Site fidelity and association patterns of a rare species: Pygmy killer whales (*Feresa attenuata*) in the main Hawaiian Islands

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Abstract

Most of what we know about cetacean biology and ecology comes from studies of relatively common species. Despite their distribution throughout the tropics and sub-tropics, pygmy killer whales (*Feresa attenuata*) are rare throughout their range and are one of the most poorly-known species of odontocetes. During a 22-yr study of short-finned pilot whales (*Globicephala macrorhynchus*) off the island of Hawai'i, we opportunistically photo-identified pygmy killer whales whenever encountered. As part of a directed multi-species study throughout the main Hawaiian Islands from 2000 through 2007, we also photo-identified individuals and obtained information

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on habitat use and behavior. This species was extremely uncommon (representing only 1.2% of odontocete sightings in directed efforts). Given the low encounter rates, assessing trends of this population cannot be feasibly done with line-transect surveys. Despite their rarity, 80% of the distinctive individuals within groups documented off the island of Hawai'i were seen on multiple occasions, individuals were resighted over periods of up to 21 yr, and there was evidence of year-round use of the area. Association analyses indicate stable long-term associations in mixed-sex groups. High resighting rates indicate a small population of island-associated individuals that may be at risk from anthropogenic impacts.

Key words: pygmy killer whale, *Feresa attenuata*, rarity, social organization, site fidelity, Hawai'i.

Species may be considered rare if they are seldom seen, occupy a small range, or if they have few individuals. The risks that a species faces, and uncertainty regarding the status of a species, may be related to all three of these possibilities (Simberloff 1988). Seldom-seen species are not necessarily rare; in the case of cetaceans, species may be seen infrequently because of their habits (*e.g.,* open ocean species), their conspicuousness (*e.g.*, small species such as dwarf sperm whales, *Kogia sima*), their behavior (*e.g.*, long diving species such as beaked whales), or when they are truly rare (*i.e.*, due to low density). Because of the difficulty in studying rare species and the lack of resources available for studies of such populations, unless obvious threats have been identified, most of what we know about the population biology, behavior, and ecology of cetaceans comes from studies of common species.

Pygmy killer whales (*Feresa attenuata*) are rare throughout their range, and are one of the most poorly known species of odontocetes. Prior to the 1950s, this species was known only from two skeletal specimens (Yamada 1954). Since then pygmy killer whales have been documented from the tropics and subtropics world-wide, but most of what has been published in subsequent decades are records of occasional strandings or reports of one or a few sightings, and nowhere has the species been reliably found to an extent that directed studies have been undertaken (Donahue and Perryman 2002). Pygmy killer whales are relatively easy to detect from visual surveys and show no obvious avoidance of vessels or evidence of extended dive durations. Yet in all areas they have been documented, pygmy killer whales have one of the lowest densities of all cetaceans. In the eastern tropical Pacific, pygmy killer whales rank 12th in abundance out of 13 species of delphinids for which population estimates exist (Wade and Gerrodette 1993). In Hawaiian waters, Leatherwood *et al.* (1988) noted that pygmy killer whales "are seen with some regularity," yet they ranked 16th in abundance out of 18 species of odontocetes documented in a large-vessel survey throughout the Hawaiian Exclusive Economic Zone (Barlow 2006). Although they are known to be taken in several fisheries (Ross and Leatherwood 1994), incidental mortality has not been identified as a major issue, thus no strong management incentive for directed research has been identified, and unlike small populations of coastal cetaceans in temperate waters, the logistics of working with a species thought to be oceanic in its habits (Reeves *et al.* 2002) have limited research opportunities. Although their typical deep-water habits and the difficulty in discriminating between pygmy killer whales and both false killer whales (*Pseudorca crassidens*) and melon-headed whales (*Peponocephala electra*) in the field have also limited the collection of information on this species, their apparent natural rarity may be the single factor most limiting our knowledge of this species.

Studying such rare species is problematic, particularly when no sites have been identified where individuals can be reliably found. Since the mid-1980s, research has been undertaken on short-finned pilot whales (*Globicephala macrorhynchus*) off the west coast of the island of Hawai'i (see Shane and McSweeney 1990). In this area, the presence of deep water (>1,000 m) relatively close to shore, and the large lee caused by the mass of the island, results in good conditions for working both with pilot whales and with other deep-water species (*e.g.*, Baird *et al.* 2006, 2008*a*; McSweeney *et al.* 2007). The presence of pygmy killer whales in the area has long been known (Pryor *et al.* 1965). When encountered during research on pilot whales, this species and other infrequently encountered odontocetes were photo-identified. While sightings were rare, with the continuation of such efforts over more than 20 yr, information on pygmy killer whales and other infrequently encountered species has slowly accumulated to the point where we can examine aspects of their biology (see McSweeney *et al.* 2007, Baird *et al.* 2008*b*). Here, we combine the results of this long-term approach with the results of a directed multi-species odontocete research effort throughout the main Hawaiian Islands undertaken since 2000 (see Baird *et al.* 2008*a*) to assess site fidelity and association patterns of this poorly known species.

