

Population structure of island-associated dolphins:
Evidence from photo-identification of common bottlenose
dolphins (*Tursiops truncatus*) in the main Hawaiian Islands

ROBIN W. BAIRD

Cascadia Research Collective,
218½ W. 4th Avenue,
Olympia, Washington 98501, U.S.A.
E-mail: rwbaird@cascadiaresearch.org

ANTOINETTE M. GORGONE

Southeast Fisheries Science Center,
NOAA Fisheries Service,
101 Pivers Island Road,
Beaufort, North Carolina 28516, U.S.A.

DANIEL J. MCSWEENEY

Wild Whale Research Foundation,
P. O. Box 139, Holualoa, Hawai'i 96725, U.S.A.

ALLAN D. LIGON

Hawaiian Islands Humpback Whale National Marine Sanctuary,
726 S. Kihei Road,
Kihei, Hawai'i 96753, U.S.A.

MARK H. DEAKOS

The Hawai'i Association for Marine Education and Research, Inc.,
PMB No. 175, 5095 Napili Hau Street 109B,
Lahaina, Hawai'i 96761, U.S.A.

DANIEL L. WEBSTER

Bridger Consulting Group,
1056 Boyland Road,
Bozeman, Montana 59715, U.S.A.

GREGORY S. SCHORR

Cascadia Research Collective,
218½ W. 4th Avenue,
Olympia, Washington 98501, U.S.A.

KAREN K. MARTIEN

Southwest Fisheries Science Center,
NOAA Fisheries Service,
8604 La Jolla Shores Drive,
La Jolla, California 92037, U.S.A.

DAN R. SALDEN

Hawai'i Whale Research Foundation,
52 Cheshire Drive,
Maryville, Illinois 62062-1931, U.S.A.

SABRE D. MAHAFFY

Cascadia Research Collective,
218¹/₂ W. 4th Avenue,
Olympia, Washington 98501, U.S.A.
and
Wild Whale Research Foundation,
P. O. Box 139, Holualoa, Hawai'i 96725, U.S.A.

ABSTRACT

Management agencies often use geopolitical boundaries as proxies for biological boundaries. In Hawaiian waters a single stock is recognized of common bottlenose dolphins, *Tursiops truncatus*, a species that is found both in open water and near-shore among the main Hawaiian Islands. To assess population structure, we photo-identified 336 distinctive individuals from the main Hawaiian Islands, from 2000 to 2006. Their generally shallow-water distribution, and numerous within-year and between-year resightings within island areas suggest that individuals are resident to the islands, rather than part of an offshore population moving through the area. Comparisons of identifications obtained from Kaua'i/Ni'ihau, O'ahu, the "4-island area," and the island of Hawai'i showed no evidence of movements among these island groups, although movements from Kaua'i to Ni'ihau and among the "4-islands" were documented. A Bayesian analysis examining the probability of missing movements among island groups, given our sample sizes for different areas, indicates that interisland movement rates are less than 1% per year with 95% probability. Our results suggest the existence of multiple demographically independent populations of island-associated common bottlenose dolphins around the main Hawaiian islands.

Key words: bottlenose dolphin, Hawai'i, movements, population structure, *Tursiops truncatus*.

Despite no obvious geographic barriers to movement and a low cost of locomotion (Williams 1999), populations of many species of whales and dolphins appear to be restricted in range or subdivided, resulting in demographically independent units that are more at risk from localized anthropogenic impacts. Proper management of these species depends upon correct identification of these units. In the United States, the agency responsible for managing cetacean populations is NOAA Fisheries Service (aka National Marine Fisheries Service or NMFS). NMFS divides all species under its jurisdiction into management units called stocks. For each stock, NMFS uses information on the stock's geographic range, population size, population trends, and estimates of human-caused mortality and serious injury to assess whether human-caused mortality is sustainable (Wade and Angliss 1997).

Evidence used to determine whether multiple stocks exist includes genetics (*e.g.*, Chivers *et al.* 2002, 2007; Sellas *et al.* 2005), individual movements (based on either

photo-identification or tagging, *e.g.*, Calambokidis *et al.* 2001, Heide-Jorgensen *et al.* 2006), pollutant ratios (*e.g.*, Calambokidis and Barlow 1991), and association patterns (*e.g.*, Bigg 1982, Wells 1991). Such evidence exists both for coastal and offshore populations (*e.g.*, Escorza-Trevino *et al.* 2005). In mainland waters of the United States there are a number of cetacean species that are subdivided into multiple stocks. For example, along the Atlantic coast of the United States, NMFS recognizes eight stocks of common bottlenose dolphins, *Tursiops truncatus* (Waring *et al.* 2007), while among all the Pacific states of the United States, NMFS recognizes seven stocks of killer whales, *Orcinus orca* (Carretta *et al.* 2006, Angliss and Outlaw 2007).

In each of these cases, the designation of multiple stocks has been the result of considerable research into the population structure of the species in question. In the absence of such efforts, NMFS (and management agencies in other countries) usually manages all individuals of a species within a particular geopolitical boundary (*e.g.*, off California/Oregon/Washington, or within the Hawaiian Islands Exclusive Economic Zone [EEZ]) as a single stock. Most species of cetaceans found within Hawaiian waters are broadly distributed across the tropical Pacific and, until recently, little effort has been extended toward assessing the potential for population subdivision within the Hawaiian EEZ. NMFS currently recognizes 24 stocks of cetaceans in Hawai'i, with the boundaries of 22 generally considered to be the Hawaiian EEZ (Carretta *et al.* 2006). Two species, blue whales (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*), are known to have ranges that encompass much larger areas and the individuals in Hawaiian waters are considered part of much larger stocks (Carretta *et al.* 2006, Angliss and Outlaw 2007). For those species where the boundaries of the EEZ are considered the stock boundaries, only a single stock for each species is currently recognized.

Population subdivision within Hawaiian waters may be important for conservation and management for several reasons. The types and extent of anthropogenic threats varies with distance from the main Hawaiian Islands. Longline fisheries, in which cetaceans are occasionally killed or injured (Forney and Kobayashi 2007), occur primarily in offshore waters (greater than 45 km from the islands). In near-shore waters there are a number of potential threats, with various species of cetaceans: (1) interaction with a variety of commercial and sports fisheries (Nitta and Henderson 1993), (2) exposure to high levels of directed (*e.g.*, dolphin or whale watching) or incidental vessel traffic, (3) being approached regularly by swimmers in the water (*e.g.*, Danil *et al.* 2005), and (4) exposure to high levels of sounds from mid-frequency sonars used in military exercises (*e.g.*, Southall *et al.* 2006). The degree to which these anthropogenic activities occur also varies among the main Hawaiian Islands with: the greatest degree of shipping traffic off O'ahu; the highest levels of military activity off O'ahu, Kaua'i, and Ni'ihau; the greatest degree of dolphin/whale-oriented vessel traffic in the 4-island area and off Hawai'i; and the highest levels of commercial and sports troll fisheries off Hawai'i. If populations are subdivided into small, demographically independent units, they may be at risk simply due to their small size or restricted ranges. In addition, using population estimates for the entire Hawaiian EEZ may result in an underestimate of the proportion of individuals within a population that are exposed to and potentially at risk from such anthropogenic influences.

In near-shore waters around the Hawaiian Islands, evidence of island-associated populations of a number of species of cetaceans is available. Based on photo-identification of distinctive individuals, several primarily deep-water species appear to exhibit high levels of fidelity to the islands, including rough-toothed dolphins (*Steno bredanensis*), and Blainville's (*Mesoplodon densirostris*), and Cuvier's (*Ziphius*

cavirostris) beaked whales (McSweeney *et al.* 2007, Baird *et al.* 2008a). Evidence from photo-identification (Norris *et al.* 1994) and genetic analyses (Andrews *et al.* 2006) suggests that there may be multiple, demographically independent units of spinner dolphins (*Stenella longirostris*) within the Hawaiian Island chain, including among the main Hawaiian Islands. Evidence of island-associated and offshore populations of false killer whales (*Pseudorca crassidens*) within the Hawaiian EEZ is available both from photo-identification and genetics (Chivers *et al.* 2007, Baird *et al.* 2008b). Another species seen both close to shore and in offshore waters in Hawai'i is the common bottlenose dolphin. A survey of the entire Hawaiian EEZ, an area of approximately 2.4 million km², suggests the overall density of common bottlenose dolphins (hereafter bottlenose dolphins) in the Hawaiian EEZ is low, with a population estimate of only 3,215 individuals (CV = 0.59; Barlow 2006). Bottlenose dolphins were the 11th most abundant species out of the 18 species of odontocetes documented (Barlow 2006). In an area around the main Hawaiian Islands extending out to approximately 140 km from shore, Barlow (2006) estimated a population size of 465 individuals. Elsewhere, both coastal and offshore forms of bottlenose dolphins are frequently found and can typically be distinguished by one or more morphological traits, as well as by ecological and sometimes genetic differences (*e.g.*, Hoelzel *et al.* 1998).

