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Familial social structure and socially driven genetic differentiation in Hawaiian short-finned pilot whales

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Abstract

Social structure can have a significant impact on divergence and evolution within species, especially in the marine environment, which has few environmental boundaries to dispersal. On the other hand, genetic structure can affect social structure in many species, through an individual preference towards associating with relatives. One social species, the short-finned pilot whale (*Globicephala macrorhynchus*), has been shown to live in stable social groups for periods of at least a decade. Using mitochondrial control sequences from 242 individuals and single nucleotide polymorphisms from 106 individuals, we examine population structure among geographic and social groups of short-finned pilot whales in the Hawaiian Islands, and test for links between social and genetic structure. Our results show that there are at least two geographic populations in the Hawaiian Islands: a Main Hawaiian Islands (MHI) population and a Northwestern Hawaiian Islands/Pelagic population (F_{ST} and Φ_{ST} $p < .001$), as well as an eastern MHI community and a western MHI community (F_{ST} $p = .009$). We find genetically driven social structure, or high relatedness among social units and clusters ($p < .001$), and a positive relationship between relatedness and association between individuals ($p < .0001$). Further, socially organized clusters are genetically distinct, indicating that social structure drives genetic divergence within the population, likely through restricted mate selection (F_{ST} $p = .05$). This genetic divergence among social groups can make the species less resilient to anthropogenic or ecological disturbance. Conservation of this species therefore depends on understanding links among social structure, genetic structure and ecological variability within the species.

KEYWORDS
cetacean, divergence, gene-culture co-evolution, genomics, *Globicephala macrorhynchus*, population structure, relatedness

1 | INTRODUCTION

While the concept of culture has traditionally been reserved for human societies, more recently biologists have identified and described aspects of culture in nonhuman species, such as elephants, birds, primates, pinnipeds and cetaceans (e.g., de la Torre & Snowdon, 2009; Kershenbaum, Ilany, Blaustein, & Geffen, 2012; Kessler et al., 2014; Lachlan & Slater, 1999; Laland & Janik, 2006; McComb & Semple, 2005; Mundinger, 1980; Rendell & Whitehead, 2001, 2003; Riesch, Barrett-Lennard, Ellis, Ford, & Deecke, 2012; Wittemyer et al., 2009). Theoretical studies have long suggested the existence of gene-culture co-evolution outside humans, and integrative studies of genomic and cultural traits are beginning to provide evidence of gene-culture co-evolution in social mammals, both in a narrow sense (i.e., direct links between genes and cultural phenotypic traits), and a broad sense (i.e., population-level genetic

differences among groups with different cultures or societies). Sociality has been shown to increase inclusive fitness in cooperative species (e.g., Connor, Smolker, & Richards, 1992; Rendell & Whitehead, 2001) and therefore be an evolutionarily advantageous trait. Socially driven, fine-scale genetic structure has been documented in primates and some other social mammals, such as elephants, rock wallabies (*Petrogale penicillata*), prairie dogs (*Cynomys ludovicianus*), killer whales (*Orcinus orca*) and sperm whales (*Physeter macrocephalus*) (e.g., Cantor et al., 2015; Dobson, Chesser, Hoogland, Sugg, & Foltz, 1998; Foote et al., 2016; Hazlitt, Sigg, Eldridge, & Goldizen, 2006; Pope, 1992; Wittemyer et al., 2009). These species all form socially defined groups that are genetically distinct due to nonrandom mating and dispersal patterns, and are often characterized by matrilineal societies with male-biased dispersal. These types of societies, if stable over many generations, could lead to the co-evolution of genes and culture.

Because cetaceans live in an environment with few boundaries to dispersal, social structure may play an important role in driving population structure and evolution. Stable social structures (i.e., hierarchical group associations that remain stable for decades to generations) have been identified in four species of cetacean—sperm whales, killer whales, long-finned pilot whales (*Globicephala melas*) and short-finned pilot whales (*G. macrorhynchus*) (e.g., Amos, Schlotterer, & Tautz, 1993; Baird & Whitehead, 2000; Cantor et al., 2015; Mahaffy, Baird, McSweeney, Webster, & Schorr, 2015). Whitehead (1998) suggests that the dearth of mitochondrial diversity in these four highly social cetaceans may be driven by selection for maternally inherited cultural traits. In killer whales and sperm whales, the effects of social structure and cultural learning (e.g., foraging techniques, migration patterns, predator avoidance and vocal traditions) as drivers of genetic structure have been well documented (e.g., Cantor et al., 2015; Filatova et al., 2012; Foote, Newton, Piertney, Willerslev, & Gilbert, 2009; Foote et al., 2016; Ford & Fisher, 1982; Janik & Slater, 1997; Rendell, Mesnick, Dalebout, Burtenshaw, & Whitehead, 2012; Riesch et al., 2012; Weilgart & Whitehead, 1997). However, little is understood of the social and genetic structure of pilot whales, or the links between the two.

Just as social structure can affect genetic structure, genetic structure can have a driving effect on social structure, if individuals choose to associate with close relatives rather than disperse throughout their range, even though it may or may not provide an evolutionary advantage (Beck, Kuningas, Esteban, & Foote, 2011). The positive feedback loop created by these two complementary processes may stabilize social units or clusters, allowing co-evolutionary genetic and social divergence to occur. While many aspects of this theory have been discussed (e.g., Findlay, 1991; Lachlan & Slater, 1999; Laland, 1992), empirical evidence of stable gene-culture co-evolution outside of humans is limited (Rendell & Whitehead, 2001). Although research in this area is increasing (e.g., Foote et al., 2016), the relationship between ecology, culture and genetics is poorly understood in all species (Laland, Odling-Smee, & Myles, 2010).