METHODS

Field Methods

Field work was undertaken periodically off the west coast of the island of Hawai'i from April 1985 through December 2007 (hereafter "west coast Hawai'i") using small and medium-sized vessels (5–15 m). Groups encountered were photographed, but information on search effort and sightings of all species was not consistently recorded. Directed odontocete surveys were undertaken around all of the main Hawaiian Islands on a periodic basis from February 2000 through August 2007. Methods for these surveys have been described by Baird *et al.* (2008*a*) so are only summarized here. Primary research vessels used ranged from 6 to 8.4 m in length and had two to six observers scanning 360° around the survey vessel. Survey routes attempted to cover as wide a survey area and as broad a range of depths as possible while generally remaining in areas with sea states of Beaufort 3 or less, and also minimizing overlap with previous survey track lines. Survey effort was quantified with vessel locations recorded with a GPS automatically every 5 min. All odontocetes observed were approached for species identification, estimation of group size and determination of sighting locations. Groups were defined as all individuals visible to the observers; in practice, there were no days with more than one sighting of a group of pygmy killer whales. In order to assess the spatial extent of groups, for encounters in 2005 through 2007, the "group envelope" was described by estimating the distance between the most widely spaced individuals in two dimensions (*e.g.*, for a group traveling north the distances between individuals spread both east-west and north-south were estimated). Primary observers were trained in distance estimation using laser range finders (Bushnell Yardage Pro 800s and 1000s, Bushnell Corporation, Overland Park, KS, U.S.A.) during each field effort. Information on associated species and general group behavior was recorded for all encounters from directed odontocete surveys. Factors used for assigning group behavior included directionality of movement (directional or non-directional), speed (motionless, slow (<4 km/h), medium (4–11 km/h)), the general positioning of individuals relative to conspecifics or other

species observed, and observations of interactions with potential prey species (*e.g.*, chasing fish or carrying prey in the mouth). Group behavior categories were: milling (non-directional, slow speed), resting (motionless, but diving), logging (motionless at surface), slow travel (directional, slow), travel (directional, medium), and social (body contact or frequent changes in orientation relative to other individuals, *e.g.*, following). Attempts were made to photograph all individual pygmy killer whales encountered. Pygmy killer whale photographs were also obtained from a small number of opportunistic encounters by other researchers or dolphin watching operators from various locations among the islands, between 2000 and 2007. Photographs from all sources prior to 2003 were typically color slides or black-and-white negatives, while those available from 2003 onwards were digital.

Individual Photo-Identification

Within encounters, photographs were sorted by individual using a variety of characteristics. Clearly distinct individuals were sorted using body scars and notches on or immediately adjacent to the dorsal fin. Other individuals were identified within encounters using subtle differences in dorsal fin shape, and/or relative size (*i.e.*, animals that are obviously small calves or neonates based on relative size in photographs where adult individuals were in the same photographic frame). For determining the number of neonates or small calves (that were unmarked) within a group, close associations with identifiable adults were used (*i.e.*, if two or more identifiable adults each had a neonate in close attendance, each neonate was counted separately).

For every individual within each encounter, the best photograph obtained was given a photo quality rating as: (1) poor, (2) fair, (3) good, or (4) excellent; based on the focus, size, and angle of the body relative to the photographic frame, and proportion of the body visible (Fig. 1). Each individual was assigned one of four "distinctiveness" categories: (1) not distinctive, (2) slightly distinctive, (3) distinctive, or (4) very distinctive. Those considered "not distinctive" included individuals with no notches on the dorsal fin or scratches on the body (typically neonates or small calves), as well as those with body scratches or extremely small notches that would usually allow for individual identification within an encounter with excellent quality photographs. These marks could usually be used to match individuals between encounters separated by days or weeks when calves or neonates were associated with the same adult in consecutive encounters, but not between encounters separated by months or years.

Slightly distinctive animals typically had one or two small notches on the trailing edge of the dorsal fin that allowed for individual identification within and between encounters, but required excellent quality photographs. Distinctive animals had multiple notches on the fin and could be identified among encounters with fair, good, or excellent quality photographs, while very distinctive animals had multiple large notches that would allow for matching individuals among encounters even with poor quality photographs. Matches between encounters were based on fin shape, and the number, size, shape, and relative positioning of dorsal fin notches. Matches between encounters separated by relatively short intervals (*e.g.,* up to several months) could also be confirmed using body scars, but most scars were observed to repigment within 6 mo to a year, with only a few scars visible over periods of 1–2 yr. All matches of individuals were agreed upon by at least two experienced matchers. Matches of some individuals were made where notch number, size, or

