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Population structure of island-associated dolphins: Evidence from mitochondrial and microsatellite markers for common bottlenose dolphins (*Tursiops truncatus*) around the main Hawaiian Islands

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ABSTRACT

We used mitochondrial and nuclear genetic markers to investigate population structure of common bottlenose dolphins, *Tursiops truncatus*, around the main Hawaiian Islands. Though broadly distributed throughout the world's oceans, bottlenose dolphins are known to form small populations in coastal waters. Recent photo-identification data suggest the same is true in Hawaiian waters. We found genetic differentiation among (mtDNA $\Phi_{ST} = 0.014$–0.141, microsatellite $F'_{ST} = 0.019$–0.050) and low dispersal rates between (0.17–5.77 dispersers per generation) the main Hawaiian Island groups. Our results are consistent with movement rates estimated from photo-identification data and suggest that each island group supports a demographically independent population. Inclusion in our analyses of samples collected near Palmyra Atoll provided evidence that the Hawaiian Islands are also occasionally visited by members of a genetically distinct, pelagic population. Two of our samples exhibited evidence of partial ancestry from Indo-Pacific bottlenose dolphins (*T. aduncus*), a species not known to inhabit the Hawaiian Archipelago. Our findings have important implications for the management of Hawaiian bottlenose dolphins and raise concerns about the vulnerability to human impacts of pelagic species in island ecosystems.

Key words: population structure, genetic differentiation, demographic independence, management units, Hawaii, *Tursiops*.

Within the Hawaiian Archipelago, several studies have shown the presence of island-associated populations within wide-ranging pelagic species, including spinner dolphins (*Stenella longirostris*; Galver 2002, Karczmarski *et al.* 2005, Andrews *et al.* 2010), rough-toothed dolphins (*Steno bredanensis*; Baird *et al.* 2008*b*), and false killer whales (*Pseudorca crassidens*; Chivers *et al.* 2007, Baird *et al.* 2008*a*). The presence of island-associated populations in otherwise pelagic species has important conservation implications. Many human impacts on marine ecosystems tend to be concentrated near coasts, including pollution, fisheries bycatch, prey depletion by commercial and recreational fisheries, marine ecotourism, and boat traffic. If the animals being affected by these anthropogenic activities are actually members of small, island-associated populations rather than large, pelagic populations, then the human impacts are much more likely to result in local depletion or even extirpation of potentially genetically and ecologically distinct populations.

Common bottlenose dolphins (*Tursiops truncatus*; hereafter bottlenose dolphins) are another broadly distributed open ocean species that may have evolved island-associated populations around the Hawaiian Islands. Bottlenose dolphins have been found to exhibit population structure in many coastal continental habitats. Distinct coastal and pelagic forms of bottlenose dolphins have been documented in the North Atlantic (Hoelzel *et al.* 1998*b*; Parsons *et al.* 2002; Natoli *et al.* 2004, 2005; Parsons *et al.* 2006), Gulf of Mexico (Sellas *et al.* 2005), Gulf of California (Segura *et al.* 2006), and eastern Pacific (Curry 1997, Sanino *et al.* 2005, Lowther 2006). Fine-scale structure within coastal and estuarine areas has also been detected (Sellas *et al.* 2005, Parsons *et al.* 2006, Möller *et al.* 2007, Rosel *et al.* 2009). Relatively little is known about the genetics of bottlenose dolphins around oceanic islands. However, the limited data that are available suggest that bottlenose dolphins are less likely to develop population structure in oceanic habitats than in continental habitats. A photo-identification (ID) study at Cocos Island suggests the animals there are part of a large, pelagic population (Acevedo-Gutierrez 1999). Around the Azores and

Madeiran Archipelagos, photo-ID data suggested the presence of resident animals (Silva 2006). However, a genetic study of those archipelagos revealed high rates of gene flow within and among the archipelagos and between the archipelagos and the eastern North Atlantic pelagic population (Querouil *et al.* 2007). The lack of genetic structure observed was attributed to a low density of prey throughout the region (Silva *et al.* 2008).

Bottlenose dolphins have been documented around all of the main Hawaiian Islands and many of the Northwestern Hawaiian Islands all the way to Kure Atoll at the northwestern end of the island chain (Rice 1998). Abundance within the U.S. Exclusive Economic Zone (EEZ) around Hawaii, an area of over 2,383,000 km^2, is estimated at 3,215 individuals (CV = 0.59; Barlow 2006). Abundance around the main Hawaiian Islands is estimated at only 1,245 individuals (correcting for the proportion of marked individuals; Baird *et al.* 2009). Hawaiian bottlenose dolphins are currently managed as a single stock encompassing the entire U.S. Hawaiian EEZ (Carretta *et al.* 2009). Baird *et al*. (2009) recently suggested the occurrence of four demographically independent populations around the main Hawaiian Island groups based on photo-ID data. They reported high resighting rates and no movement of animals among island groups, suggesting small populations with high site fidelity and interisland dispersal rates less than 1% per year. However, the short time span (7 yr) of the photo-ID study makes it unlikely to detect rare dispersal events.

The management scheme used for species protected by the U.S. Marine Mammal Protection Act (MMPA) is vulnerable to undetected population structure. Under the MMPA, stocks are defined as demographically independent populations for which "population dynamics . . . is more a consequence of births and deaths within the group (internal dynamics) rather than immigration and emigration (external dynamics)" (Wade and Angliss 1997). This definition is essentially identical to the definition of Management Units proposed by Palsbøll *et al.* (2007) and falls into the "Ecological paradigm" of population definitions described by Waples and Gaggiotti (2006). Under this paradigm, detecting population structure through genetic analysis can be quite challenging, as the expected level of differentiation can be quite low. The presence of unrecognized population structure within the Hawaiian stock of bottlenose dolphins, as suggested by Baird *et al*. (2009), represents a serious management concern. Hawaiian bottlenose dolphins are known to interact with numerous near-shore commercial and recreational fisheries, including gill net fisheries. Because these fisheries are not observed or monitored, it is impossible to quantify their impacts on bottlenose dolphins and other cetaceans. However, entanglement in gill nets is known to be a major cause of cetacean mortality in other areas of the world (Perrin *et al.* 1994, Read *et al.* 2006). The relatively low abundance of bottlenose dolphins around the main Hawaiian Islands means that even a low level of human-caused mortality could pose a serious threat. Under the current stock structure, the risks posed by human-caused mortality around the main Hawaiian Islands are assessed relative to the total abundance of the entire EEZ (N = 3,215). However, such an assessment would overestimate the level of human impact that could be sustained by the island-associated populations if they are, in fact, demographically independent.

In this study, we used data from both mitochondrial (mtDNA) and nuclear (nDNA) genetic markers to investigate the population structure of bottlenose dolphins around the main Hawaiian Island groups. We tested the hypothesis suggested by Baird *et al*. (2009) that each island group supports a demographically independent population. We used the approach outlined by Palsbøll *et al.* (2007), in which results are

interpreted relative to the critical level of dispersal and differentiation necessary to meet conservation objectives. Taylor (1997) showed that, for dolphin species, the critical level of dispersal below which populations requires separate management if the conservation goals of the MMPA are to be met is typically several percent per year. Given the estimated 21 yr generation time for bottlenose dolphins (Taylor *et al.* 2007), a 1% per year dispersal rate corresponds to a per generation dispersal rate (m) of 0.21. The expected level of genetic differentiation (F_{ST}) between two populations can be calculated using Wright's (1965) formulae:

$$F_{ST}\,(mtDNA) = 1/(2N_em + 1)$$

$$F_{ST}\,(nDNA) = 1/(4N_em + 1)$$

where N_e is the effective population size. The average abundance estimate (N) at the four main Hawaiian Islands groups is 312 (correcting for the proportion of marked individuals; Baird *et al.* 2009). Nunney (1993, Eq. 22) shows that the approximate ratio of N_e to the number of breeding adults for long-lived species can be calculated from the age of maturation and average lifespan. Using the life history values reported in Taylor *et al*. (2007) (age at first reproduction is 9.5 yr, mature adults comprise 62% of the population, and average life span of 12.4 calculated from juvenile survival rate of 0.76 and adult survival rate of 0.95), the average N_e for the four main Hawaiian Islands groups is approximately 81 for mtDNA and 163 for nuclear DNA. Thus, the expected level of differentiation for a dispersal rate of 1% per year (21% per generation) is 0.028 for mtDNA and 0.007 for nDNA. The actual level of differentiation resulting from this dispersal rate could differ substantially due to differences between the life history values of Hawaiian bottlenose dolphins and those reported in Taylor *et al*. (2007), violations of the assumptions of the models of Wright (1965) and Nunney (1993), and the stochastic nature of genetic drift and dispersal (Taylor *et al.* 2000). For instance, the actual differentiation for high-diversity markers will be lower than the expected value due to their high mutation rates (Balloux *et al.* 2000). Nonetheless, these calculations give a sense of the magnitude of differentiation expected from a 1% annual dispersal rate between the main Hawaiian Islands.

