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Rolling stones and stable homes: social structure, habitat diversity and population genetics of the Hawaiian spinner dolphin (*Stenella longirostris*)

KIMBERLY R. ANDREWS,*† LESZEK KARCZMARSKI,‡§ WHITLOW W. L. AU,*† SUSAN H. RICKARDS,¶ CYNTHIA A. VANDERLIP,** BRIAN W. BOWEN,* E. GORDON GRAU* and ROBERT J. TOONEN*

**Hawai'i Institute of Marine Biology, University of Hawai'i, PO Box 1346, Kaneohe, Hawai'i 96744, USA, †Marine Mammal Research Program, PO Box 1106, Kailua, Hawai'i 96734, USA, ‡The Swire Institute of Marine Science, The University of Hong Kong, Cape d'Aguilar, Shek O, Hong Kong, §Mammal Research Institute, University of Pretoria, C/o Whale Unit, PO Box 61, Cape Town 8000, South Africa, ¶Hawai'i Marine Mammal Consortium, PO Box 1493, Kamuela, Hawai'i 96743, USA, **State of Hawai'i Department of Land and Natural Resources, Division of Forestry and Wildlife, 2135 Makiki Heights Dr., Honolulu, Hawai'i 96822, USA*

Abstract

Spinner dolphins (*Stenella longirostris*) exhibit different social behaviours at two regions in the Hawaiian Archipelago: off the high volcanic islands in the SE archipelago they form dynamic groups with ever-changing membership, but in the low carbonate atolls in the NW archipelago they form long-term stable groups. To determine whether these environmental and social differences influence population genetic structure, we surveyed spinner dolphins throughout the Hawaiian Archipelago with mtDNA control region sequences and 10 microsatellite loci (n = 505). F-statistics, Bayesian cluster analyses, and assignment tests revealed population genetic separations between most islands, with less genetic structuring among the NW atolls than among the SE high islands. The populations with the most stable social structure (Midway and Kure Atolls) have the highest gene flow between populations (mtDNA $\Phi_{ST} < 0.001$, $P = 0.357$; microsatellite $F_{ST} = -0.001$; $P = 0.597$), and a population with dynamic groups and fluid social structure (the Kona Coast of the island of Hawai'i) has the lowest gene flow (mtDNA $0.042 < \Phi_{ST} < 0.236$, $P < 0.05$; microsatellite $0.016 < F_{ST} < 0.040$, $P < 0.001$). We suggest that gene flow, dispersal, and social structure are influenced by the availability of habitat and resources at each island. Genetic comparisons to a South Pacific location (n = 16) indicate that Hawaiian populations are genetically depauperate and isolated from other Pacific locations (mtDNA $0.216 < F_{ST} < 0.643$, $P < 0.001$; microsatellite $0.058 < F_{ST} < 0.090$, $P < 0.001$); this isolation may also influence social and genetic structure within Hawai'i. Our results illustrate that genetic and social structure are flexible traits that can vary between even closely-related populations.

Keywords: dispersal, habitat availability, insularity, microsatellites, mtDNA, population structure

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Introduction

Levels of dispersal and genetic divergence can vary between populations within species, and this variation is thought to be driven by habitat differences such as abundance and predictability of resources, level of predation pressure, and level of habitat isolation (reviewed in Bowler & Benton 2005). In cetaceans, intraspecific variation in dispersal patterns and genetic structure may also correspond to patterns of social group formation, or 'social structure', such as the size and stability

Correspondence: Kimberly R. Andrews, Fax: +1 808 236 7443; E-mail: andrewsk@hawaii.edu

of groups, the sex and relatedness of individuals within groups, and dispersal ranges of groups. For example, two sympatric forms of killer whale (*Orcinus orca*) in the northeast Pacific have different group sizes, group stability, prey type, foraging behaviour and dispersal patterns; these differences are thought to be driven by the distribution of prey and facilitated by social transmission (Hoelzel 1998; Baird & Whitehead 2000). Bottlenose dolphins (*Tursiops* spp.) also show intraspecific variation in group size, prey type, dispersal patterns and genetic structure (Wells *et al.* 1987; Lusseau *et al.* 2003; Sellas *et al.* 2005; Quérouil *et al.* 2007); in some regions this variation has been attributed to habitat differences between sheltered nearshore regions vs. open coastline or offshore regions (Ballance 1992; Gowans *et al.* 2008). The frequent association between habitat, genetic structure and social structure illustrates the inter-relatedness of these factors within cetacean species.

The spinner dolphin (*Stenella longirostris*) shows intraspecific variation in dispersal, genetic structure and social structure across a worldwide distribution in tropical and subtropical waters. In the Eastern Tropical Pacific (ETP), spinner dolphins are pelagic and form groups that are thought to range over wide geographic distances (Reilly 1990). Average group size in the ETP is around 120 individuals, but group sizes can reach hundreds or thousands (Gerrodette & Forcada 2005). These extensive movements and large groups are thought to promote greater foraging efficiency in the pelagic environment where prey are unpredictable, and greater protection where no shelter from predators is available (Gowans *et al.* 2008). Population genetic analyses in the ETP reveal little genetic divergence in mitochondrial DNA (mtDNA) or microsatellite loci even between four morphotypes that exist in this region (Galver 2002).

In contrast to the pelagic spinner dolphins in the ETP, most other Pacific populations rely heavily on the shelter and resources available in nearshore habitats. Island-associated dolphins feed nocturnally on the mesopelagic boundary community associated with the underwater slopes of the islands within several kilometres from shore (Norris *et al.* 1994; Benoit-Bird & Au 2003). During daylight hours, the dolphins use nearshore habitat for resting and social behaviour, with preferences for calm, sandy-bottom bays and lagoons (Norris *et al.* 1994). The consistent presence of these dolphins in nearshore island habitats is likely driven by the predictability of prey along the slopes of the islands and the predictability of resting habitat in the shallow waters surrounding islands (Norris *et al.* 1994).

The social structure of island-associated spinner dolphins has been studied in the Society and Hawaiian Archipelagos. In the Society Archipelago, photo-identification data indicate that group size and composition varies from day-to-day (a 'fission-fusion' society) within relatively closed island communities (Poole 1995; Oremus *et al.* 2007). Although some dolphins were observed to move between islands, no evidence of permanent relocation was observed even between Moorea and Tahiti, only 17 km apart. Genetic data reinforced the indication that permanent migration and interbreeding between islands are rare in the Society Archipelago, with many island populations being genetically distinct (Oremus *et al.* 2007).

In the Hawaiian Archipelago, the social structure of spinner dolphins differs between regions. They regularly occur at all of the Main Hawaiian Islands (MHI), three atolls in the far-Northwestern Hawaiian Islands (far-NWHI; low carbonate atolls), and one intermediate atoll at French Frigate Shoals (with both basaltic and coralline features; Fig. 1). Along the Kona Coast of Hawai'i Island (also known as the Big Island) in the MHI, the dolphins have a fission-fusion social structure and group sizes (≈30–70 dolphins) similar to the Society Archipelago (Norris *et al.* 1994; Östman 1994). Limited information exists on social structure at other MHI; however, there is evidence that spinner dolphins at O'ahu exhibit long-term site fidelity (Marten & Psarakos 1999) and a fission-fusion grouping pattern with possibly even greater fluidity than at the Kona Coast (Lammers 2004).

In contrast, the social structure at the two most northwestern atolls, Midway and Kure, differs substantially from that at the Kona Coast and the Society Archipelago. Spinner dolphins form large groups at each atoll (≈120 at Kure, ≈260 at Midway) and their group stability is greater than in any other spinner dolphin population studied to date (Karczmarski *et al.* 2005a,b). Kure and Midway also differ from the MHI in that there is usually only one large and coherent group of long-term associates that uses each atoll lagoon on a daily basis; in contrast, multiple groups are present at each MHI. The differences in social structure in the far-NWHI are thought to be driven by the limited availability of resting habitat and the geographic insularity of the atolls (Karczmarski *et al.* 2005b). In particular, the presence of a single, small area of resting habitat at each atoll is thought to preclude the presence of multiple groups. Karczmarski *et al.* (2005b) propose that the geographic distance (97 km of deep oceanic waters) separating these two atolls may be energetically expensive and potentially dangerous to traverse, and that these factors may reinforce social bonds and promote long-term stability of the communities at each atoll.