shape was different (*i.e.,* individuals with mark changes). These matches were based on fin shape and individuals having at least two or more marks in common (*i.e.,* with the same size, shape, and relative positioning on the fin). Within encounters, all photos were used to estimate the proportion of animals within groups that were "distinctive" or "very distinctive." Due to the small number of photos available from other islands, all photos were used to assess whether movements among islands may occur. For other analyses (*e.g.*, mark change rates, association analyses, intervals among resightings), only those individuals considered "distinctive" or "very distinctive" with photo quality ratings of good or excellent were used. Capture-recapture estimates of abundance will be presented elsewhere. To examine the likelihood of individuals within encounters having multiple records within our catalog, we calculated the percentage of distinctive and very distinctive individuals within each encounter that were seen on more than one occasion. In order to assess the likelihood of missing matches due to changes in marks, two types of mark change rates were estimated. Whether each acquisition of a new notch or change in notch shape occurred independently, or if multiple changes occurred in one event, is unknown, so we tallied the minimum number of mark change events that had occurred at successive sightings of individuals (*e.g.*, if an individual had two new notches the next time it was seen that was recorded as one mark change event). We also tallied the number of new notches or changes in notch shape at successive sightings of individuals. Minimum (using mark change events) and maximum (using all new notches/change in notch shape) mark change rates were estimated by dividing these numbers by the sum of all intervals from when individuals were first seen until they were last seen.

Association Analyses

For the purposes of interpreting association patterns in relation to sex, only individuals seen on multiple occasions over an extended period were considered. Individuals photographed with a neonate (based on fetal folds) or small calf (<1/2 body length) in close attendance were considered to be adult females. Individuals that appeared to be full adult size based on relative size to others in photos and without evidence of a small calf or neonate in close proximity at any point over their sighting history were considered adult males. The presence/absence of a ventral post-anal keel visible in underwater photographs, a potential indicator of sex for pygmy killer whales,[1] was also used to support sex determinations.

To illustrate associations among individuals, a social network diagram was produced with *Netdraw* 2.043 (Analytic Technologies, Needham, MA, U.S.A.). Association levels were assessed with *Socprog* 2.3[2] (Dalhousie University, Halifax, Nova Scotia, Canada), using a half-weight index of association, which is most appropriate when not all individuals in a group are identified (Cairns and Schwager 1987, Ginsberg and Young 1992). Calculations of mean and maximum association indices, and tests for preferred/avoided associations (following Bejder *et al.* 1998) included individuals seen on two or more occasions. Tests for preferred/avoided associations compared the real association indices against 20,000 randomly permuted variations, with all individuals seen within a year treated as possible associates. *P*-values were determined based on the proportion of the 20,000 permutations that had higher SDs

[1] Baird et al. unpublished data.
[2] Available from http://myweb.dal.ca/~hwhitehe/social.htm.

of the association indices than the SD of the real association indices, thus P-values that were large ($P > 0.95$) indicated a significant difference. *Socprog* was used to produce a sociogram showing associations among individuals seen on two or more occasions. Temporal trends in association patterns were examined by calculating standardized lagged association rates (Whitehead 1995). To illustrate the stability of associations, individuals with seven or more identifications with good or excellent photo quality (those seen over a long enough period to identify sex) were tabulated by encounter. As the likelihood of misidentifying individuals due to photo quality is lower for those seen on multiple occasions (due to the ability to document mark changes), intervening sightings of these individuals with fair photo quality were also tabulated. While modeling approaches used to help describe and interpret social structure and movement patterns are available in *Socprog*, they were not employed here as our sample size is insufficient to support such analyses (Whitehead 2008).

Other Analyses

Because we could not quantify seasonality of effort for the west coast Hawai'i efforts, to assess whether individuals used the study area year-round we examined the seasonal distribution of sightings of individuals seen on five or more occasions. Sighting months were classified as oceanographic season based on Flament (1996): winter (February–April), spring (May–July), summer (August–October), and fall (November–January).

Depths of sightings and 5-min effort locations from directed odontocete surveys were determined by overlaying point location data on a bathymetric raster surface in *ArcGIS* 9.1 (ESRI, Redlands, CA, U.S.A.). Underlying depth values (in meters) were transferred to point locations using the "intersect point tool" in Hawth's analysis tools (Beyer 2004). We used a gridded 50 m × 50 m multibeam synthesis bathymetry model from the Hawaii Mapping Research Group.[3] The model had areas of no data, so the grid was overlaid on 3-arc second (90 m × 90 m) U.S. Coastal Relief Model bathymetry from the National Geophysical Data Center[4] to provide 90-m resolution data where 50-m resolution data were absent. Sighting rates in relation to effort by depth were calculated using 500-m depth bins (*e.g.*, 1–500, 501–1,000 m, *etc.*).

