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Identifying social clusters of endangered main Hawaiian Islands false killer whales

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ABSTRACT: The presence of distinct social groups within an animal population can result in heterogeneity in many aspects of its life history and ecology. The ability to accurately assess social group membership increases with the number of times individuals are identified, but obtaining sufficient sightings of rarely encountered species can be difficult. Three social clusters were previously identified for the endangered population of false killer whales *Pseudorca crassidens* around the main Hawaiian Islands, using modularity among associations within a 12 yr photographic dataset with no restrictions on the number of times seen. In this study, we used photo-identification data over a 23 yr period to reassess the number and membership of social clusters, restricted to individuals seen on at least 5 different days. We compared the robustness of clustering assignments from 6 community detection algorithms using modularity and found that the 3 highest-ranking algorithms all identified the same number (4) and membership of social clusters. Spatial use of clusters varied among the islands, with 3 of the 4 clusters encountered regularly only off 1 or 2 of the 3 main island study areas. Comparison of genetic differentiation among social clusters revealed significant differentiation in nuclear DNA. Furthermore, all individuals in 2 of the clusters possess the same mitochondrial DNA haplotype, while in the other 2 clusters, approximately 40% of animals possess a second haplotype. This level of clustering and associated heterogeneity within the population may have implications for mark–recapture abundance estimation, as well as for mitigating exposure to anthropogenic activities, including interactions with fisheries.

HŌʻULUʻULU MANAʻO: Pili nā ʻano like ʻole o ka nohona a me ke kālaikaiaola o nā pūʻuo holoholona i ka loaʻa ʻana o nā pūʻulu kikoʻī. Piʻi aʻe ka hiki ke helu kūponoʻia ka māhuahua ʻana o nā heluna o ia mau pūʻulu i ka helu ʻana i nā wā e ʻike ʻia ai kēlā me kēia holoholona, ʻo ka lawa ʻana naʻe o ka ʻike ʻana i nā lāhulu ʻane halapohe kekahi ālaina. Hōʻia ʻia ʻekolu pūʻulu o ke koholā ʻane halapohe, ʻo ka *Pseudorca crassidens*, a puni nā mokupuni nui ʻewalu o Hawaiʻi, ma ka hoʻowaeʻanona ʻana i ka pilina i loko o kekahi ʻikepili kiʻa he ʻumikūmālua makahiki me ke kāohi ʻole i ka nui o ka ʻike ʻia ʻana. Ma kēia kilo ʻana, ua hoʻohana mākou i ka ʻikepili ma o nā makahiki he iwakāluakūmākolu i mea e hōʻoia hou ai i ka heluna a me nā lālā o nā pūʻulu launa i loko o kekahi pūʻuo holoholona, a pāpā ʻia nā kālailaina i nā mea i ʻike ʻia ma ʻelima mau lā ʻokoʻa ma ka liʻiliʻi loa. Hoʻohālikelike mākou i ke ʻano me ka ikaika o kēia mau pūʻulu launa ma ka hoʻohana ʻana i ka hoʻowaeʻanona ʻana ma ʻeono pūʻulu haʻilula a ʻo ka mea i loaʻa, ʻo ia hoʻi ka ʻike ʻana, ma o nā haʻilula nui ʻekolu, i ka heluna a me ka lālā hoʻokahi o nā pūʻulu launa. Loli ka hoʻohana ʻana i ke koana o nā pūʻulu ma waena o nā mokupuni, ʻike ʻia ʻekolu pūʻulu ma hoʻokahi a ʻelua paha mokupuni mai loko mai o nā mokupuni nui ʻekolu e kālailai ʻia ana. Ma ka hoʻohālikelike ʻana aku i nā hiʻohiʻona ōewe ʻokoʻa o nā pūʻulu launa, ʻike ʻia ka ʻokoʻa ʻano nui ma ka piko ōewe o nā pūʻulu. A no laila, loaʻa i nā mea a pau o ia mau pūʻulu ʻelua ke ōewe hoʻoilina hoʻokahi, a ma nā pūʻulu ʻē aʻe ʻelua, loaʻa he hiʻohiʻona ōewe ʻelua i nā holoholona he 40 pākēneka. Hiki nō paha i kēia ʻano hoʻopūʻulu ʻana me kēia ʻano waeʻanona ōewe hoʻopili ma kekahi pūʻuo ke pili i ke kuhi ʻana i ka nui ma ka hopu kaha ʻana, a i ke kāohi a hoʻēmi ʻana mai i nā hopena o nā hana kanaka, e laʻa hoʻi me ka hana ma ke kai lawaiʻa.

