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Short-finned pilot whales (*Globicephala macrorhynchus*) of the Mariana Archipelago: Individual affiliations, movements, and spatial use

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Abstract

Little is known about short-finned pilot whales (*Globicephala macrorhynchus*) in the western North Pacific outside of Japanese coastal waters. To expand understanding of short-finned pilot whale ecology in the region, we conducted small-boat surveys in 2010–2016 within the Mariana Archipelago to investigate individual associations, movements, spatial use, and dive behavior of short-finned pilot whales. We collected genetic, photo-identification, and satellite-tag data and identified 191 distinctive individuals. A preliminary social network diagram of photo-cataloged individuals revealed a main cluster that comprised 82% of individuals, representing all five mitochondrial DNA haplotypes identified within the population. Kernel density estimates for tagged short-finned pilot whales (n = 11) during summer were used to identify areas with the highest probability of use (10% probability density contour), core area (50%) and home range (95%). The area with highest

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probability of use by short-finned pilot whales was off the northwest side of Guam. Satellite tag data also suggest that some individuals are island-associated year-round. Data from five location-dive tags demonstrated that the short-finned pilot whales dove more often to intermediate depths at twilight and night, suggesting they may target prey that forage on the deep scattering layer as it migrates to and from the surface.

Key words: *Globicephala macrorhynchus*, kernel density estimation, Mariana Archipelago, photo-identification, satellite tagging, short-finned pilot whales, social network diagram, biopsy sampling, genetic analysis.

Short-finned pilot whales (*Globicephala macrorhynchus*) are distributed throughout tropical to warm-temperate oceans worldwide (Olson 2018). In the western North Pacific, they are best known off Japan where two genetically and morphologically distinct types occur (Kasuya *et al.* 1988, Kage *et al.* 1999 in Oremus *et al.* 2009, Oremus *et al.* 2009). Off Japan, the two types have distinct geographic distributions, which led to the designation of their names ("northern" and "southern" form) by Kasuya *et al.* (1988). Recent analysis of mitochondrial DNA (mtDNA) sequences from the Pacific and Indian Oceans indicates that these two short-finned pilot whale forms have distinct distributions throughout the Pacific Ocean basin that are not strictly divided by north and south (Van Cise *et al.* 2016). Because the geographic identifiers are inconsistent at a broader scale, Van Cise *et al.* (2016) used the terms originally assigned by Yamase (1760 in Kasuya *et al.* 1988) for two kinds of short-finned pilot whales found off Taiji, "Naisa" (for the southern form) and "Shiho" (for the northern form) to distinguish between the two. In addition to the known Naisa and Shiho form haplotypes, a number of other haplotypes were identified from live short-finned pilot whales, and have been classified as "Naisa type" or "Shiho type" based on their phylogenetic relationships, in the absence of morphometric data (Morin *et al.* 2015, Van Cise *et al.* 2016). Analysis of complete short-finned pilot whale mitogenomes from the Pacific and Indian Oceans revealed a third genetic clade, which recently diverged from the Naisa form short-finned pilot whale (Morin *et al.* 2015). This clade could represent a third form, as has been speculated by Kasuya *et al.* (1988) and Oremus *et al.* (2009), or could be part of the Naisa form short-finned pilot whale (Van Cise *et al.* 2016).

Within the central North Pacific, Naisa and Naisa type short-finned pilot whales occur in the Hawaiian Islands where extensive research has been conducted on their population structure, social structure, and habitat use (Baird *et al.* 2013*b*, Abecassis *et al.* 2015, Mahaffy *et al.* 2015, Van Cise *et al.* 2016). Van Cise *et al.* (2016) found that short-finned pilot whales in the Hawaiian Archipelago are genetically distinct from other strata within the Pacific and globally, indicating very restricted female-mediated gene flow. Research on the site fidelity and association patterns of short-finned pilot whales off Hawai'i Island revealed a

community structure made up of multiple populations with different patterns of site fidelity and residency (Mahaffy *et al.* 2015). Most of the photo-identified individuals were linked by association within a single social network and had strong long-term and short-term preferential associations. An integrative study using satellite tag, oceanographic, and active acoustic data to characterize a short-finned pilot whale foraging hotspot off Hawai'i Island demonstrated that the best predictors of short-finned pilot whale density were bathymetry, temperature at depth, and a high density of midwater micronekton in the deep scattering layer (DSL) (Abecassis *et al.* 2015). The highest densities of short-finned pilot whales were located between the 1,000 m and 2,500 m isobaths, and both the short-finned pilot whales and the DSL shifted into shallower nearshore waters during the night.

Both the Naisa type and the third genetic clade have been identified in the Mariana Archipelago located in the western North Pacific, and two mitochondrial haplotypes appear to be unique to the region (Martien *et al.* 2014*b*), indicating that the Mariana Archipelago is an area of unusually high diversity. Additional information on short-finned pilot whales in the Mariana Archipelago is limited to stranding records (Kami and Hosmer 1982, Donaldson 1983), anecdotal sighting reports (Birkeland 1977; Eldredge 1991, 2003; Wiles 2005), and a small number of encounters during a 2007 line-transect shipboard visual survey primarily within offshore waters of the Mariana Archipelago (Fulling *et al.* 2011). The purpose of this study is to investigate individual and group associations, movements, spatial use, and dive behavior of short-finned pilot whales encountered in the waters around the southernmost islands of the Mariana Archipelago using encounter location data, individual photo-identification, additional genetic data, and satellite telemetry in order to gain insight into the ecology of short-finned pilot whales in this region. Knowledge of regional differences or similarities in short-finned pilot whale social structure, habitat associations, and diel diving behavior may provide a greater understanding of the ecology of short-finned pilot whales within the North Pacific and worldwide.

Methods

Study Area and Surveys

The Mariana Archipelago is located in the western North Pacific Ocean and consists of 15 islands that stretch in a north-south arc with a distance of approximately 890 km between the northernmost and southernmost islands. The southern islands, from Farallón de Medinilla (FDM) south to Guam, are geologically older than the islands to the north, some of which are still volcanically active. The region is most notably characterized by the Mariana Trench where the deepest part of the world's oceans is located, which parallels the Mariana Archipelago about 148 km to the east, arcing westward to within 120 km south of Guam.

The Pacific Islands Fisheries Science Center's (PIFSC) Cetacean Research Program (CRP) conducted nonsystematic visual surveys for cetaceans in the waters off the southernmost islands of the Mariana Archipelago (Fig. 1) aboard small vessels (5.8–12.2 m) during 2010–2016 in partnership with the U.S. Navy. The survey vessels traveled at a speed of 15–26 km/h, depending on the size of the vessel and sea conditions. A handheld Global Positioning System (GPS) automatically recorded the vessel's track at 1 min intervals. Four to six observers scanned for marine mammals with unaided eye or occasional use of binoculars, collectively searching 360° around the vessel.

The survey team approached short-finned pilot whale groups for group size estimates, photo-identification, and biopsy sampling. Individuals were considered part of an encounter group if they were within a kilometer of other individuals. Observer consensus on best, high, and low group size estimates and best estimates of young-of-the-year (YOY) and neonates[2] were made during each encounter. The team used digital SLR cameras with zoom lenses to collect photos and a Barnett RX-150 crossbow with Ceta-Dart bolts and disinfected stainless steel biopsy tips (25 mm length × 8 mm diameter) to collect biopsy samples.