The Hawaiian Islands are the most geographically isolated archipelago in the world, located centrally in the tropical Pacific. The islands are of volcanic origin, rising directly from the ocean floor in depths of over 5,000 m. The closest major land mass is the North American continent, approximately 3,670 km to the northeast. The next closest island, Johnston Atoll, is over 1,100 km to the southwest. Such isolation suggests that bottlenose dolphins around the Hawaiian Islands would be more likely to have originated from an offshore population, rather than the spread of a preexisting, coastally adapted population.

The islands are generally considered in two main groupings, the eight "main" Hawaiian islands in the east, and the northwestern Hawaiian islands, a series of more than 100 small islands, islets, and atolls that start approximately 250 km to the west-northwest of the main islands and stretch northwest over a distance greater than 2,000 km. Based on bathymetry and distance between islands, the main Hawaiian islands can generally be divided into four main groupings ("island areas"), each separated by channels ranging in depth from between 500 to about 2,000 m (Fig. 1). These island areas are (from west to east): (1) Ni'ihau and Kaua'i, (2) O'ahu, (3) the "4-island region" (Moloka'i, Lana'i, Maui, Kaho'olawe), and (4) Hawai'i. Distances between islands within the 4-island region range from 11 to 15 km, while Kaua'i and Ni'ihau are separated by about 28 km. By contrast, distance between island areas range from approximately 44 km (O'ahu–Moloka'i) to 112 km (Kaua'i–O'ahu).

Using photo-identification of individual bottlenose dolphins from around all of the main Hawaiian Islands to infer movements, we assessed whether there was evidence for small-scale population structure, and discuss potential implications for management. High levels of site fidelity have been documented for numerous bottlenose dolphin populations (see *e.g.*, Scott *et al.* 1990), although studies in multiple areas or from radio-tagging have provided evidence that individuals from coastal, offshore, and island-associated populations may move much greater distances than those among the island areas in Hawai'i (*e.g.*, Würsig 1978; Tanaka 1987; Wells *et al.* 1990, 1999; Defran *et al.* 1999; Klatsky *et al.* 2007). A recent study of offshore bottlenose dolphins from two archipelagos in the North Atlantic found high levels of gene flow between the archipelagos and with pelagic populations (Quérrouil *et al.* 2007). Thus movements among the main Hawaiian Islands would be expected.

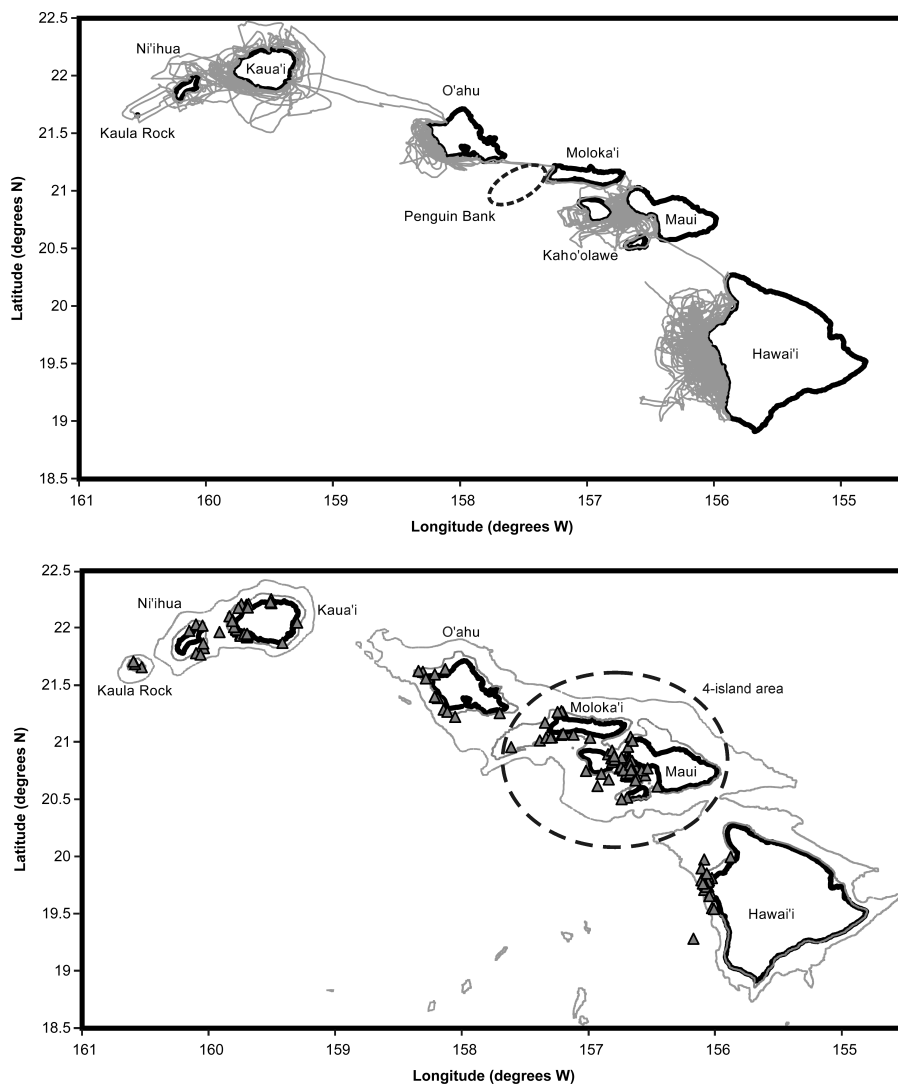


Figure 1. Top. Distribution of search effort from directed odontocete surveys. Opportunistic efforts were in areas that were also surveyed in directed efforts, with the exception of Penguin Bank, indicated, where additional opportunistic surveys were undertaken. Bottom. Bottlenose dolphin sightings from which usable photo-identifications were obtained. The 200 m and 2,000 m depth contours are shown.

METHODS

Individual identification photographs were obtained from a number of sources. Dedicated surveys for odontocete cetaceans were undertaken around all of the main Hawaiian Islands from 2000 through 2006. Methods for these surveys have been described in detail in Baird *et al.* (2008a) so are only briefly summarized here. In

dedicated surveys, survey effort was documented with locations recorded every 5 min on a GPS. Survey effort was nonrandom and nonsystematic; efforts were made to maximize the spatial extent of survey coverage and range of depths surveyed, given the limits of vessel size, distance from harbors, and fuel limitations, while remaining in areas with relatively calm (less than Beaufort 4) sea conditions. Given the prevailing wind direction, surveys were based out of the western or southwestern (lee) sides of the islands. All odontocete groups seen were approached for species identification and estimation of group size. For bottlenose dolphins, attempts were made to obtain left- and right-side photographs of all individuals present in each group, and obtain biopsy samples of as many adult and subadult individuals as possible using either a pole spear or crossbow. Information on results of genetic analyses of biopsy sampling will be reported elsewhere.¹ Photographs were also taken incidental to humpback whale research off Maui, Lana'i, and Moloka'i in 2004–2006, off Kaua'i in 2004 and 2005, and incidental to short-finned pilot whale (*Globicephala macrorhynchus*) and beaked whale research off Hawai'i in 2003–2006 (see McSweeney *et al.* 2007). Additional opportunistic photographs were obtained from several other researchers. From 2000 to 2002, photographs were taken on film (color transparencies), and from 2003 to 2006 photographs were taken with digital cameras, all with telephoto lenses (100–400 mm). Vessels used ranged in length from 6 to 16 m. In general, efforts were made to photograph all individuals within groups. Sighting locations were taken onboard each research vessel using a GPS. For each sighting the closest island(s) were noted, for comparisons of movements among islands.

Dolphins were identified from photographs based primarily on the size, location, and pattern of notches on the dorsal fin and on the back immediately adjacent to the dorsal fin (*cf.* Wells and Scott 1990, Würsig and Jefferson 1990). Body scarring and pigmentation patterns were also used to identify individuals within each encounter. For every individual within each encounter, the best photograph obtained was given a photo-quality rating as poor, fair, good, or excellent, based on the focus, size, and angle of the body relative to the photographic frame, and proportion of the body visible. Each individual was given a distinctiveness rating of: (1) not distinctive, (2) slightly distinctive, (3) distinctive, or (4) very distinctive. These ratings were based on the presence of one or more notches on the dorsal fin or immediately in front of or behind the dorsal fin (which could be detected from either left- or right-side photographs), scars on the fin, or scars on the body immediately around the fin. Left- and right-side dorsal fin images of each individual within an encounter were entered into a digital database using the software *Finscan* 1.6.1 (Hillman *et al.* 2003), which was used to assist in matching individual dolphins. We estimated the proportion of individuals within groups that were categorized as distinctive or very distinctive using only good- or excellent-quality photographs from a subset of encounters (those documented from dedicated surveys in digital format). Photographs of all quality ratings, and distinctiveness ratings of “slightly distinctive” or greater were compared both within and among island areas, although for the purposes of calculating resighting rates, only distinctive and very distinctive individuals with photo qualities of good or excellent were used.

