Residency and Movement Patterns of Common Bottlenose Dolphins (*Tursiops truncatus*) off Oʻahu and Maui Nui Carry Implications for Current Stock Boundaries

Annette E. Harnish[1,5], Robin W. Baird[1], Jens J. Currie[2], Stephanie H. Stack[2], Tori Cullins[3], Lynn Opritoiu[4], Antoinette M. Gorgone[1], John B. Kirkpatrick[5]

[1]Cascadia Research Collective, Olympia, WA, aharnish@cascadiaresearch.org
[2]Pacific Whale Foundation, Wailuku, HI, [3]Wild Dolphin Foundation, Waiʻanae, HI,
[4]Captain Steve's Rafting, Lahaina, HI, [5]The Evergreen State College, Olympia, WA

Abstract

Accurate descriptions of population structure are critical to inform effective management of protected species. Here we present the results of a reassessment of the structure and residency of two common bottlenose dolphin (*Tursiops truncatus*) stocks from the main Hawaiian Islands. Previous photo-identification and genetic studies have shown that bottlenose dolphins in the main Hawaiian Islands live in four small (~100 individuals), demographically independent and genetically differentiated island-associated populations around Kauaʻi/Niʻihau, Oʻahu, Maui Nui (Maui, Lānaʻi, Kahoʻolawe, and Molokaʻi), and Hawaiʻi. A recent abundance estimate demonstrated that three of these four populations, designated as stocks, show evidence of decline, particularly the Maui Nui stock. However, photo-identification and satellite-tagging data has shown that some individuals do occasionally move between island areas, especially between Oʻahu and Maui Nui. These movements may have important consequences, as even a few dispersing individuals can impact genetic diversity and allow for the transmission of culturally-mediated behaviors. We reassessed the population structure of the Oʻahu and Maui Nui stocks by analyzing over two decades' worth of photo-identification data representing 472 individuals, and satellite tag data from six individuals. While we found that social connections between the two populations were minimal, there were important geographic overlaps in spatial use that crossed current stock boundaries. This was caused by a small subset of individuals (n=14, 3%) from the Oʻahu population that occasionally travel between island areas, using SW Oʻahu, SW Molokaʻi, SW Lānaʻi, SW Kahoʻolawe, and S Maui. Satellite tag data from three inter-area travelers reveals that these animals made extensive use of Penguin Bank, indicating this area may be of importance to inter-area travelers. Inter-area travelers were sighted in both island areas at all times of the year, though they were consistently sighted more frequently off Oʻahu than off Maui Nui. Further research will be needed to identify the possible drivers of this behavior.

Introduction

Both inshore and offshore ecotypes of common bottlenose dolphins (*Tursiops truncatus*, hereafter bottlenose dolphins) can be found in Hawaiian waters, and are currently divided into one offshore pelagic stock and four island-associated stocks, centered around Kauaʻi/Niʻihau, Oʻahu, Maui Nui (Maui, Lānaʻi, Kahoʻolawe, and Molokaʻi), and Hawaiʻi (Carretta et al., 2019). Both photo-identification and genetic analyses have shown that these stocks are demographically independent, with high re-sighting rates indicative of resident populations and genetic differentiation between stocks (Baird et al., 2009; Martien et al., 2011). Boundaries for the four island-associated stocks are currently drawn at the 1,000 m depth contour, with the exception of the Oʻahu and Maui Nui stocks, which are separated at the Kaʻiwi Channel between the islands at approximately 500 m depth (Carretta et al., 2019). A 2009 abundance estimate based on photo-identification data placed the abundance of each of the four island-associated stocks in the low hundreds, with the exception of Oʻahu, which was around 700 (Baird et al., 2009). However, the relatively high abundance for the O‘ahu stock in the 2009 estimate was likely a consequence of data limitations, and a more recent abundance estimate has placed the O‘ahu stock's abundance in the low hundreds as well (Baird et al., 2009; Van Cise et al., 2021).

Hawaiian inshore bottlenose dolphins are distributed primarily throughout shallow waters, with over 95% of sightings at depths shallower than 1,000 m, and over 50% of sightings at depths shallower than 500 m (Baird et al., 2013; Baird, 2016). Sightings have occurred year-round at each island area, further supporting the existence of resident populations (Baird et al., 2009; Baird, 2016). Both satellite-tagging efforts and photo-identification have shown that animals rarely leave their island areas, though occasional inter-area movements have been documented through both methodologies, especially between Maui Nui and O‘ahu, the two island areas that are closest in proximity (Baird, 2016). The significance of these inter-area movements remains unknown, but one possible consequence is that it changes the exposure of some individuals to spatially variable anthropogenic threats.

There is evidence that three of the four resident stocks are in decline, with significant declines in the Maui Nui stock, and non-significant declines in the O‘ahu and Kaua‘i/Ni‘ihau stocks (Van Cise et al., 2021). Model-derived apparent survival rates are also lower than expected in all four stocks, with the lowest apparent survival rate in the O‘ahu stock (0.84, se = 0.023; Van Cise et al., 2021). The factors driving these declines are uncertain, but exposure to nearshore anthropogenic stressors such as pollution, ambient noise, boat traffic, and fisheries interactions likely plays a role (Van Cise et al., 2021). Overall, spatial variation in anthropogenic impacts to the resident bottlenose dolphins emphasizes the need for accurate stock delineation to inform management efforts for these populations, which is especially critical now given the evidence that at least one of these stocks is in decline.

Methods

Survey Effort, Photo Identification, Sex Determination, and Quality Control

Photographs were collected from both dedicated and opportunistic efforts. Dedicated efforts include Cascadia Research Collective (CRC; see Baird et al., 2013 for details) and Pacific Whale Foundation (PWF; see Stack et al., 2019 for details) survey efforts, which spanned 1996-2018[1], and covered extensive areas on the leeward sides of the islands. Opportunistic encounters were contributed by other researchers and community members. While the circumstances of these opportunistic encounters varies widely, and exact locations of encounters were not always recorded, information about the island area where encounters took place was always available. Seasonality of encounters was categorized into two periods: summer (May-October) or winter (November-April). All depths were determined using the R package marmap v. 1.0.5 (Pante & Simon-Bouhet, 2013) in conjunction with imported NOAA bathymetric data at a 1-minute resolution.

All photographs of bottlenose dolphins were matched to a long-term catalog following previously described methods (see Baird et al., 2009 for details) to establish sighting histories. Briefly, each individual was assigned a distinctiveness score between 1 and 4 (1 = not distinctive, including unmarked fins; 2 = slightly distinctive, with 1-2 notches; 3 = distinctive, with 3-5 notches; 4 = very distinctive, e.g., with 5 or more notches), and a best photo quality

[1]Photographic data from 2019 and 2020 are also being added to our photo-identification catalog for inclusion in analyses, and identification and association information of tagged individuals from this period is included to aid in interpretation of movements.

score between 1 and 4 (1 = poor, 2 = fair, 3 = good, 4 = excellent) for every encounter. To ensure that the data was robust and included no misidentifications or duplicate identifications, the dataset was then restricted to include only individuals with photo quality scores of 3 or 4, and distinctiveness scores of 3 or 4.

Sex was determined based on recorded calf presence, morphology (e.g., clear view of the genital slit or penis), or on genetic analysis of biopsy samples. Genetic analysis of the samples for sex determination using Real-Time PCR was undertaken by Southwest Fisheries Science Center following the protocols described in Morin et al. (2005).

Residency Assignments and Social Networks

Residency was initially assigned to each ID based on the island(s) and span of years that each was encountered across, with all tagged individuals (regardless of distinctiveness or photo quality) included. Individuals with a sighting history span greater than three years on a single island were classified as long-term residents. Individuals with a sighting history span greater than one year, but less than three years were classified as short-term residents, and individuals with a sighting history spanning less than one year were classified as visitors. It should be noted that individuals that are actually long-term residents that became marked part way through the study, or die part way through the study, might be inaccurately classified as short-term residents or visitors based on this scoring system. Individuals that were seen off both Oʻahu and Maui Nui were classified as inter-area.

Residency assignments were then reassessed based on social associations. A social network containing all individuals with photo quality scores of 3 or 4 and distinctiveness scores of 3 or 4 was built using a half-weight association index in SOCPROG 2.4 (Whitehead, 2008), and visualized using Netdraw 2.158 (Borgatti, 2002) with spring embedding. Any visitors that connected to the main components of the network were reassigned as associative residents for the component that they most closely linked to (i.e., Oʻahu or Maui Nui), to account for the fact that these individuals may be resident animals that were infrequently sampled, rather than true visitors. Residency assignments for visitors that did not connect to the main components were not revised.

Subarea Stratification

To explore how spatial use impacts residency, encounters with GPS locations were divided into five different geographic subareas based on demographic and geographic separation, three of which are located within the Oʻahu island area, and two of which are located in the Maui Nui island area (Figure 1). These subareas are: Oʻahu North (ON), Oʻahu West (OW), Oʻahu East (OE), Molokaʻi/Penguin Bank (MPB), and Maui Nui (MN, representing Maui, Lānaʻi , and Kahoʻolawe). These subareas align with the subareas designated in Van Cise et al. (2021), with the addition of an Oʻahu East subarea. The Oʻahu North subarea encompasses the northwest coast of Oʻahu, northward of Kaʻena Point (~21.6° N, 158.3° W), and west of Kahuku Point (~21.7° N, 158.0° W). The Oʻahu East subarea encompasses the northeast coast of Oʻahu, eastward of Kahuku Point and southward to Makapuʻu Point (~21.3° N, 157.7° W). The Oʻahu West subarea encompasses both the west and south coasts of Oʻahu, south of Kaʻena Point along the Waiʻanae coast, and southwest of Makapuʻu Point along the south coast. The Molokaʻi/Penguin Bank subarea includes the waters surrounding Penguin Bank (a large shallow water area to the southwest of the island of Molokaʻi), and the waters surrounding the island of Molokaʻi itself, extending to midway between Molokaʻi and Lānaʻi and midway between Molokaʻi and Maui. The Maui Nui subarea is geographically the largest subarea, encompassing the waters surrounding the islands of Maui, Lānaʻi, and Kahoʻolawe. Subareas were further divided based on depth at the 500 m bathymetric contour in subareas where deep-water encounters (i.e., encounters in water deeper than 500 m) took place, resulting in the creation of three additional subareas: Oʻahu West Deep (OWD), Oʻahu East Deep (OED), and Maui Nui Deep (MND). The subareas where individuals were encountered were also mapped on the social network to explore how spatial stratification impacts social relationships, and the distribution of residency classifications by subarea was described.

The total area of each subarea ranged from 934 km^2 (Oʻahu West) to 6,174 km^2 (Maui Nui), with all three of the Oʻahu subareas smaller than the Maui Nui subareas (Table 1). All subareas had more shallow water (0-500 m bathymetric depth) than deep water (500-1,000 m bathymetric depth), but the Maui Nui and Molokaʻi/Penguin Bank subareas in particular had extensive shallow water habitat, with 4,030 km^2 and 2,570 km^2 of shallow water respectively.

The shape and relative exposure of shallow water within subareas varied substantially (Figure 1). The Oʻahu West and Oʻahu West Deep subareas consist of a narrow band of habitat along the west coast of Oʻahu that widens off the south coast, while the Oʻahu North subarea consists of a broader expanse of shallow water. Oʻahu East consists of intermediate-sized bands of shallow and deep water compared to Oʻahu West/Oʻahu West Deep and Oʻahu North. Molokaʻi/Penguin Bank consists of an extensive shallow-water shelf (Penguin Bank) and shallow area surrounding Molokaʻi, with a band of deep water encompassing Penguin Bank. The Maui Nui subarea has a broad shallow-water area, with some nearshore deepwater habitat off the west coast of Lānaʻi and the south shore of Kahoʻolawe. All of the Oʻahu subareas are highly exposed to the open ocean, while a large portion of the Maui Nui subarea is enclosed by the islands of Maui, Lānaʻi, and Kahoʻolawe. Penguin Bank is also highly exposed, but the waters to the south of Molokaʻi are partially enclosed by Maui and Lānaʻi.