In addition to our PIFSC survey effort, the U.S. Navy contracted two separate research groups to conduct marine mammal surveys within the Mariana Archipelago. Geo-Marine conducted line-transect shipboard surveys (the Mariana Islands Seabird, Turtle, and Cetacean Surveys; MISTCS) within the waters around Guam and the Commonwealth of the Northern Mariana Islands (CNMI) extending from 10°N to 18°N during January–April 2007. This effort included the collection of photo-identification images (Fulling *et al.* 2011). HDR Environmental, Operations and Construction, Inc. (HDR) conducted small-boat cetacean surveys in the waters surrounding Guam and Saipan during 17 February–3 March 2011 and 15–29 March 2012, which included the collection of photo-identification images (HDR 2011, 2012) and in cooperation with PIFSC, biopsy samples. The U.S. Navy contributed photos resulting from these surveys to the present analyses.

In 2013 we began satellite tagging short-finned pilot whales to investigate movements of individuals and deployed two types of satellite tags using a Dan Inject air rifle with deployment arrows designed by Wildlife Computers. One type of tag was a location-only Wildlife Computers SPOT-240C tag. The other tag type was the Wildlife Computers SPLASH10-292B, which provided depth, as well as location. We deployed both tag types in the Low Impact Minimally Percutaneous Electronic Transmitter (LIMPET) configuration (Andrews *et al.* 2008). We programmed both tag types to transmit continuously for the first 24 h after deployment, followed by a duty cycle to conserve battery life. The SPLASH tags also collected summary statistics (start time, maximum dive depth, and dive duration) for dives equal to 30 m depth or greater and durations of 30 s or greater.

[2] Neonates were identified by visible fetal folds and YOYs were identified as individuals less than half the size of an associated adult.

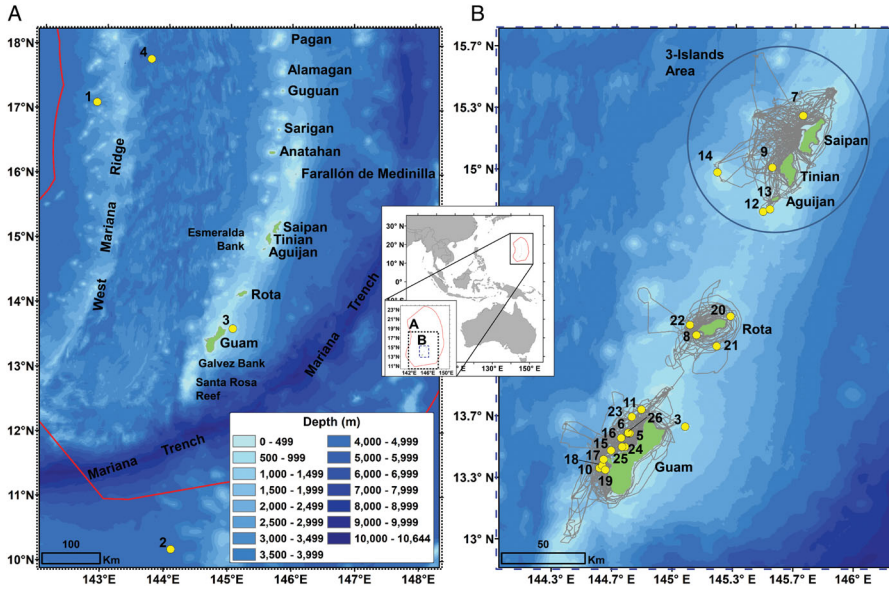

Figure 1. Inset: Location of the Guam and Commonwealth of the Northern Mariana Islands (CNMI) exclusive economic zone (EEZ) (red outline) in the western Pacific Ocean; expanded to show the boundaries of panels A and B. Panel A: Southern portion of the Guam and CNMI EEZ (red line: boundary); including the islands from Guam to Pagan. Short-finned pilot whale on-effort encounter locations (yellow circles) during a 2007 Navy shipboard survey (Mariana Islands Sea Turtle and Cetacean Survey; MISTCS) contributed by the U.S. Navy. Panel B: Survey location within the southern portion of the Mariana Archipelago. Pacific Islands Fisheries Science Center's (PIFSC) survey tracklines (gray lines; 196 d in 2010–2016) and short-finned pilot whale encounter locations of PIFSC and the U.S. Navy contributions (3: MISTCS; 5, 10: HDR). Numbers correspond to encounter location IDs listed in Table 1. Location IDs 12, 13, and 14 were those of the single encounter groups.

Data Analyses

Survey Effort and Short-finned Pilot Whale Encounters

We processed the vessel GPS tracks and short-finned pilot whale encounter locations in ArcCatalog 10.1 (Esri, Redlands, CA), projected in the WGS 1984 UTM Zone 55N coordinate system and then overlaid them onto bathymetric rasters within ArcMap 10.1. For visualization and analysis of spatial data, we used bathymetric data sets of varying resolutions, which included high-resolution, multibeam, color-shaded bathymetry for nearshore waters from the Pacific Islands Benthic Habitat Mapping Center.[3] For offshore areas not covered by the other data sets, we used a

[3] School of Ocean and Earth Science and Technology, University of Hawai'i at Manoa. http://www.soest.hawaii.edu/pibhmc/pibhmc_cnmi.htm.

Global Multi-Resolution Topography (GMRT)[4] custom bathymetric grid encompassing the U.S. Exclusive Economic Zones (EEZ) of CNMI and Guam. Within ArcMap, we extracted depths of GPS track points and encounter locations from the highest resolution data set available. We summarized survey effort by depth in bins of 100m increments. We then determined distance from the closest shoreline for each encounter location.

Photo-Identification

We created a photo-identification catalog of individuals by using marks along the leading and trailing edges of the dorsal fins as the primary identifiers and marks or scars on the body, dorsal fin surface, and peduncle as secondary identifiers (Alves *et al.* 2013*b*). Matching was conducted by two to three experienced analysts and all matches were checked for false-positives and false-negatives. A senior photo analyst rated each individual fin in each photo for quality using numeric scores within four categories (focus/clarity, contrast/lighting, angle, extent visible) and assigned an overall quality rating based on the combined scores (Q-1 = high, Q-2 = moderate, Q-3 = poor). Two photo analysts assigned distinctiveness ratings to each individual based on the number, size, and shape of the features located on the leading and trailing edges of the dorsal fin (D-1 = high, D-2 = moderate, D-3 = low, D-4 = clean fin and no marks directly behind the dorsal fin). If there was a disagreement between analysts on the distinctiveness rating, a third analyst was consulted. The catalog included only those fins with a distinctiveness of D-1 or D-2 and a quality rating of Q-1 or Q-2. We retained recaptures of cataloged individuals with lower quality photos for individual sighting histories. Field-based estimates of group size were updated if the number of cataloged individuals was greater than the field estimate.

We examined the potential for social structure within Mariana Archipelago short-finned pilot whales through creation of a social network diagram using SOCPROG 2.5 (Whitehead 2009) and Netdraw 2.146 (Borgatti 2002). All occurrences of cataloged individuals were included, with individuals considered associated if they were present within the same encounter.

Genetics

Skin and blubber biopsy samples were archived in the National Marine Mammal and Sea Turtle Research (MMASTR) Collection at the Southwest Fisheries Science Center (SWFSC), and were either stored at −80°C, or fixed in either a salt-saturated 20% DMSO solution or 100% ethanol and stored in a −20°C freezer. Geneticists from SWFSC extracted DNA from the samples using a sodium chloride precipitation protocol (Miller *et al.* 1988) or Qiagen DNeasy Blood and Tissue Kit (#69506, Qiagen, Germantown, MD). They amplified and sequenced the

[4] Ryan *et al.* 2009; Marine Geoscience Data System http://www.marine-geo.org/portals/gmrt.

hypervariable mtDNA control region in two parts of approximately 420 base pairs (bp) and 560 bp, with approximately 20 bp of overlap between the two sequences. Martien *et al.* (2014) previously described the primers, PCR, and sequencing methods. Using Geneious (version 6.1.5, Biomatters Ltd, Auckland, New Zealand), the geneticists assembled the resulting combined sequence of 962 bp. New sequences have been submitted to the NCBI GenBank (accession numbers KM624042, KM624062, KM624044, MH425574, and MH425575).

