times they were documented, as the standardized lagged association rate is meant to describe the entire population, not just those most frequently encountered (Whitehead 2008).

Within the core resident population social "units" of pilot whales were delineated, defined as key individuals and their constant companions following Ottensmeyer and Whitehead (2003) and de Stephanis *et al.* (2008*a*). Criteria for the selection of key individuals were designed to capture those with longitudinal sighting histories in the study area and were defined as individuals sighted in at least four different years and on eight different occasions. Constant companions were defined as individuals sighted with key individuals in at least three different years and on five different occasions. Sightings between years were required to be separated by a minimum of 180 d to avoid artificial inflation of sighting records.

Using the above criteria, it was possible for multiple key individuals with overlapping sighting histories to belong to the same unit or to assign constant companions to more than one unit; in such instances, association indices were also examined to determine whether unit allocation was truly representative of longitudinal association preferences or was simply an artifact of extensive sighting histories. Thus, a minimum dyadic association index of 0.50 was also required in order for key individuals and constant companions to be placed in the same unit; in situations in which the association index was below 0.50 for one or more dyads, a key individual or constant companion was only allowed to remain in the unit if the majority (>50%) of dyadic associations were above the 0.50 criterion. Similarly, key individuals that did not meet the minimum criteria for inclusion in a given unit, but which did have multiple dyadic associations above 0.50 with other key individuals, were also considered on an individual basis. A minimum association index of 0.50 mirrors an established criterion for designating "pods" of killer whales in coastal North Pacific waters (Bigg *et al.* 1990) and allows for some comparison between killer whale populations and the study group.

Once units were established using the outlined criteria, each was examined quantitatively and qualitatively to ensure unit membership was an accurate depiction of social structure; any discrepancies and subsequent changes are addressed in the results section. Elapsed time between photos of individuals was examined to ensure key individuals and constant companions were in close association (*i.e.*, seen ≤1 min apart) during an encounter and were not an artifact of how groups were defined in the field.

Results

Effort and Sightings

Short-finned pilot whales were encountered an average of once every 105 km (or every 6.5 h) of directed research effort. A total of 30,470 km of trackline (265 d on the water, 1,899 h of survey effort) were covered during surveys that were conducted between 2003 and 2007 in all months except June. Including the WWRF sightings, pilot whales were encountered off the island of Hawai'i in every month surveyed.

For photo-identification, 295 pilot whale encounters were photographed off the main Hawaiian Islands, 51,520 photographs were analyzed for the current study (Table S1). The majority of both effort and sightings from which photos were available occurred off the leeward side of Hawai'i Island (Fig. 1): 123 from directed research efforts and 144 from WWRF efforts. Good photographic coverage of these groups (coverage index ≥2) occurred in 241 of these encounters (Table S1). Data were also included from 28 encounters (directed or opportunistic) from other islands (Table S1). Off the island of Hawai'i, the mean proportion of individuals within groups that were considered distinctive was 81.2% (SD ± 16.2%; median = 82.4%; range = 47.1%–100%).

Group Composition

The mean group size from directed research efforts off the island of Hawai'i was 20.8 (range 1–53, SD ± 9.3, n = 123). Neonates were observed in 8.9% of these sightings (11 times in four different years) and young of the year were observed in 37.4% of sightings (46 times). All sightings of neonates occurred between July and November, and five of the 11 sightings with neonates occurring in July. Sightings of young of the year occurred in all months of the year with effort except March. Adult male presence/absence was recorded in the field for 89 of the 123 directed research encounters (72.4%); of these, one or more (range 1–8) adult males were present in 77

(86.5%) encounters in all months with effort. Neonates were observed in the same group as adult males on six occasions (54.5% of sightings that included neonates).

Individual Sightings and Residency to the Study Area

A total of 448 distinctive individuals were identified off the island of Hawai'i during the study period. Individual sighting histories varied substantially, ranging from individuals seen once over the entire course of the study to individuals seen in a total of 27 encounters and in all 5 yr of the study (range of number of times seen 1–29, median = 3). Based on established residency criteria, 156 core residents, 150 residents, and 142 visitors were identified. All but one core resident, 52.7% of residents, and 36.6% of visitors, were first identified in 2005 or earlier. The majority of core residents were seen during all times of year; 87.7% of core residents and 13.3% of residents were seen in at least three seasons. A social network diagram identified a core social network of 322 individuals (71.9% of the Hawai'i Island study group) and 10 satellite clusters containing 126 individuals (membership range 2–32; mean = 13.4) that did not link back to the main component (Fig. 2).