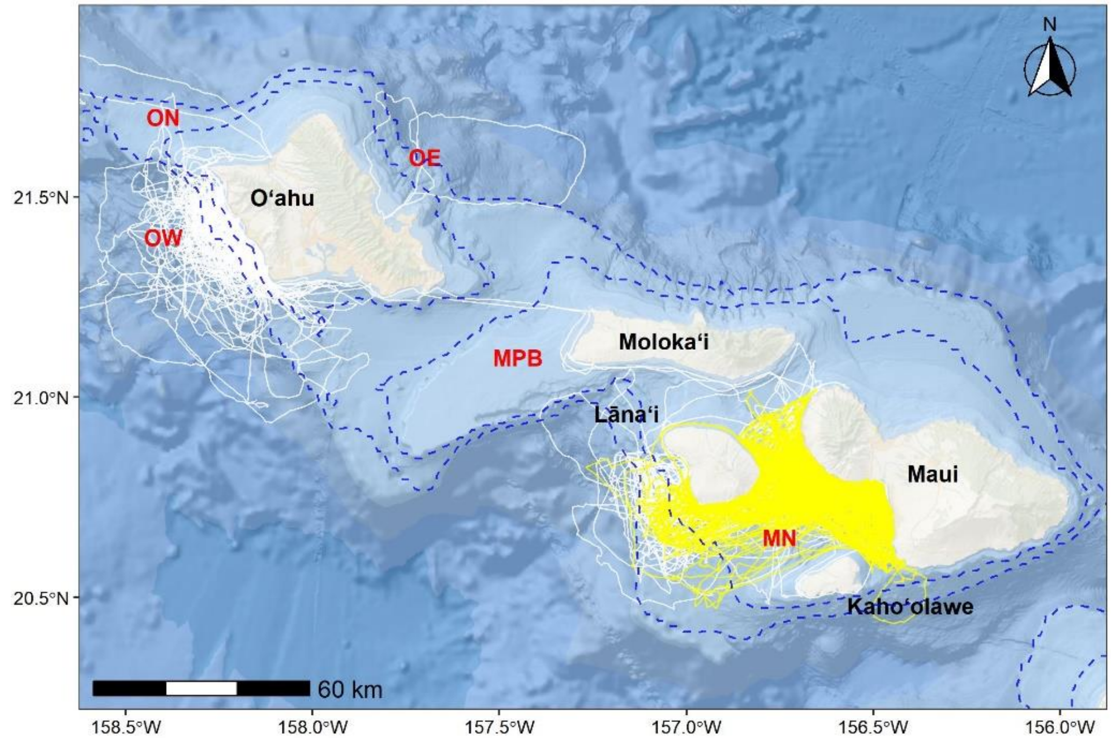


Figure 1. Effort tracklines for CRC (white - 2000-2018) and PWF (yellow - 2010-2018). PWF effort data from 1996-2009 were not available. Subareas are abbreviated in red, with ON for O‘ahu North, OW for O‘ahu West, OE for O‘ahu East, MPB for Moloka‘i/Penguin Bank, and MN for Maui Nui (subarea). Subarea divisions based on depth (O‘ahu West Deep, O‘ahu East Deep, and Maui Nui Deep) are not shown. Depth contours (blue dashed lines) are shown at 500 m and 1,000 m.

Table 1. Total area (in km^2) by depth (m) for each island area and subarea. Values have been rounded to the nearest integer. For island areas, O = O‘ahu island area, MN = MN island area. For subareas, OE = O‘ahu East, OW = O‘ahu West, ON = O‘ahu North, MN = Maui Nui subarea, MPB = Moloka‘i/Penguin Bank.

Island Area	Sub-area	Amount of available habitat (km^2) by depth (m) range												
		0-1000	0-500	500-1000	0-100	100-200	200-300	300-400	400-500	500-600	600-700	700-800	800-900	900-1000
O	**-**	3041	1683	1358	748	174	180	284	297	368	270	281	255	184
MN	**-**	10103	6600	3503	2497	1283	1031	917	872	1049	1001	590	415	448
O	**OE**	1145	612	533	296	58	74	100	84	126	132	152	71	52
O	**OW**	962	559	403	262	32	42	94	129	155	90	52	74	32
O	**ON**	934	512	422	190	84	64	90	84	87	48	77	110	100
MN	**MN**	6174	4030	2144	1267	801	707	652	603	541	603	419	253	328
MN	**MPB**	3929	2570	1359	1230	482	324	265	269	508	398	171	162	120

Inter-Area Movements

An inter-area movement was considered to be any movement that crossed the stock boundary between Maui Nui and O‘ahu, regardless of direction. Inter-area movements were described at the individual level and summarized seasonally, as well as identified on both the residency class and subarea social networks to explore social connections.

Satellite Tags: Movements and Spatial Use

LIMPET satellite tags (Wildlife Computers, SPOT6 or SPLASH10-A) were deployed on seven bottlenose dolphins, once off O‘ahu, and six times off Maui Nui, in accordance with protocols described elsewhere (Schorr et al., 2009). One of the tags deployed off Maui Nui failed on deployment and yielded no locations.

Satellite tag data processing was performed following established internal protocols (e.g., Baird et al., 2021). Briefly, location data were processed by Argos with the Kalman smoothing algorithm (Lopez et al., 2015), then with a Douglas-Argos filter through Movebank (Kranstauber et al., 2011) to clean the location data of any apparent errors based on a realistic measure of speed, with higher-quality locations (Argos location-quality 2 or 3) exempt from filtering (Douglas et al., 2012). The user-defined settings of the Douglas-Argos filter set the maximum sustainable rate of movement (MINRATE) at 20 km per hour, the maximum distance between consecutive locations (MAXREDUN) at 3 km, and the tolerance for turning (RATECOEF) at 25. Previously conducted CRC distance analyses have shown that none of the animals moved in concert while tags were deployed, so pseudoreplication of location data was not a concern (CRC, unpublished data).

The distribution of depths was determined for all tagged individuals, using the depths of all Douglas-filtered locations between 0 and 1,000 m bathymetric depth. Significant differences in depth preferences between the tagged individuals were tested for with a Kruskal-Wallis ranked sums test, in conjunction with Dunn’s test.

Interchange Indices

Dispersal rates were calculated as the interchange index both between areas and subareas, based on the methods of Urbán et al. (2000). Interchange indices increase when populations are small, as well as when there is a high degree of movement between areas, and decrease when populations are large or there is minimal movement between areas. First, to contextualize the interchange indices, within-area re-sighting indices were calculated as:

$$RWA = (NR / (NA^2)) \times 1{,}000$$

where RWA is the within-area or within-subarea re-sighting index, NR is the number of animals re-sighted over multiple years within the area or subarea, and NA is the total number of animals seen in an area. Interchange indices were then calculated as:

$$RAB = (NAB / (NA \times NB)) \times 1{,}000$$

where RAB is the interchange index for areas A and B, NAB is the number of animals sighted in both areas, NA is the total number of animals sighting in area A, and NB is the total number or animals sighted in area B. Interchange indices that fall within the same magnitude as within-area re-sighting rates for the corresponding areas indicate that movements between areas are just as likely as movements within-areas, and are especially significant.

Results

Survey Effort, Quality Control, and Photo-Identification

From 2000-2018, CRC conducted 588 hours and 9,626 km of survey effort off O‘ahu, and 969 hours and 14,021 km of survey effort off Maui Nui (Figure 1). From 1996-2018, PWF conducted 7,488 hours and 48,112 km of survey effort off Maui Nui (Figure 1). Survey effort was heavily biased towards the leeward sides of the islands, owing to restrictions caused by weather conditions on the windward side, but covered a wide range of depths and potential habitats. During this time, bottlenose dolphins were encountered by CRC and PWF on 18 occasions off O‘ahu and on 265 occasions off Maui Nui. When restricted to the number of photographed encounters with at least one individual of photo quality score ≥ 3 and distinctiveness score ≥ 3, these numbers drop to 14 encounters off O‘ahu, and 221 encounters off Maui Nui. From 2000-2018, other researchers and community scientists have also contributed photos from 528 encounters with bottlenose dolphins to CRC. When these are restricted to the number of encounters with at least one individual with a photo quality score ≥ 3 and a distinctiveness score ≥ 3, 234 encounters from O‘ahu and 136 encounters from Maui Nui were retained.

GPS locations were available for all but two CRC encounters off Maui Nui (97% of all retained CRC encounters), and 140 of the PWF encounters (89% of all retained PWF encounters), but were not available for most contributed encounters. Overall, of the total 605 encounters in the entire dataset, 292 (48%) had corresponding GPS locations, most off Maui Nui (89% of all encounters with GPS data; Figure 2). Among the encounters with associated GPS location data, depths for encounters off Maui Nui ranged from 1 m to 1,629 m, and off O‘ahu from 3 m to 872 m. However, encounters were heavily skewed in favor of shallower waters, with the vast majority (96%) of encounters taking place at depths < 500 m.

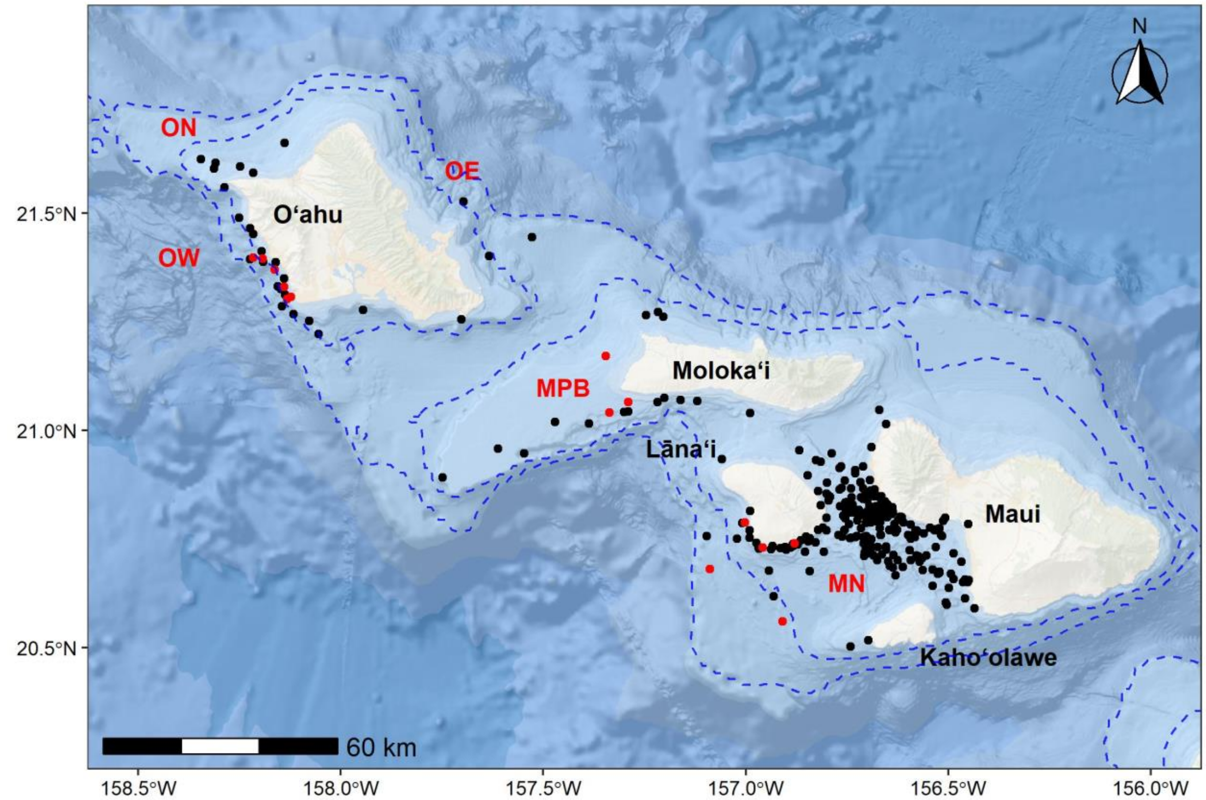


Figure 2. Encounter locations and subareas. Encounter locations are represented by black dots, with encounters where inter-area individuals were present shown as red dots. Subareas are abbreviated in red, with ON for O‘ahu North, OW for O‘ahu West, OE for O‘ahu East, MPB for Moloka‘i/Penguin Bank, and MN for Maui Nui (subarea). Subarea divisions based on depth (O‘ahu West Deep, O‘ahu East Deep, and Maui Nui Deep) are not shown. Depth contours (blue dashed lines) are shown at 500 m and 1,000 m.