Short-finned pilot whales, due to their social nature, may be affected by this reciprocal link between social structure and genetic structure. Stable social units (Mahaffy et al., 2015) and a long period of postreproductive senescence in females (Marsh & Kasuya, 1986) may contribute to gene-culture divergence in this species, both at the population and subpopulation level, as is true of killer whales (Brent et al., 2015). In the Pacific Ocean, two types of short-finned pilot whale have been identified, distinct in their morphology, genetics, distribution and vocal repertoire (Kasuya, Miyashita, & Kasamatsu, 1988; Oremus et al., 2009; Van Cise, Roch, Baird, Aran Mooney, & Barlow, 2017; Van Cise et al., 2016). Little is known of the mechanism of divergence between these two types, but due to their similarity to killer whales in several life history characteristics (e.g., stable social units, reproductive senescence in females and distinct vocal repertoires), we hypothesize that cultural adaption to distinct ecological environments (e.g., diet preference or foraging techniques) promoted the divergence of the two types (Riesch, Ford, & Thomsen, 2006), which may be distinct subspecies or species.

The Hawaiian archipelago is home to one of these types, the Naisa-type short-finned pilot whale (Van Cise et al., 2016). Their density is highest around the Main Hawaiian Islands (MHI), but they are also found in the Northwestern Hawaiian Islands (NWHI) and pelagic waters surrounding the archipelago. Photograph ID and observations suggest little overlap between these three regions (Baird, 2016).

Longitudinal observations and photograph identification (photograph ID) data collected since 2000 have been used to calculate the rate of association between pairs of individuals (called the association index, and ranging from 0 to 1), using a half-weight index (HWI) to control for effort (Mahaffy et al., 2015; Whitehead, 2008). This revealed that short-finned pilot whales in Hawai'i form stable social units of approximately 12 individuals for periods of at least a decade and that these social units will often associate with a number of other social units in affiliations called clusters, with an average of 23 individuals (Mahaffy et al., 2015). Social units, the smallest group in the social hierarchy, have a mean association index of 0.76. Clusters, the next hierarchical level, comprise one or more social units with mean association index of 0.48.

Additionally, satellite tag and photograph ID data indicate that, within the MHI, three island-associated communities may exist: an eastern MHI community, around Hawai'i Island, a western MHI community around O'ahu and Kaua'i Islands, and central MHI community around O'ahu and Lāna'i Islands (Baird, 2016). The presence of these communities suggests that, in regions with highly heterogeneous habitat such as island archipelagos, habitat preference may be an important driver of local structure. Individuals are philopatric to their island communities, although some social units have been observed on rare occasions visiting other communities, and there is some overlap in geographic range among communities (Baird, 2016). Communities represent the highest level of social organization, comprised of multiple clusters (Baird, 2016; Mahaffy et al., 2015); therefore, habitat preference may be a socially learned behaviour.

Based on studies from short-finned pilot whale populations in the Atlantic Ocean, social units are thought to be matrilineal (Alves et al., 2013; Heimlich-Boran, 1993). These two studies suggest that

males remain in their natal social unit but mate outside of that group. However, in at least some cases, all-male groups have been observed (Baird, 2016), suggesting that males do not always exhibit natal philopatry. It is unknown whether males' extra-unit mate choices are random or socially driven, or whether genetic relatedness affects association or social structure at any level higher than that of social units.

In this study, we aim to improve our understanding of local population structure and divergence in Hawaiian short-finned pilot whales. We analyse genetic differentiation between three geographic strata: the MHI, NWHI and pelagic waters surrounding the Hawaiian Islands; we then examine genetic differentiation between observed island communities within the MHI, test for sex-biased dispersal between those communities, and look for evidence that individual island preference is a driver of the amount of time that individuals spend together.

We further hypothesize that relatedness drives social structure and that, in turn, social structure affects genetic divergence among groups, for example by affecting mate selection. If genetic structure affects social structure, insomuch as close relatives form lifelong associations and travel in close-knit groups, we would expect to see higher relatedness within social units than expected at random. Similarly, if social structure affects genetic structure we might expect to see genetic divergence in the allele frequency among clusters. These patterns, along with a statistical relationship between genetic and social structure, could indicate a reciprocal relationship between genetic and social structure in Hawaiian pilot whales.

2 | METHODS

2.1 | Genetic data collection

Skin samples (n = 254) were collected from wild short-finned pilot whales throughout the MHI and NWHI using biopsy darts, in collaboration with Cascadia Research Collective and NOAA's Southwest Fisheries Science Center (SWFSC). Biopsy darts are deployed using a crossbow and collect a tissue sample approximately 8 mm in diameter and up to 20 mm in length, from the area below the dorsal fin. Samples were collected opportunistically, as social groups were encountered in the field, with priority given to sampling as many adults in each social group as possible. Samples were archived in the SWFSC Marine Mammal and Sea Turtle Research Collection, and were either stored at −80°C or preserved in either a salt-saturated 20% DMSO solution or 100% ethanol and stored in a −20°C freezer. In the MHI, known social units were heavily sampled in order to test for relatedness; additional samples were chosen randomly, with consideration given to ensuring that samples represented unrelated individuals from multiple social groups per stratum.

2.2 | Photograph ID/social network data collection

Photographs, used to generate social stratification data as well as pairwise association indices between individuals, were collected according to Mahaffy et al. (2015). Photograph identification data from that publication and from subsequent field observations, between 2003 and 2015 (Baird, Webster, Aschettino, Schorr, & McSweeney, 2013), are included in this study. Association indices were calculated using SOCPROG 2.4, with a sampling period of 1 day and a HWI of association with control for effort (Whitehead, 2008, 2009). We used the photograph identification, association indices and terms (social units, clusters and communities) used by Mahaffy et al. (2015) to characterize the hierarchical nature of short-finned pilot whale social organization in the MHI.