KEY WORDS: *Pseudorca crassidens* · False killer whale · Social organization · Social network · Modularity · Associations · Hawaiʻi

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1. INTRODUCTION

Social networks represent patterns of associations among individuals. Preferential long-term associations among individuals within a population can lead to the presence of discrete clusters within social networks, referred to as 'communities' in network analyses. A well-studied example of social organization comes from killer whales *Orcinus orca*, long-lived social odontocetes in which clusters are typically referred to as 'pods'. These pods are semi-permanent groupings of related individuals (Baird & Whitehead 2000, Beck et al. 2012, Esteban et al. 2016) that may exhibit group-specific variability in demography (e.g. Brault & Caswell 1993), spatial use (e.g. Olsen et al. 2018), foraging strategies (e.g. Baird & Dill 1995), and interactions with fisheries (e.g. Tixier et al. 2017), among other traits.

False killer whales *Pseudorca crassidens* are also long-lived social odontocetes (with a life span of up to 63 yr, based on tooth sectioning; Ferreira et al. 2014) known to have enduring bonds among individuals (Baird et al. 2008, Baird 2016). Individuals are slow to reproduce and slow to mature; life history data collected from drive fisheries in Japan indicate that females reach sexual maturity between 8 and 10.5 yr of age, males mature roughly between the ages of 10.5 and 18.5 yr, and individuals of both sexes continue growing until 25–30 yr of age (Ferreira et al. 2014). Females have relatively low pregnancy rates when compared to 8 other species of delphinids (though comparable to a population of killer whales) and are one of a few mammalian species thought to undergo a lengthy post-reproductive period (Ferreira et al. 2014, Photopoulou et al. 2017). Social network analyses of the main Hawaiian Islands insular population of false killer whales have previously been used to identify 'social clusters' that are largely analogous to killer whale 'pods' (Baird et al. 2012, Martien et al. 2019). Based on long-term photo-identification, genetic analyses, and movement data from satellite tags, this population is known to reside around the main Hawaiian Islands and is demographically isolated from 2 other populations of false killer whales with partially overlapping ranges (Baird et al. 2008, 2012, 2013, Martien et al. 2014). The main Hawaiian Islands insular population was listed as federally endangered in 2012 (National Oceanic and Atmospheric Administration 2012), due to a combination of population decline and a number of anthropogenic threats (Baird & Gorgone 2005, Reeves et al. 2009, Ylitalo et al. 2009, Oleson et al. 2010). The abundance of this population was estimated using photo-identification and open mark–recapture methods at 167 individuals (SE = 23) in 2015 (Bradford et al. 2018).

Previous analyses of association patterns for this population used an eigenvector-based modularity method (Newman 2004, 2006) to identify social clusters (hereafter referred to as clusters). As with many studies of social organization, association rates among individuals were estimated using an association index, effectively, the proportion of time pairs of individuals spend associated in the same social group (Cairns & Schwager 1987). Patterns of repeated associations over time are typically used to describe the social structure of a population (Hinde 1976), and one commonly accepted method to detect socially meaningful clusters within a population or social network is through modularity optimization (Girvan & Newman 2002, Newman & Girvan 2004). This approach groups individuals within a network in such a way as to maximize the within-cluster rates of association and minimize those between clusters (Newman 2004, 2006, Shizuka & Farine 2016). The maximum modularity value is the proportion of connections between individuals (referred to as edges in social network analyses) within a cluster relative to the expected proportion of within-cluster connections if associations were random.