¹MARTIEN, K. K., R. W. BAIRD, N. HEDRICK, A. M. GORGONE, J. LOWTHER, D. J. MCSWEENEY, K. ROBERTSON AND D. L. WEBSTER. Unpublished. Mitochondrial and microsatellite markers reveal multiple resident populations of common bottlenose dolphins (*Tursiops truncatus*) around the main Hawaiian Islands.

For the purposes of comparisons of movements, based on distances among islands, and the spatial distribution of research effort, the study area was stratified into four areas: (1) Kaua'i and Ni'ihau (including Ka'ula Rock); (2) O'ahu; (3) the "4-island" area, including Moloka'i, Lana'i, Kaho'olawe, and Maui; and (4) the island of Hawai'i. Based on resighting locations of photo-identified individuals, the 4-island area was further subdivided for some analyses into three areas: (1) Moloka'i, (2) Lana'i and Maui, and (3) Kaho'olawe.

To illustrate association patterns, social network diagrams were produced with *Netdraw* 2.043 (Analytic Technologies, Needham, MA, USA). No social network analyses were undertaken; such diagrams simply represent all associations among individuals present within groups, with nodes representing the individuals and lines between nodes representing presence in the same group. Individuals that are sighted in more than one group with changing group membership thus result in linkages among groups.

For opportunistic data, depths of sighting locations were determined from nautical charts. For sighting and 5-min effort locations from dedicated surveys, depths were determined by overlaying the point location data on a bathymetric raster surface in *ArcGIS* 9.1 (ESRI, Redlands, CA, USA). Underlying depth values (in meters) were transferred to point locations using the "intersect point tool" in Hawth's analysis tools (Beyer 2004). We used gridded 3-arc second U.S. Coastal Relief Model bathymetry ($\sim 90 \text{ m} \times 90 \text{ m}$) from the National Geophysical Data Center.²

When encounter locations were available, distances between encounters were calculated using *Workstation ArcInfo* 9.0 (ESRI), taking into account shorelines (*i.e.*, actual minimum distances an animal would have to move, not straight-line distances potentially through intervening land masses). Within each area, distances among all possible combinations of encounter locations were calculated. For each individual seen on more than one occasion, the distances among all possible encounter locations where that individual was documented were calculated, including both within-year and between-year resightings of each individual. Comparisons within areas of distances among all possible encounter locations and distances among resightings of individuals (using the median value for each individual) were made with nonparametric tests, as the distributions of distances were nonnormal.

To evaluate the significance of the between-area resighting rates, we used a Bayesian analysis to estimate the interisland dispersal rate. We estimated the likelihood of a dispersal rate given that we did not observe any interisland resighting events by first calculating the expected number of identified immigrants (*i.e.*, animals previously sighted at a different island) present at island group j at sampling event y (I_{jy}) using the formula

$$I_{jy} = I_{j(y-1)} \times (1 - d) + \left(\sum_{i \neq j} M_{iy} - I_{j(y-1)} \right) \times \frac{d}{3} \quad (1)$$

where M_{iy} is the catalog size at island group i prior to sampling event y and d is the dispersal rate from each island group (equal for all island groups).

The first term in Equation (1) represents identified immigrants that were present at island group j at sampling event $y - 1$ and were still present at sampling event y . The second term represents individuals sighted at an island group other than j

² Available at <http://www.ngdc.noaa.gov/mgg/coastal/coastal.html>.

prior to sampling event y that immigrated to j between sampling events $y - 1$ and y . The dispersal rate is divided by three in this term to reflect the assumption that an animal emigrating from island group i is equally likely to go to any of the other three island groups.

Once I_{jy} had been calculated for each island group in each year, the probability of failing to observe any interisland immigrants in each year/island group combination was calculated using the binomial probability density function

$$L_{jy} = \Pr(x, U_{jy}, p_{jy}) = \binom{U_{jy}}{x} p_{jy}^x (1 - p_{jy})^{(U_{jy} - x)} \quad (2)$$

where x is 0, U_{jy} is the number of unique individuals sighted at island group j during sampling event y , p_{jy} is I_{jy}/n_j , and n_j is the abundance at island group j , which is assumed to remain constant over the period of the study.

The overall joint likelihood of a given dispersal rate (d) and set of abundances (n_j) was then calculated as

$$L = \prod_j \prod_y L_{jy}. \quad (3)$$

The parameters required for the likelihood calculation are the annual dispersal rate (d) and abundance at each island group (n_j). For d , we used a uniform prior between 0% and 4% per year. Prior distributions for abundances were normal distributions truncated at the lower end of the distribution by the catalog size for each island group (Table 2). The normal distributions were parameterized using the mean and standard deviation of Petersen estimates (Seber 1982) of abundance at each island group. For the two samples required for calculating the Petersen estimates, we used the number of identifications obtained in the final year of sampling for each area, and all unique identifications from the previous years combined, with the number of recaptures being the subset of individuals from the final year that had been seen in one or more previous years. The Petersen estimates produced estimates of the number of distinctive and very distinctive animals for each island group. Estimates of actual population size (taking into account the proportion of marked individuals in the population and various biases that may influence population estimates) will be reported elsewhere.

We used a sample-importance resample (SIR) algorithm (Rubin 1988) to estimate the posterior distributions of n_j and d . We estimated the likelihood for 500,000 sets of parameters drawn from the prior distributions for d and n_j and then resampled the resulting parameter sets, weighted by their likelihood, 5,000 times to generate posterior distributions. Because we considered only marked individuals in our likelihood calculations, the dispersal rate estimates from our analysis are for the marked portion of the population. However, because there is no reason to expect differential dispersal rates between marked and unmarked individuals, these estimates generalize to the entire population.

RESULTS

Search effort around all islands was primarily concentrated on the western and southern (leeward) sides due to unfavorable sea conditions elsewhere, with the

exception of Kaua'i, Ni'ihau, and Lana'i (Fig. 1). In directed efforts, bottlenose dolphins were encountered 126 times (14.8% of 852 total odontocete sightings), with group sizes ranging from 1 to 40 individuals (median = 5). Bottlenose dolphins were the third most frequently encountered odontocete after pantropical spotted dolphins (*Stenella attenuata*) (21.6% of sightings) and short-finned pilot whales (19.2% of sightings). From dedicated surveys, 43.5% of all effort was in waters of depths greater than 1,000 m, although only two encounters (1.6%) were in depths greater than 1,000 m. Although directed search effort did extend as far as 70 km offshore, the vast majority of directed search effort (94%) was within 25 km of shore. Some search effort was available from 11 mo of the year, although the majority of effort was spread from November through April. Bottlenose dolphins were encountered around all the main Hawaiian Islands, with encounters in nine different months of the year. The 2 mo when there was search effort and no sightings (July and September) had efforts primarily focused in deep (>1,000 m) waters off the island of Hawai'i. There were no encounters in the deep-water channels between the islands, although there was little search effort in those channels (Fig. 1). From both dedicated and opportunistic efforts, bottlenose dolphins were photo-identified in 156 encounters over the period 2000–2006 (Table 1), with identifications obtained from all of the main Hawaiian Islands. Limited sampling effort was available off O'ahu (7% of all bottlenose dolphin encounters, from 3 yr, although with only a single ID in 1 of the 3 yr), though reasonable sample sizes were available for Kaua'i/Ni'ihau (25.6% of all bottlenose dolphin encounters, from 3 yr), the 4-island area (47.4% of all bottlenose dolphin encounters, from 7 yr), and Hawai'i (19.9% of all bottlenose dolphin encounters, from 5 yr). Within the 4-island area, due to the geographic distribution of effort, the majority of the bottlenose dolphin sightings (56 of 74) and identifications (133 of 197) were obtained from Maui or Lana'i (or midway between the two), where identifications were available for each of the 7 yr. From Moloka'i, identifications were only available from 2 yr (13 encounters, 40 identifications), while from Kaho'olawe (or with Kaho'olawe the closest island) identifications were available for 3 yr, although the number of encounters (four) and identifications (22) was small, as vessel traffic was restricted near the island.

The percentage of individuals within groups considered distinctive or very distinctive ranged from 0% to 100%, with a median of 80.0%. Including only individuals considered distinctive or very distinctive, with good or excellent quality photographs, the total number of unique individuals was 336 (Table 2). Of these, 118 (35%) were seen on two or more occasions. Eighty-two individuals were resighted within-years (for a total of 127 within-year resightings), and 77 individuals were resighted between-years (for a total of 104 between-year resightings). For those individuals seen more than once, intervals between sightings ranged from 1 to 1,894 d (median = 68 d, $n = 231$ intervals). The interval between when an individual was first seen and last seen ranged from 1 to 1,980 d (median = 588 d, $n = 118$). Excluding within-year resightings of individuals, there were 440 identifications, and including all resightings, there were 567 identifications. Within-year resighting rates were highest off Kaua'i/Ni'ihau and the 4-islands, and lowest off O'ahu. Comparisons among areas included slightly distinctive, distinctive and very distinctive individuals, but no individuals were resighted between areas.