In order to align the new sequences, geneticists used a MAFFT alignment with default parameters (Scoring Matrix: 200PAM/k=2, Gap open penalty: 1.53, Offset value: 0.123) in the Geneious software package (Katoh and Kuma 2002). Once the alignment was completed, they reexamined the sequences for accuracy and reviewed the haplotypes with a single base-pair difference from the most similar haplotype. Once sequences were finalized, geneticists compared them with previously published sequences from throughout the global distribution of short-finned pilot whales (Oremus *et al.* 2009, Van Cise *et al.* 2016).

Satellite Telemetry

The Argos system used Kalman filtering (Lopez and Malardé 2011) to determine the Argos Doppler locations of the satellite-tagged short-finned pilot whales. We uploaded the Argos raw DIAG files to Movebank[5] and ran the Douglas Argos Filter (DAF) on the satellite tag locations, using the distance angle rate filtering method (Douglas *et al.* 2012). We set the DAF to automatically retain location classes (LC) of LC2 and LC3. The DAF retained LC1, LC0, LCA, LCB, and LCZ locations if they met certain criteria. Locations of those classes had to be separated from the next location by less than a maximum redundant distance of 3 km. We set the maximum sustainable rate of movement to 15 km/h based on maximum travel speeds noted during observations of fast-traveling short-finned pilot whales in Hawai‘i and the default Ratecoef for marine mammals (Ratecoef = 25) (Baird *et al.* 2013a). We then used ArcGIS 10.1 to plot the filtered satellite tag locations, removed those that fell on land and extracted the depths and distances to shore for each tag location by the same methods as those for the encounter locations and vessel tracks.

Using kernel densities (Silverman 1986, Worton 1989), we estimated the areas within the Mariana Archipelago that were characterized by a high probability of use by satellite-tagged short-finned pilot whales during summer months in which there were the most data (June–August 2013, 2014, 2016). In order to reduce autocorrelation bias and to standardize temporal sampling, we further reduced the DAF satellite tag locations to two best quality positions per day for each tag (approximately 12 h apart). In order to prevent pseudoreplication in the data used for the kernel density estimation (kde) analysis, we followed a similar procedure used by Schorr *et al.* (2009) and Baird *et al.* (2016) to determine whether individuals tagged within the same year were acting

[5] https://www.spatialecology.com/gme.

in concert with one another during the period of overlap. Individuals were considered to be acting in concert if the average distance between a pair of individuals was less than 5 km and the maximum distance between a pair was less than 25 km over the period with overlapping data (Baird *et al.* 2016). When coordinated pairs were identified, the shorter duration track was excluded from the kde analysis. We then used Geospatial Modeling Environment (GME)[6] to calculate the kernel density for each short-finned pilot whale with no fewer than 30 final locations (Seaman *et al.* 1999) between June and August. Using a similar procedure as Citta *et al.* (2012), we overlaid our study area with a grid of 1 × 1 km cells that was large enough to encompass the kernel densities for all tagged short-finned pilot whales. We calculated the bandwidth, which controls the width of the estimated kernel around each point and determines how much regional variation is emphasized, using Smoothed Cross-Validation (SCV) within the GME (Duong 2007). Within ArcMap, we removed kernel densities on land. Because the tags did not provide an equal number of locations, we weighted the contribution of each individual short-finned pilot whale to the overall kernel density and then rescaled the overall kernel density so that it integrated to 1 (Hauser *et al.* 2014). We calculated the 10%, 50%, and 95% probability density contours for June–August based on the estimated kernel densities following Citta *et al.* (2012) and Hauser *et al.* (2014), where the 10% contour represents the highest use area, the 50% contour represents the core area, and the 95% contour represents home range.

Dive Data

To analyze dive data, we imported the ARGOS raw DIAG files into the Wildlife Computers Data Analysis Programs (WC-DAP) 3.0[7] and exported the decoded data as .csv files. The DAP "Behavior" (DB) file listed user defined dives and surfacing bouts recorded by the tags. Qualifying dives were those ≥30 m depth with durations ≥30 s, and each dive record provided the start time, end time, duration, and maximum depth reached. Surfacing bouts represented the time between qualifying dives and included the start and end times and durations. Gaps in the records occurred when one or more Argos messages failed to be received due to factors such as no satellite coverage, surfacing behavior, weather, or duty cycling.

Based on previous classifications of short-finned pilot whale diving behavior (Aguilar de Soto *et al.* 2008, Alves *et al.* 2013*a*), we classified dives as shallow (≤100 m) and deep (≥500 m), and all other dives (101–499 m) as intermediate. Dive depth and duration and surface duration were not normally distributed (Lilliefors test, $P < 0.05$), such that we present individual median and range, and the group mean of these values to characterize events across all individuals.

To examine diel variation in diving behavior, we assigned each dive and surfacing bouts to dawn, day, dusk, and night periods based on the

[6] https://www.spatialecology.com/gme.
[7] http://wildlifecomputers.com/support/downloads.

daily values of astronomical twilight for May–June 2014 and 2016.[8] We then calculated the proportion of dive records and surface time for each dive depth category in each diel period, as well as the proportion of time within each diel period represented by gaps in the data.

Results

Survey Effort and Short-finned Pilot Whale Encounters

We surveyed a total of 19,033 km of trackline during 1,263 h around the southernmost islands of the Mariana Archipelago (Saipan, Tinian, Aguijan, Rota, and Guam) over 196 d during 2010–2016 (Table S1, Fig. 1b). Most of the survey effort was during April–September with the exception of the 2010 surveys, which we conducted in February. Most of the survey effort was off the west sides of the islands. The depth along survey tracklines extended to 3,200 m and 67% of the total effort was over water with depths >200 m (Fig. 1b). The median depth of the overall search effort was 758 m. Survey effort off Guam (80 d; 7,543 km) and the 3-Islands area (83 d; 8,316 km) was similar, while that off Rota (34 d; 3,175 km) was less than half of either of the other locations (Table S1).

Short-finned pilot whales were the fourth-most encountered species for all locations surveyed by PIFSC (Hill *et al.* 2014, 2015). Our survey team encountered 20 short-finned pilot whale groups between September 2011 and June 2016 (Table 1). We encountered no short-finned pilot whales in 2010 or 2015. The overall encounter rate was 2.2 short-finned pilot whale groups/100 h of effort over water depths >200 m. No short-finned pilot whales were encountered in waters <200 m. We encountered short-finned pilot whale groups more times off Guam (n = 11) than off the 3-Islands (n = 5) and Rota (n = 4) (Table 1, Fig. 1b). The U.S. Navy contributed location data for short-finned pilot whale encounters collected during the 2007 MISTCS surveys (n = 4), as well as the 2011 (n = 1) and 2012 (n = 2) HDR surveys. Across all short-finned pilot whale encounters (n = 26), the median depth was 774 m (range 215–4,500 m), and the median distance from shore was 6.5 km (range 0.5–344.8 km). Median group size was 23 individuals (range 4–54) (Table 1). Survey teams observed neonates during two encounters and YOY during seven encounters.

Photo-identification

The short-finned pilot whale photo-identification catalog includes 191 D-1 or D-2 individuals represented by Q-1 or Q-2 photographs. Survey teams encountered 47 (25%) of the cataloged individuals only once and nearly three-quarters (73%; n = 140) of the cataloged individuals two to five times over multiple years. We resighted four short-finned pilot whales during six encounters, which was the maximum number of

[8] Selected location 14°10′N, 145°12′E from the U.S. Naval Observatory's Astronomical Application Department. http://aa.usno.navy.mil/data/docs/RS_OneYear.php.