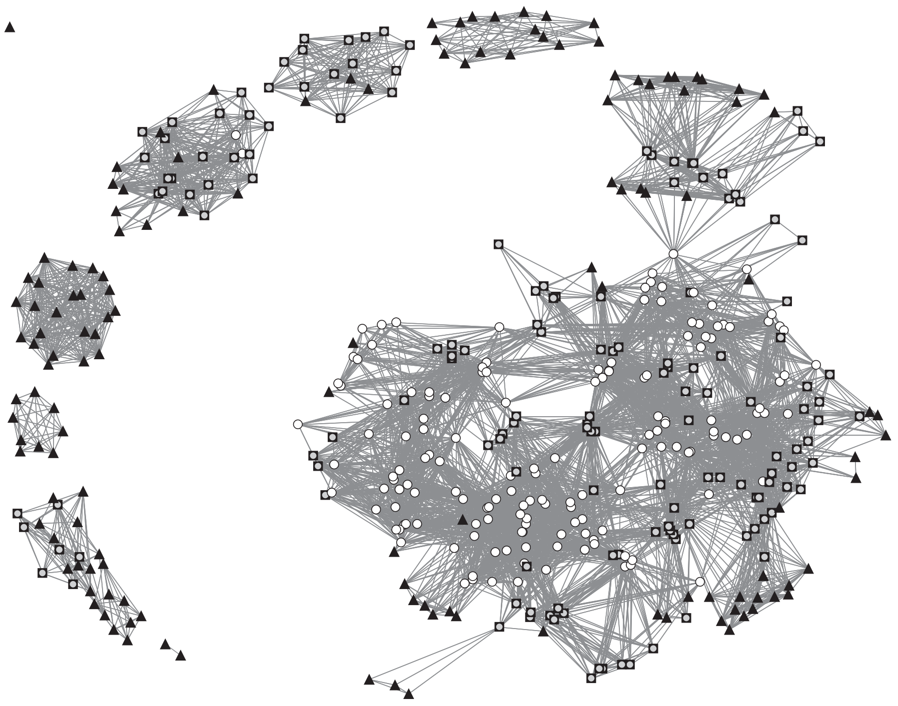

Figure 2. Social network diagram of all distinctive short-finned pilot whales (n = 448) documented off the island of Hawai'i from 2003 through 2007. Individuals are presented by nodes and lines between nodes indicate individuals seen together in the same encounter. Distances between nodes were determined using a spring-embedding algorithm to depict closeness between individuals; distances between clusters are arbitrary. Core residents are shown as white circles, residents are shown as gray boxes, and visitors are shown as black triangles. Note the two core residents that do not link by association to the main social network.

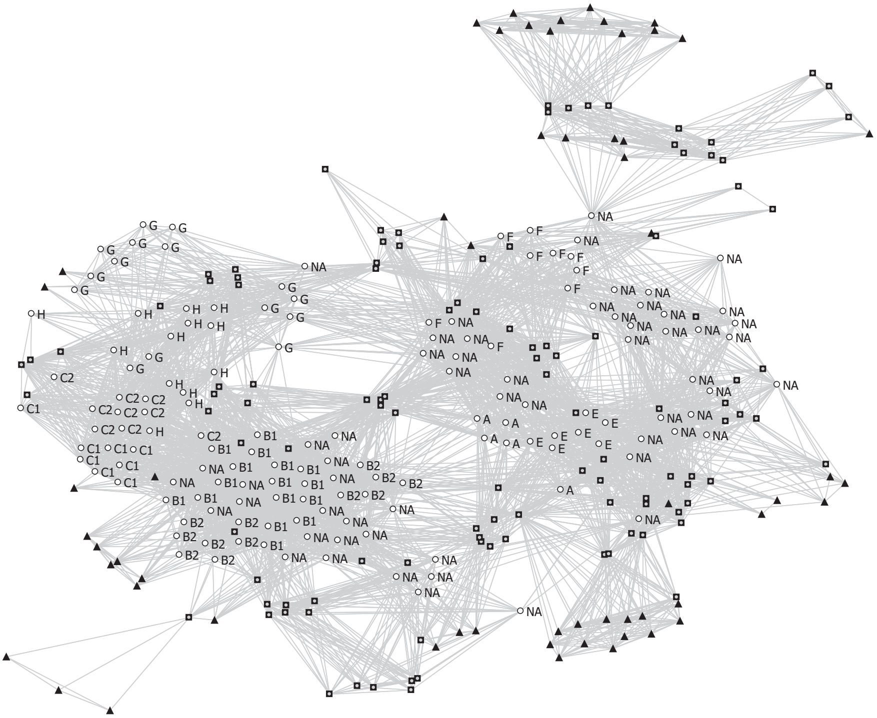

Figure 3. Social network diagram depicting all distinctive individuals documented off Hawai‘i Island that link back to the main social cluster (n = 322). Individuals are presented by nodes and lines between nodes indicate individuals seen together in the same encounter. Visitors are depicted as black triangles, residents are depicted as gray squares, and core residents are depicted as white circles; individuals assigned to units are labeled with their unit designation and core residents not allocated to a social unit are labeled “NA.”

The main cluster of the social network was composed of 57 visitors, 98 residents, and 154 core residents (Fig. 2, 3). With the exception of two individuals, all individuals present in the satellite clusters were determined to be residents or visitors based on sighting history; 85 (67.5%) of the individuals were seen on one occasion, 36 (28.6%) were seen twice, and three were seen four times. The two core residents that did not link back to the main social network were present in the largest of the satellite clusters, a cluster of 32 individuals sighted 1–5 times.

Two groups (14 individuals, 0.49% of distinctive identifications) were documented moving between islands. In February 2005, 13 individuals documented off Kaua‘i were resighted in September of that same year off Hawai‘i Island (six were removed from the analysis due to distinctiveness and photo quality restrictions). These 13 individuals had extensive sighting histories off Hawai‘i Island between 2005 and 2007; each of the seven distinctive individuals was documented on 13–18 occasions (mean = 16.3) in three separate years, and those individuals were not documented with any other individuals off Kaua‘i.