Social network diagrams of distinctive and very distinctive individuals (Fig. 2) showed that for the two areas (Kaua'i/Ni'ihau, 4-islands) with the largest ratio of identifications to the catalog sizes, a large proportion of individuals (88.2%, 90 of 102 from Kaua'i/Ni'ihau; 52.0%, 51 of 98 from the 4-islands) were associated in

Table 1. Number of encounters (groups) and identifications (distinct and very distinct individuals with photo qualities of good or excellent only) by area and year, including within-year resightings. For each area, the total number of encounters and identifications (second-to-last line) and number of identifications per encounter (last line) are shown.

Year	Kaua'i/Niihau		O'ahu		4-islands		Hawaii'i	
	No. of Enc.	No. of IDs	No. of Enc.	No. of IDs	No. of Enc.	No. of IDs	No. of Enc.	No. of IDs
2000	—	—	—	—	19	47	—	—
2001	—	—	—	—	18	61	—	—
2002	—	—	3	37	9	16	5	11
2003	16	50	7	41	5	16	3	3
2004	9	46	—	—	6	15	11	29
2005	15	80	—	—	12	35	1	12
2006	—	—	1	1	3	7	11	60
Total	40	176	11	79	74	197	31	115
IDs/Enc.		4.4		7.2		2.7		3.7

Table 2. Number of unique individuals (distinct and very distinct with photo qualities of good or excellent only), and number of individuals seen in more than 1 yr, for each island area by year. The total number of identifications of distinct/very distinct individuals (total IDs) for each area is shown (second-to-last line). The catalog size (number of unique individuals excluding between-year resightings) for each area, and the number and percentage of those individuals seen in more than 1 yr is shown (last line).

Year	Kaua'i/Ni'ihau		O'ahu		4-islands		Hawai'i	
	No. of unique ind.	No. seen >1 yr	No. of unique ind.	No. seen >1 yr	No. of unique ind.	No. seen >1 yr	No. of unique ind.	No. seen >1 yr
2000	—	—	—	—	29	19	—	—
2001	—	—	—	—	38	20	—	—
2002	—	—	28	1	10	9	9	7
2003	42	14	40	2	13	11	3	3
2004	35	14	—	—	14	8	21	11
2005	53	26	—	—	34	7	12	5
2006	—	—	1	1	7	4	49	18
Total IDs	130		69		147		94	
Catalog size	102	27 (26.5%)	67	2 (3.0%)	98	29 (29.6%)	69	19 (27.5%)

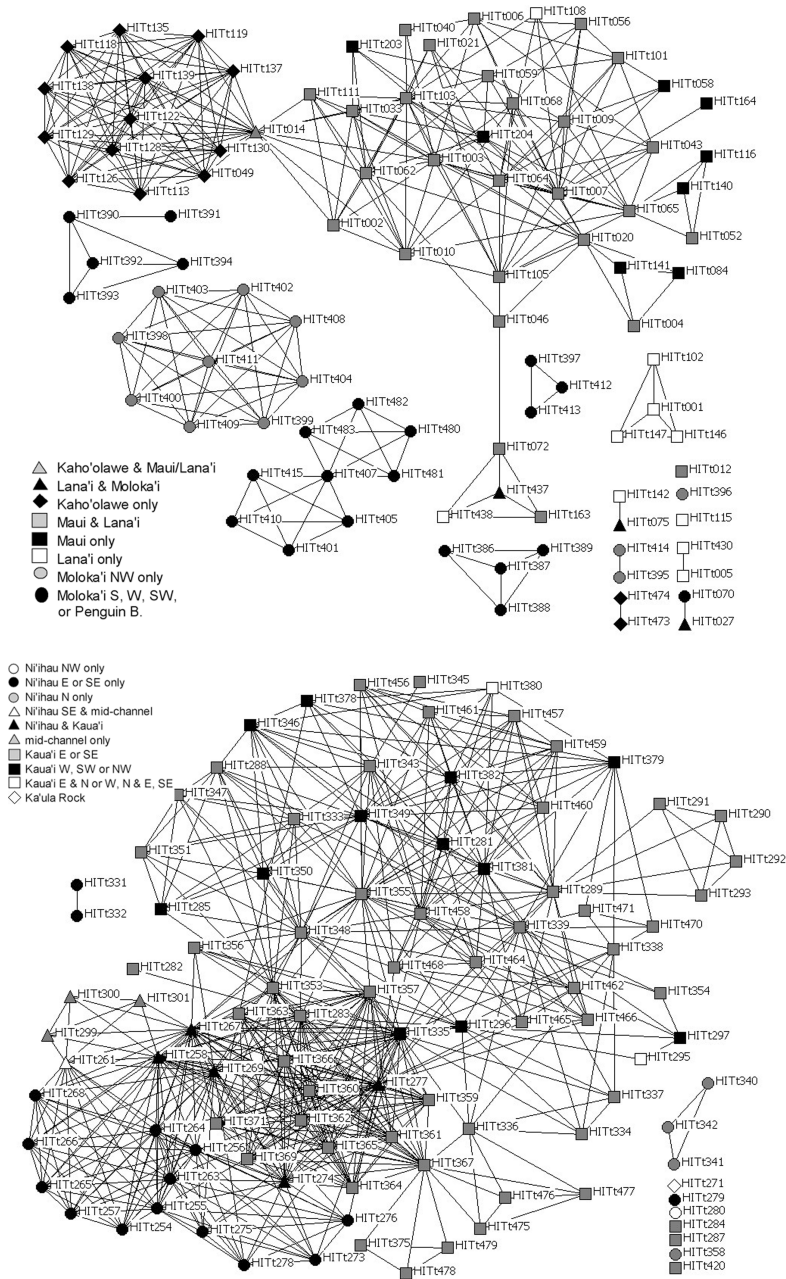


Figure 2. Social network diagrams for bottlenose dolphins in the 4-island area (top) and off Kaua'i/Ni'i'hau (bottom). Nodes in the network represent individual dolphins, with symbol type/shading representing islands documented for each individual (see Key). Lines between nodes represent associations among individuals. Completely symmetrical clusters are groups of individuals seen on only a single occasion or (rarely) with constant group membership.

single networks. For Kaua'i/Ni'ihau, the only individuals that were not in the main cluster were seen on only a single occasion each, with from one to three individuals identified in each encounter. Thus the likelihood of detecting links to the main cluster for these individuals was small. For the 4-islands, 33 of the 47 individuals not in the main cluster were documented off Moloka'i (Fig. 2), an area with limited sampling effort. For O'ahu, the number of identifications relative to the catalog size was small (79 identifications of 67 individuals), thus the likelihood of detecting links among clusters was small; the largest cluster contained only 35.8% (24 of 67) of the individuals (Fig. 3). The two clusters off O'ahu that represented multiple sightings included individuals sighted in both shallow (<200 m) and deep (>200 m) water (Fig. 3). A social network diagram produced for individuals documented off the island of Hawai'i (Fig. 3) also showed multiple clusters, with the largest cluster containing 43.5% (30 of 69) of the individuals. The ratio of identifications to catalog size for Hawai'i (1.67) was similar to that from Kaua'i and Ni'ihau (1.72), and examination of sighting depths for individuals within clusters suggested some evidence of habitat partitioning, with clusters generally either in deep (>200 m) or shallow (<200 m) water (Fig. 3).

The posterior median interisland dispersal rate from the Bayesian analysis was 0.002 per year (95% CI = 0, 0.010; Fig. 4). The Petersen estimates of the number of marked individuals around each island group, which were used to parameterize the prior distributions on abundance, are given in Table 3. Posterior distributions for abundances of each of the island groups were nearly identical to the prior distributions, indicating that the analysis was relatively insensitive to this parameter (Fig. 4).

Within the 4-island area, numerous sighting locations midway between Maui and Lana'i (Fig. 1), and frequent resightings of individuals from one island to the other suggested that most individuals documented off Maui also regularly move to Lana'i, and *vice versa*. Movements of individuals from Kaho'olawe to Maui/Lana'i (1 of 16 individuals documented off Kaho'olawe), or from Moloka'i to Maui/Lana'i (3 of 37 individuals documented off Moloka'i) were less common. Off Kaua'i, movements of individuals around the island were documented, with records of individuals moving from the east coast to the west and north coasts, from the south to the west coast, and from the north to the south coasts. The greatest distance an individual was documented moving was from the west to the east coast of Kaua'i, a distance of 70.6 km. The time interval over which this movement was documented was almost 1 yr. Individuals were also documented moving from Ni'ihau to Kaua'i (5 of 26 individuals documented off Ni'ihau). Median distances among all possible pairs of encounter locations within each island area ranged from approximately 12 to 32 km (Table 4). Median distances among sighting locations for individuals that were resighted ranged from 9 to approximately 21 km, and were significantly smaller than the distances among all possible pairs of locations for three of the four areas (Table 5). The shortest straight-line distance between encounter locations for different areas was 34.4 km, between the westernmost sighting in the 4-island area and the easternmost sighting off O'ahu (Fig. 1).