Table 1. Details of short-finned pilot whale encounters in the Mariana Archipelago including the location (description, latitude, longitude), location depth (m), distance to shore (km), best group size estimate, number of neonates and young of the year (YOY), number of individuals from the photo-identification catalog, number of biopsy samples collected, and number of satellite tags deployed. Observer consensus on best, high, and low group size estimates were made during each encounter. The best group size estimate is reported here. Corrections were made for encounters in which the number of cataloged individuals was greater than the best estimate from the field. Location IDs correspond to sites pictured in Figure 1.

Location ID	Date	Location	Latitude (N)	Longitude (E)	Depth (m)	Shore distance (km)	Best group size estimate	Neonates/ YOY	No. cataloged individuals	No. biopsy samples	Tags deployed
1[a]	2/11/2007	Offshore	17.1000	142.8500	3,395	307.8	25	—	0	0	0
2[a]	3/16/2007	Outside EEZ	10.1833	144.1167	4,500	344.8	15	—	0	0	0
3[a]	3/20/2007	Guam	13.6167	145.0667	987	12.1	7	—	4	0	0
4[a]	3/28/2007	Offshore	17.7833	143.7167	4,339	213.1	9	—	0	0	0
5[a]	2/22/2011	Guam	13.5785	144.7613	766	6.0	23	—	16	0	0
6	8/27/2011	Guam	13.5791	144.7501	825	7.1	14	0	10	7	0
7	9/8/2011	3-Islands	15.3039	145.7113	570	8.2	34	2	22	7	0
8	9/15/2011	Rota	14.1136	145.1259	215	0.5	38	1	32	9	0
9	9/29/2011	3-Islands	15.0219	145.5413	724	4.4	33	1[b]	30	6	0
10[a]	3/21/2012	Guam	13.3889	144.5954	1,429	6.0	20	—	20	3	0
11	5/26/2012	Guam	13.7076	144.8246	469	7.0	30	1	19	3	0
12	6/8/2012	3-Islands	14.7827	145.4912	676	8.3	22	1	20	3	0

13	6/8/2012	3-Islands	14.7960	145.5292	553	5.1	19	1	5	0	0
14	6/10/2012	3-Islands	14.9935	145.2356	720	36.3	23	1	9	2	0
15	6/30/2013	Guam	13.4847	144.6589	809	2.1	29	1[b]	20	2	1
16	6/30/2013	Guam	13.5526	144.7137	967	8.1	4	0	4	2	1
17	7/1/2013	Guam	13.4023	144.6097	781	3.9	17	0	15	5	1
18	5/19/2014	Guam	13.4360	144.6175	341	0.6	23	0	22	2	2
19	5/25/2014	Guam	13.37885	144.6274	587	2.5	20	0	20	5	2
20	6/16/2014	Rota	14.21588	145.31385	794	3.8	48	1	41	9	3
21	6/17/2014	Rota	14.05443	145.23831	1,443	7.3	36	0	35	2	1
22	6/18/2014	Rota	14.16741	145.08898	987	5.7	15	0	13	0	0
23	5/29/2016	Guam	13.66795	144.77207	737	8.5	48	0	48	12	1
24	6/2/2016	Guam	13.50448	144.73507	607	2.7	54	0	54	18	4
25	6/5/2016	Guam	13.50494	144.71929	693	2.8	31	0	21	1	0
26	6/5/2016	Guam	13.58108	144.75283	814	6.9	50	0	50	0	1
Median (range)					774 (215–4,500)	6.5 (0.5–344.8)	23 (4–54)		20 (0–54)	98	17

[a]Encounter data contributed by the U.S. Navy.

[b]Neonates.

resights for all individuals. Those four whales occurred together during encounters in three different years. Five years was the longest duration between resights of individuals. During three of the four 2007 MISTCS short-finned pilot whale encounters, distinctive individuals were photographed but no matches were found in the photo-identification catalog and they were not added due to poor photo quality. Those three encounters were >200 km from shore.

The preliminary social network diagram reveals a main social cluster that contains 82% of all individuals within the photo-identification catalog (Fig. 2). Three other groups, all seen only once within the 3-Islands area in 2012, are not connected to the main social cluster. The largest of these three single encounter groups (single encounter group 1; SEG 1) was 8 km south of Aguijan, while the SEG 2 was near Esmeralda Bank (36 km west of Tinian) and SEG 3 was 5 km south of Aguijan (Table 1, Fig. 1b, 2).

Genetics

From 2011 to 2016, 98 biopsy samples were collected from 80 short-finned pilot whales in the Mariana Archipelago (Table 1). The 80 sampled individuals included 43 females, 34 males, and three that could not be genetically sexed (Table 2). After eliminating duplicate samples, the SWFSC successfully generated 79 sequences, (42 of which were previously reported by Martien *et al.* 2014*b*). The genetic analyses revealed five haplotypes (A1, A2, C, 17, 18); two of which have only been found in the Mariana Archipelago (17, 18) (Martien *et al.* 2014*b*). Of the 79 individuals for which sequences were successfully generated, more than half (65%; n = 51) had haplotype A2. Of the remaining 28 individuals, 15 had haplotype A1, five had haplotype 17, five had haplotype C, and three had haplotype 18 (Table 2).

Seventy-eight of the 80 sampled individuals were in the photo-identification catalog, while two did not have distinctive enough fins to be included in the catalog but were distinguishable from one another. Individuals representing all five identified haplotypes were present within the main social cluster. Individuals with different haplotypes have been seen together multiple times over multiple years (Table S2, Fig. 2). Two haplotype A2 females and two haplotype 17 females were seen together five times in 5 yr, and two haplotype A2 individuals (one male, one female) and two haplotype C individuals (one male, one female) were seen together five times in 4 yr. A haplotype A1 male was seen with two male and one female haplotype A2 individuals three times in 3 yr. The SEG 1 and SEG 2 also included individuals with different haplotypes (Fig. 2). No samples were collected from SEG 3.

Satellite Telemetry

Location Depths and Distances from Shore

Between 2013 and 2016, we deployed 17 satellite tags on short-finned pilot whales (12 males, 5 females; sex was determined by genetics)

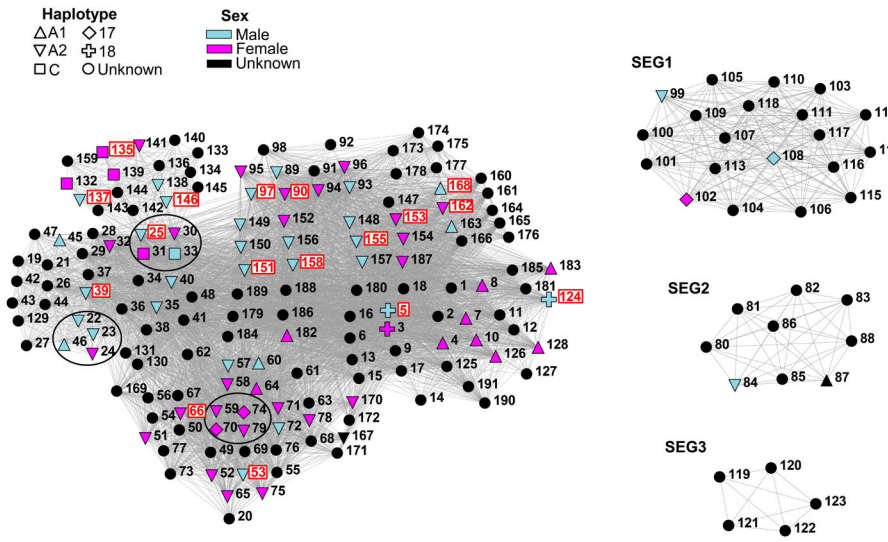

Figure 2. Preliminary social network diagram of short-finned pilot whales in the Mariana Archipelago. One main social cluster includes 82% of photo-identified individuals (from 22 encounters). Single-encounter groups (SEG) are also shown. Nodes represent individuals within the photo-identification catalog (191 individuals) and reflect known information on sex (from genetic analysis) and haplotype. Numbers (to the right of) each node correspond to photo-identification catalog IDs. IDs with red font and red boxes correspond to satellite-tagged individuals (see Table 3). Grey lines represent connections between individuals present during the same encounters. Encircled nodes represent individuals with different haplotypes encountered together multiple times over three or more years.