2.3 | Genetic sequencing and assembly

DNA was extracted from skin and muscle samples as previously described (Martien et al., 2014). The hypervariable mtDNA control region was amplified and sequenced in two parts of approximately 420 and 560 bp, with approximately 20 bp of overlap between the two sequences. Primers, PCR and sequencing methods have been previously described by Martien et al. (2014). The resulting combined sequence was 962 bp and was assembled using SEQED, version 1.0.3 (ABI), Sequencher software (versions 4.1 and 4.8; Gene Codes, Ann Arbor, MI, USA) or Geneious (Kearse et al., 2012).

Mitochondrial sequences were aligned using a MAFFT alignment with default parameters (Scoring Matrix: 200PAM/k = 2, Gap open penalty: 1.53, Offset value: 0.123) in the Geneious software package (Katoh & Kuma, 2002). Once the alignment was completed, sequences were re-examined. Any haplotypes represented by only a single sequence or haplotypes with a single base-pair difference from the most similar haplotype were reviewed for accuracy. Unique haplotypes were repeat sequenced to ensure the accuracy of the sequence. Sequences were combined with previously published sequences from Van Cise et al. (2016) to generate the final mtDNA data set.

Sequencing of 78 targeted nuclear loci for single nucleotide polymorphisms (SNPs) analysis was completed using a custom capture enrichment array designed at SWFSC based on common bottlenose dolphin (*Tursiops truncatus*) genome sequences (Supplemental File S1), followed by highly parallel sequencing (Hancock-Hanser et al., 2013; Morin et al., 2015). Four libraries of genomic DNA were prepared using protocols described in Meyer and Kircher (2010) and Hodges et al. (2009), with modifications described in Hancock-Hanser et al. (2013). Up to 400 ng of extracted DNA in 80 μl total volume was sonicated using a Bioruptor UCD-200 (Diagenode). Blunt ends of the DNA were repaired using 20 μl of the sonicated product, adaptors were ligated to the DNA, and indexes were added to each sample library via PCR with indexed primers (Meyer & Kircher, 2010). Once indexed, each sample was quantified using qPCR to estimate the number of nuclear DNA copies in each sample, and approximately 100,000 copies per sample were pooled and hybridized to a capture array. The capture-enriched product was amplified and then sequenced on Illumina HiSeq (1 × 100 bp) or NextSeq (1 × 75 bp) instruments by The DNA Array Core Facility (The Scripps Research Institute, La Jolla, CA).

Nuclear sequences were assembled as in Morin et al. (2015), using common bottlenose dolphin reference sequences (used for capture enrichment) for sequence assembly and SNP genotyping. The cut-off for calling a genotype at any position was set to 10 reads for both homozygous and heterozygous positions, to minimize genotype error (Fountain, Pauli, Reid, Palsbøll, & Peery, 2016). Potential SNPs were identified using scripts developed at SWFSC (Dryad data repository https://doi.org/10.5061/dryad.cv35b) in the R computing environment (R Core Team, 2016). From the pool of sequenced loci, candidate SNPs were selected if at least five individuals were heterozygous at that locus. Those SNPs with coverage at fewer than 55% of samples were removed, and samples with coverage at fewer than 70% of the SNP loci were also removed. Next, sequenced regions with multiple SNP loci were examined for signs of paralogous reads within the assembly (e.g., excess heterozygosity across multiple SNPs in a region, discrete regions of high coverage), and SNPs were removed if assembly of paralogous loci was determined to have occurred. Finally, quality control analyses were performed on this set of SNPs and samples using the strataG package for R (Archer, Adams, & Schneiders, 2016). SNPs were removed if the quality control analysis indicated that the locus was an outlier for homozygosity (>80% homozygous, based on the distribution of homozygous genotypes across all loci), and we additionally tested for outliers from HWE, using a Bonferroni adjustment for multiple tests. Loci that deviated significantly from HWE equilibrium were closely re-examined for evidence of assembly of paralogous loci. Additionally, samples that had highly similar SNP genotypes and could be duplicates were checked against photograph ID records to confirm that they were distinct individuals; if this could not be determined, one from each pair of duplicate samples was removed. Loci with multiple SNPs (see Table S1) were phased based on allele frequencies in the three regional strata, with a phase cut-off probability of 0.5, to generate a single multi-SNP genotype per sample at each locus for analyses of genetic differentiation (Morin et al., 2012). For analysis of relatedness within Hawaiian social units, the highest heterozygosity SNP at each locus (N = 51 after removal of one locus that was invariant in these populations) was chosen for the analysis.

2.4 | Data analysis: Population structure and diversity

We tested for both geographic and socially driven genetic structure using both mitochondrial control regions and nuclear SNPs. Table S2 lists sample stratifications used for data analysis in this study. For mitochondrial DNA analysis, samples were divided into three strata: MHI, NWHI and pelagic samples (Figure 1). Samples were placed in one of these three strata primarily based on their sampling location, with the exception that samples collected near the MHI were placed in the pelagic stratum if photograph ID data verified that the individuals did not associate with MHI communities. MHI mtDNA samples were not further stratified because all samples except one have the same haplotype. We placed samples from the NWHI in a separate stratum because several studies have shown strong differentiation between the MHI and NWHI for other marine mammals (Andrews et al., 2010; Courbis, Baird, Cipriano, & Duffield, 2014; Martien et al., 2014).