DISCUSSION

Despite encounters with bottlenose dolphins spread among all the main Hawaiian Islands, and identifications of from 79 to 197 distinctive individuals from each of

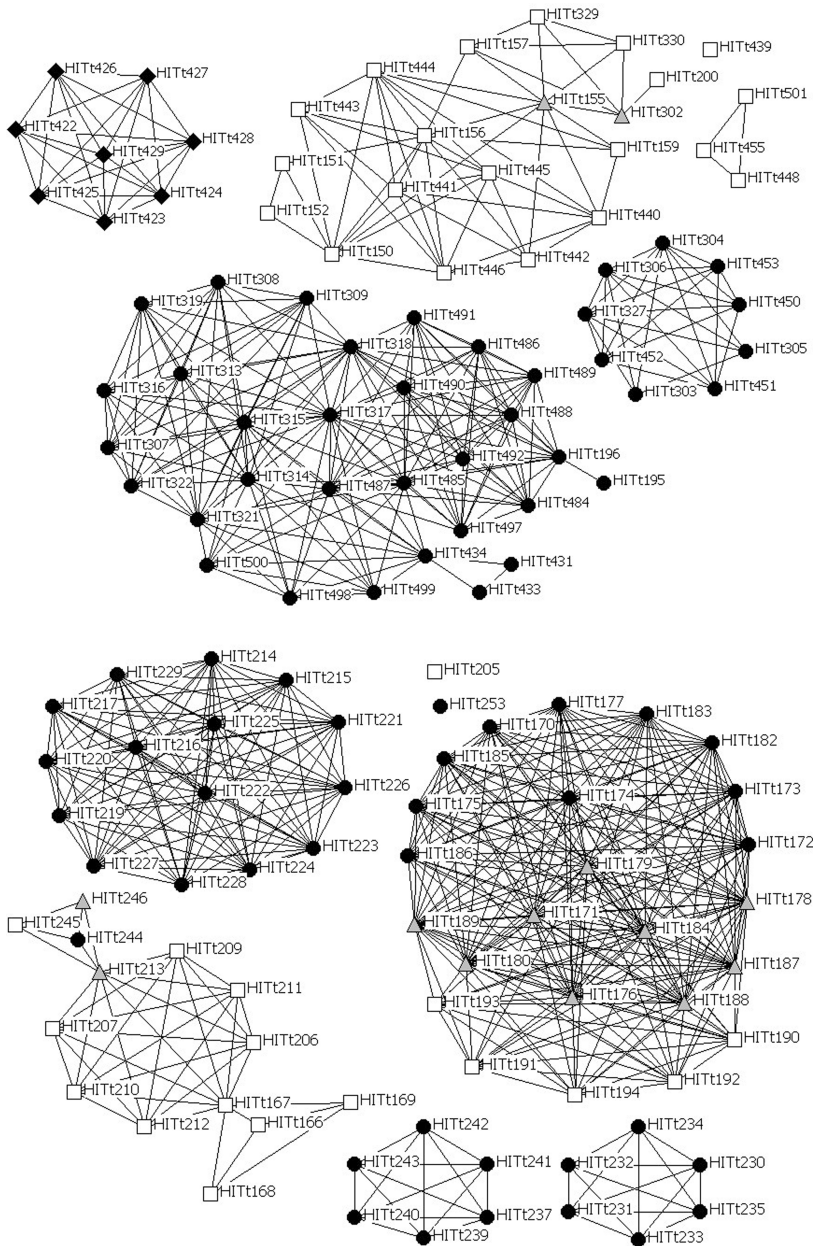


Figure 3. Social network diagrams for bottlenose dolphins off the islands of Hawai'i (top) and O'ahu (bottom). Nodes in the network represent individual dolphins, with symbol type representing depth ranges that individuals were identified in (white square = 0–200 m; black circle = 201–1,000 m; gray triangle = both < and > 200 m; black diamond = > 1,000 m). Completely symmetrical clusters are groups of individuals seen on only a single occasion or (rarely) with constant group membership.

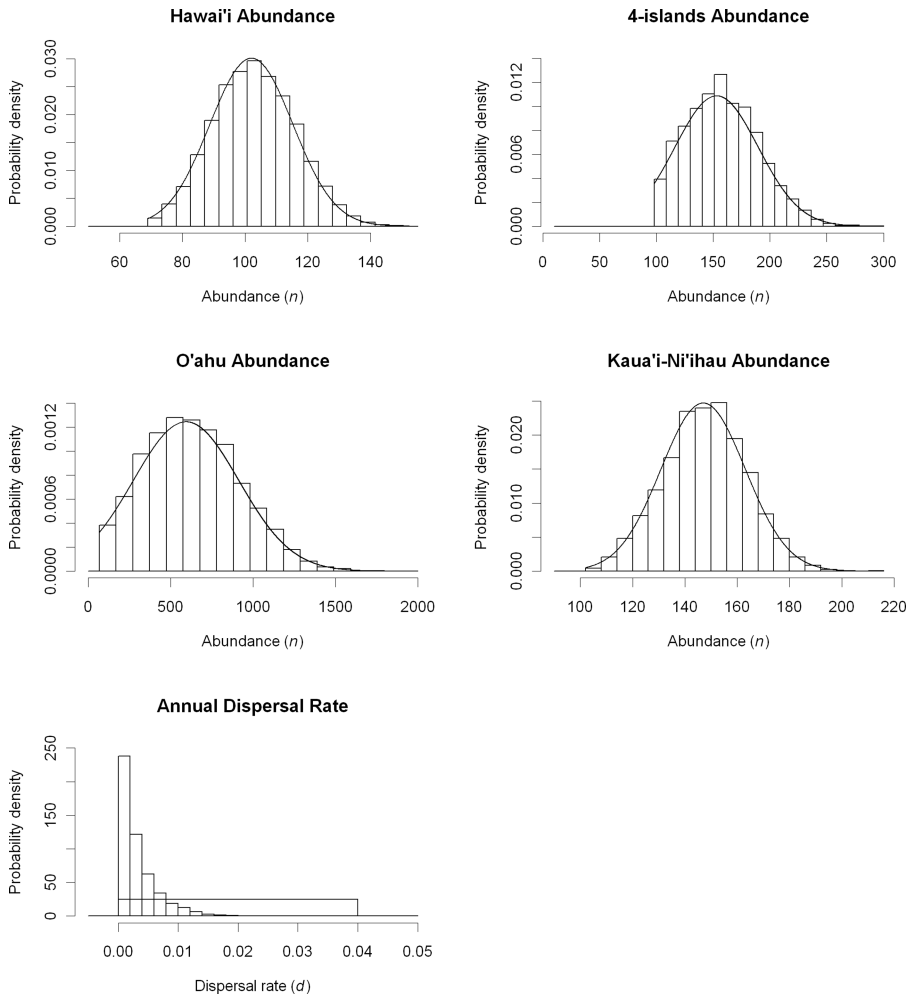


Figure 4. Posterior distributions (bars) of abundance of marked animals at each island group and of the annual dispersal rate between islands. Prior distributions are shown by solid lines.

four “island areas,” we documented no evidence of movement of individuals among these areas. For three of the four areas, Kaua'i/Ni'ihau, the 4-islands, and the island of Hawai'i, frequent within-year and between-year resightings (Tables 1 and 2) indicate that the individuals show fidelity to the areas. A Bayesian analysis designed to determine what range of dispersal rates are consistent with our photo-identification data indicate that interisland dispersal rates are less than 1% per year. We estimated that 80% of the individuals within groups were considered “distinctive” or “very distinctive.” As the marks used in identifying individuals accumulate with age, a majority of the “not distinctive” or “slightly distinctive” individuals are likely small calves and dependent juveniles, thus our analyses of dispersal rates, although restricted to distinctive/very distinctive individuals, should be representative of the

Table 3. Estimates of the number of marked animals for each area used in the simulation, determined using Petersen capture–recapture estimates.

Island area	Last year sampled	No. of unique IDs in last year	No. from last year seen in previous years	No. of IDs from previous years	Estimated no. of marked animals	SD of estimate	CV of estimate
Kaua'i/Ni'ihau	2005	53	26	73	147	16	0.11
O'ahu	2003 ^a	40	1	28	594	323	0.54
4-islands	2006	7	4	95	153	37	0.24
Hawai'i	2006	49	18	38	102	13	0.13

^a As only a single bottlenose dolphin identification was obtained from O'ahu in 2006, 2003 is used as the last year sampled in simulation analyses.

Table 4. Median and range of distances among all possible pairs of locations where bottlenose dolphins were photo-identified, by island area. Number of sightings for two areas lower than in Table 1 due to missing location information.