We also compared the Hawaiian samples to samples collected nearly 1,700 km southwest at Palmyra Atoll in order to gain insight into how the Hawaiian insular animals relate to animals from surrounding waters. Our results provide insight into both the proper management of bottlenose dolphins within the Hawaiian EEZ and the likelihood of finding island-associated populations of other pelagic species in insular habitats.

METHODS

Sample Collection

A total of 146 biopsy samples from 54 groups of live, free-ranging bottlenose dolphins, and one sample from an animal that stranded dead on O'ahu were analyzed for this study (Table S1). A total of 116 of these samples were collected as part of the photo-ID study conducted by Baird *et al*. (2009), while the remainder were collected opportunistically by researchers at the Hawaiian Islands Humpback Whale National Marine Sanctuary and during Southwest Fisheries Science Center (SWFSC) research

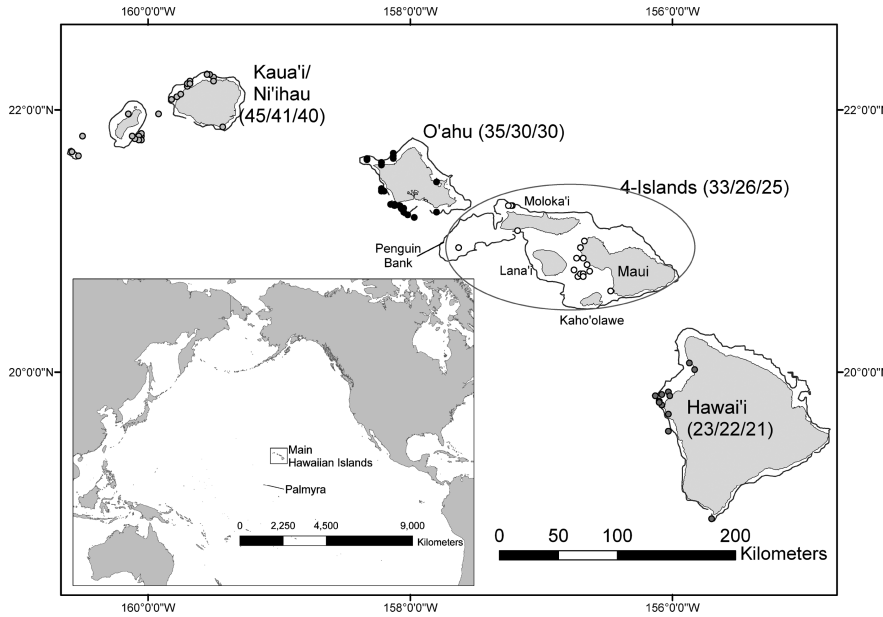

Figure 1. Map showing the sampling locations around the main Hawaiian Islands. Samples are shaded according to the island group from which they were sampled. Sample sizes (initial/final mtDNA/final microsatellites) are shown for each stratum. The black lines surrounding the island groups indicate the 400 m depth contour. The inset shows the locations of the Hawaiian Islands and Palmyra within the Pacific Ocean.

cruises. Of these 147 samples, 136 were collected around the main Hawaiian Islands (Fig. 1) and 11 were collected around Palmyra Atoll/Kingman Reef. In addition, seven *Tursiops aduncus* samples collected at the Hong Kong Aquarium from animals originally captured in Taiwan and Indonesia were included in the microsatellite analyses. All samples were part of the SWFSC Marine Mammal and Turtle Molecular Research Sample Collection (http://swfsc.noaa.gov/PRD-TissueCollection) and were either stored frozen at −80°C or at −20°C in a salt-saturated 20% dimethyl sulfoxide solution prior to laboratory analysis.

Samples collected around the main Hawaiian Islands were stratified into island groups consistent with those defined by Baird *et al*. (2009) (Fig. 1). Baird *et al*. combined Mau'i, Lana'i, Moloka'i, Kaho'olawe, and Penguin Banks into a single "4-Islands" stratum based on photo-ID data showing that individuals move freely through this region, which is characterized by contiguous shallow water (<200 m) habitat. Kaua'i and Ni'ihau were also combined based on photo-ID data (Baird *et al.* 2009).

Laboratory Analyses

Standard protocols were used for DNA extraction (Qiagen DNeasy Blood and Tissue Kit, Valencia, CA) and amplification, as well as for mitochondrial DNA (mtDNA) sequencing (Saiki *et al.* 1988, Sambrook *et al.* 1989, Palumbi *et al.* 1991). A 400 basepair region of the 5′ end of the hypervariable mtDNA control region

was amplified using primers D (5′-CCTGAAGTAAGAACCAGATG-3′; Rosel *et al.* 1994) and TRO (5′-CCTCCCTAAGACTCAAGG-3′; developed at SWFSC). The polymerase chain reaction (PCR) cycling profile for mtDNA sequencing consisted of 94°C for 2.5 min, followed by 35 cycles of 94°C for 45 s, 1 min at 48°C annealing temperature, and 72°C for 1.5 min, then a final extension at 72°C for 5 min. Both the forward and reverse strands of the amplified DNA product were sequenced as mutual controls on the Applied Biosystems Inc. (ABI; Foster City, CA) model 3100 sequencer. All sequences were aligned using Sequencer v4.1 software (Gene Codes Corp., 2000; Ann Arbor, MI).

Microsatellite DNA primers for 11 loci (all dinucleotide repeats) were analyzed for all samples. Primer sets for loci KWM1b, KWM2a, KWM2b, and KWM12a were derived from killer whales (*Orcinus orca*; Hoelzel *et al.* 1998*a*); loci D5 and D12 from beluga whales (*Delphinapterus leucas*; Buchanan *et al.* 1996); and loci Ttr11, Ttr34, Ttr48 (Rosel *et al.* 2005), TexVet7 (Rooney *et al.* 1999), and D08 (Shinohara *et al.* 1997) were derived from bottlenose dolphins (*Tursiops* sp.). Extracted DNA was amplified using a 25 μL reaction of 1 × PCR buffer (50 mM KCl, 10 mM Tris-HCl, pH 8.3, and either 1.5 mM or 2.0 mM $MgCl_2$), 0.15 mM of each dNTP, 0.3 μM of each primer, 0.5 units of Taq DNA polymerase, and approximately 10 ng of DNA. The PCR cycling profile for the loci that amplified with the 1.5 mM $MgCl_2$ buffer (KWM1b, KWM2a, KWM2b, KWM12a, TexVet7, and D08) consisted of 90°C for 2.5 min, followed by 35 cycles of 94°C for 45 s, 1 min at annealing temperature, and 72°C for 1.5 min, then a final extension at 72°C for 5 min. The optimal annealing temperature was 55°C for the loci D08 and TexVet7 and 45°C for KWM1b, KWM2a, KWM2b, and KWM12a. For the loci that amplified with the 2.0 mM $MgCl_2$ buffer (D5, D12, Ttr11, Ttr34, and Ttr48), the PCR cycling profile was 90°C for 2.0 min, followed by 50 cycles of 94°C for 5 s, 10 s at annealing temperature, and 72°C for 10 s, then a final extension of 72°C for 3 min. The optimal annealing temperature for loci D5, D12, and Ttr34 was 57°C and for Ttr11 and Ttr48 was 55°C.