Although social structure is known to vary within the Hawaiian spinner dolphins, little is known about pat-

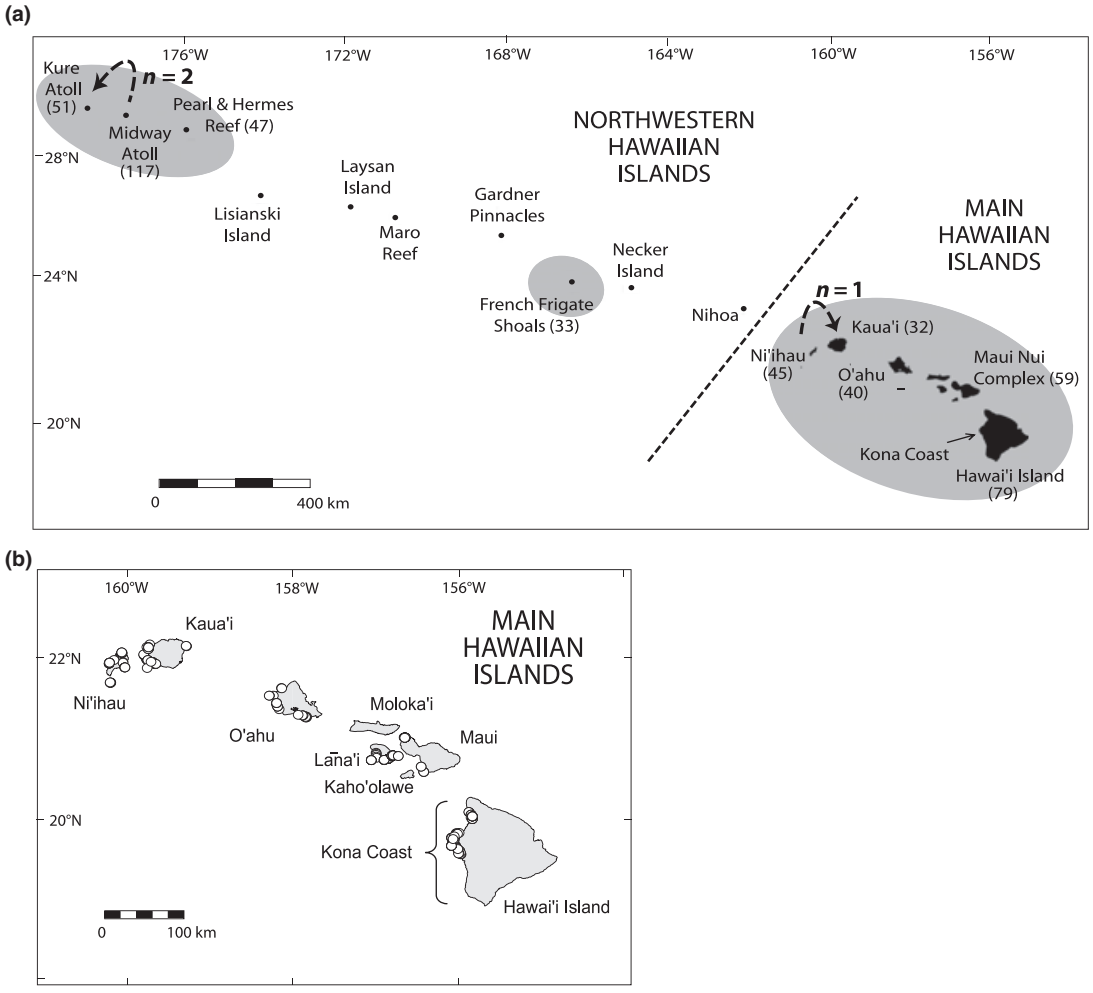

Fig. 1 (a) Map of the Hawaiian Archipelago. Dashed line separates the Northwestern Hawaiian Islands from the Main Hawaiian Islands. Gray shaded circles highlight the islands and atolls where spinner dolphins are regularly sighted. Numbers following location names represent sample sizes. Dashed arrows represent interisland movement observed by genetic recapture; and (b) Detailed map of the Main Hawaiian Islands. Circles represent spinner dolphin (*Stenella longirostris*) sampling locations at each island.

terns of genetic diversity or dispersal across the region. To examine whether variation in habitat and social structure correspond to variation in genetic diversity in Hawai'i, we examined population genetic structure across the archipelago by sampling at each island or atoll where spinner dolphins regularly occur. A preliminary study (Andrews *et al.* 2006) found genetic structure across the Hawaiian Archipelago based on mtDNA control region sequences, with lower genetic diversity and less genetic structure within the NWHI than within the MHI. Our current study provides a more detailed analysis of population genetic structure in Hawai'i by utilising larger sample sizes, larger numbers of locations sampled, nuclear as well as mtDNA markers, and comparisons with a South Pacific population at American Sāmoa. The results of these analyses were compared with existing demographic data for spinner dolphins in Hawai'i and elsewhere, to examine the relationships between dispersal, social structure and habitat variation. Hawai'i offers both high and low-island habitats in proximity, allowing direct comparisons without the confounding factors of ocean-basin separations, ecological discontinuities and evolutionary divergence.

Materials and methods

Study site and sample collection

Skin specimens were collected from spinner dolphins at each island group or atoll in the Hawaiian Archipelago where this species regularly occurs (at some islands/atolls in the NWHI spinner dolphins do not occur regularly) (Fig. 1a). Specimens were also collected at the island of Tutuila in American Sāmoa. All samples were

collected between 2001 and 2005 using previously described biopsy methods (Andrews *et al.* 2006) including a Paxarms rifle (Krützen *et al.* 2002) and a Hawaiian sling with a biopsy tip. Additionally, a skin-swabbing technique (Harlin *et al.* 1999) was used to collect many of the specimens at Midway Atoll. Specimens were stored in 20% dimethyl sulfoxide NaCl-saturated solution (modified from Amos & Hoelzel 1991). Additional specimens were provided by the National Marine Fisheries Service, Southwest Fisheries Science Center (SWFSC) Genetics Archive in the form of extracted genomic DNA, corresponding to accession numbers 7185–7202, 15510, 17432, 30411–30420, 30449, 30512–30516. SWFSC samples were collected between 1997 and 2002.

mtDNA sequencing and genetic sexing

Genomic DNA was extracted using Qiagen DNeasy extraction kits. Polymerase chain reactions (PCRs) amplified a portion of the 5′ mtDNA control region as described in Andrews *et al.* (2006). PCR products were sequenced in both the forward and reverse directions with an ABI 3730 automated sequencer, and sequences were aligned and edited manually using SEQUENCHER 4.8 (Genecodes Corporation). Primer sequences and ambiguous sequences were removed, resulting in a 417 bp fragment. The sex of each dolphin was determined by dual PCR amplification of a fragment of the *sry* gene on the Y chromosome and a fragment of the *ZFX/ZFY* genes on the X chromosomes as described by Gilson *et al.* (1998).

Microsatellite genotyping

Ten microsatellite loci obtained from three previous studies (Amos *et al.* 1993; Valsecchi & Amos 1996; Galver 2002; Table 1) were amplified by PCR carried out in 12 μl volume reactions containing 1 X Reaction Buffer (Promega Corporation), 200 μM of each dNTP, 2.0–2.75 mM $MgCl_2$, 0.38 units *Taq* DNA polymerase (Promega Corporation), and 0.21 μM each primer. Cycle conditions were as follows: 94 °C for 2.5 min, followed by 33 cycles of 94 °C for 30 s, annealing temperature for 30 s (Table 1), and 72 °C for 30 s, followed by a final 72 °C extension for 15 min. For skin swabs, the number of cycles was increased to 40. PCR products were separated on a Beckman CEQ8000 automated sequencer (Beckman Coulter), and fragment sizes were scored using the CEQ 8000 Genetic Analysis System software 8.0 (Beckman Coulter).