Group sizes, restricted to CRC encounters for consistency, were larger off O‘ahu (mean=12.8, sd = 10.4, min = 1, max = 40), than off Maui Nui (mean=6.1, sd = 4.4, min = 1, max = 18). Based on Shapiro-Wilk tests, group sizes for O‘ahu were normally distributed (Shapiro-Wilk test, $p = 0.061$), but were not off Maui Nui ($p < 0.001$). A Mann-Whitney U-test (given the mixed results regarding normality) indicated that group sizes were significantly different between the two areas ($p = 0.008$).

Without restrictions there were 3,278 total identifications, representing 775 individuals from 748 encounters. When restricted by photo quality and distinctiveness there were 1,830 total identifications from 605 encounters, representing 472 individuals. Of these, 947 identifications (representing 285 individuals) from 248 encounters were off O‘ahu, and 883 identifications (representing 201 individuals) from 357 encounters were off Maui Nui.

The discovery curve for Maui Nui is approaching an asymptote, indicating comprehensive sampling (Figure 3). In contrast, the discovery curve for O‘ahu has mostly started to level off, but continues to rise and is higher overall, indicating a continued influx of new IDs in spite of fair sampling effort (Figure 3).

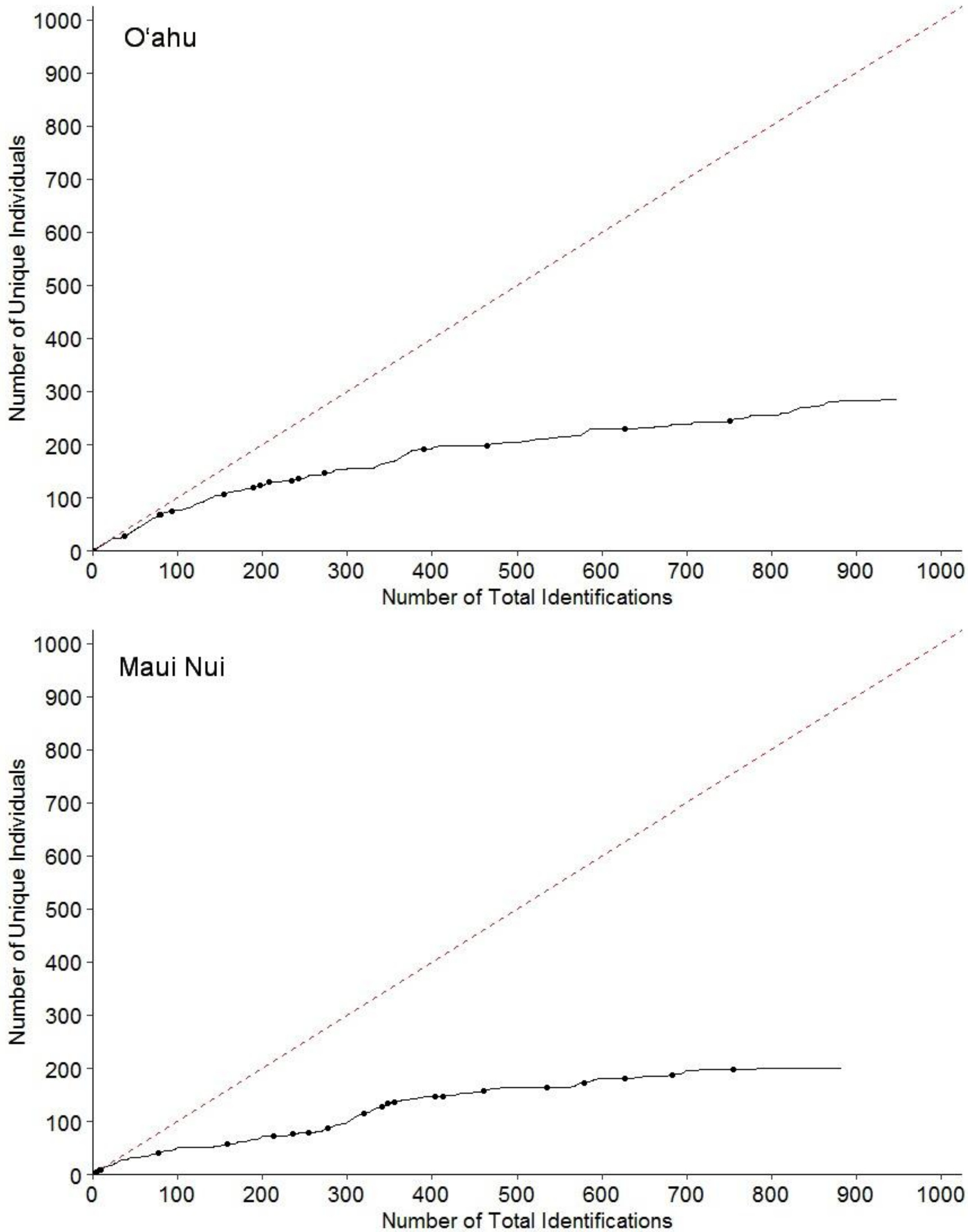


Figure 3. Discovery curves of individuals by island area, restricted to distinctive or very distinctive individuals with good or excellent quality photographs, with a reference 1:1 dashed trendline shown in red. Curves are constructed chronologically, with black dots showing the start of each year. Top: O'ahu (2002-2018). Bottom: Maui Nui (1996-2018).

Residency Assignments and Social Networks

Island areas where individuals were encountered were mapped onto a social network of all 472 individuals included in the study, along with one tagged individual who did not meet minimum distinctiveness or photo quality requirements, to evaluate initial impressions of connectedness between island areas (Figure 4). The entire network includes 6,360 ties linking the

473 individual nodes, and includes two easily identifiable main components that represent animals encountered largely off Oʻahu, and animals encountered off Maui Nui. When restricted to the main components, there are 5,970 ties connecting 381 nodes. Only three ties (representing < 0.1% of all ties in the network) link the main Oʻahu and Maui Nui components. There are 17 peripheral clusters including more than one connected individual, and 16 individuals that are unconnected to any other individuals on the network. Of the 16 individuals unconnected to any other animals in the network, eight were encountered by themselves.

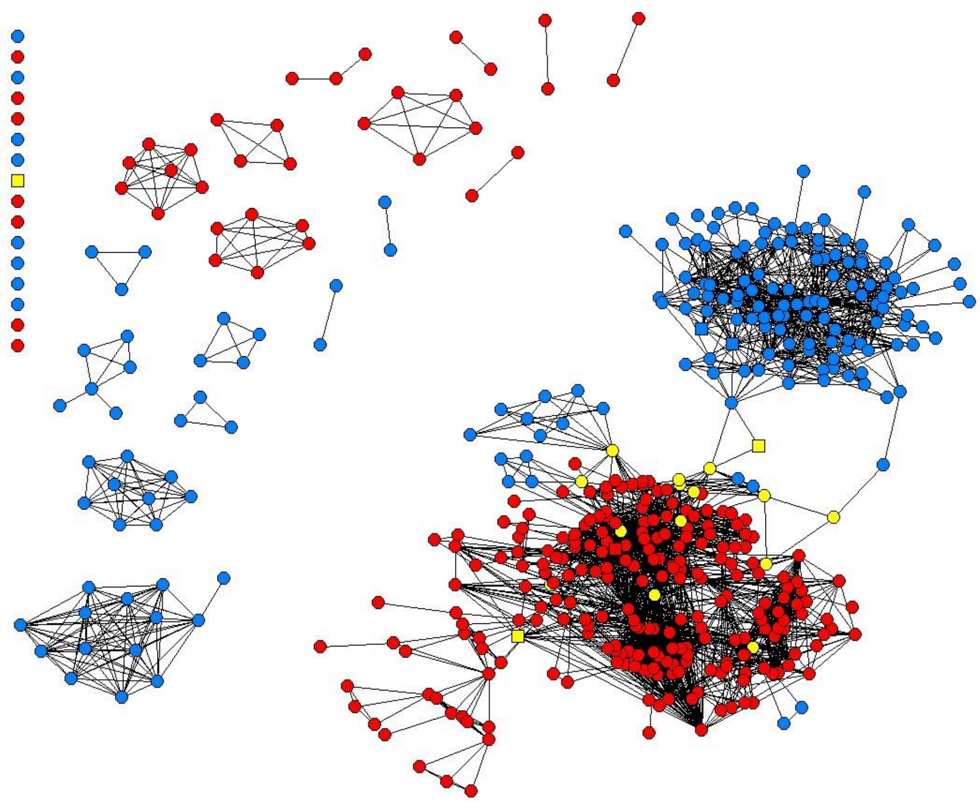


Figure 4. Social network with island areas of the individual nodes indicated by color, restricted to distinctive or very distinctive individuals with good or excellent quality photographs. All individuals with no included associations with other animals are shown in the upper left corner. All tagged animals (n=6), regardless of distinctiveness or photo quality, are represented as square nodes. Red nodes are animals encountered only off Oʻahu, blue nodes are animals encountered only off Maui Nui, and yellow nodes are animals encountered in both island areas. One isolated tagged individual (seen on the upper left) recently linked to the Oʻahu cluster through partially matched photos (see section below on tagged animals for details) has been color coded as an inter-area individual in this figure for illustrative purposes.

Revised residency assignments are summarized in Table 2. Briefly, 152 of the 190 Oʻahu visitors were reassigned as Oʻahu associative residents on the basis of their connection to the main Oʻahu component of the network, along with the 16 of the 95 Maui Nui visitors that linked most closely to the Oʻahu cluster through connections with inter-area individuals. These results were also mapped onto the same social network diagram as the initial residency assignments (Figure 5). All Maui Nui long-term residents were connected to one another in the social network, along with all but two Maui Nui short-term residents. Oʻahu long-term residents were not all directly connected to one another, with a single long-term and a single short-term resident in peripheral clusters.

Table 2. Revised residency assignment results by island area. Percentages indicate the proportion of the total number of unique identified individuals from all island areas combined, rounded to the nearest integer.

Island Area	Total # (%) of Individuals	# (%) Long-Term Residents	# (%) Short-Term Residents	# (%) Associative Residents	# (%) Visitors
O‘ahu	288 (61%)	59 (13%)	22 (5%)	169 (36%)	38 (8%)
Maui Nui	171 (36%)	66 (14%)	26 (6%)	29 (6%)	50 (11%)
Inter-Area	14 (3%)	-	-	-	-
All Island Areas	**473**	125 (26%)	48 (10%)	198 (42%)	88 (19%)

Most individuals in the peripheral clusters were visitors, with two exceptions: HITt1145, classified as an O‘ahu long-term resident, and HITt1169, classified as an O‘ahu short-term resident. HITt1145 was first seen in 2008, then again in 2018, both times in the company of a single O‘ahu visitor. HITt1169 was first seen in 2016 by itself, then again in 2017 in the company of three other individuals, all of whom are O‘ahu visitors.