Preferential Associations

Individuals within the study differed in the number of individuals with whom they were associated; estimated using the sum of association indices (Jarman 1974), the typical number of associates ranged from 2 to 18.1 (mean = 12.2, SD ± 2.6) (Fig. 4), and individuals were found to have significant differences in gregariousness ($P = 0.999$). While mean association across the population was low (AI 0.06 ± 0.01, range 0.01–0.09), maximum association was high (AI 0.91 ± 0.08, range 0.50–1.00), indicating the presence of strong dyadic associations (Fig. 4). Associations were found to be nonrandom for both short-term and long-term companionship. Long-term preferential associations between individuals were indicated

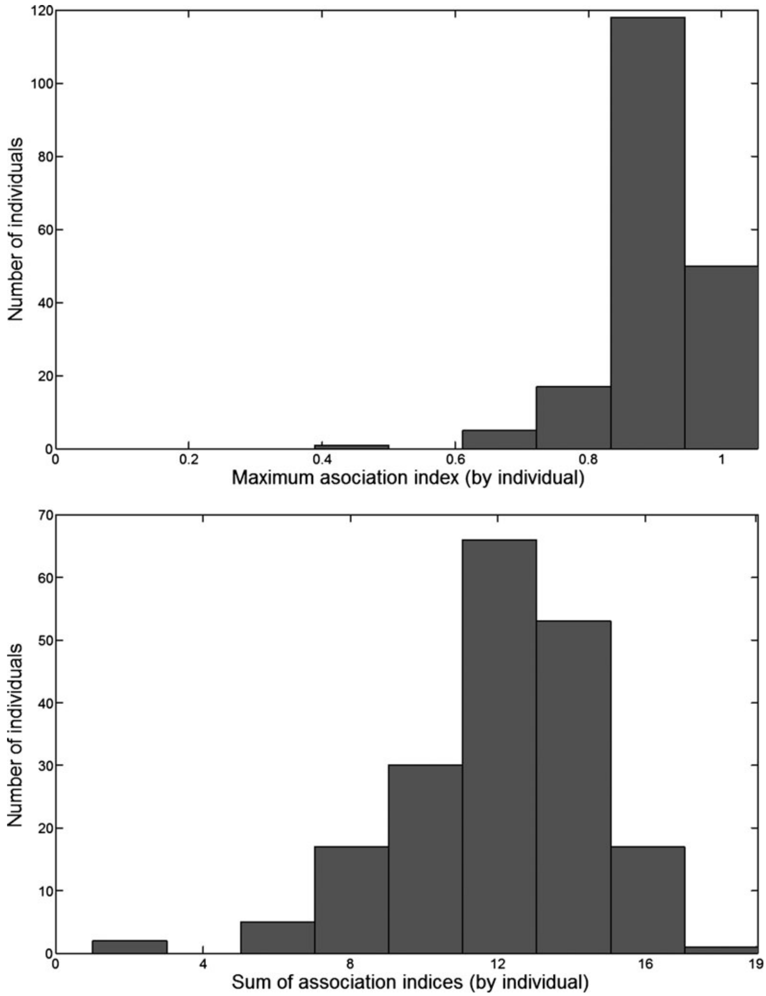

Figure 4. Distribution of association indices for distinctive individuals seen off the island of Hawai‘i five or more times: (top) maximum association index, and (bottom) average number of associates (*i.e.,* group size) for each individual.

by significantly higher SD and CV of the real data set compared to the permuted data set for both permutation tests, while long-term avoidance of some individuals was indicated by a lower proportion of nonzero association indices in the real data for both tests (Table 2). Further, for groups permuted within samples, a significantly lower mean of the real association indices indicated short-term preferential associations. All P-values stabilized at 50,000 random permutations.

Of 35,958 possible dyadic associations, 4,042 (11.2%) were considered "preferred associations" (*i.e.,* had an association index ≥0.12). The majority of dyads (29,956; 83.3%) were never documented in association; dyads that did associate but that fell below the 0.12 association index threshold for preferential associations accounted for 1,960 (5.45%) of all possible dyadic associations.

Community Structure

Division of distinctive individuals within the study into clusters was supported using both hierarchical cluster analysis and social network analysis when examining association preferences in conjunction with sighting history. Maximum modularity values were the same for both cluster analysis and social network analysis (Q = 0.798; AI = 0.048), resulting in the division of the study group into nine highly representative (CCC = 0.983) clusters of variable size and association strength (Fig. 5). Cluster membership ranged from 2 to 34 individuals, and mean association indices within clusters ranged from 0.27 ± 0.05 to 1.00 ± 0.00. Cluster 9 differed substantially in both number of individuals (two) and mean association index (1.00); membership for the remaining eight clusters ranged from 16 to 34 (mean = 23.25 ± 7.80) individuals and mean association indices ranged from 0.27 ± 0.05 to 0.78 ± 0.06. Cluster 9 also appeared to be socially

Table 2. Tests for nonrandom associations among distinctive short-finned pilot whales seen ≥5 times off the island of Hawai'i; permutation tests performed in SOCPROG 2.4 were used to test for short-term and long-term preferred or avoided associations and for differences in individual gregariousness. P-values > 0.95 are considered significant.

	Permute groups within samples (short-term and long-term test)	Permute associationswithin samples (long-term test)
Standard deviation	Observed: 0.18249 Permuted: 0.14379 P = 1.00000	Observed: 0.18249 Permuted: 0.14453 P = 0.99998
Coefficient of variation	Observed: 3.10469 Permuted: 2.42543 P = 0.99998	Observed: 3.10469 Permuted: 2. 50255 P = 1.00000
Proportion of nonzero AIs; proportion of nonzero AIs from permuted data	Observed: 0.16185 Permuted: 0.27765 P = 0.00002	Observed: 0.16185 Permuted: 0. 26133 P < 0.000001
Mean association index	Observed: 0.05878[a] Permuted: 0.059298[a] P = 0.00012[a]	
Standard deviation of typical group size	Observed: 2.46529 Permuted: 2.20822 P = 0.99998	

[a] Results reported are from short-term test.