The amplifications were assessed electrophoretically on a 2% agarose gel for quality and size before loading onto the ABI 3100 Genetic Analyzer. ABI Genemapper v4.0 was used along with an internal standard marker, Genescan-500 ROX, ABI, to determine allele fragment size. Allelic frequency per population was assessed using the program CONVERT (Glaubitz 2004). Both mtDNA sequencing and microsatellite genotyping analyses included at least 10% replication for data quality assurance. Replication was designed to test for both random errors (*e.g.*, miscalled basepairs or alleles) and systematic errors (*e.g.*, errors affecting an entire extraction plate or PCR reaction).

Samples were genetically sexed by amplification and Real-Time PCR (Stratagene) of the zinc finger (ZFX and ZFY) genes (Morin *et al.* 2005).

Molecular Diversity

Micro-Checker (Van Oosterhout *et al.* 2004) was used to check all loci for evidence of null alleles and allelic dropout. Deviation from Hardy–Weinberg equilibrium (HWE) was assessed for microsatellite loci using Genepop version 3.4 (Raymond and Rousset 1995). Both exact tests of HWE (Guo and Thompson 1992) and tests for heterozygote deficiency were conducted. The same software was used to evaluate linkage disequilibrium for each pair of loci using Fisher's method and the Markov

chain method. All HWE and linkage disequilibrium tests were conducted using program defaults for the Markov chain parameters (1,000 dememorization steps, 100 batches, 1,000 iterations per batch). Tests were first conducted for all Hawaiian samples combined into a single group and then repeated separately for each island group. For the island-specific HWE tests, a sequential Bonferroni correction (Rice 1989) was applied across all tests conducted for each island group.

Individuals that matched in sex, mtDNA haplotype, and microsatellite genotype were deemed duplicate samples and one copy was discarded from the sample set. The data set was also screened for possible near-match duplicates, *i.e.*, samples whose genotypes differed at three or fewer loci and therefore might represent duplicate samples with genotyping errors. We used the program GenAlEx v.6 (Peakall and Smouse 2006) to examine our ability to discriminate unique individuals using our microsatellite data set. We calculated both the probability that two randomly chosen individuals would possess the same multilocus genotype and the probability that full siblings would share the same genotype (Taberlet and Luikart 1999).

Relatedness within each island group was estimated using the method of Queller and Goodnight (1989) as implemented in the program Relatedness 5.0. Because the populations around each island group are small (Barlow 2006, Baird *et al.* 2009), we expect that our sample will include many close relatives. So long as each island group is sampled randomly, the inclusion by chance of close relatives will not introduce a bias into our sample. However, if closely related individuals are sampled preferentially, we could be misled into believing there is differentiation between island groups when in fact the signal we detect is simply due to sampling bias. This could happen, for example, if closely related individuals travel together and are sampled during the same encounter. In order to avoid this potential bias, we used the program Kinship 1.2 (Goodnight and Queller 1999) to identify all pairs of individuals that shared at least one allele at every microsatellite locus. These pairs represent all possible parent–offspring pairs. We excluded from our data set one member of each pair only if the two samples were taken during the same encounter.

Haplotype and nucleotide diversity for each island group and for all samples combined was calculated using Arlequin (Excoffier *et al.* 2005). We used the program jModelTest (Guindon and Gascuel 2003, Posada 2008) to select the model of nucleotide substitution that best fit our data. We calculated likelihoods for all 88 models implemented by the program and used Akaike's Information Criterion (AIC) for model selection. A median-joining network of the unique haplotypes was used to look for phylogeographic patterns in the mtDNA data. The network was constructed using the algorithm of Bandelt *et al*. (1999), as implemented by the software package Network 4.5.1.0 (Fluxus Technology, Ltd., Suffolk, England; available at http://www.fluxus-engineering.com/sharenet.htm). The maximum parsimony (MP) option (Polzin and Daneschmand 2003) was used to identify and eliminate unnecessary median vectors and links.

For the microsatellite data, the program FSTAT (Goudet 2001) was used to calculate allelic richness (based on a minimum sample size of three) and number of alleles per locus, while Genepop (Raymond and Rousset 1995) was used to calculate observed and expected heterozygosity.

Population Differentiation

The global null hypothesis of no population structure among the island groups was first tested for both the mtDNA and microsatellite data sets by conducting

global tests of genetic differentiation. Pairwise comparisons were then conducted between all pairs of island groups. Differentiation was assessed in the mtDNA data set using Fisher's exact test (Raymond and Rousset 1995) as implemented in Arlequin (Excoffier *et al.* 2005) and in the microsatellite data set using a *G*-test (Goudet *et al.* 1996) as implemented in Hierfstat (Goudet 2006, R Development Core Team 2006). Fisher's exact test has been shown to be more powerful than an F_{ST} permutation test for evaluating statistical significance in mtDNA data sets (Hudson *et al.* 1992), while the *G*-test is more powerful than F_{ST} permutation tests for microsatellites (Goudet *et al.* 1996). Statistical significance was determined through 10,000 random permutations of the original data sets.

We used three F_{ST} analogues to estimate genetic differentiation between populations. For both data sets, we calculate Weir and Cockerham's (1984) θ, using Genepop (Raymond and Rousset 1995) for the nuclear data set and Arlequin (Excoffier *et al*. 2005) for the mtDNA data set. Like most F_{ST} analogues, θ exhibits a downward bias when within-population diversity is high. We therefore also calculated two F_{ST} analogues that do not exhibit this bias. For the mtDNA, we calculated Φ_{ST} (Excoffier *et al.* 1992), as implemented in Arlequin (Excoffier *et al.* 2005). Φ_{ST} is an extension of Weir and Cockerham's (1984) θ that takes into account the evolutionary distances between haplotypes, which we calculated using the nucleotide substitution model receiving the highest AIC score in the jModelTest analysis. Because Φ_{ST} explicitly accounts for the mutation process, it is independent of mutation rate and therefore does not require a correction for diversity (Meirmans and Hedrick 2011). Furthermore, it has been shown to correspond to the expected levels of divergence based on Wright's formulae (Kronholm and Loudet 2010). For the nuclear data set, we used RECODE (Meirmans 2006) and Genepop (Raymond and Rousset 1995) to calculate F'_{ST} ($= \theta/\theta_{max}$; Hedrick 2005, Meirmans 2006). F'_{ST} corrects for within-population diversity, making it more appropriate for making demographic inferences than θ (Meirmans and Hedrick 2011). However, F'_{ST} was not derived from Wright's (1965) formulae and does not track the expected values from those formulae (Kronholm and Loudet 2010). Therefore, we focus on Φ_{ST} for the mtDNA data set and θ the for nuclear data set when determining whether the observed levels of genetic divergence between the main Hawaiian Islands are consistent with Baird *et al*.'s (2009) dispersal rate estimates. We follow standard convention by henceforth referring to θ as F_{ST}.

We tested for evidence of sex-biased dispersal in the microsatellite data set using the biased dispersal test of FSTAT (Goudet *et al.* 2002). We examined differences between males and females with respect to mean and variance of assignment indices, F_{IS}, F_{ST}, relatedness, and within-group gene diversity (H_S) and assessed significance through 1,000 permutations. To test for evidence of sex-biased dispersal within the mtDNA data set, we used the R package Hierfstat (Goudet 2006, R Development Core Team 2006) and custom R code (available from KKM upon request) to create an mtDNA implementation of the same sex-biased dispersal test used for the microsatellite data set. For the mtDNA data set, we only compared F_{ST} values between males and females, and again assessed significance through 1,000 permutations.