RESULTS

Directed odontocete surveys from 2000 through 2007 covered 40,709 km of trackline on 386 d, with 2,764 h on effort. The majority of the effort (56.7%, based on hours) was off the island of Hawai'i, where effort was spread fairly equally out to approximately 2,500 m depth (accounting for 76.8% of total effort off that island), with the remaining effort to approximately 5,000 m depth. Only 16.2% of the effort off the island of Hawai'i was in depths of less than 500 m, while off other islands effort was primarily concentrated (70.0%) in waters less than 500-m deep.

During these surveys, there were 899 sightings of 17 species of odontocetes, of which 11 sightings (1.2%) were pygmy killer whales (the 14th most frequently encountered species of odontocete). On average there was one encounter with this species for every 35 d (251 h) of effort. The only species documented less often

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[3] Available from http://www.soest.hawaii.edu/HMRG/Multibeam/index.php.
[4] Available from http://www.ngdc.noaa.gov/mgg/coastal/.

were pygmy sperm whales, *K. breviceps* (three sightings), Risso's dolphins, *Grampus griseus* (two sightings), killer whales, *Orcinus orca* (one sighting), and Longman's beaked whales, *Indopacetus pacificus* (one sighting). One pygmy killer whale sighting was in response to a radio report, as were 29 sightings of other species. Excluding sightings cued by radio reports, pygmy killer whales represented just 1.1% of all odontocete sightings. Ten of the 11 sightings were off the island of Hawai'i, with only a single sighting elsewhere (off Ni'ihau). Encounter durations ranged from 30 min to 2 h 27 min (median = 59 min). Group sizes ranged from four to an estimated 33 individuals (median = 13). Sightings were in depths ranging from 113 to 2,862 m (median = 1,218 m), from 2.8 to 16.0 km offshore (median = 6.3 km). Although 39.5% of the effort was in depths of 500 m or less, only one sighting was in less than 500 m depth. Sighting rates in less than 500 m (0.093 sightings/100 h) were approximately 15% of those in waters greater than 500 m (0.61 sightings/100 h). There was insufficient effort in depths greater than 2,500 m to assess whether sighting rates in waters deeper than 2,500 m declined.

Pygmy killer whales were recorded associating with three other species of cetaceans in four encounters: false killer whales (one encounter), short-finned pilot whales (one encounter), bottlenose dolphins (one encounter), and both short-finned pilot whales and bottlenose dolphins (one encounter). The area covered by groups in 2005 through 2007 ($n = 7$) ranged from 20 m × 20 m to 600 m × 1,200 m (median = 20 m × 80 m). Initial behavior recorded during directed efforts included milling (five encounters), resting (one encounter), logging (one encounter), slow travel (two encounters), travel (one encounter), and socializing with pilot whales (one encounter). There were no observations of feeding or chasing prey either in encounters from directed efforts ($n = 11$) or from west coast Hawai'i efforts ($n = 61$).

A total of 3,431 photographs were obtained from the 11 encounters from directed odontocete surveys. The number of individual identifications per group of all photo qualities and distinctiveness ratings ranged from 4 to 25 (median = 11.5), while the number of identifications per group of distinctive and very distinctive individuals with good or excellent quality photos ranged from 3 to 19 (median = 6.5). From west coast Hawai'i field efforts 3,157 photographs were available from 61 different encounters between 1985 and 2007. The number of individual identifications per group of all photo qualities and distinctiveness ratings ranged from 1 to 31 (median = 7), while the number of identifications per group of distinctive and very distinctive individuals with good or excellent quality photos ranged from 0 to 10 (median = 3). An additional 300 photographs were available from seven different opportunistic encounters, one from Lana'i (in 2000), two from O'ahu (in 2007), and four from Hawai'i (from 2006 and 2007). From the opportunistic encounters, the number of individual identifications per group of all photo qualities and distinctiveness ratings ranged from 1 to 8 (median = 4), while the number of identifications per group of distinctive and very distinctive individuals with good or excellent quality photos ranged from 0 to 1 (median = 0). The lower number of photographs, individual identifications, and identifications of distinctive/very distinctive individuals with good or excellent photo qualities available from west coast Hawai'i field efforts and opportunistic encounters suggests that not all individuals within these groups were photo-identified, thus negatively biasing association analyses (see below).

The proportion of individuals within groups that were considered "distinctive" or "very distinctive" ranged from 25% to 100% (median = 73.2%, mean = 73.7%, SD = 22.8%, $n = 79$). Considering only distinctive and very distinctive individuals with good or excellent quality photographs, we obtained 264 individual

Table 1. Summary of encounters and identifications by year for pygmy killer whales off the island of Hawai'i.