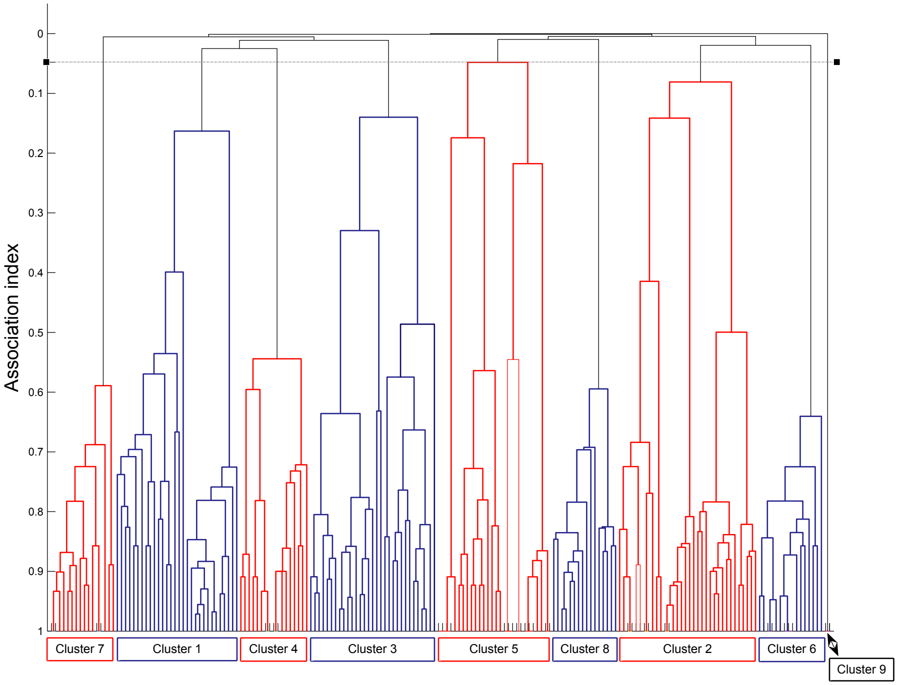

Figure 5. Dendrogram constructed using average-weight linkage hierarchical cluster analysis of distinctive short-finned pilot whales documented off the island of Hawai'i on five or more occasions. The dashed line indicates cluster division occurs at AI = 0.48 (modularity = 0.798).

isolated on the dendrogram, having no links to any of the other clusters (each of the other eight clusters were linked to at least one other cluster at some low level of association).

Individuals within clusters had significantly higher mean levels of association (0.48 ± 0.20) than those among clusters (0.00 ± 0.00, Mantel permutation test, P = 1.00). Maximum association indices were also substantially greater within clusters than among clusters (0.91 ± 0.08 *vs.* 0.08 ± 0.05). These indices and a large, positive matrix correlation coefficient of 0.768 supported rejection of the null hypothesis that no significant difference in association strength within or among clusters existed. Removing Cluster 9 from the analysis had a negligible effect, reducing the mean association index within clusters to 0.47 ± 0.20 and the maximum to 0.90 ± 0.08; all other values remained the same.

Examination of individual clusters using community division indicated the presence of meaningful subclusters in four of the nine clusters (Q = 0.321–0.441, n = 4,); Clusters 1 and 3 were each divided into two subclusters, and Clusters 2 and 5 were each divided into three subclusters. Although cluster subdivision was supported, maximum modularity values obtained were lower than for the overall study group, indicating that within-cluster divisions were not as strong. Clusters that were successfully subdivided were substantially larger than those in which subclusters were not supported (membership ranges: 26–34 and 2–17, respectively), indicating that cluster subdivision could partially be an artifact of size rather than (or as well as) social partitioning. Considering only subclusters, and Clusters 1–8, where subdivision was not supported, membership ranged from 8 to 18 individuals (mean = 12.5 ± 3.6), substantially less than the mean group size encountered in the field. Although not highlighted in the dendrogram, subclusters are evident when viewing the configuration of relevant clusters in Figure 5.

Temporal Aspects of Social Structure and Delineating Stable Groups

When defining a group as a set of individuals documented within the same encounter, the model fit to the standardized lagged association rate that best described the study group suggests some disassociation over a period of a few years (defined as "casual acquaintances," by Whitehead (1995); Fig. 6). However, adjusting the definition of a group to a set of individuals documented within the same day did not show such a disassociation (Fig. 6).

Initial analysis produced eight longitudinally stable social units (membership range 2–28, mean = 9.75) from 154 core residents. When pairwise association indices were applied to members within each unit, many dyadic associations fell below the 0.50 criterion, suggesting that further inspection of unit membership was necessary. Final unit delineation (see Table 3) resulted in nine social units (membership range 5–16, mean = 10.44, SD ± 3.75). Fifty-nine core residents were not allocated to social units since they did not share sufficient sighting histories with any key individuals, although it is possible that these individuals may in fact form stable social units with each other and might emerge as key individuals as more data are collected.