(Table 3, Fig. 3, S1). All of the tags were deployed off of Guam and Rota and the individuals were all a part of the main social cluster (Fig. 2). We received 7,490 satellite tag locations for the 17 tagged short-finned pilot whales from Argos. One individual (tag ID 128914) was excluded after the tag distance analysis because he was found to be acting in concert with another tagged short-finned pilot whale (tag ID 128910). After running the DAF and removing the locations that fell on land, 5,472 satellite tag locations remained (Table 3, Fig. S1). Tag durations for the filtered locations ranged from 6.8 d to 234.7 d. Median depth of the filtered tag locations was 948 m (range 6–9,661 m), median distance from shore was 13.4 km (range 0.1–416.6 km). All but one of the tagged short-finned pilot whales remained within 140 km from shore (Table 3, Fig. 3, S1). Over 10 d in July 2013, a male short-finned pilot whale (tag ID 128885, photo catalog ID MIGm-39) traveled 417 km south of Guam across the Mariana Trench and outside of the Guam EEZ boundary before turning around and returning to the Mariana Archipelago.

Table 2. Summary of haplotype and sex data of biopsy-sampled short-finned pilot whale individuals. Morin *et al.* (2015) grouped haplotype 17 with haplotypes A1 and A2 into the Naisa-type clade and grouped haplotype 18 with haplotype C, which may represent the third genetic stock or clade. Haplotypes 17 and 18 have only been identified in the Mariana Archipelago. See Table S2 for details on haplotypes and sex by encounter.

	Haplotype						
	A1	A2	C	17	18	Unknown	Total
Female	9	25	4	4	1	0	43
Male	5	25	1	1	2	0	34
Unknown	1	1	0	0	0	1	3
Total	15	51	5	5	3	1	80[a]

[a]A total of 98 biopsy samples were collected from 78 individuals within the photo-identification catalog. An additional two biopsy-sampled individuals did not have distinctive enough fins to be added to the photo-identification catalog but could be distinguished from one another.

Our longest tag deployment, with a duration of nearly eight months (tag 128886, photo catalog ID MIGm-146, July 2013–February 2014), includes 98.6% of filtered tag locations within 74 km from shore, with a median of 10.7 km. This individual made a single long-distance trip away from the islands during the life of the tag. On 21 January 2014, he was 48 km off the coast of Rota. On 26 January the tag recorded nine locations that ranged 108.9–139.7 km from the eastern tip of Rota. Five days later, when the tag recorded locations again, this whale was within 25 km of Guam's shoreline and remained there until the tag stopped recording on February 20. We encountered him again in May 2014 2.5 km from the Guam shoreline and only 3 km from the July 2013 encounter location.

Kernel Densities, Highest Use Areas, Core Areas, and Home Ranges

We excluded six tagged short-finned pilot whales (tag IDs 128889, 128914, 137728, 141722, 141724, and 141728) from kernel density estimates because their tags had fewer than 30 of the 12 h summer (June–August) locations, or because they were found to be acting in concert with another tagged short-finned pilot whale. The final data set for the kernel density and probability density contour estimation consisted of 1,007 locations during the 2013, 2014, and 2016 summer for 11 satellite-tagged short-finned pilot whales (Table 3, Fig. 3). The estimated home range (95% probability density contour) extended from approximately 60 km south of Santa Rosa Reef to approximately 30 km north of FDM and encompassed 51,849 km^2 around the southernmost islands of the Mariana Archipelago including FDM. The estimated core area (50% probability density contour) centered on Guam and Rota, stretching south to Santa Rosa Reef and north beyond Rota approximately 25 km encompassing 7,145 km^2. The area with the highest probability of use

Table 3. Details of satellite tags deployed on short-finned pilot whales in the Mariana Archipelago in 2013, 2014, and 2016 including the tag ID, tag type, photo-identification catalog ID, sex (determined from genetics), deployment location, deployment date/time, tag transmission duration, number of Douglas Argos Filtered (DAF) locations, number of twice daily summer (June–August) DAF locations, median depth (m), and distance from shore (km). Depth and shore distance values are based on DAF locations. Individuals that met the criteria for the kde analysis have their qualifying number of summer locations listed. All tagged individuals were a part of the main social cluster (see Fig. 2).

Tag ID.	Tag type	Photo catalog ID	Sex	Haplotype	Deployment location	Deployment date-time (local)	Duration (d)	No. DAF locations	No. summer locations	Median depth (m) (range)	Median shore distance (km) (range)
128884	SPOT5	MIGm-53	M	A2	Guam	06/30/2013 7:08	17.9	138	35	1,563 (39–3,241)	18.3 (0.2–50.8)
128885	SPOT5	MIGm-39	M	A2	Guam	06/30/2013 8:46	64.0	449	115	1,314 (16–9,661)	26.7 (0.2–416.6)
128886	SPOT5	MIGm-146	M	A2	Guam	07/01/2013 13:20	234.7	645	111	892 (9–9,374)	10.7 (0.1–139.7)
128889	SPLASH10	MIGm-158	M	A2	Guam	05/19/2014 13:26	34.7	282		865 (30–4,176)	16.5 (1.4–91.0)
128920	SPOT5	MIGm-151	M	A2	Guam	05/19/2014 13:54	39.7	248	49	904 (32–4,266)	20.8 (0.5–96.1)
128914[a]	SPOT5	MIGm-137	M	A2	Guam	05/25/2014 8:10	35.3	299		1,082 (11–4,191)	11.1 (0.03–109.7)
128910	SPOT5	MIGm-135	F	C	Guam	05/25/2014 9:50	62.4	582	98	1,263 (29–4,276)	13.5 (0.1–110.2)
128899	SPOT5	MIGm-162	F	A2	Rota	06/16/2014 9:36	83.5	514	121	1,387 (49–4,606)	19.1 (1.2–88.0)
137726	SPOT5	MIGm-168	M	A1	Rota	06/16/2014 11:27	50.9	427	99	1,386 (58–4,564)	18.1 (0.3–88.3)
137727	SPOT5	MIGm-66	F	A2	Rota	06/16/2014 13:12	94.6	275	109	1,189 (28–4,494)	17.5 (0.2–85.3)
137728	SPOT5	MIGm-155	M	A2	Rota	06/17/2014 10:07	10.5	77		1,103 (49–2,297)	10.2 (0.8–39.9)
141721	SPLASH10	MIGm-25	M	A2	Guam	05/29/2016 11:40	24.6	297	37	808 (51–2,577)	9.7 (0.7–39.5)
141724	SPLASH10	MIGm-97	M	A2	Guam	06/02/2016 7:23	12.5	169		787 (50–1,860)	8.6 (0.1–32.1)
141713	SPOT5	MIGm-90	F	A2	Guam	06/02/2016 9:21	79.9	657	125	768 (7–2,568)	8.2 (0.1–68.3)
141722	SPLASH10	MIGm-153	F	A2	Guam	06/02/2016 9:45	7.4	90		702 (28–2,613)	10.9 (0.2–24.7)
141714	SPOT5	MIGm-5	M	18	Guam	06/02/2016 12:06	58.7	539	108	796 (6–2,711)	7.4 (0.2–44.5)
141728	SPLASH10	MIGm-124	M	18	Guam	06/05/2016 11:12	6.8	83		906 (41–2,971)	11.5 (0.4–30.6)
Total								5,472	1,007	948 (6–9,661)	13.4 (0.1–416.6)

[a]Individual's values excluded from the summary total because it was determined to be moving in concert with tag ID 128910.