The earlier study analyzed 1174 identifications from 50 945 photos from this population taken between 2000 and 2011 and found 7 clusters within the main Hawaiian Islands insular false killer whale population, with 3 main clusters (termed Clusters 1, 2, and 3) and 4 peripheral clusters (Baird et al. 2012). The peripheral clusters were believed to be primarily composed of individuals that had been born or died partway through the study and thus had limited encounter rates, although these clusters could also have reflected social groups seen so infrequently that there was insufficient power to accurately assess association patterns (Baird et al. 2012). Importantly, this analysis was restricted to distinctive and very distinctive individuals but was not restricted to individuals seen on multiple occasions, potentially influencing the interpretation of association patterns. Restricting the number of days an individual has been seen is important when determining the number and membership of social clusters, as including individuals sampled infrequently will introduce uncertainty that can obscure or bias underlying patterns (Whitehead 2008a).

Genetic comparisons of the 3 main clusters identified by Baird et al. (2012) suggested that cluster membership is stable over time, with limited dispersal of individuals between clusters. Martien et al. (2014, 2019) found significant genetic differentiation in mitochondrial DNA between Cluster 3, in which all individuals possess the same haplotype (termed haplotype 1), and Clusters 1 and 2, in which approximately 40% of individuals possess a second haplotype (termed haplotype 2). Nuclear DNA showed weak, but statistically significant, differentiation among all 3 clusters (Martien et al. 2014), suggesting limited dispersal of individuals between clusters. Similarly, Martien et al. (2019) used these 3 clusters when examining genetic relatedness and found that individuals within clusters were closely related, with mating occurring both within and between clusters, but found evidence of strong fidelity to the natal cluster in both males and females.

Subsequent analyses all have shown that aspects of this population's biology vary by cluster. For example, using sighting histories for individuals available from 1986 to 2010 and satellite tag data from 2007 to 2010, Baird et al. (2012) reported differences in spatial use among individuals from 2 of the clusters. Whales from Cluster 1 preferentially used areas off northwest Molokaʻi, southwest Lānaʻi, and north of Hawaiʻi Island, while whales from Cluster 3 primarily used areas north of Maui and Molokaʻi (Baird et al. 2012). Baird et al. (2012) did not have sufficient data to characterize habitat use of whales from Cluster 2, although a later analysis did reveal differences from Clusters 1 and 3 (Baird et al. 2019). For the purposes of mark–recapture abundance estimation, Bradford et al. (2018) used cluster as a covariate, with individuals in the peripheral clusters assigned to 1 of the 3 main clusters based on their highest level of association. Bradford et al. (2018) found that capture probability varied by cluster, with particularly low estimates for Clusters 2 and 3, consistent with their low sighting rates (Baird et al. 2021). Overall, previous studies indicate the importance of these strong associations between individuals in interpreting other aspects of the biology of this endangered population, emphasizing the need for an updated assessment of association patterns.

Since the analyses by Baird et al. (2012), directed research effort and community scientist contributions for this population have increased, allowing for further examination of social structure. Baird et al. (2019) undertook an analysis using 2484 identifications from 162 651 photos available from February 2000 through April 2019, and identified 9 clusters in this population using the same methods as the earlier study. When restricted to individuals seen on 3 or more occasions with dyadic half-weight association indices of 0.3 or greater, 5 clusters were apparent (Baird et al. 2019), with 2 of the 5 comprising primarily individuals that had been in 2 of the peripheral clusters first identified by Baird et al. (2012). This suggests that the frequency of encounters of some social groups in the analyses by Baird et al. (2012) was insufficient to tease apart the existence of these clusters. A better understanding of spatial use from satellite tag deployments has also allowed for more targeted field efforts to focus on poorly sampled social groups. Using satellite tag data from 2009 to 2018, Baird et al. (2019) reported that whales from Cluster 2 preferentially used areas off southeast Maui and west and north of Hawaiʻi Island and whales from Cluster 4 primarily used areas off northwest Molokaʻi, south and west Lānaʻi, and southeast Oʻahu.