Year	# Encounters	# IDs distinct/very distinct with good or excellent photos	# Individuals	# Seen > once
1985	1	0	0	0
1986	4	10	9	3
1987	1	0	0	0
1988	4	3	3	3
1989	2	4	4	1
1990	2	1	1	0
1991	7	13	7	7
1992	2	1	1	1
1993	2	4	4	3
1994	7	21	17	11
1995	7	37	31	16
1996	2	6	5	5
1997	6	23	11	7
1998	1	3	3	3
1999	1	4	4	3
2000	2	6	6	5
2002	2	5	5	2
2003	1	8	8	8
2004	2	9	7	7
2005	3	8	8	5
2006	9	58	50	23
2007	7	26	17	16
Total	76	250		

identifications from 63 encounters (250 identifications from 59 encounters off Hawai'i, 1 off Lana'i, 1 off O'ahu, and 12 from one encounter off Ni'ihau), representing 126 individuals. Distinctive individuals ($n = 52$) had from 1 to 13 notches on the dorsal fin (median = 3), while very distinctive individuals ($n = 74$) had from 1 to 16 notches on the dorsal fin (median = 7). No matches of individuals among islands were found.

The 250 individual identifications off Hawai'i represented 112 distinctive/very distinctive individuals (Table 1). Of the 112 individuals, 103 (91.96%) were linked by association in a single association network (Fig. 2). The nine remaining individuals were only documented on a single occasion each (in five different groups: two groups of three and three singletons). Thus, the likelihood of documenting links of these nine individuals to the larger social network was small.

Off the island of Hawai'i, within groups the percentage of distinctive and very distinctive individuals seen on more than one occasion ranged from 0% to 100% (median = 100%; mean = 80%, SD = 33%, $n = 59$ groups). The high proportion of individuals within groups seen on more than one occasion reflected a large number of resightings of the 40 individuals (of 112, 35.7%) seen on two or more occasions. For these individuals, there were 88 between-year resightings and 50 within-year resightings. Resighted individuals were seen a maximum of 21 times (median = 2) in up to 12 different years (median = 2). Resighting intervals ranged from 1 day to 12.73 yr (median = 305 d). The interval from when an individual was first seen
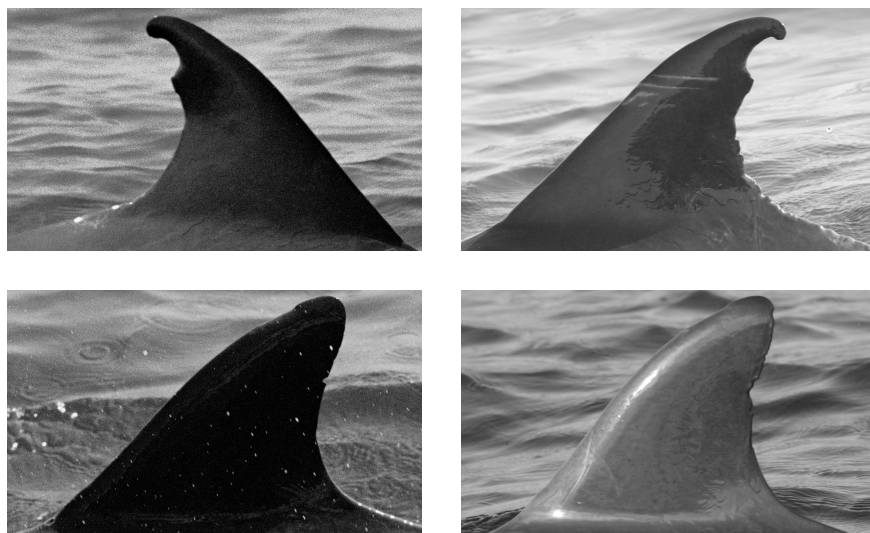
Figure 1. Two long-term matches of pygmy killer whales off the island of Hawai'i illustrating photo quality, distinctiveness ratings, and mark changes. Top: A very distinctive individual (HIFa001) photographed 31 January 1986 (left photo quality "good") and 21 August 2007 (right photo quality "excellent"). HIFa001 was photographed 19 times in the intervening 20 yr, allowing for documentation of nine mark changes (new notches or changes in notch shapes). Bottom: A distinctive individual (HIFa109) photographed 5 October 1995 (left photo quality "good") and 4 December 2006 (right photo quality "excellent"). HIFa109 was photographed eight times in the intervening years, allowing for documentation of eight mark changes.

until when it was last seen ranged from 26 d to 21.55 yr (median = 6.45 yr). Mark changes were noted for 22 of the 40 resighted individuals. A total of 71 mark changes were documented in a minimum of 45 mark change events, with the addition of 50 new notches, 16 changes in notch shape, and five notch losses (due to two notches joining). Using the sum of all intervals from when an individual was first seen until when it was last seen (276.6 yr), marks were estimated to change (either acquisition of new notches or change in notch shape) at rates from once every 3.9 yr (based on 71 mark changes) to once every 6.1 yr (based on 45 mark change events). Given the long intervals between resightings and the possibility that subsequent mark changes could obscure earlier changes, these are likely underestimates of the true rate of mark changes.