Microsatellite loci were tested for departures from Hardy Weinberg equilibrium and linkage equilibrium using ARLEQUIN 3.11 (Excoffier *et al.* 2005). Microsatellite loci were also tested for null alleles, large allele dropout and scoring errors due to stutter peaks using MICROCHECKER 2.2.0.3 (Van Oosterhout *et al.* 2004). To estimate microsatellite scoring error rate, 278 PCR reactions were repeated using biopsy samples (between 19 and 38 reactions for each locus), and 629 PCR reactions were repeated using skin swab samples (approximately equal numbers of reactions for each locus). The error rate was calculated as the ratio of the number of allelic differences observed to the total number of allelic comparisons (Bonin *et al.* 2004).

The average nonexclusion probability for the identity of individuals was estimated using CERVUS 3.0.3 (Kalinowski *et al.* 2007). Matching genotypes were identified using MSTOOLS 3.1 (Park 2001) and were assumed to be replicate samples from the same individual. In these cases only one copy of the genotype was retained for subsequent analyses.

To test for the presence of closely related individuals within a priori defined populations, pairwise genetic relatedness values were calculated for each pair of individuals at each island using the relatedness coefficient

Table 1 Diversity in the Hawaiian Archipelago for microsatellite loci (*k*: total number of alleles found; H_o: observed heterozygosity; H_e: expected heterozygosity), and polymerase chain reactions (PCR) annealing temperatures used

Locus	*k*	H_o	H_e	Annealing temp (°C)	Reference
EV1	21	0.842	0.864	48	Valsecchi & Amos (1996)
EV37	13	0.755	0.727	50	Valsecchi & Amos (1996)
EV94	16	0.851	0.841	50	Valsecchi & Amos (1996)
415/416	12	0.815	0.812	45	Amos *et al.* (1993)
SD8	15	0.672	0.688	49	Galver 2002
SL1-25	16	0.724	0.743	52	Galver 2002
SL4-16	4	0.396	0.385	50	Galver 2002
SL8-49	18	0.787	0.802	50.5	Galver 2002
SL9-69	9	0.734	0.728	53.5	Galver 2002
SL10-26	20	0.781	0.782	55	Galver 2002

in the program RELATEDNESS 5.0.8 (Queller & Goodnight 1989; Goodnight & Queller 1998). The highest pairwise relatedness value for each island was compared with the highest pairwise relatedness value for each of 100 randomisations of the dataset for each island. Similarly, the average of the five highest pairwise relatedness values for each island was compared with the values from 100 randomised datasets. Each randomisation was conducted by permuting alleles across individuals for each locus, retaining the presence and positions of missing data. Identification of close relatives within populations is important because their presence can bias measures of population differentiation.

Genetic diversity

For mtDNA data, nucleotide (π) and haplotypic (h) diversities were calculated using ARLEQUIN. The nucleotide substitution model used to calculate genetic distance was the Tamura and Nei model (Tamura & Nei 1993). This was the model available in ARLEQUIN that most closely matched the best-fit model determined using AIC in MODELTEST 3.06 (Posada & Crandall 1998), which was K81uf + I (Kimura 1980). Data from samples collected in Sāmoa were not used in MODELTEST analyses. To test whether mtDNA haplotype and nucleotide diversities differed between islands/atolls, standard error values were calculated from 10 000 bootstrap replicates for each island/atoll, and Welch's *t*-tests were used for pairwise comparisons between locations due to inequality of variances. Observed heterozygosity, expected heterozygosity, allelic richness, and total number of alleles were calculated per microsatellite locus and per location using FSTAT 2.9.3.2 (Goudet 2001) and ARLEQUIN. Welch's *t*-tests were used to assess differences in microsatellite allelic richness between islands/atolls.

Population structure

To investigate population structure within the Hawaiian Archipelago, genealogical relationships between mtDNA haplotypes were examined using a statistical parsimony network in TCS 1.21 (Clement *et al.* 2000) with a 95% connection limit. Additionally, pairwise *F*-statistics were calculated for mtDNA and microsatellites using ARLEQUIN and RECODEDATA 0.1 (Meirmans 2006), with each island or atoll treated as an a priori defined population. Three different *F*-statistics were used: a measure that incorporates mtDNA sequence divergence (Φ_{ST}), a measure based on microsatellite allele frequencies or mtDNA haplotype frequencies (F_{ST}), and a standardised version of F_{ST} that takes into account within-population genetic variation for both mtDNA and microsatellites (F'_{ST}) (Hedrick 2005; Meirmans 2006). Significance of pairwise *F*-statistics was tested using 10 000 permutations.

Population structure was also investigated in a Bayesian clustering analysis to estimate the most probable number of populations using the program STRUCTURE 2.3.2 (Pritchard *et al.* 2000) using sampling location as a prior (Hubisz *et al.* 2009) and using the admixture and correlated allele frequency models. The burn-in length was set at 10^5 steps, followed by 10^6 steps. Five independent runs were conducted for each value of K ranging between one and 10 to test the consistency of estimates of $P(X|K)$. To investigate the influence of the geographically distant Sāmoa sample, these analyses were conducted with and without the Sāmoa dataset. Population structure was further investigated using Bayesian likelihood methods to assign each individual to a population based on multilocus microsatellite genotypes as implemented in GENECLASS 2 (Piry *et al.* 2004). Assignment tests are thought to provide information about recent gene flow, since they identify migrants, or recent descendents of migrants, by identifying disequilbrium within multilocus genotypes (Wilson & Rannala 2003).

To examine the possible influence of sex-biased dispersal, measures of genetic structure were compared between males and females in the Hawaiian Archipelago with the biased dispersal methods implemented in FSTAT (Goudet *et al.* 2002) using microsatellite data. These methods test for differences between the sexes for the mean and variance of corrected assignment indices (*mAIc* and *vAIc*), F_{ST}, inbreeding coefficients (F_{IS}), relatedness, and within-group gene diversity (H_S). These tests were performed for the entire sample set from Hawai'i. After taking into account the results of genetic structure analyses, these tests were also performed separately for the subset of samples only from the far-NWHI, and the subset of samples only from the MHI plus French Frigate Shoals.

Relationships between geographic distance and genetic isolation within the Hawaiian Archipelago were investigated using GENEPOP 3.1b (Raymond & Rousset 1995). Correlations between genetic distinction (F_{ST}/1-F_{ST}) (Rousset 1997) and geographic distance were assessed with a Mantel test (10 000 permutations) and a Spearman's rank correlation test for each of the *F*-statistics calculated for mtDNA and microsatellites. Geographic distances were calculated from the approximate centres of the sampling locations at each island or atoll.

Results

Samples

A total of 589 specimens were collected from spinner dolphins at nine islands or atolls in the Hawaiian

Archipelago (Fig. 1a,b) and at the island of Tutuila in American Sāmoa (Table 2). However, some specimens were removed from the dataset for final analyses (see below). Samples collected at the islands of Maui and Lāna'i were considered as one location (here abbreviated as 'Maui') because of their close proximity (≈14 km) and the shallow waters separating the islands, as well as photo-identification data indicating that spinner dolphins move between these two locations (R Baird, unpublished data).