Both males and females were present in all six groups where sex was determined for more than one animal (Table 4). Of the 36 individuals for which sex was determined genetically, both males and females were found to be present in units (n = 6) where sex was known for more than one animal (Table 4). Although qualitatively assigning age and sex descriptors to individuals is somewhat subjective, broad inferences may still be drawn about the overall structure of the social unit and the genetic results obtained here have supported qualitative assignments. Adult males were visually identified in eight of the nine social units and genetically confirmed in five. The social unit without any adult males (Unit B1) contained five females and six males (genetically identified) and almost twice as many calves and juveniles as the other social units (Table 4). More than half of the social units did not have calves or juveniles in attendance. Known adult females were only present in four of the nine social units; however, the criteria used to define adult females was more restrictive than for adult males, suggesting that some of the individuals simply listed as "unknowns" or genetically confirmed simply as females were likely adult females without younger individuals in close association.

A social network diagram showed visitors mainly confined to the outer fringes of the main component and residents clustered in interior portions of the network between dense clusters of core residents (Fig. 2, 3). Removal of residents and visitors from the main component of the social network diagram provided a more direct comparison of core residents allocated to various social units with those left unallocated; the majority of unallocated core residents remained clustered together, further suggesting that they might constitute new social units (Fig. S1).

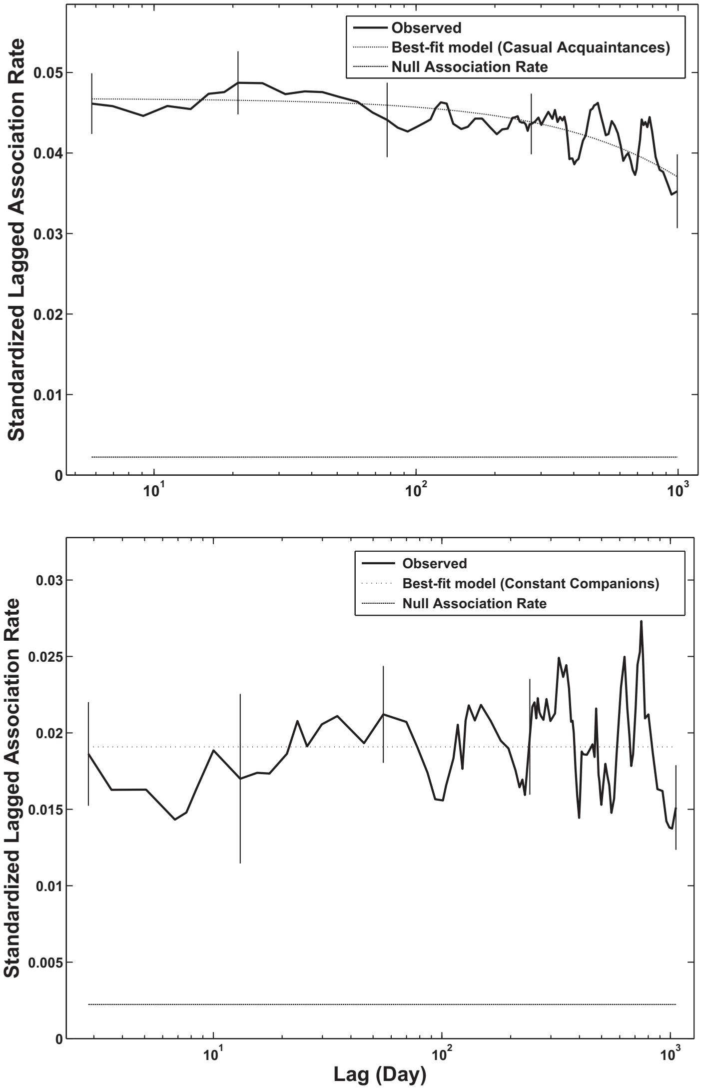

Figure 6. Standardized Lagged Association Rate for individuals documented off Hawai‘i Island using a moving average of 200,000 (top) and 250,000 (bottom) associations to create a smoother curve. Associations are defined as individuals grouped within an encounter (top) and individuals seen on the same day (bottom). Approximate standard error bars (±1 SE) were produced by jackknifing on each sampling period. The best-fit model (top: casual acquaintances, $g' = 0.046{*}e^{-0.0002\tau}$) and (bottom: constant companions, $g' = 0.0191$) was obtained using maximum likelihood methods; the null association rate is included for reference.

Social Units vs. Cluster Analysis

To illustrate the difference between social units established using sighting histories and clusters established using eigenvector methods, a dendrogram was constructed

Table 3. Longitudinally stable social units of short-finned pilot whales off the island of Hawai'i constructed from shared sighting histories and composed of key individuals and constant companions.

Unit	No. key individuals	No. constant companions	Total no. unit members	Association index range	Mean association index
A	2	3	5	0.83–0.93	0.897
B1	16	0	16	0.44–0.87	0.618
B2	0	12	12	0.64–0.97	0.827
C1	8	0	8	0.50–0.91	0.766
C2	9	0	9	0.65–0.95	0.807
E	2	5	7	0.76–0.96	0.878
F	2	7	9	0.43–0.83	0.676
G	13	2	15	0.43–0.97	0.687
H	11	2	13	0.36–0.96	0.689

Table 4. Visually estimated age/sex classes of adult males and females within social units with genetically confirmed sexes indicated as (G); see section on *Age/Sex Classification* for a review of terms and criteria.