Mean association values for the 40 individuals seen more than once was 0.08 (SD = 0.05), while the mean of the maximum association levels was 0.72 (SD = 0.25). Association values were known to be negatively biased for two reasons: (1) the number of good and excellent quality identifications of distinctive and very distinctive individuals was less than half of the estimated group size from directed encounters, despite estimates of the proportion of distinctive individuals with groups equal to approximately 74% and (2) the number of distinctive individual identifications with good/excellent photos per encounter from west coast Hawai'i efforts was less than half that of directed encounters. Tests for preferred/avoided associations were significant ($P = 1.000$), indicating that individuals associated preferentially
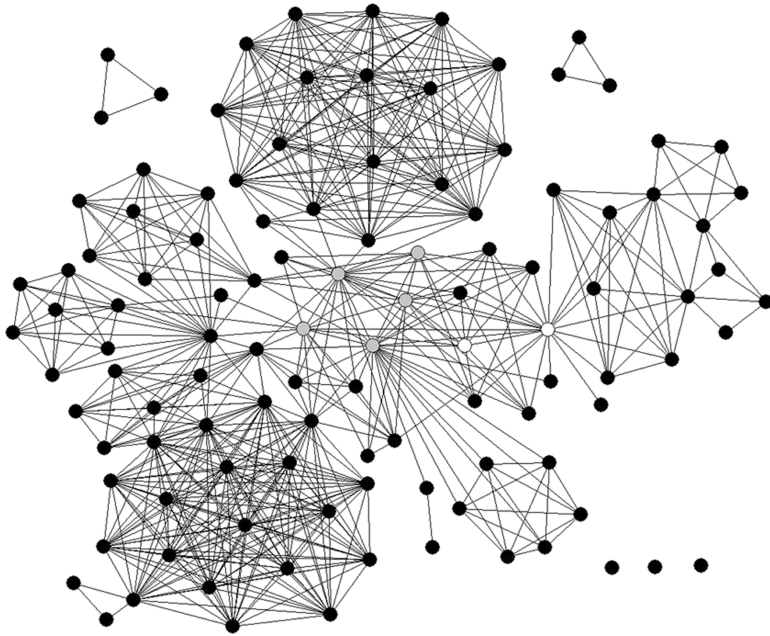
Figure 2. A social network diagram showing associations among individual pygmy killer whales documented off the island of Hawai'i. All individuals considered distinctive or very distinctive with good or excellent quality photographs are included ($n = 112$). The majority (103, 92%) were linked by association in a single social network. To illustrate group affiliation, individuals listed in Table 2 are indicated in white (HIFa005, HIFa006) or in gray (others).

with certain other individuals, rather than at random with those that were available within a period of a year (Fig. 3). Standardized lagged association rates (Fig. 4) indicated that associations were stable over periods of many years. To assess association patterns by sex, we considered seven individuals, seen from 7 to 23 times, in 7–12 yr, spanning 11–19 yr (Table 2). Given their size relative to other individuals when first photographed, all of these individuals were likely adults when first seen. Three of these individuals were seen with neonates or small calves, while four were never seen with neonates or calves in attendance. Underwater photos showing the presence/absence of a ventral post-anal keel were available for six of the seven individuals (two of the three individuals with neonates/small calves and all four seen without). Both of the individuals with neonates/small calves lacked a post-anal keel, while all four individuals seen without had pronounced post-anal keels. As such, we considered the individuals with neonates to be adult females and the others to be adult males. Sighting histories of these individuals (Table 2) indicate that associations between individuals of the same sex as well as opposite sex associations may be stable for periods of at least 15 (same sex) and 16 yr (opposite sex).

The seasonal distribution of resightings was examined for 11 individuals seen on five or more occasions (median = 7, range = 5–21). These individuals were seen in two to nine different months (median = 6) in two to four different seasons (median = 3). Five of the 11 individuals were seen in all four oceanographic seasons. There was
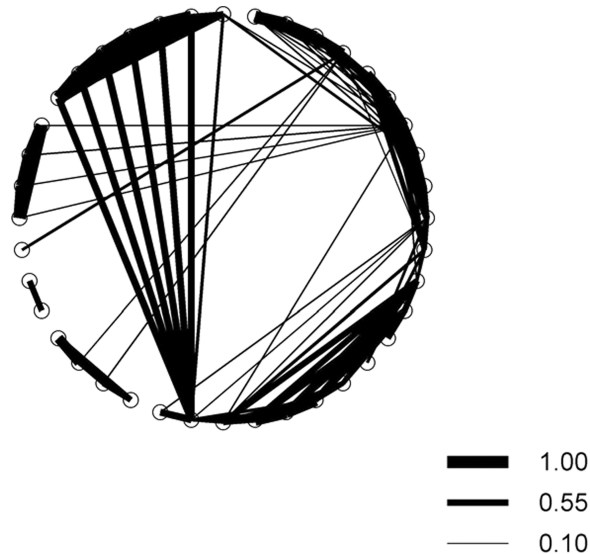
Figure 3. A sociogram showing strength of associations (represented by the thickness of the connecting lines) among distinctive and very distinctive pygmy killer whales (represented as points on the outside of the circle) seen two or more times. Individual ID labels are excluded due to space limitations. Association index values determined using a half-weight index of association.

a strong positive relationship between the number of records and the number of months in which an individual was recorded (regression, $r^2 = 0.50$, $P = 0.014$).