All microsatellite loci were highly polymorphic overall (Table 1) and at each location (Table 3). Based on these ten loci, the average nonexclusion probability for the identity of individuals was 1.42×10^{-11}, indicating a high probability that samples with matching genotypes were the same individual. Identification of matching genotypes revealed that when the biopsy sampling technique was used, 27 individuals had been re-sampled once. When the skin-swabbing technique had been used, 31 individuals had been re-sampled once, three individuals had been re-sampled twice and one individual had been re-sampled four times. A total of 30 individuals were re-sampled one or more years apart. Twenty-seven of these were re-sampled at the same island/atoll (including samples collected from all islands except Ni'ihau, Kaua'i and O'ahu), and three were re-sampled at a different location: two juveniles (one male and one female) were sampled at Midway in 2001 and at Kure in 2003 (≈97 km apart), and one adult female was sampled at Ni'ihau in 2003 and at Kaua'i in 2005 (sampling locations 37 km apart). All analyses were carried out with these three 'migrants' included in the location at which they were first sampled, and also with these migrants removed from the dataset. Results did not differ with or without the migrants included in the dataset, and here we report the results obtained

Table 2 Sample location, abbreviations and numbers of spinner dolphin skin specimens collected in the Hawaiian Archipelago and American Sāmoa

				Sex		
Location	Abbrev.	Individuals	Groups	Males	Females	Unknown
Kure Atoll	Kure	51	*NA*	30	21	0
Midway Atoll	Midway	119	*NA*	80	29	10
Pearl & Hermes Reef	PHR	47	*NA*	29	18	0
French Frigate Shoals	FFS	33	10	22	10	1
Ni'ihau		45	8	16	29	0
Kaua'i		32	13	13	19	0
O'ahu		40	15	23	15	2
Maui Nui complex	Maui	59	10	32	26	1
Kona Coast	Kona	79	14	45	34	0
Tutuila	Sāmoa	16	1	10	6	0
Total		521	71	300	207	14

Table 3 Mitochondrial (mtDNA) control region and microsatellite diversity statistics for spinner dolphins sampled at each location: π, nucleotide diversity; h, haplotype diversity; k, average number of alleles; H_o, observed heterozygosity; H_e, expected heterozygosity

	mtDNA			Microsatellites			
	No. of haplotypes	π	h	k	Allele richness	H_o	H_e
Kure Atoll	3	0.00237	0.395	7.9	6.31	0.710	0.718
Midway Atoll	4	0.00179	0.405	8.4	6.27	0.716	0.713
Pearl & Hermes Reef	3	0.00141	0.200	7.6	6.17	0.710	0.707
French Frigate Shoals	5	0.00396	0.491	8.3	7.10	0.750	0.762
Ni'ihau	9	0.00642	0.656	8.6	7.02	0.733	0.801
Kaua'i	5	0.00548	0.429	8	6.76	0.734	0.718
O'ahu	6	0.00476	0.582	8.3	6.88	0.726	0.737
Maui Nui	5	0.00431	0.461	9.4	6.98	0.727	0.732
Kona Coast	12	0.00883	0.721	9.9	6.89	0.742	0.747
Sāmoa	13	0.01977	0.975	9.6	9.60	0.856	0.814

when migrants were removed from the dataset. After removal of replicate and migrant specimens, the dataset consisted of 521 dolphins (Table 2), based on 420 biopsies and 101 skin swabs. Of the biopsies, two were collected from dolphins that stranded on O'ahu. All of the skin swabs were collected at Midway.

For each island/atoll the highest pairwise relatedness value and the average of the five highest pairwise relatedness values were within the 95% confidence intervals of the null distributions, with the exception of the highest pairwise relatedness value for O'ahu. To investigate the influence of the related pair of individuals in the O'ahu dataset on tests for population structure, *F*-statistics analyses (see below) were conducted with and without one of the individuals in the pair of related individuals from O'ahu. Pairwise *F*-statistic values differed by no more than 0.006 between these analyses, and the significance of *P*-values did not change. Therefore, a bias correction for the presence of closely related individuals was not implemented in this study, and the analyses reported here include the pair of related individuals from O'ahu.

Microsatellite quality control

No microsatellite loci deviated from Hardy Weinberg equilibrium or linkage equilibrium at any island or atoll after Bonferroni correction. Loci showed no evidence for null alleles, large allele dropout, or scoring error due to stutter peaks at any island or atoll after Bonferroni correction, although deviation from the expected level of homozygosity was found for locus 415/416 at Ni'ihau.

The average amount of missing allelic data per locus was 0.7% for biopsies and 4.4% for skin swabs. Scoring error rate was estimated at 0.7% for biopsies and 0.9% for skin swabs. These error rates are similar to others reported in the literature for studies utilising microsatellite data (Bonin *et al.* 2004).

Genetic diversity and population structure

Mitochondrial DNA analyses revealed a total of 29 haplotypes and 43 variable sites (GenBank Accession Numbers GU253256 to GU253284). Both haplotype and nucleotide diversities for mtDNA (Table 3) were significantly higher ($P < 0.05$) at Sāmoa than at any island/atoll in the Hawaiian Archipelago, with the exception of nucleotide diversity at the Kona Coast (nearly significant, $P = 0.054$). Within the Hawaiian Archipelago, haplotype diversities were significantly different ($P < 0.05$) for all pairwise comparisons except Kure vs. Midway; French Frigate *vs.* Maui; and Kaua'i vs. Kure, Midway, French Frigate, and Maui. For nucleotide diversity, most pairwise comparisons were not significant within the Hawaiian Archipelago, with the exceptions ($P < 0.05$) of the Kona Coast vs. each of the far-NWHI; O'ahu vs. each of the far-NWHI; and Pearl & Hermes vs. French Frigate and Ni'ihau (see Table 3). For microsatellite allelic richness, pairwise comparisons were significant for Sāmoa vs. the far-NWHI (Kure, Midway, and Pearl & Hermes) ($P < 0.05$) and were nearly significant for Sāmoa vs. the other Hawaiian Islands ($P \leq 0.069$), with Sāmoa having higher allelic richness in all cases. Allelic richness was not significantly different for any pairwise comparisons within the Hawaiian Archipelago.

The mtDNA haplotype network showed strikingly different patterns for Hawai'i vs. Sāmoa (Fig. 2). When taking into consideration the difference in sample sizes between these two locations (Sāmoa $n = 16$, Hawai'i $n = 505$), proportionately far more haplotypes were observed in Sāmoa (13 haplotypes) than Hawai'i (19 haplotypes), and Sāmoan haplotypes were more genetically distant from each other than were Hawaiian haplotypes ($\pi = 0.0198$ vs. $\pi = 0.0014$–0.0088). The dataset from Hawai'i was dominated by two haplotypes, whereas haplotypes were relatively equifrequent in the dataset from Sāmoa (Fig. 2). Three haplotypes were shared between Hawai'i and Sāmoa, but the most common haplotypes in Hawai'i were not detected in Sāmoa. However, the network showed no evidence for phylogeographic structuring of mtDNA lineages between Hawai'i and Sāmoa; the haplotypes found exclusively at Sāmoa or Hawai'i were scattered throughout the network.

One mtDNA haplotype was highly distinct from all other haplotypes in the network (Fig. 2). This haplotype was at least nine mutational steps from any other haplotype, and therefore did not connect to any other haplotype in the 95% TCS connection limit. This haplotype was observed at French Frigate Shoals, Kaua'i, and Sāmoa. To confirm that individuals with this haplotype were not mis-identified congeners, the haplotype was compared in a neighbour-joining phylogenetic tree with mtDNA control region haplotypes from all recognized members of the genus *Stenella*, as well as seven other odontocete species. The haplotype consistently fell within the well-supported and monophyletic spinner dolphin group (data not shown).