Island area	Median distance (range) km	No. of sightings	No. of sighting pairs
Kaua'i/Ni'ihau	37.3 (0.3–153.1)	40	780
O'ahu	32.7 (3.0–90.4)	11	55
4-islands	24.6 (0.4–135.9)	71	2,485
Hawai'i	12.7 (0.4–91.7)	25	300

Table 5. Median and range of distances among sighting locations for resighted individuals, by island area. *P*-values associated with statistical comparisons with distances among all possible pairs of locations (from Table 4) using Mann–Whitney *U* tests are shown.

Island area	Median distance (range) km	No. of individuals seen >1	<i>P</i> -value
Kaua'i/Ni'ihau	20.9 (1.5–62.2)	49	0.0009
O'ahu	13.4 (10.0–14.7)	13	0.0006
4-islands	9.0 (3.1–52.0)	43	<0.0001
Hawai'i	11.1 (3.0–31.8)	30	0.1430

population. Such dispersal rates are low enough to render the populations around each island group demographically independent and should warrant consideration as separate stocks (Taylor 1997, Palsbøll *et al.* 2007).

Our study encompassed only a small number of years. If oceanic conditions during these years were different from the long term, our observed movement rates may not be typical for these populations. Similarly, if these populations experience infrequent, large-scale dispersal events, we may have failed to detect that. However, if the low dispersal rates we observed were to exist for extended periods, genetic differentiation may result. In fact, preliminary genetic analyses of samples collected from many of the groups encountered here do indicate evidence of limited gene flow among island areas.¹ Completion of these genetic analyses will provide necessary corroboration of the demographic independence between islands suggested by our photo-identification data.

Our survey efforts (Fig. 1) were primarily restricted to the western and southwestern shores of the islands, with the exceptions of Kaua'i, Ni'ihau, and Lana'i, where we were able to work off all coasts. Bottlenose dolphins are also found on the northern and eastern coasts of the other islands (Mobley *et al.* 2000), as well as in far offshore waters of the Hawaiian EEZ (Barlow 2006). Given the relatively low sighting rate in waters greater than 1,000 m, our limited effort in the deep-water channels between some of the islands and in far offshore waters likely does not greatly bias our results. However, clearly effort off the eastern and northern shores of the other islands and in the channels among the islands would be of value, as well as additional effort off western Moloka'i and on Penguin Bank (Fig. 1). Regardless, the movements of individuals we documented from one side of Kaua'i to the other, and from Kaua'i to Ni'ihau, suggest that the geographic biases in our sampling likely do not invalidate our conclusions regarding low dispersal rates among the islands. Overcoming these geographic biases will be difficult, because the direction and strength of the trade winds make photo-identification less feasible on the eastern and northern sides of the

islands or in the channels. Similarly, although our field efforts were undertaken 11 mo of the year, the majority of the survey effort was between November and April. Little is known regarding potential seasonality of reproduction in bottlenose dolphins in Hawai'i, which might influence timing of movements. Seasonal fluctuations in sea surface temperature in Hawai'i are small however, with sea surface temperature averaging 24°C in winter and 27°C in summer (Flament 1996). In our directed efforts, bottlenose dolphin neonates have been documented in 5 mo of the year spanning an 8-mo period, ranging from fall through spring (Baird, unpublished), suggesting that reproduction is at most diffusely seasonal. In Florida, bottlenose dolphins reproduce year-round, although with a diffuse peak in births in spring and summer (Urian *et al.* 1996). Short-beaked common dolphins (*Delphinus delphis*) in the eastern tropical Pacific reproduce year-round (Danil and Chivers 2007), while spinner dolphins in the main Hawaiian Islands exhibit a diffuse peak in reproductive behavior in the summer and fall (Johnson and Norris 1994). Nonetheless, additional survey effort in the spring and summer (May through October) would be of value, and it is possible that dispersal may be greater during that period.

Bottlenose dolphins typically exhibit a fission–fusion form of social organization (Connor *et al.* 2000). Some stable associations among pairs or occasionally trios of individuals, usually of the same sex, have been documented in various populations of bottlenose dolphins, although there appears to be considerable variability among populations in the types and degree of such stable associations (Connor *et al.* 2000). If such stable associations are prevalent in the Hawaiian Islands and associated individuals tend to disperse together, our movement analyses would be positively biased, resulting in an overestimate of the dispersal rates consistent with our data. Although our data set is not extensive enough to allow us to reliably detect such associations, any bias resulting from this effect would be in a direction that would strengthen our conclusion of interisland independence rather than weaken it.

Off O'ahu, between-year resighting rates were much lower than for the other three areas. The low resighting rate for O'ahu resulted in an estimate of marked animals in the population (Table 3) that seems likely to be artificially high, given the estimate of 465 bottlenose dolphins for all the main Hawaiian islands, out to 140 km from shore, based on a large vessel line-transect survey (Barlow 2006). Although lower resighting rates may reflect a much larger population size off O'ahu, there are several reasons why the low resighting rates (and large estimate of marked animals) off O'ahu may be at least partly due to sampling biases/limitations. The sample size, in terms of the number of encounters, is smallest off O'ahu (only 35% of the next largest sample of encounters, off Hawai'i). The average number of individuals identified per encounter off O'ahu (7.2) was almost twice that of Hawai'i (3.7), and thus although the catalog sizes (the number of unique individuals) were almost the same for O'ahu and the island of Hawai'i (67 and 69 individuals, respectively), the potential for resightings is lower off O'ahu. Although identifications were available from O'ahu from three different years, 1 yr was represented by only a single opportunistic identification, thus effectively the O'ahu sample only includes 2 yr. Encounters off O'ahu were also spread over a much larger area than off Hawai'i (median distance among encounter locations of 28.4 km off O'ahu, *vs.* 12.4 km off Hawai'i; Table 4), although the spread among encounters was similar to those off Kaua'i/Ni'ihau or the 4-islands. It is also possible that groups of bottlenose dolphins that were part of an open-ocean population were photo-identified, thus the low resighting rates reflect sampling of more than one population.

The main Hawaiian islands are separated only by channels ranging from 11 to 112 km, with channels between islands from our four different study areas ranging from 44 to 112 km wide. With one sighting from the 4-island area on Penguin Bank, a shallow bank extending to the west from the island of Moloka'i, and one sighting off the southeast tip of O'ahu (Fig. 1), the shortest straight-line distance between encounters from different areas was only 34 km. Within areas, the maximum distance an individual was documented moving was 70.6 km. Although they were primarily found in the shallower parts of our study area, individuals were documented crossing the relatively shallow (<200 m) channels in the 4-islands area, as well as the deeper (~700 m) channel between Kaua'i and Ni'ihau. Coastal bottlenose dolphins in California have been documented moving 670 km (Wells *et al.* 1990), while an individual offshore bottlenose dolphin in the western Atlantic moved over 2,000 km (Wells *et al.* 1999). Given such known dispersal abilities, the lack of movements among areas documented in our study is surprising.

Studies of bottlenose dolphins around other oceanic islands are limited, although the evidence that is available suggests a greater degree of movements than documented in our study. At Cocos Island, off Costa Rica, available evidence from photo-identification suggests the population is large and individuals move through the area (Acevedo-Gutierrez 1999). This study documented 111 groups of 765 distinctive individuals in a 1.5-yr period in an area of approximately 250 km²; most individuals were sighted only once. Around Bermuda, evidence from three satellite-tagged bottlenose dolphins suggest they regularly move from shallow (<200 m) to deep (>1,000 m) water, with linear ranges of at least 100 km (Klatsky *et al.* 2007). Around the main Hawaiian Islands movements of individuals appear to be limited to only a subset of islands, and bottlenose dolphins are found much more frequently in shallow (<1,000 m) water than deep water. Association analyses from the island of Hawai'i (Fig. 3) suggest that individual bottlenose dolphins off that island may show preferences for either shallow (<200 m) or deep (200–1,000 m) waters, although a larger sample size is necessary to confirm this supposition.

Ranging patterns for individuals within a population typically reflect, or are driven by, their particular ecological circumstances. Unfortunately, little is known regarding the diet of bottlenose dolphins in Hawaiian waters. During our efforts we have observed prey captures on only a few occasions, several times with relatively large (>50 cm) but unidentified fish, and once involving multiple captures out of a school of unidentified fish 20–25 cm in length. Unlike several of the other small delphinids in Hawaiian waters (*e.g.*, pantropical spotted dolphins or spinner dolphins), bottlenose dolphins are not known to feed much on deep-scattering layer-associated prey such as myctophids (Walker 1981). The maximum dive depth of bottlenose dolphins is not known, although animals tagged off Bermuda did regularly dive below 450 m (Klatsky *et al.* 2007), thus bottlenose dolphins in Hawai'i likely can feed both in the water column and on the bottom in depths of up to at least a few hundred meters. What is known is that the waters surrounding the Hawaiian Islands are oligotrophic, and productivity is higher immediately around the islands due to a number of oceanographic processes (Doty and Oguri 1956; Gilmartin and Revelante 1974; Seki *et al.* 2001, 2002). Availability of benthic prey near the islands and increased predictability and presumed availability of prey associated with the increased productivity near the islands likely were the selective forces encouraging the formation of island-associated populations. The waters surrounding Cocos Island are highly productive (Palacios *et al.* 2006). While waters surrounding Bermuda are oligotrophic, the surrounding area has higher regional chlorophyll levels than for the

central Pacific surrounding Hawai'i.³ The localized island effects in Hawai'i are likely greater than for Bermuda, given the larger expanse and size of the islands in Hawai'i. Combined with the greater size of the available shallow water habitats in Hawai'i, these factors set Hawai'i apart from either Cocos Island or Bermuda, and may be the reason why such limited movements of animals exist in Hawai'i in comparison. Such factors may explain a lack of offshore movements of island-associated animals, but are less satisfying in terms of understanding the residency of individuals to particular island areas.