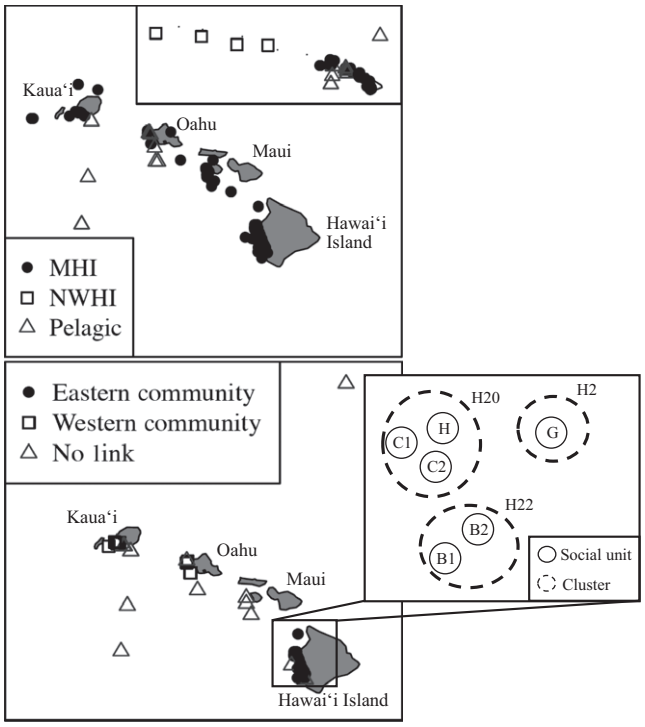

FIGURE 1 Sampling locations for samples used in this study. *Above:* samples used in mtDNA analyses. Symbols represent their stratification for geographic structure analyses. Inset shows additional samples from the NWHI and Pelagic strata. *Below:* samples used in SNP analyses. Symbols represent their stratification for genetic structure analyses. Samples labelled "No Link" are presumed to belong to the pelagic stratum, because they cannot currently be linked to any social stratum within the Main Hawaiian Islands. Inset shows social units and clusters in the eastern community that were used for relatedness analyses

SNP data were only available for the MHI and pelagic strata. Using previous knowledge of the social structure, habitat use and movements (Baird, 2016; Mahaffy et al., 2015), SNP samples were divided into two strata within the MHI (eastern and western MHI communities) based on photograph ID data, visual observations of social units and satellite tag data (Figure 1). Several social units were heavily sampled to test for relatedness within social units. Therefore, in order to remove any potential bias due to sampling regime, we randomly subsampled the data set using a random number generator to include no more than two individuals from each social unit before conducting tests of genetic differentiation among geographic strata.

Molecular diversity indices for all samples and for each region were calculated for both mtDNA (Theta [θ_H], haplotypic diversity [h], and mean nucleotide diversity [π]) and SNP genotypes (average number of alleles per locus, expected and observed heterozygosity [H_e, H_o]). Pairwise genetic differentiation was calculated among geographic strata using F_{ST} and Φ_{ST} for mtDNA. For SNP genotypes, geographic differentiation (F_{ST} only) was calculated only between

island communities within the MHI. All estimates of divergence and genetic diversity were conducted using the strataG package for R except haplotypic diversity, which was calculated in ARLEQUIN (Excoffier & Lischer, 2010).

We tested for sex-biased dispersal among island communities using the Hierfstat package in R (Goudet, 2005), which looks for first-generation immigrants within the sample set. To do this, we tested for differences among males and females in F_{ST}, F_{IS} or the mean or variance of assignment probability (Goudet, Perrin, & Waser, 2002).

2.5 | Data analysis: Genetic structure, social structure and island preference

To test the hypothesis that there are links between genetic structure, social structure and island preference in Hawaiian short-finned pilot whales, we first calculated pairwise genetic relatedness among individuals, as well as pairwise genetic differentiation among clusters, which represent one or more social units.

To calculate genetic relatedness within and among social units in the MHI, samples were stratified according to previously inferred social structure (Mahaffy et al., 2015), and social unit relatedness was calculated if at least five individuals from a social unit had been sampled. Pairwise relatedness was estimated using a dyadic maximum-likelihood estimator (Milligan, 2003) in the R package Related (Pew, Muir, Wang, & Frasier, 2014), which implements the software program COANCESTRY (Wang & Summers, 2010). Within-unit relatedness was compared to the expected relatedness by permuting a random sample 1,000 times and calculating relatedness. From one cluster, we were able to sample two social units, and we used this cluster to test the hypothesis that genetic relatedness is a driver of association among social units by comparing within-cluster relatedness with the distribution of relatedness between 1,000 randomly selected pairs of social units.

Pairwise genetic differentiation (F_{ST}) was estimated among clusters using SNP genotypes only due to the lack of mtDNA haplotypic diversity. Clusters were only included if there were at least five samples collected from that cluster. To characterize the overall degree of differentiation among social clusters, we performed this test using all available samples from clusters. Next, to characterize the extent to which gene differentiation has been affected by social structure, we removed highly related ($r > .6$) samples to reduce bias due to genetic relatedness and recalculated F_{ST} among social clusters, now considering differences in the allele frequency within each cluster.

To determine whether genetically similar social units and clusters were more likely to associate, we compared pairwise cluster genetic differentiation (F_{ST}) with mean pairwise association between clusters, using a fixed effect linear model with cluster ID controlled as a fixed effect. Association between pairs of clusters was calculated by taking the mean of association between individuals in the first cluster and individuals in the second cluster.