For *F*-statistics analyses, patterns of significance and relative values between islands and atolls throughout Hawai'i and Sāmoa were similar for mtDNA and microsatellites, and for the different types of *F*-statistics (Table 4). As expected, the highest *F*-statistic values were found between Sāmoa and the Hawaiian islands/atolls. Significant population differentiation was also found between most Hawaiian islands/atolls, with some exceptions: adjacent Midway and Kure were not

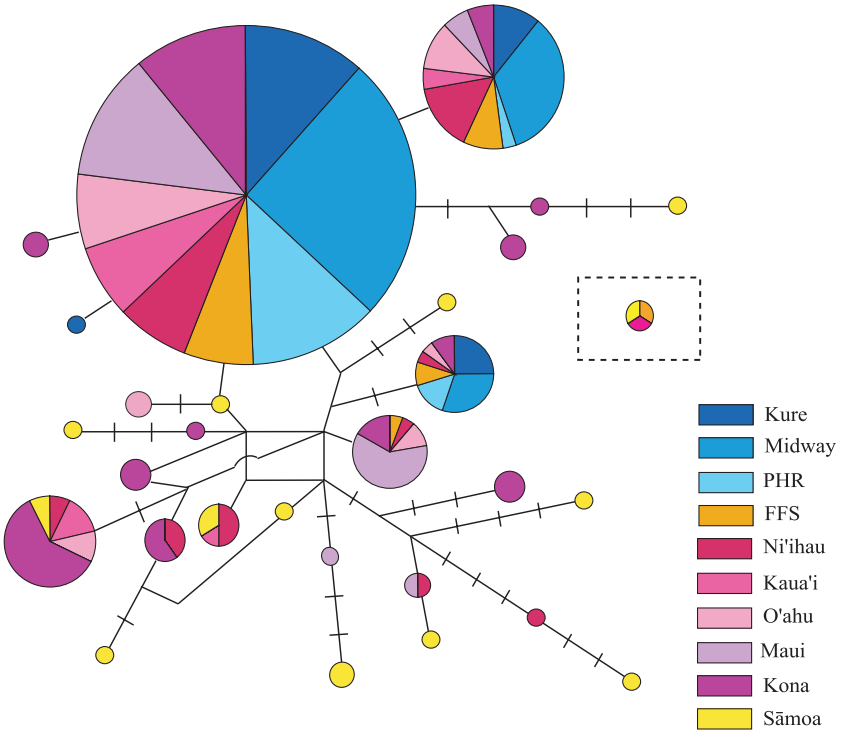

Fig. 2 Parsimony network of mtDNA control region haplotypes from different islands and atolls in the Hawaiian Archipelago and American Sāmoa. Diameters of circles are proportional to the frequency of the haplotype. Hash marks and nodes represent mutational steps separating haplotypes. Locations in the far-Northwestern Hawaiian Islands are shades of blue, and locations in the Main Hawaiian Islands are shades of red and purple. The haplotype within the dashed-line box was at least nine mutational steps from the closest haplotype and did not connect with ≥ 95% confidence anywhere in the network.

distinct for all *F*-statistics, and French Frigate Shoals, Ni'ihau, Kaua'i and O'ahu were not distinct from each other for most *F*-statistics. The highest pairwise *F*-statistic values within Hawai'i generally involved comparisons with the Kona Coast.

Bayesian clustering analyses indicated similar patterns of population structure as did *F*-statistics (Fig. 3). The highest average posterior probability occurred at $K = 4$ (Fig. 3a), although variance was relatively high for all $K \geq 4$. Despite this high variance, visual inspection of the output for all $K > 1$ indicated similar partitioning into population clusters. For example, for both $K = 4$ (Fig. 3a) and $K = 8$ (Fig. 3b), visual inspection of the output revealed partitioning into four primary population clusters including Sāmoa; the far-NWHI; French Frigate Shoals combined with all the MHI except the Kona Coast; and the Kona Coast. Based on these results, we chose $K = 4$ as the most probable value. When analyses were conducted without the Sāmoa dataset, the highest average posterior probability occurred at $K = 3$, and visual inspection of the output showed similar patterns of population clustering within the Hawaiian Islands as did the analyses that included the Sāmoa dataset (data not shown).

GENECLASS2 assignment tests provided evidence for relative migration levels consistent with *F*-statistics and STRUCTURE results (Fig. 4). For samples collected at each island/atoll except O'ahu, more individuals were assigned to the island at which they were sampled (here we refer to these individuals as 'back-assigned') than to any other island, indicating some site fidelity at each island. Migration appeared to be relatively high between the far-NWHI (Kure, Midway, and Pearl & Hermes Reef), but low between the far-NWHI *vs.* other islands/atolls; of all the individuals sampled in the far-NWHI, 75.6% were assigned back to the far-NWHI. Islands with the lowest percent back-assignments were French Frigate Shoals (18.2%) and O'ahu (15.0%), suggesting that these islands have the highest migration rates in Hawai'i. For samples collected at O'ahu, more individuals were actually assigned to adjacent Maui (27.5%) than to O'ahu. The Kona Coast had the highest percent back-assignments (59.5%) in Hawai'i, and Sāmoa had the highest percent back-assignments overall (81.3%).

None of the six tests for sex-biased dispersal showed significant differences between males and females within the Hawaiian Archipelago ($P > 0.05$). After taking into account results of the genetic structure analyses, sex-biased dispersal tests were also conducted treating the far-NWHI and MHI/French Frigate Shoals as two separate regions. These tests also showed no evidence for sex-biased dispersal in either region ($P > 0.05$).

Genetic differentiation was significantly correlated with geographic distance across the Hawaiian Archipelago (Spearman's rank correlation, $P < 0.05$) for both mtDNA and microsatellites and each type of *F*-statistic,

Table 4 Pairwise *F*-statistics for spinner dolphins between locations in the Hawaiian Archipelago and American Sāmoa for 10 microsatellite loci (below diagonals) and a 417 bp fragment of the mtDNA control region (above diagonals). (a) F_{ST} values for microsatellites and Φ_{ST} values for mtDNA. (b) Standardised F_{ST} (F'_{ST}) values for microsatellites and mtDNA. Φ_{ST} considers genetic distance between haplotypes, but F_{ST} and F'_{ST} do not. Shaded areas indicate significant values: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

(a)	Kure	Midway	PHR	FFS	Ni'ihau	Kaua'i	O'ahu	Maui	Kona	Sāmoa
Kure		0.000	−0.003	−0.011	0.048*	0.061*	0.029	0.076**	0.163***	0.506***
Midway	−0.001		0.018	0.001	0.087***	0.105***	0.054**	0.123***	0.236***	0.643***
PHR	0.009**	0.003		0.010	0.072**	0.070**	0.050*	0.089**	0.176***	0.532***
FFS	0.013***	0.009***	0.010**		0.013	0.017	−0.002	0.037	0.121***	0.396***
Ni'ihau	0.013***	0.012***	0.015***	0.004		0.000	−0.005	0.015	0.051**	0.300***
Kaua'i	0.012***	0.011***	0.013***	0.005	0.001		−0.008	0.030	0.042*	0.316***
O'ahu	0.009**	0.007**	0.013**	0.001	0.001	0.003		0.016	0.071**	0.368***
Maui	0.018***	0.015***	0.022***	0.009**	0.012***	0.013***	0.001		0.085***	0.387***
Kona	0.031***	0.028***	0.040***	0.016***	0.021***	0.024***	0.018***	0.025***		0.216***
Sāmoa	0.081***	0.089***	0.090***	0.058***	0.080***	0.077***	0.073***	0.073***	0.058***	

(b)	Kure	Midway	PHR	FFS	Ni'ihau	Kaua'i	O'ahu	Maui	Kona	Sāmoa
Kure		−0.009	0.025	−0.015	0.042*	0.015	0.017	0.042	0.102***	0.393***
Midway	−0.003		0.052*	−0.015	0.037*	0.025	0.013	0.050**	0.116***	0.416***
PHR	0.030**	0.010		0.076*	0.155***	0.046*	0.105**	0.082**	0.175***	0.538***
FFS	0.049***	0.033***	0.039**		0.002	0.011	−0.014	0.022	0.070**	0.311***
Ni'ihau	0.048***	0.041***	0.053***	0.016		0.043	−0.011	0.054*	0.033*	0.208***
Kaua'i	0.043***	0.039***	0.045***	0.020	0.002		0.012	0.039	0.055*	0.344***
O'ahu	0.032**	0.023**	0.045**	0.003	0.004	0.011		0.030	0.035*	0.264***
Maui	0.065***	0.053***	0.078***	0.035**	0.043***	0.048***	0.005		0.120***	0.370***
Kona	0.116***	0.102***	0.147***	0.065***	0.079***	0.090***	0.068***	0.096***		0.192***
Sāmoa	0.337***	0.353***	0.366***	0.269***	0.342***	0.320***	0.318***	0.309***	0.253***	