Evidence of multiple demographically independent populations of bottlenose dolphins within the main Hawaiian Islands has a number of implications for the conservation and management of these populations. From a management perspective, NMFS currently considers bottlenose dolphins inhabiting the Hawaiian EEZ as a single stock. Our results suggest that within the main Hawaiian Islands there are as many as four discrete populations corresponding to the four main island groupings. Factors potentially influencing these populations vary among the main Hawaiian Islands, including interactions with fisheries, anthropogenic noise from military exercises and vessel traffic, and potentially reduction of prey populations due to over-fishing. Furthermore, the lack of evidence for movements among the main Hawaiian Islands suggests that movements may also be limited for bottlenose dolphins in the northwestern Hawaiian Islands, as has been documented for spinner dolphins (Karczmarski *et al.* 2005, Andrews *et al.* 2006). Thus, our results indicate a need to reconsider stock structure for bottlenose dolphins within the entire Hawaiian EEZ.

ACKNOWLEDGMENTS

Dedicated field efforts were funded by the Southwest Fisheries Science Center, the U.S. Navy (N-45), the Pacific Islands Fisheries Science Center, the Wild Whale Research Foundation, Dolphin Quest, the Hawaiian Islands Humpback Whale National Marine Sanctuary, the Marine Mammal Commission, and the M. R. and Evelyn Hudson Foundation. Additional logistical support was received from David Jung of the Island Marine Institute, Hannah Bernard and Bill Gilmartin of the Hawaii Wildlife Fund, and Joe Mobley of the University of Hawai'i. MHD would like to thank the Marine Mammal Research Consultants for equipment contributions, and the Hawaiian Islands Humpback Whale National Marine Sanctuary for funding support. DRS would like to thank Whale Quest Kapalua, UFO Chuting, Central Pacific Marine, and Atlantic Submarine for support. We would like to thank Alison Stimpert/Oceanwide Science Institute and Doug Perrine for providing additional photos. A number of individuals helped in the field, but we would particularly like to thank La'Ren Antoine, Erica Busatto, Mike Christie, Amanda Cummins, Annie Douglas, Mary Grady, Sascha Hooker, Katie Jones, Saeko Kumagai, Ed Lyman, Alice Mackay, David Mattila, David Nichols, and Amy Sloan for assisting with surveys and photographing dolphins. We would like to thank Jeremy Davies for processing the depth data and Rich Cosgrove for calculating swim distances between sighting locations. Research was undertaken under NMFS Scientific Research Permits No. 587, 731, 774, and 782, and sampling within the Kaho'olawe Island Reserve was undertaken under the authorization of the Kaho'olawe Island Reserve Commission. We thank Jay Barlow, Tim Gerrodette, Aleta Hohn, Dave Johnston, Gretchen Steiger, Randy Wells, and an anonymous reviewer for helpful comments on the manuscript.

³Personal communication from M. Ondrusek, National Environmental Satellite, Data, and Information Service, NOAA, 1335 East-West Highway, Silver Spring, MD, June 2008.

LITERATURE CITED

- ACEVEDO-GUTIERREZ, A. 1999. Aerial behavior is not a social facilitator in bottlenose dolphins hunting in small groups. *Journal of Mammalogy* 80:768–776.
- ANDREWS, K. R., L. KARCMARSKI, W. W. L. AU, S. H. RICKARDS, C. A. VANDERLIP AND R. J. TOONEN. 2006. Patterns of genetic diversity of the Hawaiian spinner dolphin (*Stenella longirostris*). *Atoll Research Bulletin* 543:65–73.
- ANGLISS, R. P., AND R. B. OUTLAW. 2007. Alaska marine mammal stock assessments, 2006. NOAA Technical Memorandum NMFS-AFSC-168. 244 pp.
- BAIRD, R. W., D. L. WEBSTER, S. D. MAHAFFY, D. J. MCSWEENEY, G. S. SCHORR AND A. D. LIGON. 2008a. Site fidelity and association patterns in a deep-water dolphin: Rough-toothed dolphins (*Steno bredanensis*) in the Hawaiian Archipelago. *Marine Mammal Science* 24:535–553.
- BAIRD, R. W., A. M. GORGONE, D. J. MCSWEENEY, D. L. WEBSTER, D. R. SALDEN, M. H. DEAKOS, A. D. LIGON, G. S. SCHORR, J. BARLOW AND S. D. MAHAFFY. 2008b. False killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands: Long-term site fidelity, inter-island movements, and association patterns. *Marine Mammal Science* 24:591–612.
- BARLOW, J. 2006. Cetacean abundance in Hawaiian waters estimated from a summer/fall survey in 2002. *Marine Mammal Science* 22:446–464.
- BEYER, H. L. 2004. Hawth's analysis tools for ArcGIS[®]. Version 3.21 (computer program). Available from <http://www.spatial ecology.com/htools> (accessed 12 September 2005).
- BIGG, M. A. 1982. An assessment of killer whale (*Orcinus orca*) stocks off Vancouver Island, British Columbia. Report of the International Whaling Commission 32:655–666.
- CALAMBOKIDIS, J., AND J. BARLOW. 1991. Chlorinated hydrocarbon concentrations and their use for describing population discreteness in harbor porpoises from Washington, Oregon and California. Pages 101–110 in J. E. Reynolds and D. K. Odell, eds. *Marine mammal strandings in the United States*. NOAA Technical Report. NMFS 98.
- CALAMBOKIDIS, J., G. H. STEIGER, J. M. STRALEY, L. M. HERMAN, S. CERCHIO, D. R. SALDEN, J. URBÁN, J. K. JACOBSEN, O. VON ZIEGESAR, K. C. BALCOMB, C. M. GABRIELE, M. E. DAHLHEIM, S. UCHIDA, G. ELLIS, Y. MIYAMURA, P. LADRÓN DE GUEVARA, M. YAMAGUCHI, F. SATO, S. A. MIZROCH, L. SCHLENDER, K. RASMUSSEN, J. BARLOW AND T. J. QUINN II. 2001. Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science* 17:769–794.
- CARRETTA, J. V., K. A. FORNEY, M. M. MUTO, J. BARLOW, J. BAKER, B. HANSON AND M. S. LOWRY. 2006. U.S. Pacific marine mammal stock assessments: 2005. NOAA-Technical Memorandum-NMFS-SWFSC-388. 317 pp.
- CHIVERS, S. J., A. E. DIZON, P. J. GEARIN AND K. M. ROBERTSON. 2002. Small-scale population structure of eastern North Pacific harbor porpoises (*Phocoena phocoena*) indicated by molecular genetic analyses. *Journal of Cetacean Research and Management* 4:111–122.
- CHIVERS, S. J., R. W. BAIRD, D. J. MCSWEENEY, D. L. WEBSTER, N. M. HEDRICK AND J. C. SALINAS. 2007. Genetic variation and evidence for population structure in eastern North Pacific false killer whales (*Pseudorca crassidens*). *Canadian Journal of Zoology* 85:783–794.
- CONNOR, R. C., R. S. WELLS, J. MANN AND A. J. READ. 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. Pages 91–126 in J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead, eds. *Cetacean societies: Field studies of dolphins and whales*. University of Chicago Press, Chicago, IL.
- DANIL, K., AND S. J. CHIVERS. 2007. Growth and reproduction of female short-beaked common dolphins, *Delphinus delphis*, in the eastern tropical Pacific. *Canadian Journal of Zoology* 85:108–121.
- DANIL, K., D. MALDINI AND K. MARTEN. 2005. Patterns of use of Maku'a Beach, O'ahu, Hawai'i, by spinner dolphins (*Stenella longirostris*) and potential effects of swimmers on their behavior. *Aquatic Mammals* 31:403–412.
- DEFRAN, R. H., D. W. WELLER, D. L. KELLY AND M. A. ESPINOSA. 1999. Range characteristics of Pacific coast bottlenose dolphins (*Tursiops truncatus*) in the Southern California Bight. *Marine Mammal Science* 15:381–393.