Here, we use an expanded and updated photo-identification dataset that includes sightings of main Hawaiian Islands insular false killer whales from 1999 through 2021 to assess the number and membership of social clusters within this population. Importantly, this larger dataset increases the number of sightings available for each individual, and thus the number of individuals that meet a threshold for inclusion in the study. Previous analyses of false killer whale social clustering only used a single method, eigenvector-based modularity (Newman 2004, 2006), to determine the number and membership of social clusters (Baird et al. 2012, 2019). Here, we compared metrics from 6 community detection algorithms, combined with a method to assess the robustness of the clustering assignments (Shizuka & Farine 2016), to determine the best approach for assessing the number and membership of social clusters in this population. These analyses will help inform ongoing efforts to estimate abundance and examine trends of this endangered population, as well as allow for more robust analyses of cluster-specific spatial use, trophic ecology, fisheries interactions, and age structure.

2. METHODS

2.1. Data sources and defining groups

Data used in the current study were taken from a long-term photo-identification study of main Hawaiian Islands insular false killer whales led by Cascadia Research Collective (CRC) and updated here to include directed research from the Pacific Whale Foundation (PWF), the National Marine Fisheries Service's (NMFS) Pacific Islands Fisheries Science Center

(PIFSC), and opportunistic sightings from a variety of sources. We restricted analyses to begin in 1999 (although the first photos from this population were available in 1986; Baird et al. 2008), which excludes an early period with a number of year-long or multi-year gaps in encounters and with very strong spatial biases in effort, with almost all photos only from Hawai'i Island. Photographs were primarily obtained from small-vessel surveys undertaken throughout the main Hawaiian Islands, with most effort in leeward (west and southwest) waters (Fig. 1). Directed surveys by CRC were typically undertaken each year off 2 or 3 of the 4 different main island areas (i.e. Kaua'i and Ni'ihau, O'ahu, Maui and Lāna'i, and Hawai'i Island) (e.g. Baird et al. 2008, 2012), while surveys by PWF were typically undertaken periodically throughout the year off Maui Nui (a region consisting of the islands of Maui, Lāna'i, Moloka'i, and Kaho'olawe) (e.g. Stack et al. 2019). PIFSC undertook directed research off O'ahu between 2009 and 2021 and also worked with this population during large-scale surveys throughout the main Hawaiian Islands (e.g. Bradford et al. 2020). While these surveys involved working with a number of different species, false killer whales were always a high priority species, and attempts were made to remain with a group of false killer whales as long as possible and obtain photos of all individuals present. During CRC and PIFSC surveys, efforts were made in some cases to deploy satellite tags, obtain drone footage, and/or collect skin/blubber biopsies using a remote-biopsy system (pole spear or crossbow). Photographs obtained from opportunistic sightings throughout the islands were provided by researchers working on other species or by community scientists, primarily individuals working with ocean tour operations.

False killer whales were often observed in large aggregations composed of smaller sub-groups spread over up to 20 km and generally moving in the same direction at a similar rate of speed (Baird et al. 2008, Bradford et al. 2014). Baird et al. (2008) reported a significant positive relationship between encounter duration and group size; encounters lasting less than 2 h had a median of 7 individuals (range: 3–15) while encounters lasting more than 2 h had a median of 25 individuals (range: 12–41). Therefore, groups were defined as all individuals encountered or sighted in a particular day off one side (e.g. leeward side) of an