Unit	No. unit members (sexes genetically determined)[a]	No. adults by sex based on field characteristics (with genetic confirmations shown when known)		No. of calves (C) and juveniles (J) not included in Units[b]	Est. total Unit size including calves and juveniles[c]
		Males	Females		
A	5 (1M, 4U)	1 (1G)	–	–	5
B1	16 (6M, 5F, 5U)	–	4 (3G)	1 (C), 4 (J)	**21**
B2	12 (2M, 1F, 9U)	2 (1G)	–	–	12
C1	8 (8U)	3	–	–	8
C2	9 (1M, 8U)	1	–	–	9
E	7 (3M, 1F, 3U)	2 (2G)	–	–	7
F	9 (2M, 1F, 6U)	1 (1G)	2	2 (J)	**11**
G	15 (3M, 3F, 9U)	1	3	3 (C)	**18**
H	13 (3M, 4F, 6U)	2 (1G)	1	1 (J)	**14**

[a] M = male, F = female, U = unknown.
[b] The number of calves and juveniles was estimated for each unit based on close, consistent association with a member of the unit thought to be an adult female.
[c] Numbers in bold indicate an estimated total unit size that differs from established unit size.

using only key individuals and constant companions; individuals were then assigned to both social units and clusters (Fig. S2). As mentioned above, key individuals and constant companions were divided into a total of nine social units using longitudinal sighting histories; application of the eigenvector-based method for community division resulted in six clusters, three that corresponded exactly to previously established social units and three that were each formed from merging two social units. When subcluster membership was compared to unit membership, results were very similar: subclustering successfully predicted unit membership with the exception of Units C1 and C2, which were combined into a single cluster.

Several features of subclusters were similar to those of units; subcluster size ranged from 8 to 18 individuals (mean = 12.1, SD ± 3.7) and 9 of the 10 subclusters had an overall average association index ≥0.50 (range 0.48 ± 0.14–0.84 ± 0.02). Unlike unit membership, which required that the majority of dyadic associations for each member be ≥0.50, four of the 10 subclusters contained individuals (range 1–4) that failed to meet the ≥0.50 criterion used to determine unit membership. Dyadic associations within subclusters were also more heterogeneous than those within units; minimum dyadic association indices within subcluster ranged from 0.06 to 0.76 with 5 of the 10 subclusters having a minimum dyadic association index ≤0.50. Although all minimum association indices were below 0.50 (range 0.29–0.46), for the clusters in which within-cluster division was not supported, the average association index for each cluster was ≥0.50 (range 0.64–0.78) and there were no dyadic associations that failed the criteria for unit membership, suggesting the clusters would meet unit membership criteria if they had sufficient sighting histories.

Discussion

Preliminary Population Structure

Analysis of association patterns presented here in concert with current knowledge of movement patterns and habitat usage of short-finned pilot whales suggest the presence of both a demographically independent, island-associated population and an offshore or open-ocean population off the island of Hawai‘i. The high degree of residency and site fidelity used to define core resident individuals off the island of Hawai‘i, combined with a lack of interisland resightings, suggest core residents represent a separate, insular population. Sighting rates in relation to depth suggest pilot whales off the main Hawaiian Islands are strongly associated with the island slopes (Baird *et al.* 2013). Preliminary evidence of multi-year, within-island resightings of short-finned pilot whales off other islands within the main Hawaiian Islands (Baird *et al.* 2011), combined with a lack of interisland resightings, provide evidence of site fidelity to each island area and support the existence of additional demographically independent, island-associated populations or subpopulations within the archipelago. The existence of multiple populations is evident for several other species of odontocetes in the main Hawaiian Islands; insular and offshore populations have been described for false killer whales (Baird *et al.* 2008*a*, Martien *et al.* 2014), and demographically independent island-associated populations have been described for common bottlenose dolphins (Baird *et al.* 2009, Martien *et al.* 2011), melon-headed whales, *Peponocephala electra* (Aschettino *et al.* 2011), pantropical spotted dolphins, *Stenella attenuata* (Courbis *et al*. 2014), and spinner dolphins, *S. longirostris* (Andrews *et al.* 2010).

Residency and Site Fidelity

Short-finned pilot whales exhibited dramatically different levels of site fidelity over the course of the study, suggesting multiple populations may use the study area. The differing patterns of residency reflect the degree to which an individual's range likely overlapped with that of the study area; labeling individuals as core residents or residents suggested that the majority of their time was spent off the island of Hawai‘i. Indeed, individuals that were satellite tagged off the leeward side of the island of

Hawai'i in 2006 and 2007 were documented moving north of the study area into the 'Alenuihāhā Channel separating the northern tip of the island of Hawai'i from Maui, and individuals tagged in 2008 generally remained associated with the island (GSS, unpublished data). Only one group identified off Hawai'i Island was also photographed off another island (Kaua'i), although the sample size of encounters off other islands was relatively small.

In addition to core residents and residents, a steady influx of new individuals also used the study area. Individuals seen only once were encountered in all seasons and in all years; despite significant survey effort, more than half of the individuals that were only seen on a single occasion were first documented during the last 2 yr of the study. Individuals labeled visitors that appear within social clusters containing residents or core residents are likely whales that have only recently entered the marked population, or are members that died before the end of the study, thus limiting the number of times they could be documented.