DISCUSSION

Pygmy killer whales are one of the most poorly known species of odontocetes, with virtually nothing previously published on habitat use, seasonality of occurrence, site fidelity, or social organization of this species. In our study, despite extensive search effort in our directed odontocete surveys from 2000 through 2007, with 40,709 km of trackline in depths out to almost 5,000 m, this species was only encountered on 11 occasions, representing just 1.2% of all sightings of odontocetes. Sighting rates of pygmy killer whales were about six times higher in depths greater than 500 m than in depths less than 500 m, although we had insufficient effort (and sightings) in depths greater than 2,500 m to assess whether density was lower in extremely deep water. While there was only one sighting from directed survey efforts from islands other than Hawai'i, the majority (70%) of the effort off other islands was in depths less than 500 m, perhaps explaining, at least in part, the relative lack of sightings in other areas.

Despite their rarity, we provide the first information on site fidelity and social organization of this species. Over the 22-yr period of this study, resighting rates of individual pygmy killer whales off the island of Hawai'i were high, with a mean of 80% of distinctive or very distinctive individuals within groups being documented on more than one occasion. Although only about 36% of the total distinctive/very
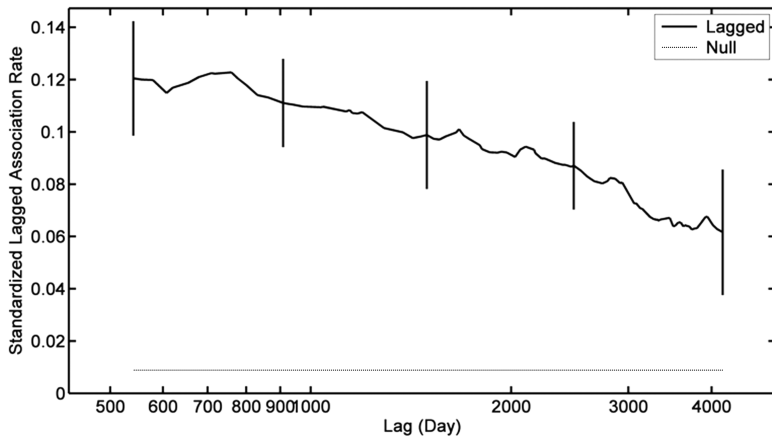
Figure 4. The standardized lagged association rate for individual pygmy killer whales. The standardized lagged association rate shows the probability that, supposing individual Y is an associate of individual X, if a randomly chosen associate of individual X is identified after a time lag, then it will be individual Y. Jackknife error bars are shown. The standardized null association rate is also shown, which indicates the value if individuals associated at random. A moving average of 4,000 was used.

distinctive individuals were documented on more than one occasion, there are several reasons why these resighting rates are negatively biased. With the long duration of our study (22 yr), there were likely a number of births and deaths in the population, and thus not all individuals were available for resighting over the duration of the study. Although we restricted our analyses to distinctive and very distinctive individuals to minimize the likelihood of missing matches, the relatively infrequent encounters and low numbers of individual identifications over the duration of the study (Table 1), combined with estimated mark changes occurring every 3.9–6.1 yr, suggests that some matches were missed due to mark changes. While we were not able to quantify the seasonal distribution of effort, the fact that individuals seen greater than five times were seen in almost as many months (median = 6) as they were encountered (median = 7), suggests that these individuals use the area year-round.

Such high resighting rates indicate there is a small population of resident pygmy killer whales off the island of Hawai'i. Despite the small number of encounters in the early years of the west coast Hawai'i efforts (Table 1), one individual was resighted over a 21-yr period (Fig. 1), suggesting long-term fidelity to the island. Virtually all distinctive individuals (92%) documented off the island of Hawai'i over the 22-yr study were linked by association into a single social network (Fig. 2), indicating that they represent a single island-associated population, rather than the existence of both an island-associated and a separate pelagic population. While no movements of individuals among islands were documented, the number of individual identifications available from other islands was extremely small (14 distinctive and very distinctive individuals), thus the likelihood of documenting movements among islands was low. Increased search effort in deep (>500 m) waters off other islands to photo-identify individuals, or satellite tagging of individuals off the island of Hawai'i to examine movements, is required to understand better the movements of individuals in this population.

Table 2. Partial sighting histories for individuals seen on seven or more occasions (for which sex is known). All individuals were thought to be adults when first documented, based on relative body size in photographs. Identifications based on "fair" photo-qualities are included.