All inter-area individuals clustered most closely with the O‘ahu component, and only represented a link between the two main components three times. These three links were identified as HITt1095 (seen three times off Maui Nui in 2012, 2014, and 2017, and once off O‘ahu), HITt1096 (seen only once off Maui Nui in 2017), and HITt1152 (seen once off Maui Nui in 1997, and twice off O‘ahu in 2015 and 2016). Additionally, several Maui Nui visitors clustered more closely with the O‘ahu component than the Maui Nui component. When inter-area individuals were filtered out of the social network, the two main components were completely separated, and all Maui Nui visitors that clustered with the O‘ahu component became isolated from both main components.

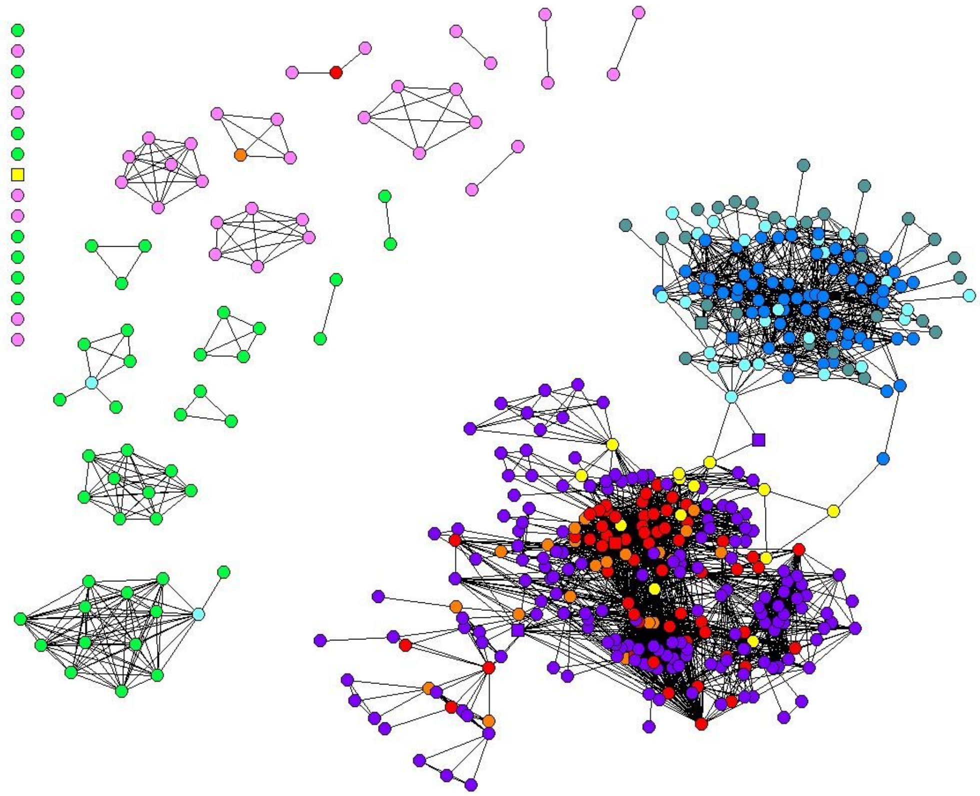


Figure 5. Social network with revised residency assignments of the individual nodes indicated by color, restricted to distinctive or very distinctive individuals with good or excellent quality photographs. All individuals with no included associations with other animals are shown in the upper left corner. All tagged animals (n=6), regardless of photo quality or distinctiveness, are indicated by square nodes. Red nodes are Oʻahu long-term residents, orange nodes are Oʻahu short-term residents, purple nodes are Oʻahu associative residents, pink are Oʻahu visitors, blue are Maui Nui long-term residents, turquoise are Maui Nui short-term residents, teal are Maui Nui associative residents, green are Maui Nui visitors, and yellow are inter-area individuals. One isolated tagged individual (seen on the upper left) recently linked to the Oʻahu cluster through partially matched photos (see section below on tagged animals for details) has been color coded as an inter-area individual in this figure for illustrative purposes.

Subarea Stratification

Spatial stratification between subareas generally aligned with social relationships (Figure 6). Oʻahu North animals in particular clustered together almost entirely separate from the main Oʻahu cluster, connected by one individual, HITt1703, which was seen twice off Oʻahu in 2018, and only once with GPS coordinates recorded. Individuals seen in both the Oʻahu West and Oʻahu West Deep subareas were frequently intermixed with Oʻahu West individuals, though there was some peripheral partitioning of a few Oʻahu West Deep individuals within the main Oʻahu cluster. Individuals seen in the Molokaʻi/Penguin Bank subarea were generally located in peripheral clusters, though a few were located on the periphery within the main Oʻahu cluster, and deep within the Maui Nui cluster. Additionally, a couple of individuals with GPS locations in both the Molokaʻi/Penguin Bank and Maui Nui subareas acted as cutpoints between the Oʻahu and Maui Nui main clusters. These two individuals were identified as HITt0027 and HITt0070, both of whom were classified as Maui Nui long-term residents.

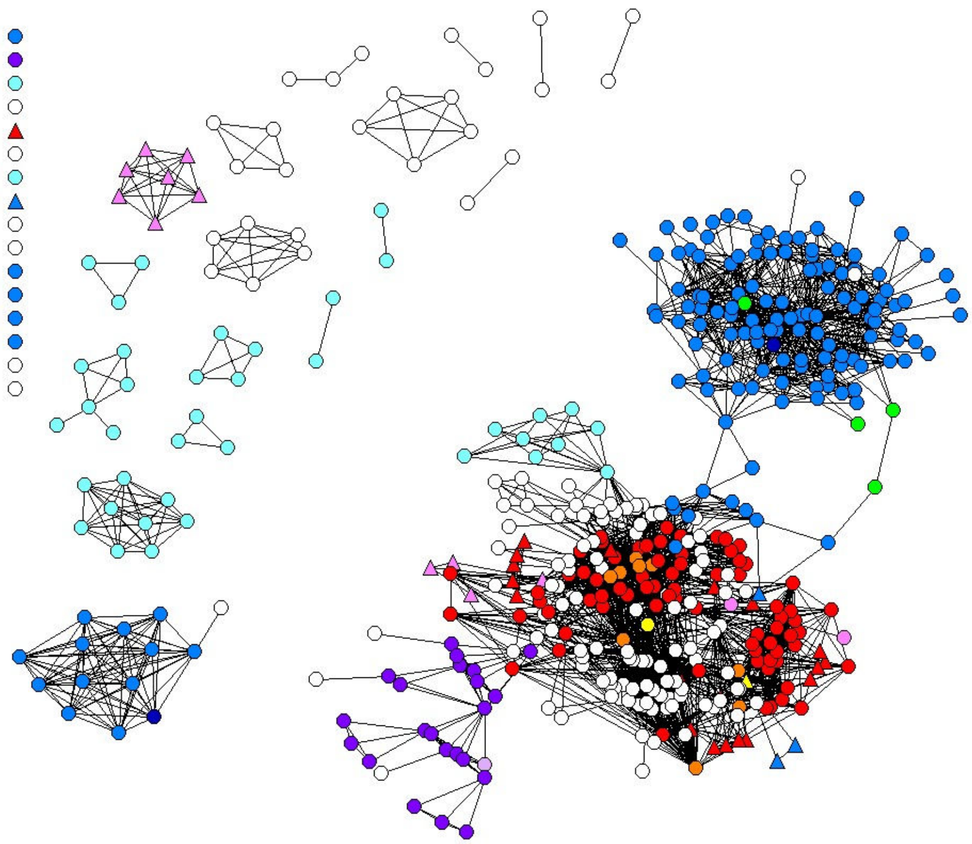


Figure 6. Social network with subareas where individuals were encountered indicated by color and shape, restricted to distinctive or very distinctive individuals with good or excellent quality photographs. All individuals with no included associations with other animals are shown in the upper left corner. Blue circles indicate the Maui Nui subarea (n= 140), dark blue indicate both the Maui Nui and Maui Nui Deep subareas (n=2), blue triangles indicate the Maui Nui deep subarea (n=4), turquoise circles indicate the Moloka‘i/Penguin Bank subarea (n=41), green circles indicate both the Maui Nui and Moloka‘i/Penguin Bank subareas (n=4), yellow circles indicate both the Maui Nui Deep and O‘ahu West subareas (n=1), yellow triangles indicate both the Maui Nui Deep and O‘ahu West Deep subareas (n=1), red triangles indicate the O‘ahu West Deep subarea (n=20), red circles indicate the O‘ahu West subarea (n=73), orange circles indicate both the O‘ahu West and O‘ahu West Deep subareas (n=9), light purple circles indicate both the O‘ahu North and O‘ahu West subareas (n=1), dark purple circles indicate the O‘ahu North subarea (n=23), pink circles indicate the O‘ahu East subarea (n=2), pink triangles indicate the O‘ahu East Deep subarea (n=11), and white circles indicate an individual lacking any GPS coordinates to assign subareas (n=142).

Based on encounters with recorded GPS locations, two individuals were sighted in subareas corresponding to two different stocks (Figure 7). Exchange between subareas within the same island area was repeatedly documented, most frequently between the O‘ahu West and O‘ahu West Deep subareas, with nine individuals documented in both subareas. Four individuals were documented in both the Maui Nui and Moloka‘i/Penguin Bank subareas, two individuals were documented in both the Maui Nui and Maui Nui Deep subareas, and one individual was documented in both the O‘ahu North and O‘ahu West subareas.

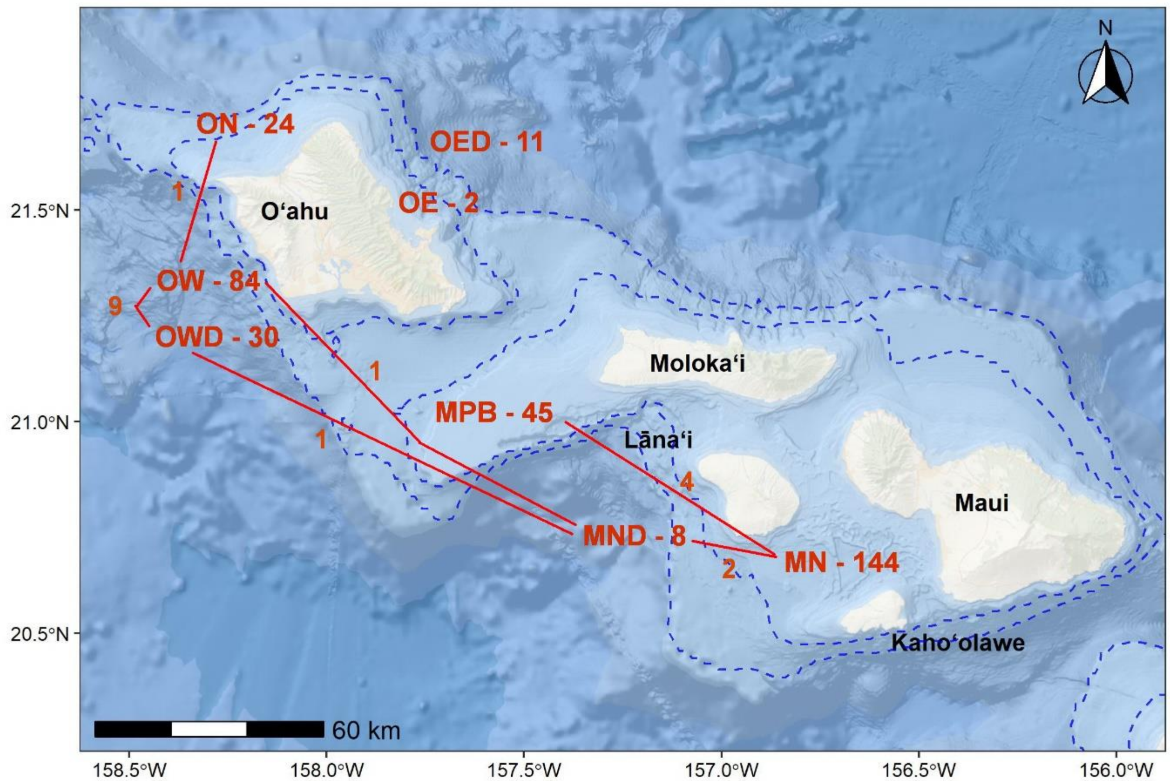


Figure 7. Map of subareas with the total number of animals identified within each subarea following the subarea abbreviation in red, and the number of individuals identified within both subareas adjacent to the red lines connecting subareas. Depth contours (blue dashed lines) are shown at 500 m and 1,000 m. ON = O‘ahu North, OW = O‘ahu West, OWD = O‘ahu West Deep, OE = O‘ahu East, OED = O‘ahu East Deep, MPB = Moloka‘i/Penguin Bank, MN = Maui Nui (subarea), MND = Maui Nui Deep.