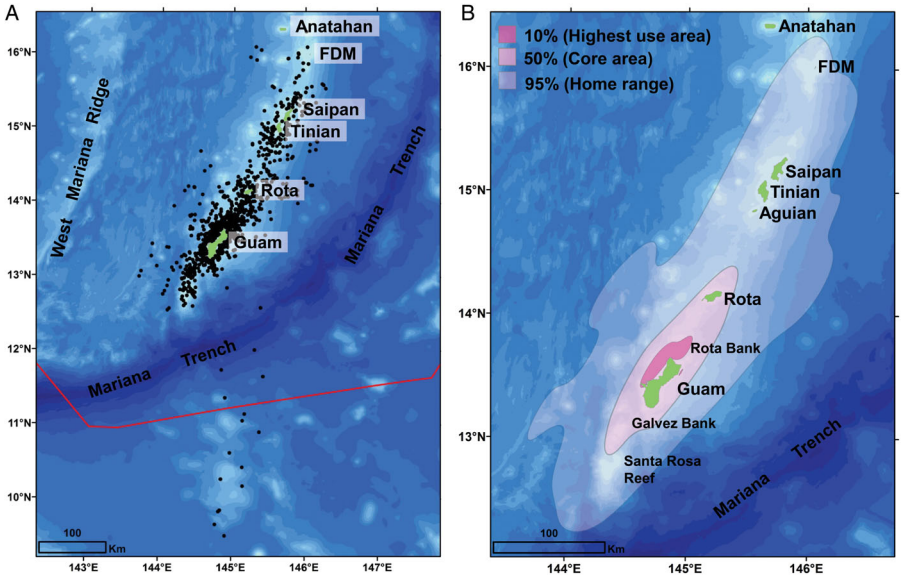

Figure 3. Panel A: Two-daily satellite tag locations (n = 1,007) from 11 short-finned pilot whales satellite tagged off Guam and Rota during summer (June–August) 2013, 2014, 2016 (black dots). Panel B: the probability density contours (magenta 10%, pink 50%, violet 95%) estimated from kernel densities of the satellite tag locations. Red line denotes the Guam and Commonwealth of the Northern Mariana Islands exclusive economic zone boundary. All individuals were a part of the main social cluster (see Fig. 2).

by short-finned pilot whales during the summer (10% probability density contour) was centered off the northwest side of Guam extending north to Rota Bank. This area encompassed 665 km^2. A small area (8 km^2) off the northeast side of Guam, separate from the larger highest use area, also was identified as an area of highest use.

Dive Behavior

We deployed five SPLASH location-dive tags on one adult female and four adult male short-finned pilot whales off Guam in May 2014 and May–June 2016 (Table 3). The tags transmitted for 6.8–34.7 d (2,064 h) and recorded 7,779 dive and surfacing bout records totaling 1,442 h (Table S3). The tags recorded more intermediate depth dives (n = 2,112) than shallow (n = 1,030) or deep (n = 744) dives, and the short-finned pilot whales' mean depth was 231 m (SD = 104) for intermediate depth dives, 673 m (SD = 113) for deep dives, and 56 m (SD = 21) for shallow dives. Maximum dive depth was 1,168 m. Dives were divided into diel periods (dawn, day, dusk, night) based on astronomical twilight. Average day length during summer was 12.9 h, twilight periods were 1.3 h, and nights were 8.5 h. Gaps within the tag data over all tags were roughly even (approximately 30% missing data) across the diel periods (Table S4).

Table 4. Summary of diel dive data from five SPLASH tags deployed on short-finned pilot whales in the Mariana Archipelago. The Wildlife Computers Data Analysis Program (WC-DAP) "Behavior" (DB) file reported dives ≥30 m depth with duration ≥30 s. For each tagged short-finned pilot whale, dive depth categories (shallow: ≤100 m, intermediate: 101–499 m, deep: ≥500 m) were assigned to diel periods (dawn, day, dusk, night) based on the daily values of astronomical twilight for May–June 2014 and 2016 at 14°10′N, 145°12′E from the U.S. Naval Observatory's Astronomical Application Department. Average day length during these periods was 12.9 h, twilight periods were 1.3 h, and nights were 8.5 h. The proportion of the number of dives in each depth category and the surface time (h) was calculated for each diel period. Median values are reported.

		Shallow Dives				Intermediate dives				Deep dives				Surface time			
Tag ID	Total no. dives	Dawn	Day	Dusk	Night	Dawn	Day	Dusk	Night	Dawn	Day	Dusk	Night	Dawn	Day	Dusk	Night
128889	1,329	0.23	0.43	0.25	0.18	0.40	0.15	0.80	0.77	0.50	0.49	0.25	0.09	0.31	0.42	0.28	0.33
141721	1,056	0.50	0.50	0.50	0.06	0.50	0.22	0.80	0.86	0.58	0.30	0.29	0.10	0.35	0.73	0.30	0.37
141722	393	0.30	0.50	0.33	0.14	0.80	0.29	0.80	0.82	0.35	0.18	0.25	0.10	0.52	0.78	0.31	0.34
141724	698	0.25	0.51	0.25	0.08	0.38	0.20	0.75	0.83	0.75	0.36	0.33	0.13	0.38	0.69	0.31	0.34
141728	410	0.66	0.53	0.00	0.12	0.37	0.28	0.90	0.85	0.58	0.21	0.25	0.08	0.33	0.33	0.27	0.37
All	3,886	0.25	0.50	0.29	0.13	0.50	0.22	0.80	0.83	0.50	0.30	0.25	0.10	0.35	0.67	0.28	0.35

Tagged short-finned pilot whales dove to intermediate depths more often during the night and twilight periods than during the day (Table 4). In addition, during dusk and night periods short-finned pilot whales performed more intermediate-depth dives than deep dives or shallow dives. During the day, the short-finned pilot whales spent most of their time (67%) at or near the surface and performed shallow dives more often than deep or intermediate dives (Table 4). The whales made their deepest dives (>600 m) during all diel periods.

Discussion

Understanding the ecology of short-finned pilot whales in different locations around the world is important for understanding the ecology of the species as a whole. Differences in habitat (*e.g.*, bathymetry, oceanographic conditions) and prey availability can influence population size and structure, social structure, and foraging behavior. This study was the first investigation of spatial use, movements, individual/group associations, and diving behavior of short-finned pilot whales in the Mariana Archipelago, and within the broader western North Pacific. Genetic, photo-identification, and telemetry data from Mariana Archipelago short-finned pilot whales reveal clues to answering questions about island association, diel diving behavior, and social structure.

Survey Effort and Short-finned Pilot Whale Encounters

More than half (51%) of our total survey effort was over water depths of 500–3,000 m where short-finned pilot whales were found most often (77% of all encounters) within the Mariana Archipelago, similar to island-associated short-finned pilot whale encounter location depths in the Hawaiian, Marquesas, Society, Madeira, and Canary Islands (Gannier 2009, Alves 2013, Baird *et al.* 2013*b*, Servidio 2014, Baird 2016).