We used Mantel tests and linear models to examine the relationship between geographic distance, genetic relatedness and associations between individuals. To do this, we first calculated geographic distance (d) as the straight-line distance between sampling locations for each sample. Three Mantel tests were calculated between all pairs of individuals, comparing genetic distance (defined as 1—genetic relatedness, r), geographic distance (d) and the amount of time a pair spends together (association index, AI).

We compared linear, exponential and logarithmic models to test the importance of geographic distance (d), genetic relatedness (r) and an interaction term ($r \times d$) as potential drivers of association (AI) between individuals, and also between clusters. For these models, we converted geographic distance to a categorical variable with two categories (inter-island, $d < 300$ mi and intra-island, $d > 50$ mi), due to the fact that, within each island community, sampling location is not representative of an individual's habitat use or distance to other individuals in the community. Further, to account for multiple observations of each individual, we included fixed effects for each pairwise individual (I). We iteratively built models by adding one predictor variable with each iteration, for a final model that included all possible predictor terms:

$$E(f[AI_{ij}]) = \alpha + \beta_1 r_{ij} + \beta_2 d_{ij} + \beta_3 r_{ij} d_{ij} + G(I_i) + G(I_j)$$

Significant parameters of the model that minimized Akaike information criterion (AIC) were considered to be potential drivers of association among pairs of individuals.

3 | RESULTS

The mtDNA data set consisted of 242 samples from throughout the Hawaiian Islands (125 previously reported in Van Cise et al., 2016). A total of 163 SNPs at 50 nuclear loci from 112 individuals were successfully genotyped from four capture-enriched library pools. The SNP and mtDNA data sets overlapped by 100 samples. Six samples were determined to be duplicates and removed from the data set, so that the final SNP data set included 106 individuals (Dryad Digital Repository http://dx.doi.org/10.5061/dryad.78521). Forty-four SNPs were removed during the quality analysis phase due to possible assembly of paralogous loci, resulting in 119 SNPs at 49 nuclear loci (Table S1).

Sample stratifications can be found in Figure 1 and Table S2. Only eight samples with SNP data were available from the pelagic stratum, and no samples were successfully genotyped from the NWHI. Cluster assignments were made for 93 of the samples; analyses of differentiation among social clusters were performed using a data set that included related individuals ($n = 93$) and a data set with individuals removed from pairs with relatedness estimates >0.6 ($n = 85$). Finally, pairwise relatedness based on the 51 unlinked SNPs was calculated for the full 106 sample SNP data set, and group relatedness was calculated for three social units, five clusters and two communities.

3.1 | Population structure and diversity

We found very low mtDNA haplotype diversity in the Hawaiian Islands (Table 1). Six haplotypes were identified among the 242

TABLE 1 Molecular diversity indices for single nucleotide polymorphism (SNP) and mtDNA data sets. MHI SNP data were tested using subsampled data sets so that diversity indices within strata were not biased by sampling technique. "All samples" includes all samples included in the study. Nuclear samples were subsampled within the eastern and western communities

	mtDNA *N*	Theta (θ_H)	Haplotype diversity (*h*)	Nucleotide diversity (π)	SNP *N*	Average number of alleles	H_o	H_e
All samples	242	0.06	0.08 ± 0.02	0.004	106	4	0.45	0.45
Regions								
MHI	205	0.007	0.01 ± 0.01	0.004	63	3.9	0.46	0.46
Western MHI community	—	—	—	—	21	3.5	0.49	0.47
Eastern MHI community	—	—	—	—	42	3.7	0.45	0.45
NWHI	17	0.33	0.44 ± 0.1	0.004	—	—	—	—
Pelagic	20	0.27	0.36 ± 0.1	0.004	—	—	—	—

N, sample size, H_o, observed heterozygosity, H_e, expected heterozygosity; MHI, Main Hawaiian Islands; NWHI, Northwestern Hawaiian Islands.

TABLE 2 Mitochondrial haplotype distribution by stratum in the Hawaiian Islands

Stratum	MHI	NWHI	Pelagic
Haplotype			
J	204	12	16
C	1	0	0
K	0	0	2
12	0	5	0
11	0	0	1
2	0	0	1

MHI, Main Hawaiian Islands; NWHI, Northwestern Hawaiian Islands.

samples (Table 2); 232 of the 242 samples had haplotype J. With the exception of one sample collected off Kaua'i, all samples from the MHI stratum had haplotype J. SNP genotypes were subsampled within each island community to control for nonrandom sampling of social groups, so that the data set used for molecular diversity and geographic differentiation included 63 samples from the MHI. Observed heterozygosity and expected heterozygosity for the phased multi-SNP genotypes in the MHI were both 0.46, with slightly higher heterozygosity in the western MHI community than in the eastern MHI community (Table 1).

Mitochondrial differentiation was significant between the MHI (N = 204) and NWHI (N = 17) strata, as well as between the MHI and pelagic (N = 20) strata (F_{ST} and Φ_{ST} p < .001, Table 3). Within the MHI, SNP differentiation was small but significant between the eastern (N = 42) and western (N = 21) MHI communities (F_{ST} p = .009). SNP differentiation was not tested between other strata (pelagic, NWHI) due to low sample size. We did not find any evidence of sex-biased dispersal between communities in the MHI (*p*-values for all indices ranged from .2 to .9).