Inter-Area Movements

Fourteen individuals were documented off both O‘ahu and Maui Nui based on photo-identification. Three of the 14 were sexed, all as females based on calf presence. The mean number of sightings for inter-area individuals was 4.4 (sd = 4.6), though the majority of re-sightings were often within the same island area. For example, HITt0518, (an adult female) was seen 20 times between 2006 and 2018, 19 times off O‘ahu, and once off Moloka‘i (in 2007). Of the inter-area individuals, six were sighted off O‘ahu in multiple years, and two were sighted off Maui Nui in multiple years. There were no strong seasonal trends to encounters with inter-area individuals (Table 3).

Encounters with inter-area individuals were more frequent off O‘ahu (Table 3). Eleven of 14 individuals were documented moving between island areas only once (e.g., moving from O‘ahu to Maui Nui), but three individuals moved between island areas more than once (e.g., moving from O‘ahu to Maui Nui and back to O‘ahu). The three individuals that moved between island areas more than once were HITt1095 (sighted first off Maui in December 2012, then off O‘ahu in June 2014, and twice again off Lāna‘i in November 2014 and March 2017), HITt1104 (first sighted twice off Oʻahu in June 2014 and February 2016, then off Lānaʻi in March 2017, and again off Oʻahu in November 2017) and HITt1439 (sighted first off Oʻahu in September 2012, then off Maui in December 2012 and off Lānaʻi in November 2014, and then again off Oʻahu in June 2017). The two inter-area individuals documented moving between islands in encounters with corresponding GPS locations were HITt0232 (sighted in the Maui Nui Deep subarea in 2002, then in the Oʻahu West Deep subarea in 2003) and HITt1104 (sighted first in the Oʻahu West subarea in 2016, then in the Maui Nui Deep subarea in March 2017, and then again in the Oʻahu West subarea in November 2017).

Table 3. Inter-area movements by season from photo-identification data. Percentages are of the total number of encounters for that particular island area and season, rounded to the nearest integer. IA = Inter-area.

Season	Total # Encounters off Oʻahu	# Encounters with IA off Oʻahu (%)	Total # Encounters off Maui Nui	# of Encounters with IA off Maui Nui (%)
Summer	126	21 (16.7%)	119	3 (2.5%)
Winter	122	16 (13.1%)	238	7 (2.9%)

Interchange Indices

Within-area re-sighting indices were 1.07 for Oʻahu, and 2.33 for Maui Nui, indicating that a higher proportion of individuals are re-sighted off Maui Nui than off Oʻahu, and reconfirming the earlier results of the discovery curves for these areas (Figure 3). The interchange index between island areas was 0.28, an order of magnitude below the Maui Nui and Oʻahu within-area re-sighting indices. This means that movement between the island areas does occur, but at much lower levels than within the island areas.

Within-area re-sighting indices by subarea for encounters with GPS coordinates ranged from 0 to 5.21 (Table 4). Sample sizes of re-sighted individuals were generally small due to limited availability of GPS coordinates, and were extremely small in subareas where there was limited sampling, including for the Oʻahu North, Oʻahu East, Oʻahu East Deep, and Molokaʻi/Penguin Bank subareas, all of which had three or fewer individuals re-sighted across multiple years. Some areas had low sample sizes of re-sighted individuals in spite of considerable effort however, including the Oʻahu West Deep and Maui Nui Deep subareas. The greatest number of within-area re-sighted individuals was within the Maui Nui subarea, with 88 out of 144 total individuals having re-sightings across multiple years. Even with the generally small sample sizes, however, movements between subareas were identified.

Interchange indices between subareas that were of the same or greater magnitude as both within-area re-sighting indices for those subareas were found for four pairs of subareas: Oʻahu West/Oʻahu West Deep, Oʻahu West/Maui Nui Deep, Oʻahu West Deep/Maui Nui Deep, and Maui Nui/Maui Nui Deep (Table 4). This indicates that movements between these pairs of subareas is as likely as movements within each of the subareas that compromise the pairs. Interchanges indices between subareas that were not of the same or greater magnitude as both within-area re-sighting indices for those subareas were calculated for two pairs of subareas: Oʻahu West/Oʻahu North, and Maui Nui/Molokaʻi/Penguin Bank. Movements between these pairs of subareas are therefore not as likely as movements within each of the individual subareas that comprise the pairs, but do still occur. The interchange indices between all remaining pairs of subareas were calculated to be zero, indicating that either no movement between those subareas takes place, or that movement is infrequent enough that it was never documented.

Table 4. Within-area re-sighting and interchange indices for individuals with designated subareas based on GPS coordinates. Re-sighting indices are based on the number of individuals seen across multiple years, and located along the diagonal. Interchange indices that are of the same magnitude as within-area re-sighting indices for both of the same subareas are shaded in grey. ON = Oʻahu North, OW = Oʻahu West, OWD = Oʻahu West Deep, OE = Oʻahu East, OED = Oʻahu East Deep, MPB = Molokaʻi/Penguin Bank, MN = Maui Nui (subarea), MND = Maui Nui Deep.

Subarea (# Within-Area Resighted Individuals, # Total Individuals)	**ON**	**OW**	**OWD**	**OE**	**OED**	**MPB**	**MN**	**MND**
ON (3, 24)	5.21	-	-	-	-	-	-	-
OW (12, 84)	0.49	1.70	-	-	-	-	-	-
OWD (1, 30)	0	3.57	1.11	-	-	-	-	-
OE (0, 2)	0	0	0	0	-	-	-	-
OED (0, 11)	0	0	0	0	0	-	-	-
MPB (2, 45)	0	0	0	0	0	0.99	-	-
MN (88, 144)	0	0	0	0	0	0.62	4.24	-
MND (0, 8)	0	1.49	4.17	0	0	0	1.74	0

Movements and Spatial Use of Tagged Individuals

Details on satellite tag deployments are presented in Table 5. Two of the tagged individuals were Maui Nui residents (one long-term (TtTag006 – HITt0788) and one associate (TtTag007 – HITt0794)), and are located within the main Maui Nui cluster of the social network (Figure 4). Both remained within the Maui Nui subarea, with movements between Maui and Lānaʻi for both, with HITt0788 moving briefly into the Molokaʻi/Penguin Bank subarea, and HITt0794 venturing into the Maui Nui Deep subarea briefly (Figure 8). Both individuals used relatively shallow water (Figure 9: TtTag006 mean=75 m (sd = 74 m); TtTag007 mean=78 m (sd = 151 m)).

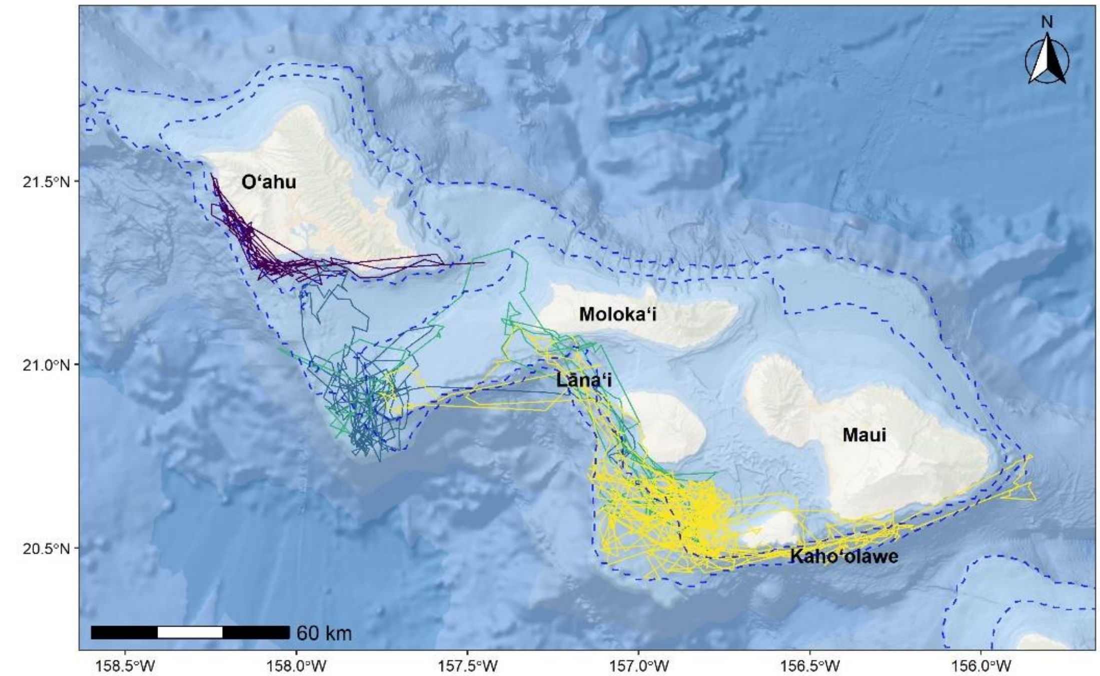
Two tags were deployed on Oʻahu residents within the main Oʻahu cluster of the social network (Figure 4), one on a long-term resident (TtTag030) tagged off Oʻahu, and one on an associative resident (TtTag036) tagged offshore of west Lānaʻi. HITt0604 (TtTag030) spent the duration of the tag deployment within the Oʻahu West and Oʻahu subareas, with most locations in the Oʻahu West subarea (Figure 8). HITt1643 (TtTag036), however, moved extensively while tagged, crossing from the Maui Nui and Maui Nui Deep subareas into the Molokaʻi Penguin Bank subarea. This animal also moved much further east than any other tagged individual, reaching past the east coast of Maui at one point, though the majority of locations were in the areas between Lānaʻi and Kahoʻolawe (Figure 8). Both of these individuals used a wide range of depths while tagged (Figure 9: TtTag030 mean = 373 m (sd = 212 m); TtTag036 mean = 484 m (sd = 273 m)).

Two tags, TtTag031 (HITt1094), TtTag032 (HITt1096) were deployed off west Lānaʻi onto animals that are more likely members of the Oʻahu stock, based on associations and movement patterns. Based on photos from 2020 that are only partially matched, HITt1094 has been linked with the Oʻahu cluster. While tagged, HITt1094 moved around extensively, crossing into the Oʻahu West, Oʻahu West Deep, Molokaʻi/Penguin Bank, Maui Nui Deep, and Maui Nui subareas, with the majority of locations taking place on the south end of Penguin Bank (Figure 8). HITt1096 is classified as an Oʻahu associative resident, and has only been encountered once, on the day when it was tagged. When it was encountered, it was seen with three other individuals, HITt1095, HITt1097, and HITt1098. HITt1098 was not assigned a residency class or included in the social network on account of a low distinctiveness score, but HITt1095 and HITt1097 were classified as an inter-area individual and a Maui Nui short-term resident, respectively. In the social network, HITt1096 occupies a location on the periphery of the Oʻahu and Maui Nui clusters, and represents one of the three links connecting the main clusters. While tagged, HITt1096 also moved around extensively, moving between the Maui Nui and Maui Nui Deep subareas, as well as the Molokaʻi/Penguin Bank and Oʻahu West Deep subareas (Figure 8). Both HITt1094 and HITt1096 spent a significant portion of their time in water ≥ 500 m (Figure 9: TtTag031 mean = 809 m (sd = 545 m); TtTag032 mean = 448 m (sd = 397 m)).