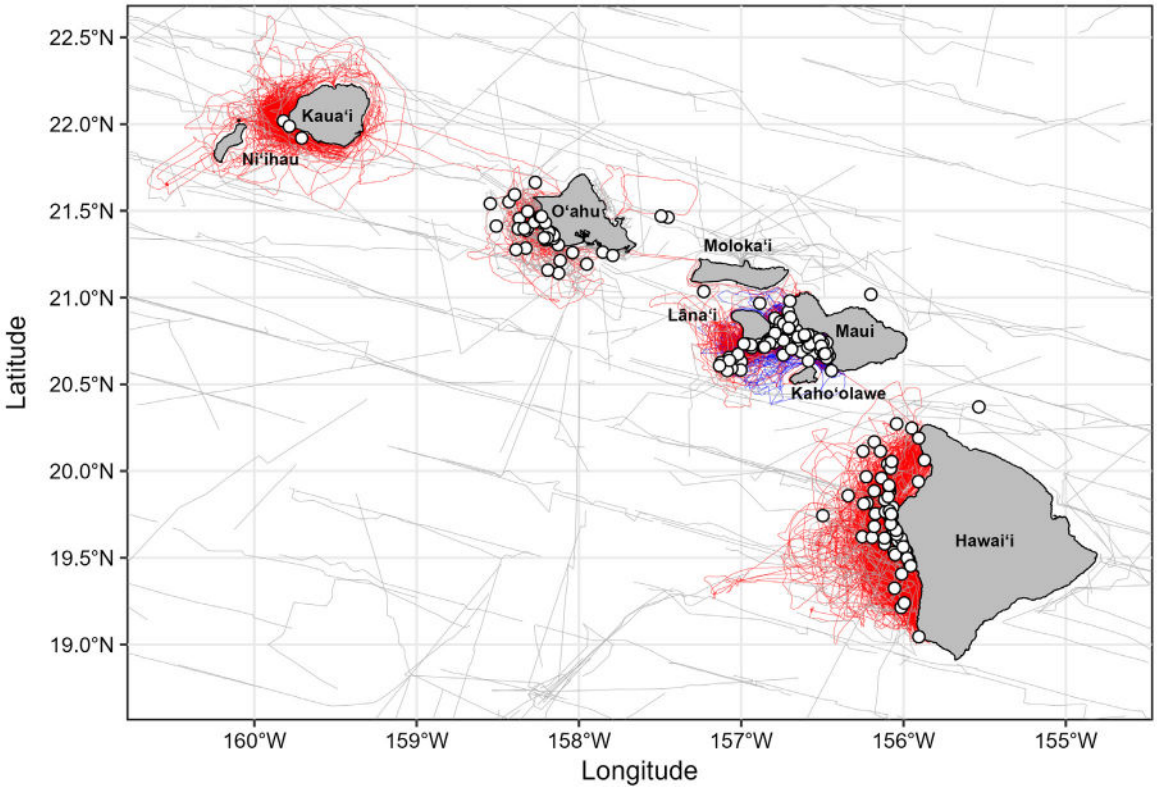

Fig. 1. Main Hawaiian Islands, showing all quantifiable effort tracklines from 1999 to 2021; data from Cascadia Research Collective (red), Pacific Whale Foundation (blue), and Pacific Islands Fisheries Science Center (gray). Sighting locations (when available) are shown as points

island area. There were no cases where groups of false killer whales were seen on both the windward and leeward side of a particular island on the same day. While our definition of a group is more expansive than what has been used in studies of other cetacean species, it follows the description by Whitehead (2008a, p. 297) of ‘sets of animals that actively achieve or maintain spatiotemporal proximity over any time scale and within which most interactions occur’. It is also similar to a definition used by Parsons et al. (2009) and Foster et al. (2012) for killer whales, where individuals photographed in the same channel of water and within 10 km of each other were assumed to be within range for acoustic communication and thus associated. During line-transect surveys conducted by NMFS for the purpose of abundance estimation, Bradford et al. (2014) reported group encounters of false killer whales from the pelagic and Northwestern Hawaiian Islands insular populations that spanned up to 35 km and were composed of up to 18 subgroups.