The waters off Guam may be an important area for Mariana Archipelago short-finned pilot whales. We encountered short-finned pilot whale groups more times off Guam (n = 11) than off the 3-Islands area (n = 5) and Rota (n = 4) (Table 1, Fig. 1b) despite the fact that our survey effort by depth was similar across locations. Although the duration of our survey effort off Guam was greater than that off Rota, there was no significant difference in the duration of survey effort between Guam and the 3-Islands area (Mann-Whitney, P = 0.5).

The mean group size of short-finned pilot whales in the Mariana Archipelago (26, SD = 13.4) is smaller than what has been observed in the Philippines (56.7, SD = 14.7) (Dolar *et al.* 2006), but similar to that observed in Hawai'i (20, SD = 16), Madeira (18, SD = 12), the Marquesas (29.7, SD=not reported), Society (24.4, SD = 11.3) and Canary Islands (16.2, SD = 0.5) (Gannier 2008, Alves *et al.* 2013*b*, Baird *et al.* 2013*b*, Servidio 2014). The maximum group sizes observed in Hawai'i (up to 195 individuals) and the Philippines (up to 350 individuals) are much larger than those observed in the Mariana Archipelago (54 individuals), Madeira (60 individuals) and the Canary Islands (80 individuals) (Dolar

et al. 2006, Alves *et al.* 2013*b*, Servidio 2014, Baird 2016). The difference in maximum group size that we have observed in the Mariana Archipelago may be related to small sample size. Baird *et al.* (2013*a*) had more than 500 sightings of short-finned pilot whales in the main Hawaiian Islands over a 13 yr period, and Dolar *et al.* (2006) recorded more than twice the number of short-finned pilot whale encounters (n = 48) during two month-long efforts in consecutive years compared to what we observed (n = 22) in the Mariana Archipelago during month-long surveys in 2011–2016. Alternatively, our estimates may be a true reflection of the maximum group size in the Mariana Archipelago. The Madeira maximum estimate resulted from encounters with 105 groups in 2003–2011 (Alves *et al.* 2013*b*).

Photo-identification

Although preliminary because of small sample size and low re-sight rates of short-finned pilot whales in the Mariana Archipelago, the analysis of photo-identification data and creation of a social network diagram demonstrates the presence of an extensive main social cluster of individuals. Three groups have been photographed on only a single occasion, suggesting some segment of the population may prefer offshore waters or those near the northern islands, and occur near the southernmost islands intermittently. During the 2007 MISTCS surveys, researchers encountered two groups of short-finned pilot whales along the northern portion of the West Mariana Ridge; west of Guguan and Alamagan and one group south of Guam outside of the EEZ boundary (Fig. 1a). Although some individuals had very distinctive fins, none of the individuals photographed during those offshore encounters matched to our photo-identification catalog and none were added to the catalog because the photos did not meet the quality threshold.

The Mariana Archipelago short-finned pilot whale social network may be made up of smaller distinct social units that include individuals with varying degrees of site fidelity as has been observed in the population of Madeira short-finned pilot whales, which included residents, regular visitors, and transients (Alves *et al.* 2013*b*). Similarly in Hawai‘i, some groups are known to be long-term residents of Hawai‘i Island and are consistently seen there, while others are seen intermittently or infrequently (Mahaffy *et al.* 2015). In addition, the resident Hawai‘i short-finned pilot whales formed strong long-term bonds and preferential associations between individuals, which was also observed in pilot whales in Madeira (Alves *et al.* 2013*b*) and the Canary Islands (Servidio 2014). The strength of individual associations of Mariana Archipelago short-finned pilot whales cannot be evaluated at this time because our individual re-sight rate is too low. Whitehead (2008) recommends a minimum cutoff of using only those individuals identified in five sampling periods when attempting to quantitatively assess social interactions and associations. Of the 191 individuals within our photo-identification catalog, only 25 were photographed on five or more separate occasions.

Genetics

Five haplotypes (A1, A2, C, 17, 18) were found in the genetic samples from short-finned pilot whales of the Mariana Archipelago. When Martien *et al.* (2014*b*) truncated the haplotypes A1 and A2 from 962 bp to 345 bp for comparison with haplotype A (Oremus *et al.* 2009) they found that all were identical. Haplotype A is found broadly in the South Pacific, southeast Asia, the Indian Ocean, the western North Atlantic, and the Caribbean (Téllez *et al.* 2014, Van Cise *et al.* 2016), while haplotype C has been found in the South Pacific, in Japanese markets, and may be the third genetic stock or clade (Oremus *et al.* 2009, Morin *et al.* 2015). Morin *et al.* (2015) grouped haplotype 18 with haplotype C and grouped haplotype 17 with haplotypes A1 and A2 into the Naisa-type clade. Martien *et al.* (2014*b*) found strong mitochondrial differentiation between short-finned pilot whales encountered in the waters off the 3-Islands area and those encountered off Rota and Guam, suggesting a lack of female-mediated gene flow between these island groups, although the differentiation between the areas may reflect familial or social structure rather than population differentiation (Martien *et al.* 2014*b*). No significant nuclear differentiation has yet been found between islands groups in the Mariana Archipelago, suggesting that there is male-mediated gene flow between these island populations (although lack of differentiation could be due to small sample size) (Van Cise *et al.* 2015).

Genetic, life-history, and photo-identification studies of other pilot whale populations have hypothesized that social groups are primarily matrilineal (Kasuya and Marsh 1984, Amos *et al.* 1993, Heimlich-Boran 1993, Alves *et al.* 2013*b*, Servidio 2014). Kasuya and Marsh (1984) examined the carcasses from 27 (southern form) short-finned pilot whale schools stranded or caught off the Pacific coast of Japan and concluded that females likely stay with their mothers for life but that males may migrate between schools after weaning and move between different breeding schools after reaching puberty. Alves *et al.* (2013*b*) found a positive correlation between association indices and genetic relatedness coefficients suggesting that individual short-finned pilot whales that associated more tended to be genetically related. Amos *et al.* (1993) used microsatellite DNA analysis to determine that long-finned pilot whale groups in the Faroe Islands consist of closely related adult females and their offspring, including adult males. However, Connor (2000) suggested that the collection of samples from individuals captured in the drive fishery may have confounded the results of Amos *et al.* (1993). He pointed out that the sampled long-finned pilot whale schools were much larger than those observed offshore and may have represented a broader social structure. Oremus (2008) found that groups of stranded long-finned pilot whales in New Zealand were composed of multiple unrelated matrilines by using mtDNA and microsatellites from samples.

The social structure of Mariana Archipelago short-finned pilot whales is not immediately evident from our existing data, but it is possible that Mariana Archipelago short-finned pilot whale groups are matrilineal and that both females and males may remain in their natal group into

adulthood. There are several adult males and females with the same haplotypes that have been seen together over multiple years (Table S2). However, Oremus (2008) cautioned that multiple matrilines in association do not necessarily indicate relatedness. Additional genetic analyses will be required to clarify whether these individuals are mothers and offspring or siblings. Other evidence from our data suggests that some groups are not strictly separated by matrilineal lines. We have observed short-finned pilot whales with different haplotypes within the same encounter for both the single-encounter groups (SEG 1 and SEG 2) and within the main social cluster (Table S2, Fig. 2). Some of our highest resight rates are for individuals with different haplotypes encountered together over multiple years. We are uncertain whether these are stable groups that remain together throughout the year or form temporary associations during the summer months. In the Canary and Madeira Islands short-finned pilot whale group sizes increased in summer and autumn and more visitors and mixed groups were observed, which was proposed to be related to breeding (Heimlich-Boran 1993, Alves *et al.* 2013*b*, Servidio 2014).