Tag location depths varied significantly between individuals (Kruskal-Wallis ranked sums test KW = 819.75, $p < 0.001$). Post-hoc pairwise comparison using Dunn's test with the Benjamini-Hochberg method revealed significant differences (p values <0.05) in tag location depths between almost all pairs, with the exception of TtTag006 and TtTag007.

Table 5. Summary of tag data when locations were obtained. Sex was determined for three individuals: HITt0788 (TtTag006) was identified as a male based on genetic analysis, HITt0604 (TtTag030) was identified as a female based on calf presence, and HITt1094 (TtTag031) was identified as a female based on morphology.

Tag ID	Individual ID	Date Tagged	Location Tagged	Depth Tagged (m)	Duration of Contact (Days)	# Douglas filtered locations
TtTag006	HITt0788	13-Dec-12	SE Lānaʻi	140	17.7	337
TtTag007	HITt0794	19-Dec-12	W Lānaʻi	93	9.0	130
TtTag030	HITt0604	17-Oct-16	W Oʻahu	479	13.0	230
TtTag031	HITt1094	07-Mar-17	Offshore W Lānaʻi	708	16.3	332
TtTag032	HITt1096	17-Mar-17	W Lānaʻi	72	13.0	246
TtTag036	HITt1643	02-Dec-20	Offshore W Lānaʻi	524	33.4	867



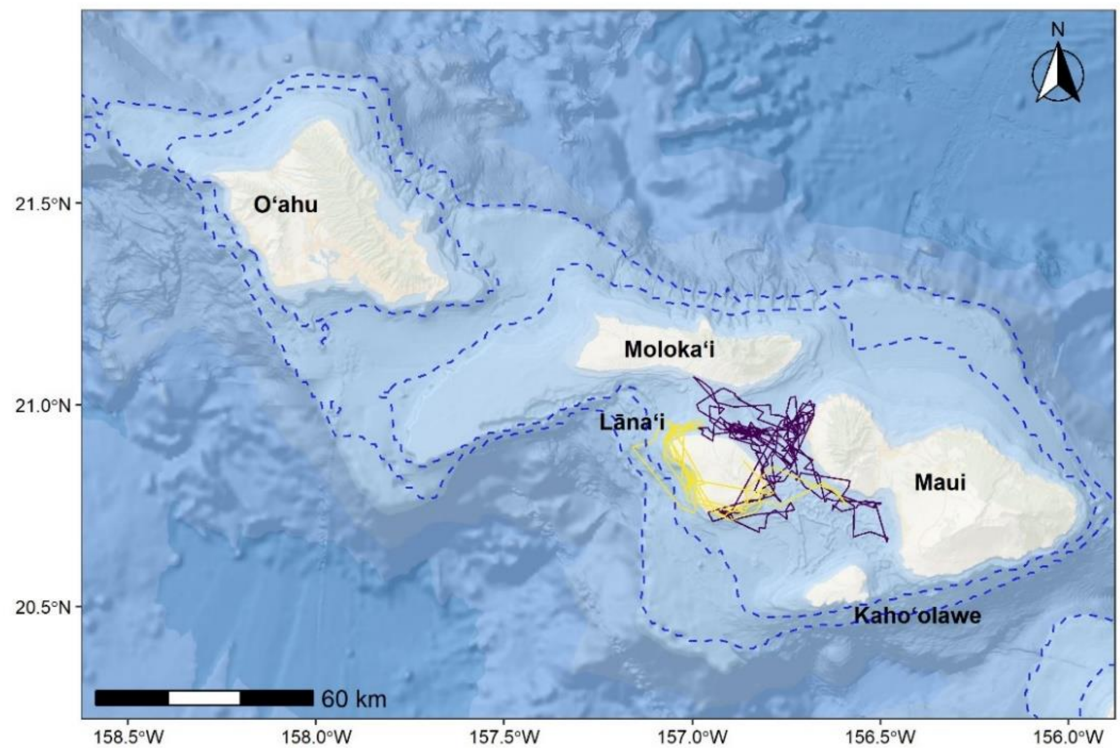


Figure 8. Douglas-filtered Argos tracklines of the four tagged individuals from the O‘ahu population (top), and two tagged individuals from the Maui Nui population (bottom). Top: TtTag030 - purple, TtTag031 - blue, TtTag032 - green, TtTag036 - yellow. Bottom: TtTag006 - purple, TtTag007 – yellow. Depth contours (blue dashed lines) are shown at 500 m and 1,000 m. See Table 5 for details on deployments.

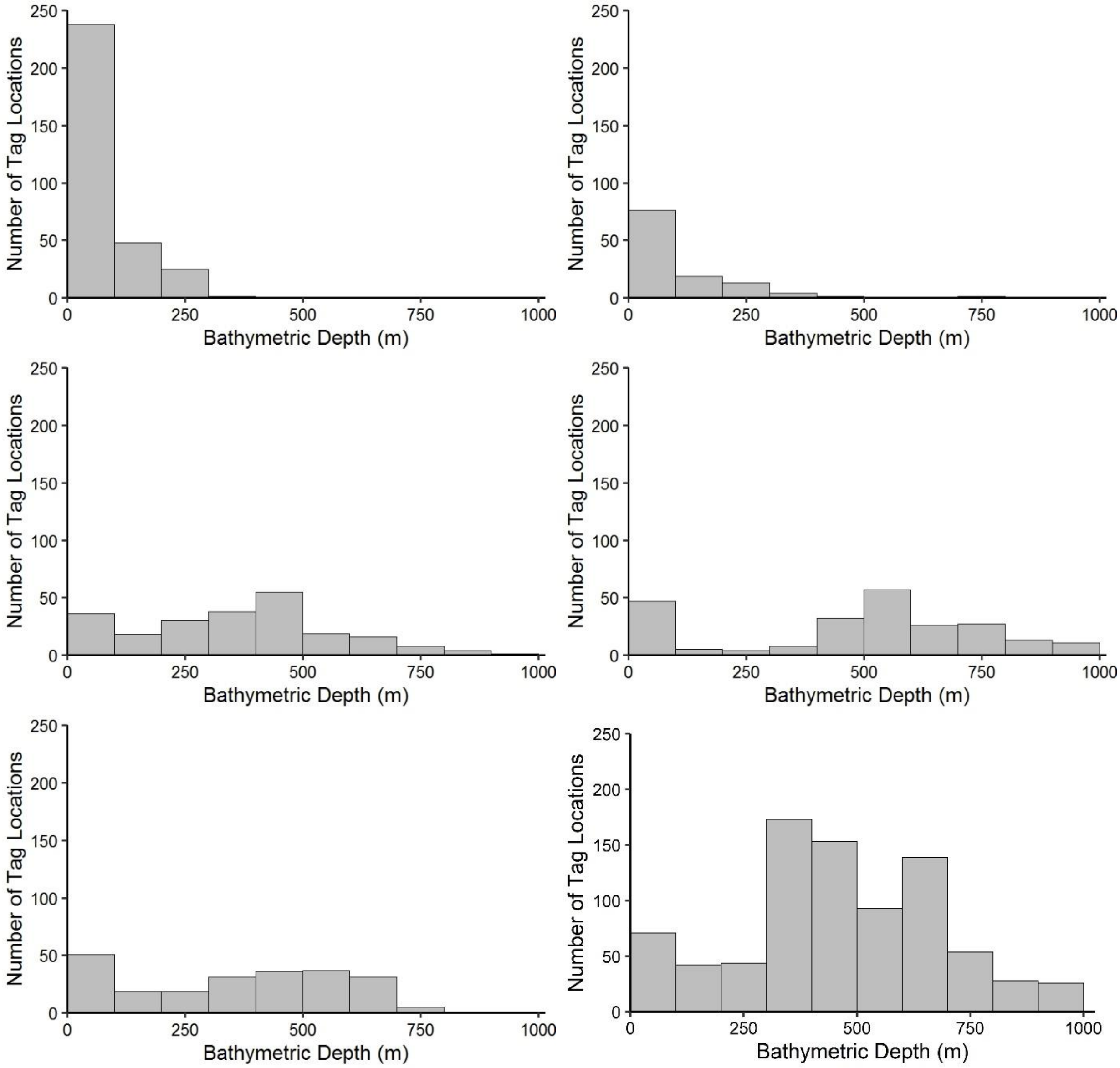


Figure 9. Range of depths from satellite tag data for five individuals. Top left: TtTag006. Top right: TtTag007. Middle left: TtTag030. Middle right: TtTag031. Bottom left: TtTag032. Bottom right: TtTag036. See Table 5 for details on deployments.

Discussion

We found that while social connections between the O‘ahu and Maui Nui populations of common bottlenose dolphins were minimal, there were important geographic overlaps in spatial use that crossed current stock boundaries. Based on photo-identification evidence, very few individuals (14 out of 472 animals included in this study, 3%) moved between island areas, all of which clustered within the main O‘ahu component in the social network (Figure 4; Figure 5). In spite of over two decades worth of data, and almost 400 identified animals with almost 6,000 links in the main components, inter-area individuals only connected the two main components three times. Inter-area travelers have associated with several individuals only seen once off Maui Nui, but without additional re-sightings and social association data for these animals it is impossible to confirm whether they are members of the Maui Nui stock, or travelers from the O‘ahu stock. Social associations between the stocks, even with occasional inter-area movements occurring, therefore appear infrequent at best. The fact that animals from separate stocks do not seem to interact aligns well with the results of Martien et al. (2011), which found significant genetic differentiation between the O‘ahu and Maui Nui stocks. Geographically, however, the areas used by inter-area animals does overlap with the areas used by Maui Nui residents, indicating that there is potential for interactions, and raising the question of why animals from different stocks do not interact.

A possible factor is the relative likelihood that separate groups of animals will encounter one another. The Maui Nui stock is small (and declining), with only an estimated abundance of 48-85 individuals (95% CI) in 2018 (Van Cise et al., 2021). The Maui Nui island area has over 10,000 km^2 of water between 0 and 1,000 m bathymetric depth, and over 6,000 km^2 of water between 0 and 500 m of bathymetric depth, so this low abundance should theoretically result in a very low density of bottlenose dolphins for the island area as a whole. Combined with the fact that inter-area movements have only been captured a handful of times through photo-ID, it seems unlikely that both an inter-area group and a Maui Nui group would happen to be in the same place at the same time, allowing them the opportunity to interact.

An alternative explanation is that even in circumstances which spatially allow for interactions, behavioral differences between groups may limit their ability or willingness to interact with one another. Encounter characteristics and tag data revealed behavioral differences between animals in different island areas, lending weight to this explanation. Similar situations have been documented with different ecotypes of killer whales in the nearshore waters of the temperate eastern North Pacific, where in spite of sympatry between mammal-eating and fish-eating populations, the two ecotypes do not interact because of behavioral differences (Baird et al., 1992). Similar to the different killer whale populations, group sizes also significantly differ between the O‘ahu and Maui Nui stocks, suggesting that there is at least some degree of behavioral differentiation between the two.