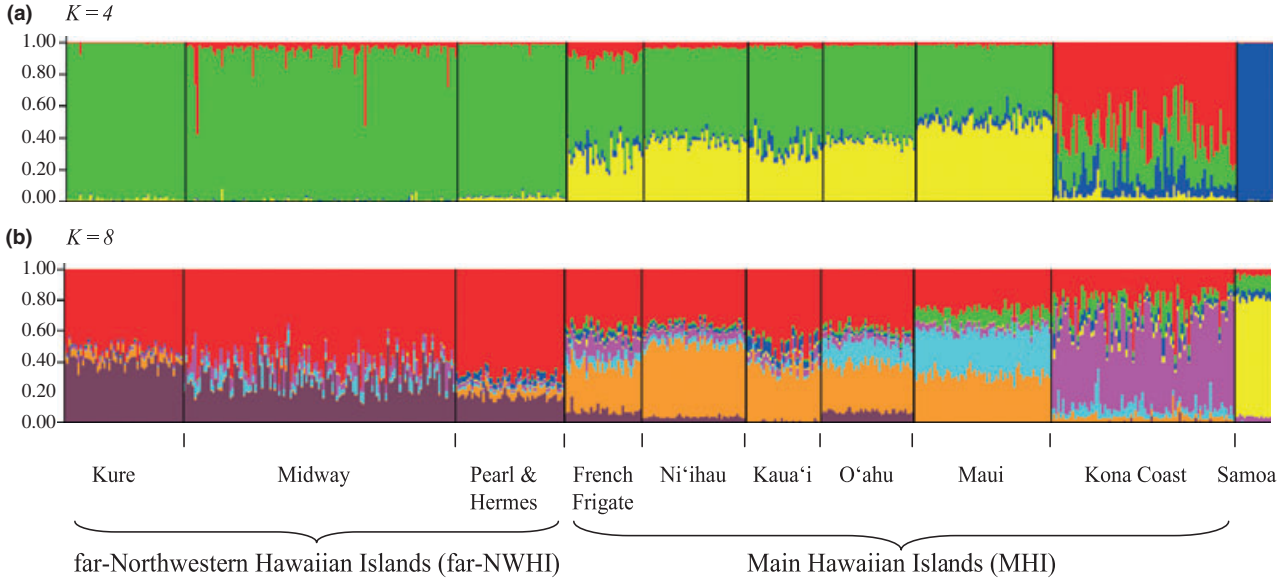

Fig. 3 Assignment probabilities of individuals to putative population clusters at: (a) $K = 4$; and (b) $K = 8$ using the program STRUCTURE 2.3.2. Locations where individuals were sampled are indicated below the graph.

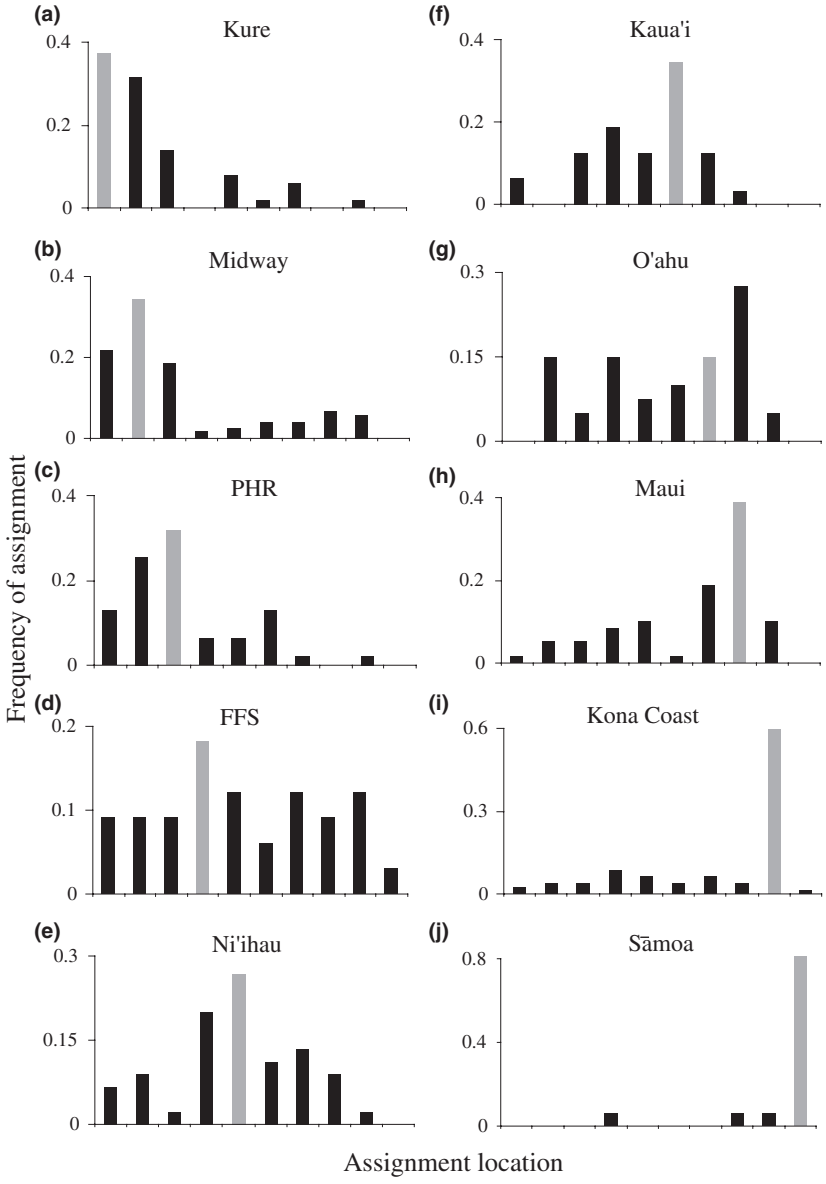

Fig. 4 Distribution of assignment locations for spinner dolphins sampled in the Hawaiian Archipelago and American Sāmoa determined using GENECLASS2. Graph headings represent the location where the individuals were sampled, and graphs are arranged from (a) the west-most island in the Hawaiian Archipelago to (i) the east-most island in the Hawaiian Archipelago, followed by (j) Sāmoa. 'Back-assignments' (assignments to the location at which the individual was sampled) are coloured in light grey.

with the exception of the mtDNA standardised *F*-statistic which was nearly significant ($P = 0.066$). We report here the relationship between unstandardised *F*-statistics and geographic distance (Fig. 5).

Discussion

Genetic structure and diversity within Hawai'i

The overall pattern of population genetic structure differed substantially between islands/atolls in the Hawaiian Archipelago. Genetic distinctions were detected between most islands, but there was little distinction between two of the three far-NWHI (Kure and Midway), and little distinction between French Frigate Shoals (in the NWHI near the middle of the archipelago) and the islands of Ni'ihau, Kaua'i, and O'ahu (in the MHI). When compared to the previous study (Andrews *et al.* 2006), less genetic distinction was found between French Frigate Shoals vs. the MHI and O'ahu vs. Ni'ihau, and greater genetic distinction was found between O'ahu vs. the far-NWHI. These differences were shaped by the inclusion of microsatellite analyses in our current study, which appeared to have greater power than mtDNA analyses to detect subtle population differences. Additionally, these differences were likely influenced by the inclusion of greater sample sizes and the exclusion of replicate samples (made possible by microsatellite analyses) in our current study.