2.2. Photo-identification

Photos taken during group encounters were manually sorted by individual, matched, and added to the photo-identification catalog using the methodology described by Baird et al. (2008, 2012). Individuals within each group encounter were rated on a scale of 1 to 4 for increasing levels of photo quality (1 = poor, 2 = fair, 3 = good, 4 = excellent) and dorsal fin distinctiveness (1= not distinctive, 2 = slightly distinctive, 3 = distinctive, 4 = very distinctive) following Baird et al. (2008). Because distinctiveness generally increases over time as an individual acquires changes to the fin, individuals were assigned their highest distinctiveness rating for use in the analysis. While not appropriate for analyses that rely on specific assumptions about capture probability (e.g. mark–recapture abundance estimation), using the highest distinctiveness rating increases the number of encounters for some individuals and thus duration of individual sighting histories, providing a more representative pattern of associations and increasing the number of individuals included in the study.

As well as including sightings after the 2012 study, additional photos taken during 1999–2011 contributed by other research groups and community scientists that had not been previously available were added to the catalog. Given the potential for new photographs to reveal missed matches, previously obscured due to limitations in photo quality, lack of sightings, or changes to the fin, all individuals were carefully compared against the entire catalog to look for any internal matches (i.e. the same individual assigned 2 or more IDs in the catalog). Any potential internal matches were reviewed and confirmed by a second experienced matcher. Additionally, older records of non-distinctive and slightly distinctive individuals were re-examined to determine whether new information on scarring obtained from recent sightings and historical contributions could be used to identify internal matches. Non-distinctive individuals (based on a lack of nicks and notches on the dorsal fin) were matched and added to the catalog whenever possible using continuity of secondary or superficial scarring on the dorsal fin and body. Non-distinctive individuals were almost always smaller than associated adult-sized individuals and were considered to be dependent calves if seen in repeated association with a known or likely (based on morphology and sighting history) adult female. While Baird et al. (2008) noted that matching non-distinctive individuals within an encounter required excellent quality photos and was not possible between encounters, subsequent advances in digital camera technology have made this feasible in some cases (e.g. Elliser et al. 2022). Given the small size of the population, emphasis was placed on matching every individual photographed, including calves and juveniles, in order to inform current and future studies of social and population structure.

2.3. Associations and defining social clusters

In order to determine how individuals in the population associate, we used the association strength (a measure of co-occurrence termed an association index) among pairs of individuals to see whether individuals in the population preferentially associate to form clusters or communities. We used a correlation coefficient to assess how well association indices reflect true associations and measured the social complexity or social differentiation of the population (i.e. how much variation exists in the proportion of time pairs of individuals spend associated) to estimate how likely individuals in the population were to form clusters. We then constructed social clusters using 6 competing algorithms (Table 1) and compared them using measures of robustness and modularity to determine how well the clusters from the top-ranking algorithms reflected true association patterns. Finally, we used a Mantel test to compare relative association strength within and between clusters

Table 1. Description of 6 community detection algorithms tested to assess social structure in main Hawaiian Islands false killer whales. Algorithms were tested in R using the 'assignment' function in the 'igraph' package

Community detection algorithm 'Assignment' function in 'igraph'	Approach	Optimization method	Description/references
Leading Eigenvector 'leading.eigenvector.community'	Divisive	Modularity	A spectral partitioning method that divides the network into communities based on the eigenvectors of the largest positive eigenvalues within a modularity matrix, which is defined as the adjacency matrix of the network minus the probability of edges being present between each dyad in a random network where the degree of each node matches the actual network (Newman 2006)
Edge Betweenness 'Edge.betweenness.community'	Divisive	Modularity	Divides the network into communities by calculating edge betweenness then iteratively removing edges with the highest edge betweenness score and recalculating modularity after each removal (Newman & Girvan 2004)
Label Propagation 'Label.propagation.community'	Label propagation	Network structure	Algorithm based on label propagation, where each node is assigned a unique label, then repeatedly updated with those used by most of the node's neighbors to identify communities. Does not use an optimization measure; instead, nodes with the same labels are considered part of the same community (Raghavan et al. 2007)
Fastgreedy 'Fastgreedy.community'	Agglomerative	Modularity	Greedy optimization algorithm that uses an adjacency matrix to repeatedly merge individuals into communities where each vertex is a community of one and each is repeatedly joined until a single community exists (Clauset et al. 2004)
Walktrap 'Walktrap.community'	Agglomerative	Modularity	Grouping nodes into communities based on the distance between nodes using random walks, and merging communities using Ward's method (Pons & Latapy 2005)
Louvain 'Cluster_louvain'	Agglomerative	Modularity	Heuristic hierarchical algorithm divided into 2 phases that each optimize modularity: (1) treats individuals as nodes and assigns them to communities and (2) treats resulting communities as nodes and aggregates them to build a new network (Blondel et al. 2008)