Additionally, satellite tag data reveals significant differences in depth preference between the tagged individuals from the two populations. The two tagged animals that are positioned within the main Maui Nui component of the social network remained exclusively in shallow water, never venturing beyond 500 m depth, while in contrast the single animal tagged off O‘ahu and the remaining three tagged animals from Maui Nui frequently ventured into deeper waters (Figure 8; Figure 9). The three tags from Maui Nui that do not cluster with the main Maui Nui component are more likely inter-area animals from the O‘ahu stock than members of the Maui

Nui stock based on their associations and movement patterns[2], explaining the differences between the distributions of their tag location depths and those of the other two animals tagged off Maui Nui. The similar depth distribution between their tag locations and that of the single tagged Oʻahu animal lends further support to the idea that they are inter-area animals, as all inter-area individuals are clustered within the Oʻahu component of the social network and appear to represent a subset of this stock (Figure 4). However, tag data is inherently short-term, and caution must be used in interpreting these results. Through photo-identification, we found that interchange between shallow and deep water subareas was generally high, with interchange indices demonstrating that movements between Oʻahu West and Oʻahu West Deep, as well as between Maui Nui and Maui Nui Deep were just as likely as movements within each of those subareas (Table 4). Movements were not detected between the Oʻahu East and Oʻahu East Deep subareas, but sample sizes in these subareas were small, limiting the ability to accurately assess movements. This suggests that most bottlenose encounters in deep water (at least up to 1,000 m bathymetric depth) likely do not represent different populations or social groups, but are occasional excursions of the same resident populations that typically prefer shallow water. Crucially, the significant interchange between the Maui Nui and Maui Nui Deep subareas revealed by photo-identification and interchange indices suggests that members of the Maui Nui population do in fact make use of deep water, something which the tag data failed to capture (Table 4). In general, however, the findings of this study indicate that Oʻahu and inter-area animals tend to use deep water more regularly than Maui Nui animals. This may be a behavioral adaptation indicative of ecological niche specialization, though to some degree this may also reflect the greater total area of shallow water habitat around Maui Nui compared to Oʻahu (Table 1). Further research will be needed to explore whether there are additional behavioral differences between the two stocks, such as different vocalization or communication patterns or unique foraging specializations, which might help to explain the lack of social interactions between these stocks.

Both CRC and PWF effort and contributed encounters were heavily biased towards the leeward sides of the islands due to weather conditions, likely excluding bottlenose that primarily use the windward sides (Figure 2). The few encounters from the windward sides (six from north Oʻahu, and three from east Oʻahu, as well as the three encounters from north of Molokaʻi) were comprised of animals that were seen only in those areas, with the single exception of an animal seen off both north and west Oʻahu. Furthermore, animals from these subareas cluster together, largely separate from the main components in the social network (Figure 6). This suggests that additional groups of bottlenose dolphins are present on the windward sides of the islands that are largely isolated from the leeward side groups, and may therefore be demographically independent. Future survey efforts in these areas would be beneficial in understanding whether windward side groups exist, and if so, what their relationships to the leeward side groups are.

Dividing the island areas into subareas allowed for a more detailed analysis of population structure and spatial use, and also helped to identify areas where encounter rates were low or survey coverage was poor. Perhaps unsurprisingly given the small calculated mean inter-annual travel distances calculated in previous analyses (Van Cise et al., 2021), social stratification aligned well with spatial stratification between subareas (Figure 6). Satellite tag data also revealed spatial stratification among tagged resident animals from the main island area clusters, with the two Maui Nui residents generally remaining within shallow waters around Maui and

[2] Subsequent to the photo-analyses presented here this individual has been linked by association with the Oʻahu cluster (CRC unpublished).

Lānaʻi, and the Oʻahu resident remaining in the waters around west and south Oʻahu (Figure 8). These three tagged individuals and the majority of our long-term photo-identification data demonstrate that Hawaiian resident bottlenose dolphins generally have strict site fidelity, as previously reported by Baird et al. (2009), supported by Martien et al. (2011), and later confirmed by Van Cise et al. (2021). This is likely behaviorally driven by distinct habitat preferences. Different subareas have unique degrees of open-ocean exposure, total areas, and different expanses of nearshore habitat that could favor niche specialization, as has been observed in other bottlenose dolphin populations worldwide (Hoelzel, 2009). Over a long time period, the limited mobility of Hawaiian bottlenose, in conjunction with their social and spatial stratification, may continue to gradually increase the genetic and cultural differentiation between groups. Already, the populations between island areas are genetically differentiated (Martien et al., 2011), and future work to investigate how genetic haplotype ratios differ between subareas would be informative.

Residency assignments revealed similar numbers of long- and short-term residents for both island areas, though there were almost six times as many associative residents in the Oʻahu island area compared to the Maui Nui island area. The greatest numbers of both long- and short-term residents were found in the Oʻahu West and Maui Nui subareas. This is unsurprising given that these subareas had both the greatest survey coverage and numbers of encounters, and improved survey coverage increases the likelihood of repeated encounters with the same individuals, allowing for a better assessment of how long individuals remain in a particular area. In contrast, the Oʻahu East, Oʻahu East Deep, Oʻahu North subareas, all with poor coverage, have low numbers of long- and short-term resident animals compared to the number of associative residents and visitors. Interestingly, the Molokaʻi/Penguin Bank subarea had the greatest number of visitors and one of the lowest re-sighting rates, in spite of having the second-largest number of encounters within the subarea, and the third largest number of total identified individuals.

Within the social network, two large main components representing the two main island areas were easily distinguishable, along with several peripheral clusters (Figure 4). Of the 473 total animals included in the study, 381 (81%) individuals are part of the main components, while 92 (19%) individuals are part of the peripheral clusters. Almost all long- and short-term residents clustered within the main components, while the peripheral components were comprised almost entirely of visitors (Figure 5). This is not unexpected, as their limited number of re-sightings reduces the number of social relationships represented in the network. Peripheral clusters may therefore be an artifact of inadequate sampling, but it is also possible that they represent visiting dolphins from the pelagic stock, or from Kauaʻi or Hawaiʻi Island, though no such movements have been identified to date through photo-identification studies (Baird et al., 2009; CRC, unpublished data). In terms of spatial use, most peripheral clusters were comprised of individuals identified in the Molokaʻi/Penguin Bank subarea, though Molokaʻi/Penguin Bank animals were also identified in both main components (Figure 6). Connections to the Maui Nui component seem to be an artifact of the way that the subareas were drawn, however. HITt0075 and HITt0437 (the two Molokaʻi/Penguin Bank subarea animals deeply embedded within Maui Nui component), and HITt0070 and HITt0027 (the two Molokaʻi/Penguin Bank animals connecting the Oʻahu and Maui Nui components) were all encountered in the easternmost portion of the Molokaʻi/Penguin Bank subarea, directly adjacent to the boundary of the Maui Nui subarea. Revised subarea boundaries may counter this effect, and further division of the Maui Nui and Molokaʻi/Penguin Bank subareas should be considered in future work. The connections to the O‘ahu component cannot be explained by subarea boundaries however, suggesting that they are not artifacts of study design.

The large number of associative residents within the O‘ahu island area is particularly striking given how similar the relative numbers of other residency classes are for both island areas (Table 2). All of these individuals are connected to the main O‘ahu component of the social network, and of similar morphology to the other animals present around O‘ahu (CRC, unpublished data), so they are likely not visiting offshore groups, but members of an inshore population. Additionally, most associative residents were identified in either the O‘ahu West or O‘ahu West Deep subareas, which were heavily surveyed. These animals have all only been seen over time spans of less than one year however, so they are either visitors from less frequently surveyed O‘ahu subareas, or are not resident to the island at all. This raises the question of what draws these individuals to the more heavily surveyed O‘ahu West subarea. One possible explanation is that the associative residents utilize certain areas of O‘ahu with high survey coverage (such as the west coast of O‘ahu) as shallow-water travel corridors on their way to somewhere else with lower survey coverage, and mingle along the way with the resident animals that use the area more consistently. This would explain the limited re-sightings of these individuals and provide a possible explanation for the larger group sizes encountered off O‘ahu. This still begs the question, however, of where these animals are coming from and where they are going. Additional tagging efforts dedicated to non-resident animals off O‘ahu may shed light on the identity and spatial use of these individuals.

In spite of the lack of social interactions between stocks, there is clearly spatial overlap, driven by the inter-area travelers. Compared to other island areas in the main Hawaiian archipelago, connectivity between the O‘ahu and Maui Nui areas is quite good for bottlenose dolphins. The channel between Hawai‘i and Maui Nui is almost 2,000 m deep and 28 km across, and the channel between O‘ahu and Kaua‘i exceeds 3,000 m depth and is 116 km wide. While distance is not necessarily an issue in that bottlenose dolphins are physically capable of travelling long distances (e.g., Wells et al., 1999), most bottlenose in the main Hawaiian Islands have fairly limited movements (Figure 8; Baird 2016). Additionally, as previously discussed, bottlenose show a distinct preference for shallow water, and especially water under 200 m bathymetric depth. This suggests that movements across the larger channels are very unlikely, given that bottlenose dolphins are not likely to travel that far or traverse into such deep waters. Only one movement of a tagged individual between Kaua‘i and O‘ahu has been documented in the two decades that CRC has studied bottlenose in the Hawaiian Islands (Baird, 2016), supporting this conclusion. In contrast, the Ka‘iwi channel between O‘ahu and Maui Nui presents a much less significant barrier to movement. It reaches only ~700 m depth, and is 42 km wide. Also, the much shallower depth does fall below the depths of the observed tag locations for four out of the six tagged animals from Maui Nui and O‘ahu (Figure 9), and three encounters with GPS locations that were included in this study.

As previously mentioned, all of the inter-area travelers identified through photo-identification clustered with the main O‘ahu component in the social network, yet utilized both island areas. Encounters with GPS locations where inter-area animals were identified were centered around southwest O‘ahu, southwest Moloka‘i, and southwest Lāna‘i (Figure 2). Interchange indices based solely on photo-identification data with GPS locations also revealed that movements between the O‘ahu West/O‘ahu West Deep subareas and the Maui Nui Deep subarea were just as likely as movements within each of these areas (Table 4). Furthermore the three satellite tags deployed on suspected or confirmed inter-area animals (TtTag031, TtTag032, and TtTag036) also made use of south O‘ahu, southwest Moloka‘i, southwest Lāna‘i, west Kaho‘olawe, and even south Maui. These tagged animals also made extensive use of Penguin Bank, hinting that this area may also be of importance to inter-area travelers (Figure 8). Combined, these data indicate that the inter-area travelers seem to have a much larger range than the current O‘ahu stock boundaries, extending from southwest O‘ahu, across Penguin Bank and southwest Moloka‘i and Lāna‘i to the southern coast of Maui. However, this range does not seem to extend into the more insular waters between western Maui and eastern Lāna‘i, where the vast majority of encounters with Maui Nui stock members are concentrated. Given the relative spatial use of the inter-area travelers versus the Maui Nui residents, future research should incorporate revisions to the subarea boundaries (i.e., breaking the Maui Nui subarea down into Maui Nui West and Maui Nui East subareas) to explore movement patterns with a more refined lens.

The forces driving inter-area movements in the Hawaiian Islands remain unclear, but may be related to limited resource availability. The O‘ahu West subarea is comparatively small (962 km^2 of water between 0 and 1,000 m bathymetric depth), especially along the western coast where there is only a narrow band of shallow-water habitat (559 km^2 of water between 0 and 500 m bathymetric depth; Table 1). The limited availability of shallow-water habitat in the subarea may not have enough resources to sustain the O‘ahu West animals, especially with the constant influx of visiting animals that was previously discussed. It is possible, therefore, that these animals are occasionally forced to travel greater distances to locate foraging opportunities, driving inter-area movements. Similar circumstances have been identified among bottlenose dolphins in the Azores, where the average distance between sightings in 25 km, but movements of up to 291 km are repeatedly detected and hypothesized to be driven by limited prey availability (Silva et al., 2008). Other possible explanations of inter-area movements, including male sex-biased dispersal (e.g. Wells et al., 1987) or seasonal migration seem unlikely, as the three sex-identified inter-area animals are females and there is no easily discernable seasonal trend to inter-area movements. Continued research will be required to identify the ecological drivers of this behavior.