We used the Bayesian clustering program STRUCTURE 2.3.1 (Pritchard *et al.* 2000, Falush *et al.* 2003, Hubisz *et al.* 2009) to cluster the samples on the basis of their microsatellite genotypes. We used an admixture model with correlated frequencies and used sampling location as a prior. We examined the sensitivity of our results to this setting by running a second set of analyses in which sampling location information was not used. We also ran an analysis in which sampling location was used as a prior but Palmyra was excluded, as excluding more divergent populations

can sometimes enhance the ability of STRUCTURE to detect more subtle population structure. We had STRUCTURE cluster the samples into $k = 1$–6 groups and ran STRUCTURE 10 times for each k. We compared estimates of likelihood and ancestry across runs to confirm convergence. We evaluated support for different values of k by comparing the average log probability of the data (Ln $P(D)$) associated with each model. For all STRUCTURE analyses, we used a burn-in of 100,000 and a run length of 5,000,000. All other parameters were left at program defaults, unless otherwise specified for specific analyses.

We used STRUCTURE to look for individuals that are immigrants between Hawai'i and Palmyra or have recent immigrant ancestry. To do this, we labeled the samples as to whether they were collected around the Hawaiian Islands or at Palmyra. We then ran STRUCTURE with the USEPOPINFO option and had STRUCTURE look for immigrant ancestry up to two generations in the past.

We also used the USEPOPINFO option to look for *T. truncatus*/*T. aduncus* hybrids in the data sets. Though *T. aduncus* has never been reported from the Hawaiian Islands, one sample from our study possessed a haplotype typical of this species (see Results). For this analysis, we added to the data set seven samples of *T. aduncus* that were collected at the Hong Kong Aquarium from animals captured in Indonesia and Taiwan. We labeled the known *T. aduncus* samples as "aduncus" and all other samples as "truncatus" and again looked for immigrant ancestry up to two generations in the past. For this analysis, we assumed that allele frequencies were independent between the two species.

We analyzed the microsatellite data set using Migrate 3.0.3 (Beerli and Felsenstein 1999, 2001) to estimate rates of gene flow within the Hawaiian Archipelago and between each of the Hawaiian Island groups and Palmyra. We used Migrate to calculate the number of migrants per generation (N_em) and the effective population size times the mutation rate ($N_e\mu$) for each population. Note that the latter quantity is referred to as θ by the Migrate software, but we refer to it as $N_e\mu$ to avoid confusion with one of the measures of genetic divergence we use, namely Weir and Cockerham's (1984) θ. We conducted a maximum likelihood analysis using 10 short chains (20,000 steps) and three long chains (200,000 steps). For both chain lengths, we used a 10,000 step burn-in and recorded the genealogy every 20 steps. The analysis was first run using simple estimates of $N_e\mu$ and N_em, calculated by Migrate using standard formulae, as initial parameter values, then rerun by initializing at the estimates provided by the initial run. This process was repeated three times, each time initializing with the estimates provided by the previous run. The estimates produced by the last two runs were consistent, indicating that convergence had been achieved. Profile likelihoods were calculated using the "Fast" option, in which percentiles are first estimated assuming all parameters are uncorrelated and then refined through one full maximization cycle for each parameter. We set Migrate to output dispersal rate estimates as $4N_em$, and then divided by four to convert to number of migrants per generation.

RESULTS

Data Editing

When all Hawaiian samples were combined into a single population, the test for heterozygote deficiency and the exact test of deviation from HWE were both significant in the global comparison, as well as for three individual loci: KWM1b,

D5, and Ttr34. Once the samples were divided into island groups, both the tests indicated that KWM1b deviated significantly from HWE in the samples from Kaua'i/Ni'ihau. No deviation was detected for any other loci at Kaua'i/Ni'ihau, and no deviation was detected for any loci at any of the other island groups. No loci showed evidence of linkage disequilibrium, null alleles, or allelic dropout. Results were not sensitive to the inclusion of KWM1b, so it was retained.

The probability of identity for our data set for unrelated individuals is 4.12×10^{-13} and for full siblings is 3.06×10^{-5}, indicating that our microsatellite data set is adequate for identifying unique individuals. Eleven pairs of samples were found to have identical microsatellite genotypes, the same mtDNA haplotype, and were of the same sex. One member of each pair was excluded from the analysis. In all cases of duplicate samples, both were collected from the same island, and three of 11 were collected during the same encounters. We found no near-match duplicates; all pairs of remaining samples had genotypes that differed by at least five alleles.

We identified six pairs of samples, all from the Hawaiian Islands, that shared at least one allele at every locus and were sampled during the same encounter. As these represent possible parent–offspring pairs sampled from the same group, we eliminated one member of each pair in order to avoid a bias in our sampling due to the sampling of family groups. Four samples (three from the Hawaiian Islands and one *T. aduncus*) were excluded from the study because we were unable to obtain reliable genotypes for them at three or more microsatellite loci. After all exclusions, the microsatellite data set contained 127 individuals from Hawai'i and Palmyra and six *T. aduncus*, all of which had been genotyped for at least 10 of 11 microsatellite loci, while the mtDNA data set contained 130 individuals, all from Hawai'i and Palmyra (Table S1).

Molecular Diversity

We identified 25 unique haplotypes (GenBank accession numbers EF672700-EF672723 and EF672725) among the 130 unique individuals we sequenced from the Hawaiian Islands and Palmyra (Table S2). Eighteen haplotypes were only found around the Hawaiian Islands, five were only detected in the Palmyra samples, and two haplotypes (haplotypes 9 and 10) were shared (Table 1). Haplotype 20, which was represented by a single sample collected off the coast of Kaua'i (sample 34066), differed from all others by an average of 19.5 mutations (range 18–23). We resequenced sample 34066 using a subsample that had been stored independently. We obtained an identical sequence from the subsample, eliminating the possibility of a sample mix-up in the SWFSC Tissue Collection. Using searches in BLAST (http://www.ncbi.nlm.nih.gov/BLAST/) and DNA Surveillance (http://www.cebl.auckland.ac.nz:9000/), we found haplotype 20 to be more similar to *T. aduncus* than to other *T. truncatus* samples. Haplotype 20 differed from the *T. aduncus* haplotypes published by Wang *et al*. (1999) by an average of 5.3 base pairs (range 3–9 bp). Wang *et al*. (1999) identified seven fixed differences between *T. truncatus* and *T. aduncus.* Haplotype 20 possessed the *T. aduncus* character at all seven of these diagnostic sites. We ran all mtDNA analyses both with and without sample 34066 and found that results were not sensitive to its inclusion (Φ_{ST}s were 0.001–0.007 lower when 34066 was included). We therefore included this sample in all results reported below.

Haplotype diversity for the five islands ranged from 0.779 to 0.909 (Table 2). Nucleotide diversity ranged from 0.018 to 0.022 (Table 2). The model of nucleotide

Table 1. Frequencies for 25 mtDNA haplotypes detected in the data set. See Table S2 for haplotype definitions.

Genbank accession number	Haplotype ID	Palmyra (11)	Hawai'i (22)	4-Islands (26)	O'ahu (30)	Kaua'i (41)
EF672600	1		5	7	8	8
EF672601	2		1	10	3	6
EF672602	3		3	3		2
EF672603	4		6	1	8	8
EF672604	5			3		
EF672605	6		2		4	
EF672606	7		1			
EF672607	8					1
EF672608	9	3	2			
EF672609	10	2	1			
EF672610	11			1		
EF672611	12		1		3	6
EF672612	13				4	1
EF672613	14					1
EF672614	15					1
EF672615	16					1
EF672616	17					2
EF672617	18					1
EF672618	19			1		2
EF672625	20					1
EF672619	21	1				
EF672620	22	2				
EF672621	23	1				
EF672622	24	1				
EF672623	25	1				

substitution favored by jModelTest was the Tamura-Nei model with rate variation among sites and some invariant sites (denoted TrN+I+G in jModelTest), and gamma shape parameter of 0.179. The median-joining network (Fig. 2) revealed a sparse tree with many missing haplotypes. There was little geographic concordance in the clustering of the island groups, though most of the samples from Palmyra had haplotypes that clustered together and were either not shared with the other islands or were shared only with the island of Hawai'i.