and examined the demographics and haplotypes for each cluster.

Association analyses were undertaken both in SOCPROG 2.9 (Whitehead 2009) using MATLAB (MATLAB 2016) and in R v. 4.2.1 (R Core Team 2022). In both, dyadic (pair-wise) associations were measured on a scale of 0–1.0 (ranging from individuals never seen in association to individuals always associated) with a half-weight index (HWI) to account for situations where not all individuals were photographed and identified (Cairns & Schwager 1987, Whitehead 2008a, Farine 2013). Individuals were considered associated if they were in the same group (see above). Data used to analyze associations and determine the most appropriate clustering algorithm (see below) were restricted to individuals seen on 5 or more days and considered at least slightly distinctive (highest distinctiveness ≥2) with fair or better quality photos (photo quality ≥2) (hereafter referred to as the restricted dataset) to minimize errors associated with lower quality data (Whitehead 2008a). The decision to include slightly distinctive individuals and fair photo qualities was based in part on the characteristics of the study population (i.e. a small resident population with limited range composed of well-known individuals), all of which increase capture probability (Urian et al. 2015). As mentioned, uncertainty associated with less well-known individuals was reduced by restricting analyses to individuals seen on at least 5 days.

Three additional types of analyses were undertaken in SOCPROG on the restricted dataset. First, the level of social differentiation (S) of a population (i.e. the coefficient of variation of the true association indices) measures how widely association indices vary within the study population. Measures of S of <0.3, >0.5 to <2.0, and >2.0 indicate homogeneous, well differentiated, and extremely well differentiated societies, respectively (Whitehead 2008a,b). Social differentiation was estimated using maximum likelihood within SOCPROG (Whitehead 2008a,b). Although not biased by sampling regime, social differentiation is a measure applied to the entire study population, and can be artificially inflated by the presence of distinct communities (i.e. clusters) that may themselves lack differentiation (Whitehead 2008a,b). To determine whether the level of *S* is affected by clusters, social differentiation was estimated for each cluster after determining the best clustering algorithm (see below), then averaged and compared to the population-wide estimate. Second, the ability of *S* to detect variation in the social system (i.e. how association rates vary among dyads) was estimated using a correlation coefficient scaled from 0.0 (not helpful) to 1.0 (extremely helpful) between the true association indices and those generated using the HWI. Precision was assessed using standard errors (SEs) from 100 bootstrap replications. Third, once the most appropriate community (i.e. cluster) detection algorithm was determined, clusters generated were assessed to determine whether association rates significantly differed within and between clusters (i.e. whether within-cluster associations were strong compared to those between clusters) using a Mantel test with 1000 permutations and expressed as a *t*-value, p-value, and matrix correlation coefficient.

Subsequent analyses were all undertaken in R on the restricted dataset. To determine the number and membership of clusters in the population, we tested 6 different community detection algorithms (Table 1) using community assignment functions within the 'igraph' package in R (v.1.3.4) (Csardi & Nepusz 2006), and then used an approach outlined by Shizuka & Farine (2016) to determine which algorithm best represents actual social groups (i.e. clusters) within the restricted dataset. Five of the 6 community assignment functions tested were designed to optimize modularity using a divisive (2 functions) or agglomerative (3 functions) approach, and 1 function (based on label propagation) used network structure rather than modularity optimization to detect communities. The algorithms we selected are among the most widely used and are considered 'state-of-the-art' for community detection (Yang et al. 2016).