Date	HIFa001[a]	HIFa002	HIFa003	HIFa109	HIFa012	HIFa005	HIFa006
2-Mar-88	x			x			
29-Oct-88	x			x			
20-Jun-91	x		x	x			
31-Oct-91	x		x				
13-Nov-91	x		x	x			
5-Dec-94	x	x	x	x			
6-Dec-94	x		x	x			
5-Apr-95	x	x	x	x		x	x
1-Nov-96	x	x	x	x	x		
23-Sep-97	x	x	x		x	x	x
17-Oct-97	x	x	x	x	x	x	x
27-Nov-97	x	x	x		x		
9-Dec-97	x	x	x	x	x		
19-Dec-97	x	x	x	x	x		
10-Apr-98	x	x	x	x	x		
11-Oct-03	x	x	x		x	x	x
10-Aug-04	x	x	x	x	x		
16-Dec-04	x	x	x		x	x	x
17-Sep-05	x	x	x	x	x		
25-Nov-06	x	x	x	x	x		
4-Dec-06	x	x	x	x	x		
13-Aug-07						x	x
21-Aug-07	x	x	x		x		
Sex	Male	Male	Female	Male	Male	Female	Female

[a]Individual HIFa001 first documented on 31 January 1986.

Pygmy killer whales are generally considered an oceanic species (Reeves *et al.* 2002). What might explain the high degree of site fidelity for this population? It is difficult to assess pygmy killer whale use of the area in relation to potential prey, as nothing is known of the diet of this species in Hawaiian waters. The lack of observations of feeding behavior from 72 different encounters suggest that pygmy killer whales in Hawai'i feed either at great depth or primarily at night, possibly on prey that come closer to the surface associated with the deep-scattering layer at night. Little is known of the diet of this species anywhere, although they have been reported feeding on both cephalopods and fish (Sekiguchi *et al.* 1992, Zerbini and Santos 1997). High levels of site fidelity and evidence of island-associated populations around the main Hawaiian Islands have been documented for a number of cetacean species with very diverse dietary preferences. These include Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales that likely feed primarily on bathypelagic cephalopods (Baird *et al.* 2006, McSweeney *et al.* 2007), false killer whales feeding primarily on large pelagic fish (Chivers *et al.* 2007, Baird *et al.* 2008*b*), rough-toothed dolphins (*Steno bredanensis*) feeding at least in part on a variety of epipelagic fish and squid (Baird *et al.* 2008*a*), and spinner dolphins (*Stenella longirostris*) feeding on mesopelagic fish and squid (Norris *et al.* 1994,

Benoit-Bird and Au 2003). In all cases, and presumably also for pygmy killer whales, an increase in either prey abundance or the spatial and temporal predictability of prey associated with the islands, are probably the factors that lead to high levels of site fidelity and the evolution of island-associated populations.

The relatively low number of identifications of distinctive/very distinctive individuals per group from west coast Hawai'i efforts in comparison to directed odontocete surveys likely negatively biases our association analyses. Despite such biases, maximum association rates were high (mean = 0.72), analyses of preferred/avoided associations indicated that individuals associate preferentially with certain others (Fig. 3), and standardized lagged association rates imply such associations may be stable over periods of years (Fig. 4, see also Table 2). Thus, the social organization of this species appears more similar to the stable groups documented for killer whales (Bigg *et al.* 1990, Baird and Whitehead 2000), pilot whales (Ottensmeyer and Whitehead 2003), or false killer whales (Baird *et al.* 2008*b*), than to smaller delphinids such as bottlenose dolphins, *Tursiops* sp. (Connor *et al.* 2000).

That there is a small resident population of pygmy killer whales off the island of Hawai'i has several implications for management. Sighting rates for this population are so small that the use of traditional line-transect surveys to estimate abundance and examine population trends has limited utility. Variability associated with abundance estimates from line-transect surveys is inversely related to encounter rates, and for low density populations like this the encounter rates will be so low that there will be virtually no ability to detect even a catastrophic decline in population size (see Taylor *et al.* 2007). The most likely anthropogenic threats in Hawaiian waters are interactions with fisheries and impacts from high intensity military sonars associated with naval exercises. Although impacts from sonars have not been documented for this species, the Hawaiian Islands are home to a major naval base and the site of regular naval exercises (Anonymous 2006), and given their rarity and offshore distribution, the probability of documenting impacts are low, even if they were to occur. Although pygmy killer whales have not been reported killed in the Hawai'i-based long-line fishery for tuna and swordfish, or interacting with nearshore fisheries (Nitta and Henderson 1993), one stranded animal from O'ahu did have hook and line marks in the mouth (Schofield 2007), suggesting that pygmy killer whales do interact with local fisheries. Their high level of site fidelity and apparently small population size suggest this population could be easily impacted by human activities.

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