Table 2. Haplotype and nucleotide diversity (±SE) for the island groups and overall.

	Sample size	Number of haplotypes	Haplotype diversity	Nucleotide diversity
Palmyra	11	7	0.909 ± 0.066	0.018 ± 0.010
Hawai'i	22	9	0.870 ± 0.044	0.022 ± 0.011
4-Islands	26	7	0.779 ± 0.055	0.019 ± 0.010
O'ahu	30	6	0.830 ± 0.033	0.018 ± 0.009
Kaua'i/Ni'ihau	41	14	0.892 ± 0.024	0.022 ± 0.011
Overall	130	25	0.886 ± 0.014	0.022 ± 0.011

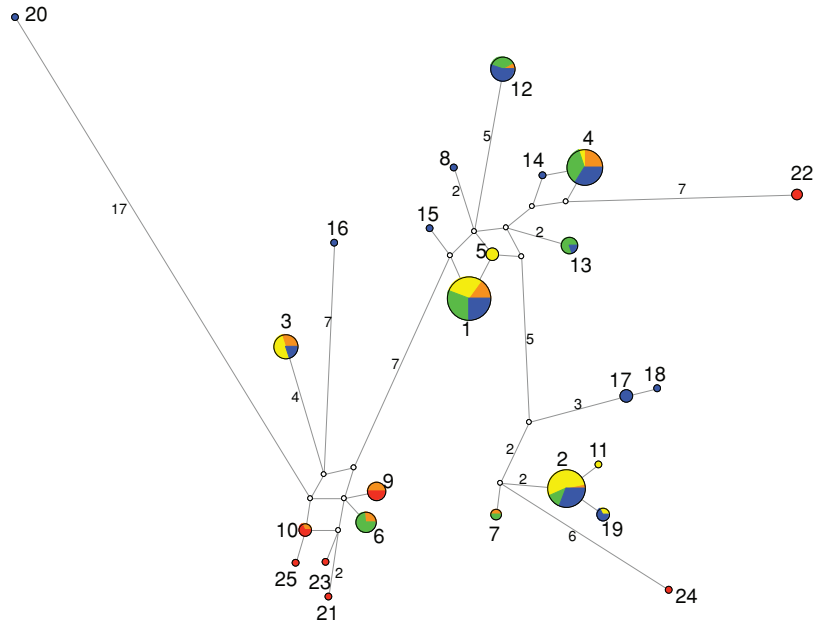

Figure 2. Median-joining network showing relationships among the mtDNA haplotypes. Numbers next to nodes correspond to "Haplotype ID" listed in Table 1. The sizes of the nodes are proportional to the frequencies of the haplotypes. Each node is shaded to indicate the fraction of individuals with that haplotype that comes from each island group: red = Palmyra, orange = Hawai'i, yellow = 4-Islands region, green = O'ahu, and blue = Kaua'i/Ni'ihau. Small open circles indicate haplotypes that were inferred by the program but not found in our sample. Numbers next to lines represent the number of pairwise differences between haplotypes. Unlabeled lines represent a single base pair difference.

For the microsatellite data, observed heterozygosity ranged from 0.656 to 0.750 for the different *T. truncatus* strata and was 0.600 for the *T. aduncus* samples (Table 3). Relatedness values within each of the Hawaiian Island groups were similar, with nearly complete overlap in 95% confidence intervals (Table 3). Relatedness was lower for Palmyra, though its 95% confidence interval did overlap slightly with

Table 3. Estimates of number of alleles, expected heterozygosity (H_e), observed heterozygosity (H_o), and allelic richness averaged across loci within populations (all ± SE), and estimates of average relatedness within each of the main island groups.

Population	*n*	No. of alleles	H_e	H_o	Allelic richness	Relatedness (95% CI)
Palmyra	11	5.4	0.695 ± 0.192	0.656 ± 0.232	3.29 ± 1.01	0.012 (0.005–0.013)
Hawai'i	21	6.4	0.736 ± 0.137	0.692 ± 0.178	3.47 ± 0.74	0.016 (0.010–0.026)
4-Islands	25	6.5	0.741 ± 0.109	0.744 ± 0.153	3.46 ± 0.69	0.021 (0.012–0.029)
O'ahu	30	6.9	0.746 ± 0.125	0.695 ± 0.141	3.53 ± 0.78	0.018 (0.010–0.024)
Kaua'i/Ni'ihau	40	7.5	0.744 ± 0.115	0.750 ± 0.156	3.53 ± 0.68	0.015 (0.013–0.033)
T. aduncus	6	4.3	0.737 ± 0.128	0.600 ± 0.296	3.26 ± 1.08	

Table 4. Pairwise divergence between the island groups. For mtDNA sequence data (A), divergence was estimated using F_{ST} (below the diagonal) and Φ_{ST} (above the diagonal), while *P*-values (in parentheses) were calculated using the Fisher's exact test. For microsatellite data (B), divergence was estimated using both F_{ST} (below the diagonal) and F'_{ST} (above the diagonal), while *P*-values (in parentheses below the diagonal) were calculated using the *G*-test. Comparisons that are statistically significant at the $\alpha = 0.05$ level are in bold.

(A)	Palmyra $n = 11$	Hawai'i $n = 22$	4-Islands $n = 26$	O'ahu $n = 30$	Kaua'i/Ni'ihau $n = 41$
Palmyra	–	**0.142**	**0.289**	**0.326**	**0.265**
Hawai'i	**0.081** (**0.003**)	–	**0.116**	0.032	0.040
4-Islands	**0.164** (**<0.001**)	**0.080** (**0.005**)	–	**0.141**	**0.033**
O'ahu	**0.135** (**<0.001**)	−0.005 (0.155)	**0.085** (**0.003**)	–	0.014
Kaua'i/Ni'ihau	**0.101** (**<0.001**)	0.002 (0.197)	**0.045** (**0.020**)	0.003 (0.344)	–
(B)	Palmyra $n = 11$	Hawai'i $n = 21$	4-Islands $n = 25$	O'ahu $n = 30$	Kaua'i/Ni'ihau $n = 40$
Palmyra	–	**0.305**	**0.357**	**0.319**	**0.322**
Hawai'i	**0.086** (**<0.001**)	–	**0.050**	**0.049**	**0.041**
4-Islands	**0.099** (**<0.001**)	**0.013** (**0.005**)	–	**0.019**	**0.031**
O'ahu	**0.088** (**<0.001**)	**0.013** (**0.002**)	**0.007** (**0.024**)	–	**0.029**
Kaua'i/Ni'ihau	**0.089** (**<0.001**)	**0.010** (**0.008**)	**0.008** (**0.001**)	**0.007** (**0.012**)	–

those of the other islands (Table 3). Summaries of diversity for each marker are presented in Table S3.

Population Differentiation

A global Fisher's exact test of differentiation with the mtDNA data set revealed significant genetic differentiation among the island groups as a whole ($P \leq 0.0001$; $\Phi_{ST} = 0.121$). Thus, the global null hypothesis of no structure within the mtDNA data set was rejected. Pairwise comparisons of mtDNA haplotype frequencies using Fisher's exact test showed that the 4-island region is significantly differentiated from all other islands, as is Palmyra (Table 4A). No significant differentiation in haplotype frequencies was detected among Hawai'i, O'ahu, and Kaua'i/Ni'ihau.