Our observations of residency patterns are consistent with those found elsewhere. In a long-term photo-identification study in the Madeiran Archipelago (using the same criteria although with different labels), Alves *et al.* (2013) found varying degrees of site fidelity, with a subsection of individuals demonstrating strong, long-term fidelity to the area. Despite comparable data sets, the majority (71%) of individuals in Madeira were only seen once, compared to 32% in the current study, and preliminary genetic analysis has suggested differing residency patterns found in the Madeira study may be due to social philopatry rather than genetic differentiation (Alves *et al.* 2013). Although not referred to as site fidelity, Heimlich-Boran (1993) reported a similar range of resighting rates for short-finned pilot whales off the island of Tenerife, with the number of sightings per individual ranging between 1 and 28 (mean = 5.3, SE ± 0.27) over a 22 mo study. Individuals were considered *resident* if sighted more than once or in the company of other *residents*, ignoring any temporal components to an individual's sighting history. While direct comparisons cannot be made, it is apparent that new individuals were identified throughout the study period and that some individuals off Tenerife exhibited a strong degree of residency.

In contrast to our findings, residency was not apparent for long-finned pilot whales off Nova Scotia (Ottensmeyer 2001, Ottensmeyer and Whitehead 2003). Although only part of the study area was covered during a survey, individuals were estimated using a lagged identification rate to remain in the study area (~85 km^2) for less than a day and new individuals were identified throughout the study.

Individual Associations and Gregariousness

Short-finned pilot whales in this study appear to form a well-differentiated society that demonstrates strong long-term and short-term preferential associations with strong interindividual bonds. These findings are supported using both quantitative techniques and social network analysis. Further analysis indicated that few casual associations existed and that the majority of associations were preferential in nature (Table 2). Similar preferential associations were found among pilot whales in the Madeiran Archipelago (Alves *et al.* 2013), off the coast of Nova Scotia (Ottensmeyer and Whitehead 2003) and in the Strait of Gibraltar (de Stephanis *et al.* 2008*a*), although information on differing levels of individual gregariousness was not available. Similarly, Ottensmeyer (2001) noted that the majority of possible associations between individuals were never documented; however, unlike the current study, the maximum association index for some members of her study group was low, suggesting no consistent associates. Ottensmeyer (2001) reasoned that strong associations may still exist for those individuals with low maximum association index values which seem possible given photographic limitations that not all potential associates were documented.

The reasons for differences in gregariousness found in our study, with some individuals consistently found in small or large groups, are unclear but could be indicative of relative social standing within the population or associated with specific age/sex classes. As analyses were restricted to the roughly 81% of the study group considered distinctive, results represent sociality only among distinctive individuals and are likely biased toward older animals. Differences reported here could in part be an artifact of the number of distinctive individuals in the different groups. From a logistical perspective, individual differences in gregariousness can negatively impact an individual's sighting history, as larger groups likely have a higher probability of being spotted. Thus, it is possible that hyper-social individuals have a higher probability of being documented in the field than less social individuals.

Detecting Community Structure

Short-finned pilot whales off the island of Hawai'i may exhibit a hierarchical social structure. Social network analysis supported the division of the core residents into nine socially meaningful clusters of varying size and association strength. The mean association index within clusters (AI = 0.48 ± 0.20) was similar to the 50% criterion used to designate pod membership in killer whales in the coastal eastern North Pacific (Bigg *et al.* 1990), and thus could be indicative of persistent social groups. Although the mean number of individuals assigned to each social cluster was similar to the mean group size estimated in the field, within-cluster mean association indices ranged from 0.27 to 0.78, suggesting that social clusters (and thus groups encountered in the field) were broadly representative of preferential associations among specific individuals, but were not necessarily indicative of strongly cohesive groups within the study group. Given the wide range in membership and association strengths among clusters, it is likely that some social clusters were aggregations of one or more smaller, more cohesive groupings. Indeed, subclustering was only supported for the social clusters that had a mean association index <0.50; resulting subcluster membership (range 8–18) was smaller than the mean group size estimated in the field, and mean association indices ranged from 0.48 to 0.84, indicating that clusters with a mean association index <0.50 likely contained multiple, smaller cohesive social groups.

The results suggest that considering the temporal aspects of social structure is important in predicting longitudinally stable social units; however, in the absence of unit information, subclusters may serve as a reasonable proxy for determining cohesive social groups provided individuals are in close association. When compared to social units constructed using shared sighting histories rather than social network analysis, mean membership and association index ranges were similar for both subclusters and for clusters where subclustering was not supported. These subclusters also contained peripheral individuals that only strongly associated with some members of the subcluster and maintained weak associations with others, suggesting subclusters are slightly less conservative than units. Whether peripheral individuals represent new additions to the social cluster or long-term associates with newly-acquired markings that have just entered the marked population (such as calves or juveniles) is not known, and will require additional research effort.

Social cluster and social unit sizes presented here are likely conservative as membership was biased toward marked, older animals and did not take into account potential associations between unmarked individuals (such as most calves, juveniles, and some subadults) and the rest of the study group. Considering the overall distinctiveness of the study group, it is possible that true mean social unit membership is closer to 12.5 individuals, similar to an estimate of pod size in Madeiran short-finned pilot whales when including nonmarked individuals (Alves *et al.* 2013). Given the discrepancy between the mean group size encountered in the field and the mean cluster, subcluster and unit sizes, groups encountered likely represent multiple social units in temporary association. This assumption has also been suggested by Alves *et al.* (2013) for pods of short-finned pilot whales and Ottensmeyer and Whitehead (2003) for units of long-finned pilot whales, but is contrary to de Stephanis *et al.* (2008*a*); however, differences in how groups were defined in the field prevent further comparison among studies.