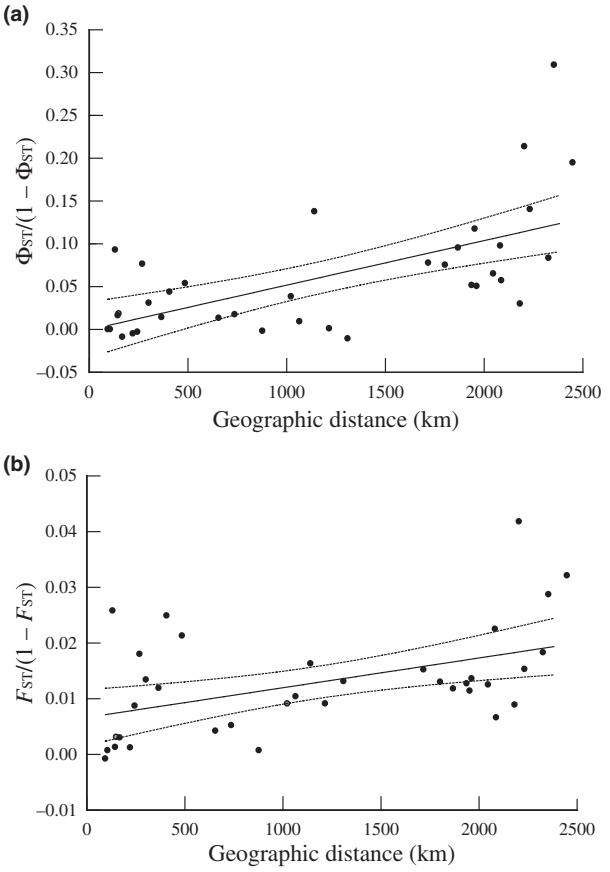

Fig. 5 Isolation by distance tests for correlation between genetic differentiation and geographic distance between islands/atolls for: (a) mtDNA ($r = 0.629$, $r^2 = 0.395$, $P < 0.001$); and (b) microsatellites ($r = 0.473$, $r^2 = 0.224$, $P = 0.004$). Outer lines represent 95% confidence intervals.

The patterns of genetic structure generally matched expectations based on dispersal data available at Kure, Midway, Pearl & Hermes and the Kona Coast. Photo-identification data indicate that dispersal between Kure and Midway is relatively high (Karczmarski *et al.* 2005b; L. Karczmarski, unpublished data), consistent with the lack of genetic distinction between these atolls (Table 4). Photo-identification data have also revealed that dispersal between Kure and Midway is greater than dispersal between Pearl & Hermes and either Kure or Midway (L. Karczmarski unpublished data). Our genetic analyses reveal a corresponding higher level of genetic differentiation between Pearl & Hermes vs. Kure and Midway (all *F*-statistic results significant for microsatellites, F'_{ST} significant for mtDNA) than between Kure vs. Midway (no significant pairwise *F*-statistic results for mtDNA or microsatellites) (Table 4). Within the MHI, photo-identification data are currently only available for the Kona Coast (Norris *et al.* 1994; Östman 1994; Jan Östman, unpublished data). These data indicate a relatively high level of site fidelity at the Kona Coast, supporting our genetic analyses which indicate strong differentiation between this location and other islands/atolls (Table 4). Overall, the concordance between genetic structure and photo-identification data indicates that the genetic structure in Hawai'i probably reflects present-day dispersal patterns, rather than historic dispersal.

Genetic diversity also varied among regions within the Hawaiian Archipelago. The mtDNA haplotype diversity differed significantly between most islands/atolls, whereas mtDNA nucleotide diversities differed mainly between the far-NWHI vs. the other islands/atolls in the archipelago, with lower diversities found in the far-NWHI. This pattern is less obvious in microsatellite diversity, although the far-NWHI had consistently lower values for all microsatellite diversity indices than did other locations in the archipelago (Table 3). The lower genetic diversities in the far-NWHI likely result from small population sizes in this region; photo-identification studies have estimated population sizes at Kure (≈120, Karczmarski *et al.* 2005a) and Midway (≈260, Karczmarski *et al.* 2005b) that are much lower than at the island of Hawai'i (at least ≈1000, Norris *et al.* 1994; and likely considerably larger, Östman 1994; B. Würsig & L. Karczmarski personal communication). This evidence for smaller population sizes in the NWHI is consistent with the scarcity of resting habitat and foraging habitat in this region.

Relationship between genetic structure and habitat

We found that regional variation in genetic structure corresponds with the geographic distance between islands/atolls in the Hawaiian Archipelago. This significant correlation indicates that dispersal is limited by the length of oceanic gaps between habitat patches. A similar relationship between dispersal and habitat patch isolation has been observed for other species which occupy habitat patches (e.g. Kuussaari *et al.* 1996; Baguette *et al.* 2000; Goodwin & Fahrig 2002; Serrano & Tella 2003). This relationship is generally assumed to arise because time spent in interpatch habitat is costly to fitness, and therefore selective pressure against dispersal will be higher when habitats are separated by greater geographic distance (MacArthur & Wilson 1967; Waser *et al.* 1994; Schtickzelle *et al.* 2006). However, geographic distance alone cannot explain the observed genetic structure in our dataset. Genetic distinctions were observed between two of the islands that were geographically closest together (the Kona Coast and Maui, ≈46 km apart), whereas genetic distinctions were not found between some of the islands/atolls that were farthest apart (e.g. French Frigate Shoals and Ni'ihau,

≈650 km apart). These examples are reflected in the variance present in the graphical relationship between genetic differentiation and geographic distance (Fig. 5) and the nonsignificant correlation for mtDNA standardised *F*-statistics.

A second environmental factor likely influencing genetic structure is the availability of resources. Resting habitat is thought to be a limiting resource for spinner dolphins in Hawai'i, influencing both population size and social structure at the different islands/atolls (Norris *et al.* 1994; Karczmarski *et al.* 2005b). Prey abundance and density may also vary between islands and may act as a limiting resource (Benoit-Bird 2004). Although resting habitat and prey abundance have not been quantified at all islands, these variables are likely closely linked with island size. Our results show a trend that spinner dolphin populations at the smallest islands (far-NWHI, French Frigate Shoals, Ni'ihau, Kaua'i and O'ahu) have the highest levels of gene flow. Because smaller islands likely have fewer resources and smaller populations than larger islands, the higher levels of gene flow between smaller islands may result from increased pressures of resource competition and inbreeding (Greenwood 1980; Johnson & Gaines 1990; Pusey & Wolf 1996).

Relationship between genetic structure and social structure

Social structure may be a third factor influencing population connectivity in Hawai'i. In particular, Midway and Kure (97 km distant) have stable groups and no genetic distinctions between atolls, whereas the Kona Coast has a fission-fusion society and is genetically distinct from Maui (46 km distant) and all other islands (Norris *et al.* 1994; Östman 1994; Karczmarski *et al.* 2005a, b). The spinner dolphins at Moorea in French Polynesia show similarities to the Kona Coast in having a fission-fusion social structure and genetic distinctions from nearby island habitats (Oremus *et al.* 2007). The apparent relationship between social and genetic structures may be counterintuitive; the islands with higher group stability (Kure and Midway) have greater interisland gene flow than the islands with the fission-fusion society (Kona Coast and French Polynesia). A greater understanding of this relationship between social and genetic structures can be gained through the photo-identification data from Midway and Kure. These data indicate that dispersal does not occur at a constant rate; rather, dispersal occurs infrequently by groups of 30–60 dolphins with approximately equal numbers of males and females, juveniles and adults. These dispersers move between dolphin communities that are otherwise stable, resident and socio-behaviourally discrete over long periods of time (Karczmarski *et al.* 2005b). Group dispersal (called *parallel dispersal*) has been observed in a few other species, including lions (*Panthera leo*, Pusey & Packer 1987) and capuchins *(Cebus capucinus*, Jack & Fedigan 2004), and is thought to function in maintaining social relationships that are important for predator avoidance, resource acquisition, intraspecific competition, or the raising of young (Handley & Perrin 2007). Group dispersal at Midway and Kure may similarly function to maintain social relationships in these highly stable social communities, while still permitting gene flow to alleviate pressures of inbreeding and resource competition.