Significant differentiation among the island groups was also detected in the microsatellite data with the global *G*-test ($P < 0.0001$; $F_{ST} = 0.038$; $F'_{ST} = 0.100$), again rejecting the global null hypothesis of no structure within the microsatellite data set. All pairwise comparisons between the island groups using the microsatellite data were statistically significant (Table 4B). Pairwise Φ_{ST} values ranged from 0.014 to 0.326 and F_{ST} from −0.005 to 0.164 in the mtDNA data set (Table 4A). In the microsatellite data set, F_{ST} values ranged from 0.007 to 0.099, while F'_{ST} ranged

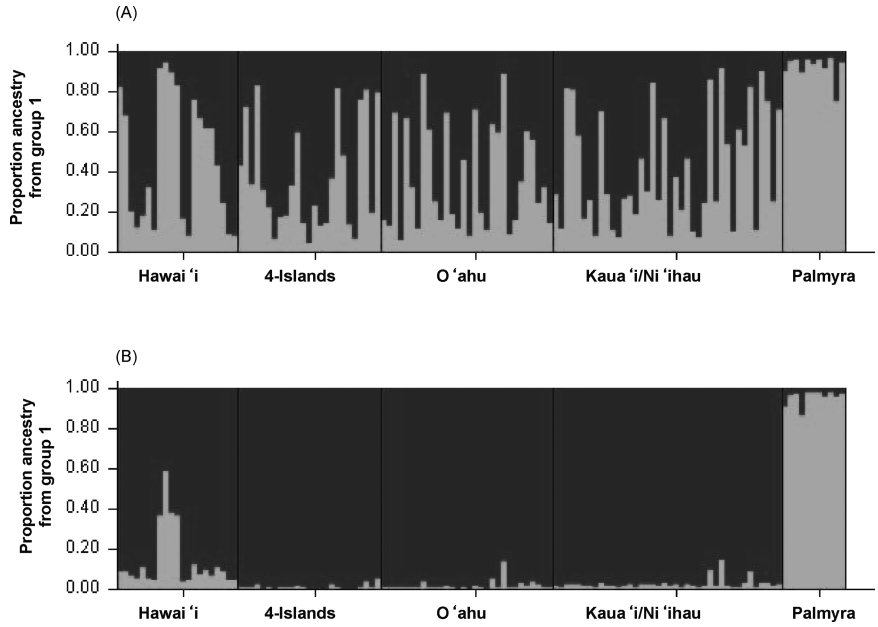

Figure 3. Graphical representation of the results of the STRUCTURE analysis for the most probable model ($k = 2$). Each vertical bar represents an individual. Bars are shaded as to the proportion of the individual's ancestry that is attributable to groups one (light gray) and two (dark gray), as defined by STRUCTURE. The top figure (A) shows results when sampling location is not used by the program, while the bottom figure (B) shows results when sampling location is used as a prior.

from 0.019 to 0.357 (Table 4B). None of the tests for sex-biased dispersal were statistically significant (all $P > 0.05$).

When all Hawaiian and Palmyran samples were included in the STRUCTURE analysis, the model that had the highest log-likelihood was the one with two groups ($k = 2$; Table S4). This result was consistent across all replicate runs of the analysis. The model with $k = 2$ was favored regardless of whether sampling location was used as a prior. Without the use of sampling location, STRUCTURE estimated that the samples from Palmyra derived on average 91% (SD = 0.07) of their ancestry from group one, while the Hawaiian samples derived only 59% (SD = 0.27) of their ancestry from group two (Fig. 3). When sampling location was used as a prior, these ancestry proportions increased to 96% (SD = 0.043) and 95% (SD = 0.089), respectively. The average ancestry proportions varied by less than 1% between replicate analyses, confirming that the analyses had converged. In models where k was greater than two, the Palmyra samples always showed strong assignment to one group, while the Hawaiian samples exhibited varying degrees of mixed ancestry to the remaining groups. The failure of STRUCTURE to detect population structure within the Hawaiian Islands was consistent regardless of whether Palmyra was included in the analysis (Table S4).

Most samples assigned strongly back to their sampled population when we used the USEPOPINFO option to look for hybrids or immigrants between the Hawaiian

Table 5. Ancestry probabilities for individuals sampled around the main Hawaiian Islands but identified by STRUCTURE as being likely migrants from or hybrids with the population to which the Palmyran samples belong. The column "Hap" indicates which haplotype each individual possessed.

Individual ID	Sampling location	Hap	Prob. exclusively Hawaiian ancestry	Prob. migrant	Prob. has migrant parent	Prob. has migrant grandparent
30495	Hawai'i	9	0.270	0.461	0.253	0.016
30496	Hawai'i	9	0.062	0.684	0.200	0.054
30498	Hawai'i	2	0.391	0.414	0.179	0.016
30499	Hawai'i	10	0.425	0.308	0.234	0.033
33876	O'ahu	13	0.443	0.333	0.162	0.062
34032	Kaua'i	1	0.405	0.269	0.320	0.005

and Palmyran samples. However, there were six individuals sampled around the Hawaiian Islands that were identified as having less than a 50% probability of being descended exclusively from the Hawaiian populations. Five of the individuals were more likely to be migrants than hybrids, while the sixth was more likely an F1 hybrid (Table 5). All six of these individuals were sampled in deep ($\geq$400 m) water (as compared to only 30% of the samples coming from deep water in the overall data set). Four of them were sampled together off the southern tip of the island of Hawai'i during an SWFSC cruise and were the only animals sampled around the main Hawaiian Islands that shared haplotypes with Palmyra. The other two individuals were both sampled by Baird *et al*. (2009), one off O'ahu and one off Kaua'i, from groups that were not linked by association to any other group. Of the 17 individuals that assigned to the "Palmyra" cluster (11 from Palmyra and six from the Hawaiian Islands), 12 (70%) had haplotypes that are also present in the southwestern Pacific (haplotypes 6, 9, 10, 21, and 22) or in Japan and China (haplotype 13; Tables 1 and 5; Tezanos-Pinto *et al.* 2009). In contrast, only 10% (11 out of 113) of the individuals assigned to the "Hawaiian Islands" cluster had haplotypes detected elsewhere in the Pacific.

When the USEPOPINFO option was used to look for *T. aduncus* ancestry among the Hawaiian Island and Palmyran samples, a single individual (sample ID 33946) sampled off the coast of Kaua'i assigned more strongly to *T. aduncus* than to *T. truncatus*. This animal possessed a *T. truncatus* haplotype (haplotype 2) but had an assignment probability to *T. truncatus* of 0.387. STRUCTURE gave the highest probability (0.572) to sample 33946 having *T. aduncus* ancestors at least two generations in the past (*i.e.*, grandparents). The probabilities of it being a pure *T. aduncus* or an F1 hybrid between the two species were estimated at 0.019 and 0.022, respectively. Sample 34066, which possessed a *T. aduncus* haplotype, did not show any evidence of recent hybrid ancestry in the STRUCTURE analysis (assignment probability to *T. truncatus* equaled 0.966).

The Migrate analysis resulted in dispersal rate (N_em) estimates ranging from 0.17 to 5.77 migrants per generation (Table 6). Dispersal rate estimates were generally higher within the Hawaiian Archipelago (mean = 1.478, SD = 1.5) than between the Hawaiian Islands and Palmyra (mean = 0.61, SD = 0.33). Within the Hawaiian Islands, most pairs of islands exhibited higher dispersal rate estimates going from the southeast to the northwest than for the reverse direction. $N_e\mu$ was lowest for the 4-Islands region and highest for Palmyra, though the 95% profile likelihood envelopes for Palmyra, O'ahu, and Kaua'i overlapped substantially (Table 6).

Table 6. Estimates of $N_e\mu$ (effective population size times mutation rate) and number of migrants per generation (N_em) from the microsatellite data set. Bidirectional mutation rates are given, with source populations in columns and recipient populations in rows. The 2.5th and 97.5th profile likelihood estimates are given in parentheses.