3.2 | Genetic structure, social structure and island preference

Average pairwise relatedness (*r*) among individuals was 0.11, with a range from 0 to 0.76. Within-unit relatedness estimates for each of three social units with five or more samples were all significantly

TABLE 3 Geographic population differentiation in Hawaiian Island short-finned pilot whales. For single nucleotide polymorphism (SNP) data, only F_{ST} was calculated; for mtDNA data, both F_{ST} and Φ_{ST} were calculated. Sample sizes for each stratum are shown in parentheses. Significant values are shown in bold

Stratum	F_{ST}	F_{ST} *p*-value	Φ_{ST}	Φ_{ST} *p*-value
mtDNA				
MHI (204) vs. NWHI (17)	0.67	**<.001**	0.58	**<.001**
MHI (204) vs. pelagic (20)	0.39	**<.001**	0.30	**<.001**
NWHI (17) vs. pelagic (20)	0.08	.07	0.01	.28
SNP				
Eastern MHI community (42) vs. western MHI community (21)	0.01	**.009**	NA	NA

MHI, Main Hawaiian Islands; NWHI, Northwestern Hawaiian Islands.

higher than expected if groups were randomly organized (Figure 2). Within-cluster relatedness for cluster H20, comprised of three social units, was also significantly higher than relatedness between randomly selected pairs of social units (r = .33, p < .03), as well as being higher than mean relatedness at the community level (r = .11).

When pairs with r > .6 were removed, clusters with more than five individuals sampled were found to be significantly differentiated from each other in eight out of ten pairwise comparisons (Table 4). Global F_{ST} was also significant when tested using all samples with cluster assignments (n = 84, F_{ST} = 0.02, p = .05). When the same analysis is performed using all samples regardless of relatedness, the number of significant pairwise differences between social clusters increases from eight to nine, likely due to an increase in both sample size and relatedness within groups (Table S3).

Pairs of clusters that exhibited higher genetic differentiation associated less often (Figure 3), according to the results of a fixed effect linear regression, which indicated a negative causal relationship between pairwise F_{ST} differentiation and association between clusters (p = .01). In this model, genetic differentiation explained 68% of the variance in association between clusters (R^2 = 0.68).

While there was no correlation between relatedness and geographic distance (Mantel test p = .13), association index was

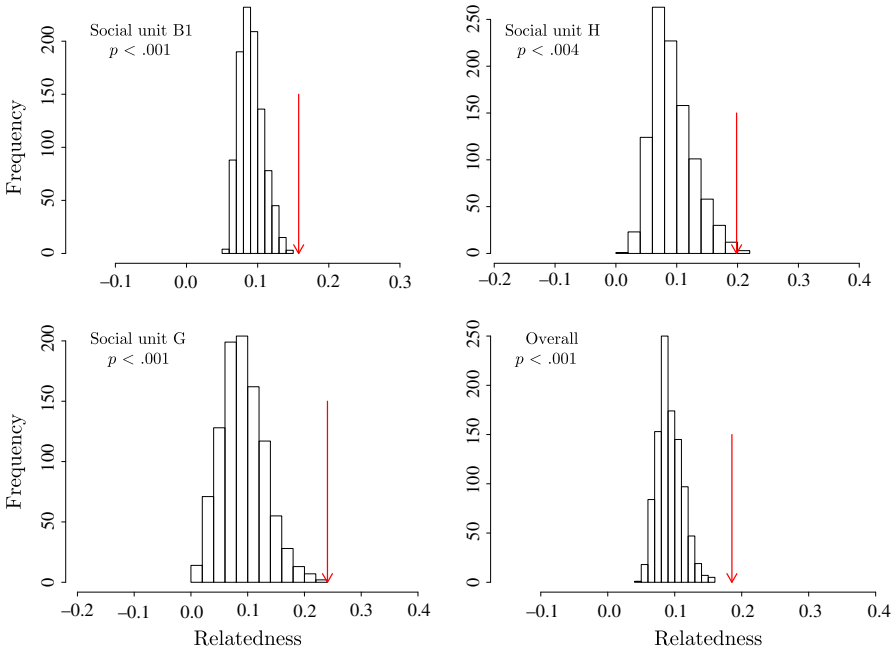

FIGURE 2 Relatedness analysis for three social units with at least five individuals sampled, and overall relatedness within groups (bottom right). Arrows indicate average within-group relatedness; histograms show the expected distribution of within-group relatedness values if groups were randomly organized but retained their original sample size

TABLE 4 Genetic differentiation (F_{ST}) between five clusters with more than five sampled individuals (related individuals not included); sample sizes for each cluster are shown in parentheses. F_{ST} *p*-values (in parentheses) are shown below F_{ST} values; significant differentiation between clusters is shown in bold

	Eastern community cluster 2 (8)	Eastern community cluster 20 (10)	Eastern community cluster 22 (10)	Western community cluster 13 (9)
Eastern community cluster 20 (10)	**0.05 (<.001)**			
Eastern community cluster 22 (10)	**0.06 (<.001)**	**0.04 (.002)**		
Western community cluster 13 (9)	**0.02 (.05)**	**0.02 (.04)**	0.01 (.12)	
Western community cluster 24 (6)	**0.05 (.02)**	**0.03 (.03)**	**0.02 (.04)**	0.002 (.39)

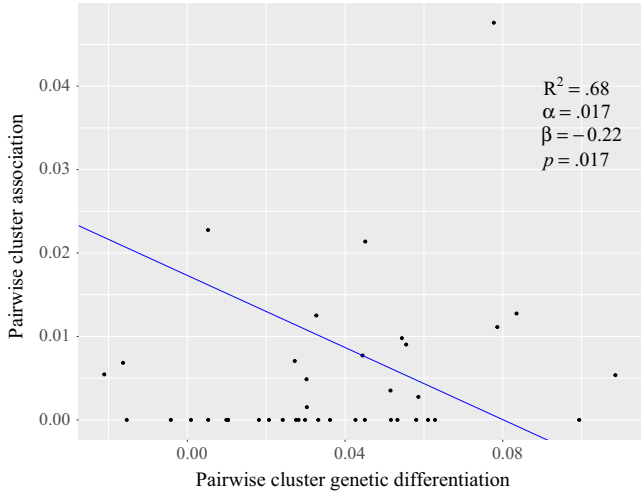

FIGURE 3 Fixed effect linear regression comparing pairwise genetic differentiation (F_{ST}) among clusters with average association index, or rate of association, among clusters. Association index is calculated using a half-weight index and a sampling period of 1 day, to control for effort

significantly correlated with both relatedness and distance (Mantel test $p < .001$ for both tests).