Sex-biased dispersal

The majority of mammalian species appear to alleviate the pressures of inbreeding and kin competition through male-biased dispersal (Greenwood 1980). In contrast, our genetic analyses indicate that spinner dolphins throughout the Hawaiian Archipelago have equal levels of dispersal for both sexes. Photographic identification data from Midway and Kure support these results, with approximately equal numbers of males and females found to disperse between these atolls (L. Karczmarski & S.H. Rickards unpublished data). However, genetic tests for sex-biased dispersal are known to have low power (Goudet *et al.* 2002), and therefore these results should be confirmed by mark-recapture studies at other islands in the archipelago. A lack of male-biased dispersal is relatively rare among odontocete species; male-biased dispersal has been found for spinner dolphins in French Polynesia (Oremus *et al.* 2007); bottlenose dolphins (*Tursiops* spp.) in western and southeastern Australia (Krützen *et al.* 2004; Möller & Beheregaray 2004); Dall's porpoises (*Phocoenoides dalli*, Escorza-Treviño & Dizon 2000); sperm whales (*Physeter macrocephalus*, Lyrholm *et al.* 1999); and belugas (*Delphinapterus leucas*, O'Corry-Crowe *et al.* 1997). However, lack of sex-biased dispersal has been reported for bottlenose dolphin in the Bahamas (Parsons *et al.* 2006), the North Atlantic (Natoli *et al.* 2005; Quérouil *et al.* 2007), and the Mediterranean and Black Seas (Natoli *et al.* 2005).

Genetic isolation of Hawai'i

Geographic and genetic isolation of Hawaiian spinner dolphins from other populations in the Pacific may also influence social and genetic structure within Hawai'i. For example, strong demographic isolation in the far-NWHI is thought to influence the stable social structure in this region (Karczmarski *et al.* 2005b). Previous studies have reported genetic distinctions between the Kona

Coast vs. other Pacific regions, providing evidence that Hawai'i may be a demographically isolated archipelago (Galver 2002; Johnston *et al.* 2008). Our results showing genetic distinctions between Sāmoa vs. all islands/atolls in Hawai'i were consistent with this prediction. Further evidence for the genetic isolation of Hawai'i comes from the low mtDNA control region diversity in Hawai'i, and especially in the far-NWHI. This diversity is the lowest observed to date among spinner dolphins worldwide (Galver 2002; Oremus *et al.* 2007), indicating the presence of relatively small and isolated populations in Hawai'i. This isolation is likely due to the large geographic distances separating Hawai'i from other spinner dolphin populations; the closest island known to host spinner dolphins is Palmyra Atoll, 1600 km south of Hawai'i.

The origin of the divergent haplotype found at French Frigate Shoals, Kaua'i, and Sāmoa is unknown. It may be a remnant haplotype from an ancestral population which colonised both Hawai'i and Sāmoa, or it may have originated from a divergent population of spinner dolphins at a location outside of Hawai'i or Sāmoa. Either way, the presence of this haplotype in both Hawai'i and Sāmoa demonstrates a genetic connection between northern and southern hemispheres in the central Pacific, although it is not clear whether this represents historic gene flow or low levels of ongoing gene flow. Oremus *et al.* (2007) suggest that low levels of gene flow occur between island-associated spinner dolphin populations across the Pacific, creating a metapopulation dynamic. This idea of a Pacific metapopulation was advanced to explain the high mtDNA diversity, despite small population sizes, at islands in French Polynesia (Oremus *et al.* 2007). However, if ongoing gene flow is occurring between Hawai'i and other locations, this gene flow is not sufficient to retain high mtDNA diversity in Hawai'i.

Comparison with other species in Hawai'i: population structure

The island fidelity and genetic structure observed for spinner dolphins are not unusual for odontocete species in the Hawaiian Archipelago, despite the capabilities of odontocetes for long-distance movement. Photo-identification and genetic data have revealed that bottlenose dolphins have unusually high fidelity to each MHI, when compared to other oceanic islands (Martien *et al.* 2005; Baird *et al.* 2009). Rough-toothed dolphins (*Steno bredanensis*) and two species of beaked whales (*Ziphius cavirostris* and *Mesoplodon densirostris*) also exhibit site fidelity at one or more Hawaiian Islands, despite being deep-water species (McSweeney *et al.* 2007; Baird *et al.* 2008b). Another species found commonly in deep waters, false killer whales (*Pseudorca crassidens*), did not exhibit fidelity to individual islands in Hawai'i (Baird *et al.* 2008a), but had lower genetic diversity in nearshore waters of Hawai'i, as well as genetic distinctions between nearshore and offshore populations. These data indicate that Hawai'i hosts a small, demographically isolated population of false killer whales (Chivers *et al.* 2007). Short-finned pilot whales in Hawai'i are also genetically distinct from other populations in the Pacific (Chivers *et al.* 2003). The fidelity of odontocetes to the Hawaiian Archipelago is probably driven by the predictability of food resources in the waters surrounding the islands, as well as the large geographic distances separating this archipelago from any other coastal habitat.

The genetic distinctions for spinner dolphins between Hawaiian Islands contrasts strongly with the limited genetic subdivision observed in similarly distributed marine fishes. Molecular surveys of the Hawaiian grouper (*Epinephelus quernus*, Rivera *et al.* 2004), three surgeonfishes (Eble *et al.* 2009), and the bigscale soldierfish (*Myripristis berndti*, Craig *et al.* 2007) all revealed little to no genetic differentiation across the archipelago. The evolutionary causes for the more pronounced genetic structure in spinner dolphins likely include stronger genetic drift due to small population sizes, as well as lower levels of population connectivity resulting from strong social structure and the lack of pelagic larval dispersal for odontocete species. However, the genetic structure of spinner dolphins also contrasts with that of a distantly related marine mammal species, the Hawaiian monk seal, which is also distributed across the Hawaiian Archipelago (J. Schultz, unpublished data). The differences in genetic structure between spinner dolphins and monk seals may be related to differences in their social structure; in contrast to spinner dolphins, monk seals are solitary.

Management implications

Anthropogenic impacts on the spinner dolphin populations in Hawai'i are a growing concern. The primary focus of this concern is the rapidly growing dolphin ecotourism industry (Carretta *et al.* 2009). Our range-wide genetic survey of Hawaiian spinner dolphins has applications under the US Marine Mammal Protection Act, to aid in defining and assessing management units. The results of genetic assignment tests indicate relatively high site fidelity at most islands, indicating that the dolphins at each island should be managed separately. Our data also highlight the potential vulnerability of these dolphins to anthropogenic disturbance by providing evidence that the populations in Hawai'i are

small and genetically isolated from locations outside of Hawai'i. The populations that are likely most vulnerable to disturbance include the population at the Kona Coast due to its higher level of philopatry, and the population in the far-NWHI due to their very small and socio-behaviourally discrete communities. Our results also provide evidence that availability of resources may be a critical factor influencing spinner dolphin distribution, dispersal patterns, genetic structure and social structure at the different Hawaiian Islands. Therefore, efforts to conserve spinner dolphins would benefit from characterisation of critical habitat at each of the Hawaiian Islands and atolls.

Conclusions

Our analyses indicate that genetic structure between islands is highly variable for spinner dolphins across the Hawaiian Archipelago, with less genetic structuring among the NHWI than among the MHI, and a trend for smaller islands/atolls to have lower levels of genetic diversity and differentiation. This variation in genetic structure corresponds with variation in both habitat and social structure, providing evidence that the population-level response of spinner dolphins to different island/atoll habitats within Hawai'i has involved shifts in social behaviour, dispersal and consequent genetic structure. Our results illustrate that social and genetic structures are flexible within spinner dolphins and can change in response to habitat differences across relatively small geographic scales.

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K.A. studies the influence of habitat and behavior on genetic structure and diversity, with application to conservation issues. L.K. studies cetacean behavioural ecology, especially sociobehavioural complexity and comparative population ecology of delphinids and other group-living mammals. S.R.'s research interests include cetacean population biology, behavioural ecology, and social organization, with an emphasis on conservation in the Hawaiian archipelago. C.V. collaborates on the collection of long term photographic-identification and behavioural data of spinner dolphins at Kure and Midway Atolls and Pearl & Hermes Reef. B.B. studies the evolution and conservation genetics of marine vertebrates, with an emphasis on how biodiversity is generated and maintained. E.G.G.'s research focuses on the role of the neuroendocrine system in orchestrating the environmental physiology of fish and other vertebrates. R.T. studies coral reef connectivity.