	Source population					
Recipient population	$N_e\mu$	Hawai'i	4-Islands	O'ahu	Kaua'i/ Ni'ihau	Palmyra
Hawai'i	2.26 (2.04, 2.52)	–	1.22 (1.07, 1.39)	2.2 (1.99, 2.41)	0.17 (0.12, 0.23)	0.49 (0.40, 0.60)
4-Islands	1.52 (1.39, 1.66)	1.59 (1.46, 1.75)	–	0.47 (0.39, 0.58)	0.74 (0.64, 0.85)	0.47 (0.39, 0.57)
O'ahu	3.29 (3.08, 3.51)	0.65 (0.56, 0.74)	1.02 (0.90, 1.14)	–	0.37 (0.30, 0.44)	0.61 (0.52, 0.70)
Kaua'i/Ni'ihau	3.33 (3.01, 3.69)	1.46 (1.20, 1.77)	2.07 (1.77, 2.40)	5.77 (5.27, 6.31)	–	1.37 (1.13, 1.65)
Palmyra	3.45 (3.11, 3.86)	0.26 (0.20, 0.34)	0.7 (0.59, 0.82)	0.46 (0.37, 0.56)	0.49 (0.40, 0.60)	–

Discussion

Our results support the hypothesis of Baird *et al*. (2009) that the main Hawaiian island groups each host a demographically independent population of bottlenose dolphins. We found significant genetic differentiation in the microsatellite analyses between all pairs of strata examined, suggesting limited movement between strata. Baird *et al*. (2009) used a Bayesian analysis of photo-ID data to estimate an interisland dispersal rate of 1% per year or less. The estimates of genetic divergence between islands (Φ_{ST} for the mtDNA ranging from 0.014 to 0.141 and F_{ST} for microsatellites ranging from 0.007 to 0.013; Table 4) are consistent with Baird *et al*.'s estimate. The results of Migrate also indicated restricted gene flow between islands, with estimates of the number of migrants per generation ranging from 0.17 (Kaua'i/Ni'ihau to Hawai'i) to 5.77 (O'ahu to Kaua'i/Ni'ihau; Table 6). Given the long generation time ($T = 21$ yr; Taylor *et al.* 2007) of bottlenose dolphins, this corresponds to annual rates of 0.008–0.263 migrants per year. Such rates of gene flow are sufficient to prevent the development of the high levels of genetic divergence characteristic of Evolutionarily Significant Units (Waples 1991), and thus have resulted in relatively low estimates of divergence within the main Hawaiian Islands (Table 4). However, from a demographic point of view, these movement rates are low enough so as to have minimal impact on population dynamics.

The interisland population structure that was revealed by the pairwise tests for population differentiation was not resolved by STRUCTURE. This result is not surprising, as STRUCTURE has been shown to be unable to reliably detect population structure at the level we expected and detected between the island resident populations (Latch *et al.* 2006, Waples and Gaggiotti 2006). STRUCTURE 2.3.1 (Hubisz *et al.* 2009) incorporates a new model in which sampling location is incorporated into the Bayesian prior for the analysis, thus increasing power to detect population structure in data sets where divergence is low or the number of loci is moderate (<20). Nonetheless, even this new model does not perform well at either determining the correct value of k or estimating admixture proportions for admixed populations with $F_{ST} < 0.2$ (Hubisz *et al.* 2009), as was the case in our study. Use

of sampling location in the prior did, however, improve STRUCTURE's ability to distinguish Hawaiian and Palmyran samples (Fig. 3).

Numerous papers have been written in recent years discussing the negative correlation between within-population heterozygosity and most F_{ST}-analogues (reviewed by Meirmans and Hedrick 2011). These papers have focused on the estimation of genetic divergence from nuclear loci, with relatively little attention paid to the problem in mtDNA data. However, our results highlight the impact that high diversity can have on estimates of mtDNA divergence. Despite the lack of a phylogeographic signal in our data set, estimates of Φ_{ST} were much higher than estimates of F_{ST} in all pairwise comparisons using the mtDNA data set (Table 4). Diversity within populations is higher for the mtDNA data set than for the microsatellite data set, both in terms of observed heterozygosity and the average numbers of alleles/haplotypes per locus (Table 2, 3). Thus, the bias introduced into the F_{ST} estimates by high within-population diversity will be greater in the mtDNA data set. Because Φ_{ST} is not subject to this bias (Kronholm and Loudet 2010), it is the more reliable estimator of genetic divergence in this case.

Estimates of genetic divergence were generally higher for the mtDNA data set than for the microsatellite data set, as expected. However, there were fewer statistically significant interisland comparisons in the mtDNA data than in the microsatellite data. This finding is unusual, especially since mammalian species often exhibit a pattern of male-biased dispersal (Greenwood 1980). Our analyses did not reveal evidence of sex-biased dispersal, though power of the test is low (Goudet *et al.* 2002). Though sex-biased dispersal is common in other cetacean species, studies of bottlenose dolphins in the Gulf of Mexico (Sellas *et al.* 2005) and the North Atlantic (Natoli *et al.* 2005, Parsons *et al.* 2006, Querouil *et al.* 2007, Rosel *et al.* 2009) have also failed to detect evidence of biased dispersal, a pattern that may reflect the importance of social bonds in this species (Rosel *et al.* 2009). A lack of sex-biased dispersal and lower statistical power in mtDNA *vs.* microsatellite data sets has also been found in two other Hawaiian cetaceans: spinner dolphins (Andrews *et al.* 2010) and pantropical spotted dolphins.[1] Larsson *et al*. (2009) showed that the relative statistical power of mitochondrial *vs.* microsatellite markers depends on many factors, including allele frequency distributions, rates of gene flow, and effective population sizes, and therefore cannot be easily generalized. However, when allele frequency distributions are similar for the two marker types and dispersal is not sex-biased, the power of mitochondrial data is comparable to that of two microsatellite markers (Larsson *et al.* 2009). Thus, the lower power of our mtDNA data set may reflect the fact that mtDNA is a single marker, whereas the microsatellite data set includes 11 independent markers.

Though all island groups were significantly differentiated in the microsatellite data set, the 4-Islands region was the only island group that exhibited significant differentiation from the other island groups in mtDNA haplotype frequencies. The significant difference in haplotype frequency between this and the other Hawaiian island groups is driven by the frequency of haplotype 2, which comprises nearly 40% of the sample for the 4-Islands region but only 4%–15% at the other island groups (Table 1). The 10 individuals with haplotype 2 sampled in the 4-Islands region were sampled from nine different groups over the course of 4 yr, ranging in size from 1 to 16

[1]Personal communication from Sarah Courbis, Portland State University, PO Box 751, Portland, Oregon 97207; unpublished data presented to the Pacific Scientific Review Group, Kona, Hawaii, November 2010.

individuals. Photo-ID data from these encounters (R. W. Baird, pers. comm.) indicate they were not repeated encounters of a single stable group of individuals. Thus, the high frequency of this haplotype is not the result of biased sampling or repeated sampling of a single stable group. The apparent stronger mtDNA divergence of the 4-islands region could be due to a smaller population size than at the other islands, a possibility that is supported by the significantly lower estimate of $N_e\mu$ (Table 6) and higher resighting rate (Baird *et al.* 2009) for the 4-Islands region compared to the other island groups. However, a smaller population size would be expected to result in greater divergence in the microsatellite data set, which we did not observe. The large variation in estimates of divergence between island groups for the mtDNA data set could also be simply a reflection of the larger variance expected from the lower effective population size of the mitochondrial genome as compared to the nuclear genome (Taylor *et al.* 2000). Averaging across loci further reduces the variance in nuclear estimates of differentiation.