Satellite tag data from Mariana Archipelago short-finned pilot whales suggest that some associations between individuals with different haplotypes may be more than ephemeral. Two satellite-tagged individuals with different haplotypes (tag ID 128914, haplotype A2 and tag ID 128910, haplotype C) moved in concert with each other for the entire 35.3 d deployment duration of tag ID 128914. It is also possible that this extended association may have been for the purpose of breeding given that these individuals were male and female. Future deployments on individuals, from the same encounters, with different haplotypes in different seasons will help to clarify this question.

Satellite Telemetry

All of the tagged Mariana Archipelago short-finned pilot whales were a part of the main social cluster (Fig. 2). The satellite tag data indicate that the whales are primarily using near-island waters (median distance from shore 13.4 km; Table 3, Fig. 3), despite occasional distant offshore movements, up to >400 km from shore. Data from the longest tag deployment of nearly eight months suggest that some short-finned pilot whales may be primarily island-associated year-round and demonstrate site fidelity. Kernel density estimates, based on location data from satellite tags deployed on short-finned pilot whales off Guam and Rota, indicate that the area with highest probability of use during the summer (June–August) was located off the northwest side of Guam (Fig. 3b).

Dive Behavior

Mariana Archipelago short-finned pilot whales demonstrated similar diving behavior as short-finned pilot whales in other locations. Like short-finned pilot whales in Madeira and Hawai‘i (Alves *et al.* 2013*a*, Baird *et al.* 2015), those in the Mariana Archipelago spent most of the daytime hours at or near the surface and diving to shallow depths ≤100 m. Maximum dive depths of Mariana Archipelago short-finned pilot

whales (1,168 m) were also similar to those recorded off Kaua'i (751–1,231 m) and the Canary Islands (1,000–1,500 m), and the whales performed their deepest dives (>600 m) during the day and night (Aguilar de Soto *et al.* 2008, Servidio 2014, Baird *et al.* 2015, Baird 2016). The Mariana Archipelago short-finned pilot whales had similar deep dive durations (maximum = 29 min, mean = 17.1 min (SD = 2.9)) as those in the Hawaiian (maximum = 16.8–24.6 min; Baird *et al.* 2015) and Canary Islands (≤21 min; Aguilar de Soto *et al.* 2008). Aguilar de Soto *et al.* (2008) suggested that the much shorter dive time of short-finned pilot whale as compared to other deep diving species, such as sperm (*Physeter macrocephalus*) and beaked whales, was necessary because of the high energy expenditure of sprinting during dives.

In Hawai'i, short-finned pilot whales spent more time at night diving to intermediate depths (300–500 m) (Baird 2016) and were located in areas with high densities of midwater micronekton (Abecassis *et al.* 2015). Active acoustic data demonstrate that there is a persistent DSL at approximately 400–600 m depth in Hawai'i (Abecassis *et al.* 2015) and at 650 m depth north of 8°N latitude in the central equatorial Pacific (Hazen and Johnston 2010), as well as shallower DSL at 400 m depth and 300–600 m depth, respectively, that make nightly migrations toward the surface (0–250 m) (Hazen and Johnston 2010, Abecassis *et al.* 2015, Au and Giorli 2016). Although the characteristics and behavior of the DSL in the Mariana Archipelago have not been described, it is possible that they are similar to those detailed above.

Similar to short-finned pilot whales in Hawai'i, the tagged Mariana Archipelago whales conducted more intermediate depth dives (101–499 m) at twilight and night than shallow or deep dives (Table 4). Passive acoustic devices mounted on the seafloor at locations off Guam, Saipan, and Tinian detected high percentages of short-finned pilot whale echolocation clicks during twilight and nighttime periods of observation suggesting that the whales were foraging (Au and Giorli 2016). Dives to intermediate depths and the occurrence of echolocation clicks by short-finned pilot whales during twilight and night hours suggest that the whales may be foraging on prey within the DSL or on prey that target the DSL. However the pattern observed off Hawai'i Island, in which the whales and the DSL moved closer to shore (into shallower waters) at night, was not evident from the Mariana Archipelago short-finned pilot whale satellite tag data. The median location depth and distance from shore for all tag locations (SPOT and SPLASH) were slightly shallower and closer to shore during the day (902 m and 12.6 km) than during night/twilight periods (1,057 m and 13.9 km). An important next step is to model the satellite track and dive data from the SPLASH tags to determine where the Mariana Archipelago short-finned pilot whales were diving and possibly foraging.

We have no information on the specific prey of short-finned pilot whales in the Mariana Archipelago, but short-finned pilot whales are known to feed on mesopelagic squid and fish in other regions (Kubodera and Miyazaki 1993, Bustamante *et al.* 2003, Abecassis *et al.* 2015). Aguilar de Soto *et al.* (2008) suggested that the high energy expenditure, for deep dives during which the short-finned pilot whales

perform sprints to capture a single prey, would require that the prey have a high caloric content and proposed muscular squid as good potential candidates. Ommastrephid squids were the most abundant prey identified in the diet of 14 short-finned pilot whales (6 southern form; 8 northern form) caught off Ayukwa, Ojika Peninsula, Japan in 1982 (Kubodera and Miyazaki 1993). In the southern form short-finned pilot whales, histioteuthid squids were the second most abundant prey species followed by gonatid squids.

Conclusion

Although short-finned pilot whales are among the most commonly encountered species of odontocetes in the Mariana Archipelago over 7 yr of surveys, our relatively few encounters limit our interpretation of the results. Additional genetic sampling, photo-ID, and telemetry data would help elucidate whether Mariana Archipelago short-finned pilot whales are a single mixed population or comprise several geographically or socially segregated groups. Continued research that includes surveys during all seasons and expands to areas north of the 3-Islands area is necessary for a broader understanding of the dynamics of movements, space use, and social networks of short-finned pilot whales within the Mariana Archipelago. However, with this multi-approach study, we have substantially broadened the existing knowledge of short-finned pilot whales in the Mariana Archipelago and within the western North Pacific. The results from this study are important for moving toward population assessments and the evaluation of potential threats to short-finned pilot whales in Mariana Archipelago.

Acknowledgments

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Supporting Information

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Figure S1. Filtered satellite-tag locations (black dots; n = 5,472) for 16 short-finned pilot whales tagged off of Guam and Rota in June–July 2013, May–June 2014, and May–June 2016. One individual's track (tag ID 128914) was removed after he was found to be moving in concert with another whale. Red line denotes the Guam and CNMI EEZ boundary. All satellite-tagged individuals were a part of the main social cluster (see Fig. 2).

Table S1. Summary of the Pacific Islands Fisheries Science Center's Cetacean Research Program nonsystematic visual surveys for cetaceans in the Mariana Archipelago by location and year including the month(s) of survey effort, number of survey days at each location, and the trackline distance surveyed within that area. The 3-Islands area includes the islands of Saipan, Tinian, and Aguijan and their surrounding waters, as well as nearby offshore reefs (see Fig. 1).

Table S2. Summary of haplotype and sex of short-finned pilot whales by encounter. The location IDs correspond to those pictured in Figure 1 and listed in Table 1.

Table S3. Summary of dive and surfacing bout records from five SPLASH tags deployed on short-finned pilot whales in the Mariana Archipelago. Dives listed by depth category (shallow: ≤100 m, intermediate: 101–499 m, deep: ≥500 m). Individual depths and durations listed as medians (ranges). Overall depths and durations listed as means (SD).

Table S4. Calculation of the total time (h) of short-finned pilot whale tag deployment durations and the gaps in the dive data within each diel period, as well as the proportion of the total duration time represented by gaps in the data.