Social and Ecological Significance of Clusters and Units

Results presented here indicate that although units represent persistent social entities, social dynamics may differ among units. Previous studies have suggested that pilot whales may exhibit natal group philopatry (Heimlich-Boran 1993, Ottensmeyer and Whitehead 2003, de Stephanis *et al.* 2008*a*, Alves *et al.* 2013); however, qualitative assignment of age and sex to individuals within each social unit indicated that there may be some segregation between adult males and female/calf pairs, or that adult males may disperse from their natal groups (Table 4). More than half of the social units did not have calves or juveniles documented in association with an adult; however, the majority of social units where calves and juveniles were present also contained putative adult males. The largest social unit defined in the study, Unit B1, was the only unit where adult males were not identified; conversely, Unit B1 also contained almost twice as many female/calf pairs as the other units. It is important to note that Units B1 and B2 were initially defined as a single unit; however, the pronounced differences in association levels within this unit supported unit division. In contrast to Unit B1, three of Unit B2's members were thought to be adult males and no known adult females (based on close association of calves), juveniles or calves were identified in the unit; thus, while Units B1 and B2 both appear to exhibit some degree of within-unit age and sex-based segregation, they also maintain interunit associations, suggesting bonds between units are socially important. The interunit association between Units B1 and B2 is supported by the fact that multiple units have been documented in association and may help explain why individuals off the island of Hawai'i were commonly observed in groups of mixed sex and age.

The suggestion by Amos *et al.* (1993) and Fullard *et al.* (2000) that grinds of long-finned pilot whales represent an extended matrilineal group demonstrating persistent associations similar to pods of killer whales in the coastal eastern North Pacific has been questioned (Connor 2000, Ottensmeyer and Whitehead 2003, Oremus 2008). Indeed, Oremus (2008) identified multiple unrelated matrilines within stranded groups of long-finned pilot whales in New Zealand and suggested that while natal group philopatry has been demonstrated within matrilines, multiple matrilines in association do not necessarily indicate relatedness. This important distinction between pilot whale social structure (s) and killer whales in the coastal eastern North Pacific may indicate an intermediate social structure between sperm whales and killer whales.

Implications for Conservation and Management

Short-finned pilot whales in Hawaiian waters are currently managed as a single stock with no recognition of population subdivision (Carretta *et al.* 2014). Shipboard (Barlow 2006) and aerial surveys (Mobley *et al.* 2000) have indicated that short-finned pilot whales are abundant throughout the main Hawaiian Islands; however, these abundance estimates assume that the whales surveyed exist as a single population, rather than multiple independent demographic units, as has been found for several species of odontocetes in the Hawaiian Islands (Baird *et al.* 2008*a*, *b*, 2009; McSweeney *et al.* 2009; Aschettino *et al.* 2011; Martien *et al.* 2011; Courbis *et al.* 2014). As Baird *et al.* (2008*a*) suggested, applying abundance estimates from the entire Hawaiian EEZ to portions of the population potentially demonstrating restricted ranges may result in an underestimate of the level of anthropogenic risks affecting that population; thus, detailed knowledge of population structure is necessary to inform management decisions. The presence of a small core resident population of short-finned pilot whales off the island of Hawaiʻi could therefore indicate an elevated risk to anthropogenic threats such as high levels of commercial and recreational vessel traffic, targeted tourist activities such as dolphin watching and swim-with-dolphin programs (Danil *et al.* 2005), and increased exposure to mid-frequency naval sonar (Southall *et al.* 2006).

In addition to management concerns associated with individuals demonstrating restricted ranges, Williams and Lusseau (2006) noted the importance of considering social structure when formulating effective management plans. Using social network analysis, Williams and Lusseau (2006) simulated removal of random and targeted individuals from the coastal eastern North Pacific population of killer whales known to demonstrate natal group philopatry. Results of Williams and Lusseau's (2006) analysis indicated that while removal of random individuals did not fracture the social network, targeted removal of individuals (as would be expected in a live-capture scenario) caused the network to splinter into smaller groups. Short-finned pilot whales in Hawaiian waters are not at risk of live capture; however, this analysis does suggest that, as a strongly matrifocal species similar to killer whales, loss of key individuals within the social unit (*e.g.,* as a result of fishery interactions) could weaken unit stability. As a small resident population demonstrating strong group cohesiveness, short-finned pilot whales off the island of Hawaiʻi may warrant special management considerations.

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SUPPORTING INFORMATION

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Figure S1. Social network diagram depicting core residents documented off Hawai'i Island that link back to the main social network: Unit A (red circle), Unit B1 (black plus sign), Unit B2 (light green up triangle), Unit C1 (gray hatched box), Unit C2 (light blue down triangle), Unit E (pink boxed-circle), Unit F (dark green diamond), Unit G (yellow square), and Unit H (orange inverted triangles). Core residents not allocated to a social unit are shown as dark blue squares.

Figure S2. Dendrogram constructed from key individuals (solid lines) and constant companions (dashed lines) documented off the island of Hawai'i to illustrate differences between social unit delineation using sighting histories and cluster assignment using the eigenvector method. Maximum modularity (*Q*) is indicated by a dashed line and an association index of 0.50 is indicated by a dotted line. Note: the asterisk in Cluster 1 refers to HIGm0211, the individual responsible for subdividing Unit C into C1 and C2. The individual that fell below the 0.50 criterion in Unit B1 was removed from the final analysis but is shown here for illustration. Cluster assignments here do not correspond to other figures.

Table S1. Directed research and opportunistic sightings off the main Hawaiian Islands from 2003 through 2007.