Regression model fits indicated that association between individuals increases with genetic relatedness. Genetic relatedness was found to be a significant driver of association time ($p < .0001$), while distance category (near or far), and the product of genetic relatedness and distance category were not found to be significant ($p = .9$ and .2, respectively). AIC was minimized using a model in which association index increased with an exponential increase in relatedness (AIC = −4,169), but a linear relationship was similar (AIC = −4,164). Relatedness explained 21% of the variance in association time between pairs of individuals ($R^2 = 0.21$).

4 | DISCUSSION

4.1 | Genetics, sociality and island preference

Our results show that short-finned pilot whales in Hawai'i exhibit links between their genetic structure, social structure and island preference, which is likely a socially learned behaviour. Similar links have been shown in other social animals, such as killer whales, sperm whales and elephants (Archie, Moss, & Alberts, 2006; Foote et al.,

2016; Rendell et al., 2012; Wittemyer et al., 2009; Yurk, Barrett-Lennard, Ford, & Matkin, 2002), and may have a stabilizing effect that promotes rapid genetic divergence among groups. In Hawaiian pilot whales, it seems that island preference and social structure influence genetic structure in the absence of any physical barriers to gene flow, based on genetic differentiation of island communities and clusters. Genetic relatedness in turn affects social organization, based on high genetic relatedness within social units and clusters.

The importance of genetic relatedness to social organization is evident when we examine the high level of relatedness within social units as compared to random (Figure 2), a pattern that has been demonstrated in pilot whales from other regions of the world (Alves et al., 2013), and may result from matrilineal fidelity. We additionally found that relatedness was higher within clusters than throughout the Hawaiian population, suggesting that relatedness plays a role in determining how groups are organized at hierarchical levels above the immediate family unit. We saw the same pattern in the regression comparing relatedness with association in pairs of individuals, which showed that animals that were more closely related were also more likely to associate.

If relatedness does not affect social structure at any level higher than that of the social unit, we would expect relatedness at the cluster level to fall to the level of relatedness within the entire population. Our results indicate that relatedness continues to drive social structure and association at higher levels in the hierarchical organization than just the matrilineal social unit. This may indicate that clusters are groups of related social units that underwent fission, similar to elephants (Archie et al., 2006) and killer whales (Williams & Lusseau, 2006). Genetic relatedness between groups can decay quickly in time due to the death of kin and would be consistent with the lower relatedness within clusters than social units that we observed in this study.

In elephants, social units that associate more often were shown to have recently split from each other due to the death of a matriarch (Archie et al., 2006). A larger, more comprehensive sample that includes all or most clusters, and a greater number of SNPs, would increase the resolution of the genetic structure among socially divided units, clusters and communities, and may allow us to determine which clusters are more genetically similar, and whether specific clusters are facilitating gene flow between island communities.

On the other hand, we were able to show significant genetic differentiation among sympatric clusters even when highly related individuals were removed from our analyses, indicating restricted gene flow among sympatric clusters. Clusters that were more genetically differentiated also spent less time together (Figure 3). This would suggest that social structure inhibits gene flow among clusters, which could accelerate genetic divergence among clusters compared to a group of randomly mating individuals. It is important to note, however, that the observed genetic differentiation among clusters may also be caused by low effective population size, sampling stochasticity or a combination of these factors.

This bidirectional influence between social structure and genetic structure creates a positive feedback between the two that may be self-stabilizing, thus encouraging continued genetic and social divergence. Similar patterns have been seen in other social animals; for example, in some bird species, social song learning has been argued to restrain genetic divergence soon after a dispersal event, but promote divergence at later stages in the process (Slabbekoorn & Smith, 2002). In killer whales, social structure and social learning are thought to have promoted rapid subspecies divergence into novel ecological niches (Foote et al., 2016). In a similar way, social structure in pilot whales may promote genetic divergence, and in turn genetic relatedness helps maintain a familial social structure.

Geographic distance is significantly correlated with association between individuals, or social structure, although it was not found to be a significant driver of association between individuals. As geographic distance (d) cannot be interpreted as a continuous variable, due to the geographic overlap of social units within island communities, it instead represents individuals that were encountered in the same island community ($d < 50$ mi) or different island communities ($d > 300$ mi). The correlation between geographic distance and association among individuals likely indicates that individual preference for one island community and association with other individuals are both driven by similar mechanisms.

While the present study did not examine genetic or social structure as drivers of ecological behaviours such as island preference, there is evidence for social and parental (i.e., genetic) learning of ecological and other behaviours in other highly social cetaceans, such as killer whales and sperm whales (Cantor et al., 2015; Foote et al., 2016). Indeed, social learning of ecological behaviours may be important to the long-term resilience of oceanic predators (Whitehead, 2007). Further studies of ecological and social behaviours in pilot whales, such as diet preference, foraging strategies, mating strategies, group movements and vocal repertoire, would help elucidate whether social structure and genetic structure also contribute to the learning and practice of these behaviours.