Conclusion

Though somewhat constrained by uneven sampling across subareas, the broader patterns revealed by this study point towards several interesting conclusions that bear relevance for current stock boundaries. Despite extensive sampling over a 20-year period, we found that there are limited social connections between the O‘ahu and Maui Nui island areas, which accounts for the significant genetic differentiation between stocks revealed by Martien et al. (2011). However, in spite of the limited social connections between stocks, there are important geographic overlaps across stock boundaries. These overlaps are caused by a subset of the O‘ahu population that moves between island areas, using an expanded range that includes southwest O‘ahu, Penguin Bank, southwest Moloka‘i, the west and southwest coasts of Lāna‘i, the west and south coasts of Kaho‘olawe, and even the south coast of Maui. These findings demonstrate that current stock boundaries may be inadequate for the O‘ahu stock, as they fail to account for exposure to any anthropogenic threats off Maui Nui. However, the proportion of the O‘ahu stock that uses this extended range and the ecological cues that drive this behavior remain unclear, and continued research will be required to address these factors. Continued research should also focus on subareas with minimal coverage, such as O‘ahu North and O‘ahu East, where social stratification in conjunction with spatial stratification suggests the possibility of additional demographically-independent populations of bottlenose dolphins.

Finally, the use of multiple datasets provided a much more robust understanding of the dynamics of movements, highlighting a general need to use multiple, long-term approaches in assessing population structure. While genetic and photo-identification data initially suggested that animals rarely move across the Ka‘iwi channel (Baird et al. 2009; Martien et al. 2011), our larger and longer photo-identification dataset and the inclusion of satellite tag data captures a larger range of movement behaviors that indicate current stock boundaries are inadequate for the O‘ahu stock. Continued reassessment of the population structure and movements of these animals should be undertaken to test the accuracy of previous work, and ensure the effectiveness of current management strategies to preserve these populations.

Acknowledgements

Research was conducted under permits 926, 731-1509, 731-1774, 15330, and 20605 issued to Robin W. Baird, and 13427 and 18101 issued to PWF. Funding for CRC’s efforts to study Hawaiian common bottlenose dolphins was provided by several groups, including the Pacific Islands Fisheries Science Center, the State of Hawai‘i, the NOAA Bycatch Reduction Engineering Program, Dolphin Quest, and the Southwest Fisheries Science Center. Funding for PWF’s research program was provided by PacWhale Eco-Adventures, the members of Pacific Whale Foundation, and a number of individual donors. We thank the many staff, interns, and volunteers who contributed to PWF’s and CRC’s odontocete projects over the years. Genetic analysis of biopsy samples was carried out at the Southwest Fisheries Science Center under the supervision of Karen Martien. Special thanks to Sabre Mahaffy, Enrico Corsi, and Michaela Kratofil for assisting in several aspects of this project. Our thanks for those who contributed photographs: Paul Johnson, Jim Ault, the Hawaiian Islands Humpback Whale Sanctuary (permits 1000-1617, 774-1437, 774-1417, 782-1438, 782-1719), Chuck Babbitt, Kim Wood, Dan Salden, Brittany Guenther, the Pacific Islands Fisheries Science Center (permits 20311, 15240, 774-1714), Becca Johnston, The Dolphin Institute, Tiffany Morgan, the Oceanwide Science Institute (permits 782-1438, 782-1719), Alison Stimpert, Andrea Bendlin, Alexis Rudd, Carlie Wiener, Doug Perrine, the Kaho‘olawe Island Reserve Commission, Mark Deakos, Robin Ernst, the University of Hawai‘i, Alexa Vitek, Alicia Franco, the Center for Whale Studies, Dani Kleinhenz, Don McLeish, Pete Donaldson, Eden Zang, Marc Lammers, Tammy Silva, Heather Harris, Heide Weber, Katie Grove-Velasquez, Paul Nachtigall, Shannon Harrison, Shaylene Curtis, and Sierra Bertini.

References

Baird, R.W. (2016). The Lives of Hawai‘i’s Dolphins and Whales: Natural History and Conservation. University of Hawai‘i Press.

Baird, R. W., Abrams, P. A., & Dill, L. M. (1992). Possible indirect interactions between transient and resident killer whales: implications for the evolution of foraging specializations in the genus Orcinus. *Oecologia, 89*(1), 125-132.

Baird, R. W., Gorgone, A. M., McSweeney, D. J., Ligon, A. D., Deakos, M. H., Webster, D. L., Schorr, G. S., Martien, K. K., Salden, D. R., & Mahaffy, S. D. (2009). Population structure of island-associated dolphins: Evidence from photo-identification of common bottlenose dolphins (Tursiops truncatus) in the main Hawaiian Islands. *Marine Mammal Science, 25*(2), 251-274. https://doi.org/10.1111/j.1748-7692.2008.00257.x

Baird, R. W., Webster, D. L., Aschettino, J. M., Schorr, G. S., & McSweeney, D. J. (2013). Odontocete Cetaceans Around the Main Hawaiian Islands: Habitat Use and Relative

Abundance from Small-Boat Sighting Surveys. *Aquatic Mammals, 39*(3). https://doi.org/10.1578/AM.39.3.2013.253

Baird, R. W., Cornforth, C. J., Jarvis, S.M., DiMarzio, N. A., Dolan, K., Henderson, E. E., Martin, S. W., Watwood, S. L., Mahaffy, S. D., Guenther, B. D., Lerma, J. K., Harnish, A. E., & Kratofil, M. A. (2021). Odontocete studies on the Pacific Missile Range Facility in February 2020: satellite-tagging, photo-identification, and passive acoustic monitoring. Prepared for Commander, Pacific Fleet, Environmental Readiness Division, Pearl Harbor, HI. https://www.cascadiaresearch.org/files/publications/Bairdetal2021_Kauai.pdf

Borgatti, S. P. (2002). NetDraw: graph visualization software (Version 2.158). Analytic Technologies. https://sites.google.com/site/netdrawsoftware/home

Carretta, J. V., Forney, K. A., Oleson, E. M., Weller, D. W., Lang, A. R., Baker, J., Muto, M. M., Hanson, B., Orr, A. J., Huber, H., Lowry, M. S., Barlow, J., Moore, J. E., Lynch, D., Carswell, L., & Brownell Jr., R. L. (2019). U.S. Pacific Marine Mammal Stock Assessments: 2018. U.S. Department of Commerce, NOAA. https://repository.library.noaa.gov/view/noaa/20266

Dinis, A., Alves, F., Nicolau, C., Ribeiro, C., Kaufmann, M., Cañadas, A., & Freitas, L. (2016). Bottlenose dolphin Tursiops truncatus group dynamics, site fidelity, residency and movement patterns in the Madeira Archipelago (North-East Atlantic). *African Journal of Marine Science, 38*(2), 151-160. https://doi.org/10.2989/1814232X.2016.1167780

Douglas, D. C., Weinzierl, R., Davidson, S. C., Kays, R., Wikelski, M., & G. Bohrer. (2012). Moderating Argos location errors in animal tracking data. *Methods in Ecology and Evolution, 3*(6), 999-1007. https://doi.org/10.1111/j.2041-210X.2012.00245.x

Hoelzel, A. R. (2009). Evolution of population genetic structure in marine mammal species. In Bertorelle, G., Bruford, M. W., Hauffe, H. C., Rizzoli, A., & Vernesi, C. (Eds.), Population genetics for animal conservation (294-318). Cambridge University Press.

Kranstauber, B., Cameron, A., Weinzerl, R., Fountain, T., Tilak, S., Wikelski, M., & R. Kays. (2011). The Movebank data model for animal tracking. *Environmental Modelling & Software, 26*, 834-835. https://doi.org/10.1016/j.envsoft.2010.12.005

Lopez, R., Malardé, J., Danès, P., & P. Gaspar. (2015). Improving Argos Doppler location using multiple-model smoothing. *Animal Biotelemetry, 3*, 32. https://doi.org/10.1186/s40317-015-0073-4

Martien, K. K., Baird, R. W., Hedrick, N. M., Gorgone, A. M., Thieleking, J. L., McSweeney, D. J., Robertson, K. M, & Webster, D. L. (2011). Population structure of island- associated dolphins: Evidence from mitochondrial and microsatellite markers for common bottlenose dolphins (Tursiops truncatus) around the main Hawaiian Islands. *Marine Mammal Science, 28*(3), E208-E232. https://doi.org/10.1111/j.1748-7692.2011.00506.x

Morin, P.A., Nestler, A., Rubio-Cisneros, N.T., Robertson, K.M., & S.L Mesnick. (2005). Interfamiliar characterization of a region of the ZFX and ZFY genes facilitates sex determination in ceteaceans and other mammals. *Molecular Ecology, 14*, 3275-3286. https://doi.org/10.1111/j.1365-294X.2005.02651.x

Pante, E., & Simon-Bouhet, B. (2013). Marmap: A Package for Importing, Plotting, and Analyzing Bathymetric and Topographic Data in R. *PLoS One, 8*(9), e73051. https://doi.org/10.1371/journal.pone.0073051

Pittman, S. J., Winship, A. J., Poti, M., Kinlan, B. P., Leirness, J. B., Baird, R. W., Barlow, J., Becker, E. A., Forney, K. A., Hill, M. C., Miller, P. I., Mobley, J., & Oleson, E. M. (2016). Ch. 6: Marine Mammals – Cetaceans. In Costa, B. M., & Kendall, M. S. (Eds.), Marine Biogeographic Assessment of the Main Hawaiian Islands (pp. 227-265). Bureau of Ocean Energy Management and National Oceanic and Atmospheric Administration. https://www.cascadiaresearch.org/files/Projects/Hawaii/MarineMammalsMHI_NOAATechMemo.pdf

Schorr, G. S., Baird, R. W., Hanson, M. B., Webster, D. L., McSweeney, D. J., & Andrews, R. D. (2009). Movements of satellite-tagged Blainville's beaked whales off the island of Hawai 'i. *Endangered Species Research, 10*, 203-213. https://doi.org/10.3354/esr00229

Silva, M. A., Prieto, R., Magalhães, S., Seabra, M. I., Santos, R. S., & Hammond, P. S. (2008). Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. *Marine Biology, 156*, 179-192. https://doi.org/10.1007/s00227- 008-1075-z

Stack, S.H., Currie, J.J, McCordic, J.A., & Olson, G.L. (2019). Incidence of Odontocetes with Dorsal Fin Collapse in Maui Nui, Hawaii. *Aquatic Mammals, 45*(3), 257-265. https:://doi.org/10.1578/AM.45.3.2019.257

Urbán, J., Jaramillo, A., Aguayo, A., Ladrón de Guevara, P., Salinas, M., Alvarez, C., Medrano, L., Jacobsen, J. K., Balcomb, K. C., Claridge, D. E., Calambokidis, J., Steiger, G. H., Straley, J. M., Von Ziegesar, O., Waite, J. M., Mizroch, S., Dahlheim, M. E., Darling, J. D., & Baker, C. S. (2000). Migratory Destinations of Humpback Whales Wintering in the Mexican Pacific. *Journal of Cetacean Research and Management, 2*(2):101-110

Van Cise, A. M., Baird, R. W., Harnish, A. E., Currie, J. J., Stack, S. H., Cullins, T., & Gorgone, A. M. (2021). Mark-Recapture Estimates Suggest Declines in Abundance of Common Bottlenose Dolphin Stocks in the Main Hawaiian Islands. *Endangered Species Research, 45*, 37-53. https://doi.org/10.3354/esr01117

Wells, R. S., Scott, M. D., & Irvine, A. B. (1987). The social structure of free-ranging bottlenose dolphins. In Genoways, H. H. (eds) Current mammalogy (pp. 247-305). Springer. https://doi.org/10.1007/978-1-4757-9909-5_7

Wells, R. S., Rhinehart, H. L., Cunningham, P., Whaley, J., Baran, M., Koberna, C., & Costa, D. P. (1999). Long Distance Offshore Movements of Bottlenose Dolphins. *Marine Mammal Science, 15*(4), 1098-1114. https://doi.org/10.1111/j.1748-7692.1999.tb00879.x

Whitehead, H. (2008). Analyzing animal societies: Quantitative methods for vertebrate social analysis. University of Chicago Press.