Hawaiian bottlenose dolphins are subject to management under the U.S. MMPA. Taylor (1997) has shown that in order to meet the management objectives of the MMPA, the threshold dispersal rate at which dolphin populations will require separate management is typically several percent per year. The results of our study, together with those of Baird *et al*. (2009), suggest that dispersal rates between the main Hawaiian Islands fall below this threshold. Our results also highlight the need for further research into the population structure of bottlenose dolphins in the Northwest Hawaiian Islands, an area of the Hawaiian Archipelago from which we currently have no data but where other species exhibit fine-scale population structure similar to that found in the main Hawaiian Islands (Karczmarski *et al.* 2005, Andrews *et al.* 2010).

Our finding of genetic differentiation among the main Hawaiian islands is in contrast to a genetic study of bottlenose dolphins around the Azorean and Madeiran Archipelagos (Querouil *et al.* 2007). No genetic differentiation was detected within either of these archipelagos or between them and the northwestern Atlantic pelagic population. The difference in the level of population structure around the Hawaiian Islands compared to the Azorean and Madeiran Archipelagos may be a result of differences in bathymetry and productivity of the surrounding areas. Each of the Hawaiian Island groups is surrounded by a relatively large area of shallow water habitat (Fig. 1). Baird *et al*. (2009) found that the majority of bottlenose dolphin sightings in Hawaiian waters were in these shallow water areas. Furthermore, productivity of the open ocean waters surrounding the Hawaiian Islands is very low, while various oceanographic processes result in higher productivity immediately around the islands (Doty and Oguri 1956; Gilmartin and Revelante 1974; Seki *et al.* 2001, 2002). In contrast, there is very little shallow water habitat around the Azorean and Madeiran Archipelagos (Querouil *et al.* 2007) and productivity in the surrounding waters is higher than around Hawai'i (Barlow *et al.* 2008, Kahru *et al.* 2009). Silva *et al*. (2008) postulate that the low prey availability around the Madeiran and Azorean archipelagos forces animals there to maintain very large home ranges and prevents the development of genetic differentiation. Habitat-driven resource specialization has been suggested as an important mechanism driving population differentiation in bottlenose dolphins and other marine mammals (Hoelzel 1998, Hoelzel *et al.* 1998*b*, Natoli *et al.* 2005, Möller *et al.* 2007). The availability of benthic prey and sharp drop in productivity with increased distance from shore may result in a sufficient habitat discontinuity to act as a barrier to movement and allow the development of island-associated populations in the Hawaiian Archipelago, but not in the Azorean or

Madeiran Archipelagos. Baird *et al*. (2009) made a similar argument for the apparent lack of a resident population around Cocos Island.

Though both the genetic and photo-ID data support the existence of demographically independent populations around each of the main islands, it is clear that these populations still experience gene flow with animals throughout the rest of the Pacific. The levels of diversity within each of the main Hawaiian Island groups were higher than those observed in coastal bottlenose dolphins from the Gulf of California (Segura *et al.* 2006), Gulf of Mexico (Sellas *et al.* 2005), or western North Atlantic (Rosel *et al.* 2009). The median-joining network for the Hawaiian samples exhibits more long branches and missing haplotypes than the haplotype networks for the aforementioned coastal populations, indicating that Hawai'i experiences higher gene flow from a large pelagic population than do the other coastal populations. This finding is consistent with a recent large-scale study of bottlenose dolphin population structure, which found that coastal populations in the western and central Pacific are significantly differentiated, but are connected by low levels of gene flow across large distances, either through occasional long-distance dispersal or gene flow with pelagic populations (Tezanos-Pinto *et al.* 2009).

Our STRUCTURE analyses revealed several animals in our Hawaiian data set that did not assign to the Hawaiian Islands. Specifically, six animals sampled around the Hawaiian Islands were identified by STRUCTURE as being likely migrants from or hybrids with the population to which the Palmyran samples belong. Though it is possible that these samples represent actual migrants from a Palmyran resident population, it is more likely that all of the samples in the "Palmyra" cluster came from a more broadly distributed pelagic population. The high estimates of divergence and low dispersal rate estimates between Palmyra and the Hawaiian Island groups suggest that, if direct dispersal occurs, it is rare. Consequently, it is unlikely that we would have detected such a large number of dispersers. Most (70%) of the samples from the "Palmyra" cluster defined by STRUCTURE possess haplotypes also detected in the southern and western Pacific (Tezanos-Pinto *et al.* 2009), suggesting higher gene flow between Palmyra and those areas than between Palmyra and Hawai'i. Further resolution of the relationships between the Hawaiian, Palmyran, and pelagic bottlenose dolphins will require additional sampling, particularly from Palmyra and pelagic waters.

Perhaps the most surprising finding of this study is the presence of two individuals sampled off the coast of Kaua'i with evidence of *T. aduncus* ancestry. Sample 34066 possesses a haplotype characteristic of *T. aduncus*. However, the microsatellite data did not reveal any evidence of *T. aduncus* ancestry in this animal's nuclear genome, suggesting that it is not the result of a recent hybridization event. Rather, this animal's haplotype could be evidence of introgression in the distant past. The microsatellite data set did, however, provide evidence of recent hybrid ancestry for sample 33946. Though this animal had a *T. truncatus* haplotype (haplotype 2), it was found to have only a 0.39 probability of being a pure *T. truncatus* in the STRUCTURE analysis designed to identify migrants or hybrids. The greatest probability (0.57) was placed on 33946 being the product of a hybridization event two generations in the past. However, with only six known *T. aduncus* samples from a small portion of the species' range, the allele frequencies of *T. aduncus* are poorly characterized in our data set. An expanded data set containing a much larger sample size from a greater number of *T. aduncus* source populations would provide more convincing evidence of hybrid origin for sample 33946. Increasing the number of loci in the data set or adding data from other types of markers (see Taylor *et al.* 2010 for a review of

markers appropriate to taxonomic studies) may also aid in the robust identification of *T. aduncus*/*T. truncatus* hybrids.

Island-associated populations have now been identified for four species of delphinids within the Hawaiian Archipelago: common bottlenose dolphins (this study, Baird *et al.* 2009), spinner dolphins (Galver 2002, Karczmarski *et al.* 2005, Andrews *et al.* 2010), rough-toothed dolphins (Baird *et al.* 2008*b*), and false killer whales (Chivers *et al.* 2007, Baird *et al.* 2008*a*). These insular populations are likely to face very different threats than their pelagic counterparts. They are likely to be exposed to higher pollutant levels, as pollution tends to be concentrated near coasts and result in higher contaminant loads in coastal marine mammals (Reijnders *et al.* 2009, Ylitalo *et al.* 2009). The main Hawaiian Islands also support numerous near-shore commercial and recreational fisheries, most of which are not observed or monitored (Carretta *et al.* 2009). Entanglement in and ingestion of fishing gear is often fatal for dolphins (Wells *et al.* 2008) and may represent a significant source of mortality for insular populations. Finally, the insular populations are exposed to greater vessel traffic, including that associated with ecotourism, and are thus more likely to suffer vessel strikes and behavioral and social disruption due to noise and direct human interaction (Constantine *et al.* 2004, Danil *et al.* 2005). The differences in threats between insular and pelagic populations necessitate separate management and highlight the need for further studies of the population structure of marine mammals around the Hawaiian Islands.

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Supporting Information

The following supporting information is available for this article online:

Table S1. Initial and final sample sizes, after exclusions, for the island groups and *T. aduncus*.

Table S2. Polymorphic sites for 25 mtDNA haplotypes detected in the data set. Position one of the alignment corresponds to position 15472 of the *Tursiops truncatus* mitochondrial genome (Genbank NC_012059). The column "Hap ID" corresponds to the haplotype IDs presented in Table 1.

Table S3. Estimates of number of alleles, expected heterozygosity (*He*), observed heterozygosity (*Ho*), and allelic richness averaged across populations (all ± SE).

Table S4. Estimates of mean Ln $P(D)$ and Pr(K) from STRUCTURE. The maximum values of each metric for each model are in bold.