- DOTY, M. S., AND M. OGURI. 1956. The island mass effect. *Journal du Conseil International pour l'Exploration de la Mer* 22:33–37.
- ESCORZA-TREVINO, S., F. I. ARCHER, M. ROSALES, A. LANG AND A. E. DIZON. 2005. Genetic differentiation and intraspecific structure of eastern tropical Pacific spotted dolphins, *Stenella attenuata*, revealed by DNA analyses. *Conservation Genetics* 6:587–600.
- FLAMENT, P. 1996. The ocean atlas of Hawai'i. University of Hawai'i. Available from <http://radlab.soest.hawaii.edu/atlas/> (accessed 6 November 2007).
- FORNEY, K. A., AND D. KOBAYASHI. 2007. Updated estimates of mortality and injury of cetaceans in the Hawaii-based longline fishery, 1994–2005. NOAA Technical Memorandum NMFS-SWFSC 412. 30 pp.
- GILMARTIN, M., AND N. REVELANTE. 1974. The 'island mass' effect on the phytoplankton and primary production of the Hawaiian Islands. *Journal of Experimental Marine Biology and Ecology* 16:181–204.
- HEIDE-JORGENSEN, M. P., K. L. LAIDRE, M. V. JENSEN, L. DUECK AND L. D. POSTMA. 2006. Dissolving stock discreteness with satellite tracking: Bowhead whales in Baffin Bay. *Marine Mammal Science* 22:34–45.
- HILLMAN, G. R., B. WÜRSIG, G. A. GAILEY, N. KEHTARNAVAZ, A. DROBYSHEVSKY, B. N. ARAABI, H. D. TAGARE AND D. W. WELLER. 2003. Computer-assisted photo-identification of individual marine vertebrates: A multi-species system. *Aquatic Mammals* 29:117–123.
- HOELZEL, A. R., C. W. POTTER AND P. B. BEST. 1998. Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphin. *Proceedings of the Royal Society of London B* 265:1177–1183.
- JOHNSON, C., AND K. S. NORRIS. 1994. Social behavior. Pages 243–286 in K. S. Norris, B. Würsig, R. S. Wells, M. Würsig, S. M. Brownlee, C. M. Johnson and J. Solow, eds. *The Hawaiian spinner dolphin*. University of California Press, Berkeley, CA.
- KARCZMARSKI, L., B. WÜRSIG, G. GAILEY, K. W. LARSON AND C. VANDERLIP. 2005. Spinner dolphins in a remote Hawaiian atoll: Social grouping and population structure. *Behavioral Ecology* 16:675–685.
- KLATSKY, L. J., R. S. WELLS AND J. C. SWEENEY. 2007. Offshore bottlenose dolphins (*Tursiops truncatus*): Movement and dive behavior near the Bermuda Pedestal. *Journal of Mammalogy* 88:59–66.
- MC SWEENEY, D. J., R. W. BAIRD AND S. D. MAHAFFY. 2007. Site fidelity, associations and movements of Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales off the island of Hawai'i. *Marine Mammal Science* 23:666–687.
- MOBLEY, J. R., S. S. SPITZ, K. A. FORNEY, R. A. GROTEFENDT AND P. H. FORESTELL. 2000. Distribution and abundance of odontocete species in Hawaiian waters: Preliminary results of 1993–98 aerial surveys. National Marine Fisheries Service Southwest Fisheries Science Center Administrative Report LJ-00-14C. 26 pp.
- NITTA, E. T., AND J. R. HENDERSON. 1993. A review of interactions between Hawaii's fisheries and protected species. *Marine Fisheries Review* 55:83–92.
- NORRIS, K. S., B. WÜRSIG, R. S. WELLS, M. WÜRSIG, S. M. BROWNLEE, C. M. JOHNSON AND J. SOLOW. 1994. *The Hawaiian spinner dolphin*. University of California Press, Berkeley, CA.
- PALACIOS, D. M., S. J. BOGRAD, D. G. FOLEY AND F. B. SCHWING. 2006. Oceanographic characteristics of biological hot spots in the North Pacific: A remote sensing perspective. *Deep-Sea Research II* 53:250–269.
- PALSBOÛLL, P. J., M. BÉRUBÉ AND F. W. ALLENDORF. 2007. Identification of management units using population genetic data. *Trends in Ecology and Evolution* 22:11–16.
- QUÉROUIL, S., M. A. SILVA, L. FREITAS, R. PRIETO, S. MAGALHÃES, A. DINIS, F. ALVES, J. A. MATOS, D. MENDONÇA, P. S. HAMMOND AND R. S. SANTOS. 2007. High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. *Conservation Genetics* 8:1405–1419.

- RUBIN, D. B. 1988. Using the SIR algorithm to simulate posterior distributions. Pages 395–402 in J. M. Bernardo, M. H. de Groot, D. V. Lindley and A. F. M. Smith, eds. Bayesian statistics 3. Clarendon Press, Oxford, UK.
- SCOTT, M. D., R. S. WELLS AND A. B. IRVINE. 1990. A long-term study of bottlenose dolphins on the west coast of Florida. Pages 235–244 in S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, San Diego, CA.
- SEBER, G. A. F. 1982. The estimation of animal abundance and related parameters. 2nd edition. Griffin, London, UK.
- SEKI, M. P., J. J. POLOVINA, R. E. BRAINARD, R. R. BIDIGARE, C. L. LEONARD AND D. G. FOLEY. 2001. Biological enhancement at cyclonic eddies tracked with GOES thermal imagery in Hawaiian waters. Geophysical Research Letters 28:1583–1586.
- SEKI, M. P., R. LUMPKIN AND P. FLAMENT. 2002. Hawai'i cyclonic eddies and blue marlin catches: The case study of the 1995 Hawaiian International Billfish Tournament. Journal of Oceanography 58:739–745.
- SELLAS, A. B., R. S. WELLS AND P. E. ROSEL. 2005. Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. Conservation Genetics 6:715–728.
- SOUTHALL, B. L., R. BRAUN, F. M. D. GULLAND, A. D. HEARD, R. W. BAIRD, S. M. WILKIN AND T. K. ROWLES. 2006. Hawaiian melon-headed whale (*Peponocephala electra*) mass stranding event of July 3–4, 2004. NOAA Technical Memorandum NMFS-OPR-31. 73 pp.
- TANAKA, S. 1987. Satellite radio tracking of bottlenose dolphins *Tursiops truncatus*. Nippon Suisan Gakkaishi 53:1327–1338.
- TAYLOR, B. L. 1997. Defining 'population' to meet management objectives for marine mammals. Pages 49–65 in A. E. Dizon, S. J. Chivers and W. F. Perrin, eds. Molecular genetics of marine mammals. Special Publication 3, Society for Marine Mammalogy, Lawrence, KS.
- URIAN, K. W., D. A. DUFFIELD, A. J. READ, R. S. WELLS AND E. D. SHELL. 1996. Seasonality of reproduction in bottlenose dolphins, *Tursiops truncatus*. Journal of Mammalogy 77:394–403.
- WADE, P. R., AND R. P. ANGLISS. 1997. Report of the GAMMS workshop, April 3–5, 1996, Seattle, Washington. NOAA Technical Memorandum NMFS-OPR-12. 93 pp.
- WALKER, W. A. 1981. Geographical variation in morphology and biology of bottlenose dolphins (*Tursiops*) in the eastern North Pacific. NOAA SWFSC Administrative Report LJ-81-03C. 52 pp.
- WARING, G. T., E. JOSEPHSON, C. P. FAIRFIELD AND K. MAZE-FOLEY. 2007. U.S. Atlantic and Gulf of Mexico marine mammal stock assessments—2006. NOAA Technical Memorandum NMFS NE 201. 378 pp.
- WELLS, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199–225 in K. Pryor and K. S. Norris, eds. Dolphin societies, discoveries and puzzles. University of California Press, Berkeley, CA.
- WELLS, R. S., AND M. D. SCOTT. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-recapture techniques. Report of the International Whaling Commission (Special Issue 12):407–415.
- WELLS, R. S., T. P. DOHL, L. J. HANSEN, D. L. KELLY, A. BALDRIDGE AND R. H. DEFRAN. 1990. Northward extension of the range of bottlenose dolphins along the California coast. Pages 421–431 in S. Leatherwood and R. R. Reeves, eds. The bottlenose dolphin. Academic Press, New York, NY.
- WELLS, R. S., H. L. RHINEHART, P. CUNNINGHAM, J. WHALEY, M. BARAN, C. KOBERNA AND D. P. COSTA. 1999. Long distance offshore movements of bottlenose dolphins. Marine Mammal Science 15:1098–1114.
- WILLIAMS, T. M. 1999. The evolution of cost efficient swimming in marine mammals: Limits to energetic optimization. Philosophical Transactions of the Royal Society of London B. Biological Sciences 354:193–201.

- WÜRSIG, B. 1978. Occurrence and group organization of Atlantic bottlenose porpoises (*Tursiops truncatus*) in an Argentine Bay. *Biological Bulletin* 154:348–359.
- WÜRSIG, B., AND T. A. JEFFERSON. 1990. Methods of photo-identification for small cetaceans. *Report of the International Whaling Commission (Special Issue 12)*:43–52.

Received: 16 January 2008

Accepted: 28 July 2008