4.2 | Population structure and diversity

Mitochondrial diversity is very low in Hawaiian short-finned pilot whales: of the six haplotypes reported in this study, haplotype J made up the majority of individuals, and although sampling was increased in the MHI from previous Pacific-wide studies (Van Cise et al., 2016), no new haplotypes were found in this study. The MHI stratum was distinct from the pelagic and NWHI strata, indicating the presence of an insular population around the MHI, as well as a pelagic/NWHI population. Insular or coastal populations have been observed in other odontocetes, such as false killer whales (Martien et al., 2014), bottlenose dolphins (Allen et al., 2016) and spinner dolphins (Andrews et al., 2010). Pilot whales exhibit strong site fidelity (Mahaffy et al., 2015), and it is possible that the MHI population has become adapted to the slope habitat it prefers (Abecassis et al., 2015; Baird, 2016) and may have different dietary preferences from the pelagic population. However, tagging data indicate that pelagic social groups will sometimes travel through the slope region of the MHI (Baird, 2016). The lack of mtDNA gene flow between these

two populations suggests that social structure prevents dispersal of females between these two populations when they come in contact with each other.

Although mtDNA differentiation between the pelagic and NWHI strata was nonsignificant, we expect that a larger sample size will differentiate the two populations. Samples from the pelagic stratum had haplotypes also found in SE Asia, the South Pacific, the Indian Ocean and southern Japan, while NWHI haplotypes were either J (MHI) or an endemic haplotype with 4 bp difference from J, suggesting that the NWHI group may have diverged from the MHI insular population, possibly due to geographic isolation. This is similar to the pattern observed in Hawaiian false killer whales (*Pseudorca crassidens*), where photograph identification, tagging and mtDNA suggest three populations, with shared maternal ancestry between the MHI and NWHI, but nuclear data showing contemporary gene flow are highest between the NWHI and pelagic populations (Martien et al., 2014). However, our nuclear SNP sample size was not large enough to test for geographic differentiation between these strata; therefore, the possibility still remains for male-mediated gene flow between the NWHI and Pelagic strata. A large data set of both mtDNA haplotypes and SNP genotypes from the NWHI and pelagic strata may provide greater insight into the historical and contemporary rates of gene flow among these geographic areas.

Within the insular MHI population, there are at least two genetically distinct island communities, with some continued gene flow between them. This may be driven by cluster philopatry to island communities, with some clusters key to gene flow between communities. Satellite tag data indicate a third possible community, around O'ahu/Lāna'i, known as the central MHI community (Baird, 2016). Additional samples from that community are needed to test whether it is genetically distinct from the eastern and western MHI communities. Individuals rarely leave their island community, instead spending the majority of their time around one island; however, on rare occasions clusters have been observed outside their island community ranges (Baird, 2016), and mating may occur during these rare excursions.

Within small groups, such as social units or clusters, inbreeding depression can be avoided through mechanisms such as sex-biased dispersal (Prout, 1981). We found no detectable difference in genetic diversity indices at the regional, MHI population or community level, indicating a lack of inbreeding, although there was no nuclear evidence for sex-biased dispersal among communities. Sugg, Chesser, Dobson, and Hoogland (1996) use a socially structured population of prairie dogs to show that an increase in COANCESTRY within a breeding group is countered by divergence among groups, which works to maintain genetic diversity at the population level. This can happen through kin recognition and behavioural avoidance of mating within a group, or if one sex remains philopatric to the group while the other sex is more likely to disperse. The advantages of social living, such as cooperative behaviours and increased genetic fitness, are thought to outweigh the costs if inbreeding can be avoided (Sugg et al., 1996). In MHI pilot whales, high levels of COANCESTRY, or relatedness, within social units and clusters may be countered by genetic divergence among these groups, thus maintaining genetic diversity at the community and population level. However, Parreira and Chikhi (2015) found that randomly permuting social unit membership within a population always produces an excess of heterozygotes and concluded that it is not necessary to use inbreeding-avoidance mechanisms to explain outbreeding signatures in small groups, but rather that social structure itself generates outbreeding signatures that can have advantageous fitness traits.

Short-finned pilot whales in Hawaiian waters are subjected to a variety of anthropogenic impacts, including interactions with fisheries, vessel strikes and exposure to high-intensity Navy sonars (Baird, 2016). Social species such as this can be more vulnerable to the removal of a single individual, as it may precipitate the loss of an entire group (Wade, Reeves, & Mesnick, 2012). If some clusters contribute more to gene flow between communities, the loss of those clusters could act to fragment communities within the MHI, which would decrease genetic diversity and increase demographic isolation in each region, thus making those communities more vulnerable to environmental or anthropogenic perturbations.

In order to avoid this vulnerability, conservation management of this species in the Hawaiian Islands could focus on maintaining gene flow between communities within the MHI populations, similar to migration corridors between fragmented terrestrial habitats. This would require the use of photograph identification and satellite tag data to identify individuals or social groups that regularly move among communities, and movement patterns associated with these events. Once these corridors are established, fisheries interactions within them could be monitored to minimize fatal injuries or inhibition of movement.

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DATA AVAILABILITY

We have deposited the sequences used in these analyses in GenBank. Accession numbers for mtDNA haplotypes are as follows:

KM624043, KM624044, KM624054, KM624055, KM624058 and KM624059. Accession numbers for nuclear sequences generated for SNP discovery are MG023261–MG023309. The *Tursiops truncatus* reference sequence and SNP genotype data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.78521.

AUTHOR CONTRIBUTIONS

A.V.C., P.A.M. and K.K.M. conceived the study and analyses. A.V.C. generated genetic data and completed all analyses. S.D.M. completed all photo ID analyses of social structure. R.W.B., P.A.M., K.K.M. and J.H.F. provided valuable input and expert guidance for data analysis. R.W.B., E.M.O. and D.L.W. provided photographs and tissue samples for the analyses.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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