For each algorithm, the modularity of the particular cluster assignment was calculated using the modularity (Q) function in the 'igraph' package, with values greater than 0.3 indicating that clusters are useful in describing how individuals in the population associate (Newman 2004, Csardi & Nepusz 2006). The robustness of community assignments was measured through community assortativity (r_{com}) and calculated in R using the 'igraph', 'assortnet' (v. 0.12), and 'asnipe' (v. 1.1.16) packages for each cluster assignment method with 1000 bootstrap replications (Csardi & Nepusz 2006, Farine 2014, 2016, Shizuka & Farine 2016). This method resamples observations of groups with replacement and generates new community assignments. As noted by Shizuka & Farine (2016), the value of r_{com} is 1 when all bootstrap replicates provide the same community assignments and approaches 0 when community assignments in the replicates are random compared to the original network. We used a combination of modularity and community assortativity values to choose the most appropriate (best) algorithm for determining the number of clusters and cluster membership. A weighted social network diagram was used to visualize associations within the study population for the algorithm with the highest modularity and r_{com} values. In each diagram, individuals are represented by nodes, with cluster membership indicated by node color and shape, and the thickness of the line or edge between nodes indicating association strength. Probability plots for the top 3 algorithms were generated in 'igraph' and represent how often individuals were assigned to different clusters in bootstrap replicate networks, where the length of the line connecting nodes represents the probability that nodes shared a community assignment in bootstrap replicates, with closer nodes more likely to share community assignments across replicates. Histograms were also constructed to evaluate variation in the number of communities generated in bootstrap replicates for each community assignment algorithm.

Once the best clustering algorithm was chosen and clusters were defined, we removed the restriction on the number of days seen (hereafter referred to as the relaxed dataset). The relaxed dataset was used to examine within-cluster demographics and distribution of mitochondrial haplotypes, and to compare cluster assignments among datasets with different sets of restrictions (included in Table A1 in the Appendix). We also analyzed the complete or unrestricted dataset (i.e. with no restrictions on number of days seen, fin distinctiveness, or photo quality) in order to assign all individuals to clusters to compare genetic differentiation among clusters. In these latter cases, individuals grouped in clusters using the restricted dataset were retained in those clusters even if the analyses using the relaxed and complete datasets resulted in some individuals switching cluster membership, as the clusters constructed from the restricted dataset were considered more robust.

However, a review of cluster assignments among all 3 datasets found that only a single individual in the relaxed and unrestricted datasets changed cluster (Table A1). Cluster membership identified in the current study was compared to the 3 main and 4 peripheral clusters identified by Baird et al. (2012), as well as to 5 clusters identified by Baird et al. (2019) using photos available at the time from 2000 through April 2019 but with more relaxed restrictions.

To determine whether individuals demonstrated long-term fidelity to their cluster, we binned the data into 2 roughly equal time periods (1999–2010 and 2011–2021) and used the best clustering algorithm (see above) to generate clusters for a modified version of the restricted dataset (restricted to slightly distinctive with fair or better photo quality but requiring individuals to be seen on 3 or more days instead of 5, given smaller number of encounters in each of the 2 time periods). Comparison of cluster membership to assess long-term fidelity was restricted to the cluster with the largest number of encounters over the period 1999–2021, as cluster assignment accuracy should increase with the number of times individuals are seen.

2.4. Demographic and genetic assessment by social cluster

We examined demographics (age class, sex) by cluster for both the restricted and relaxed datasets (1999–2021) using cluster membership determined by the best clustering method. This analysis was not to provide a demographic breakdown by cluster, but rather to assess whether clusters were of mixed age and sex, instead of being composed of only a single sex or limited age class (e.g. all adult males, or all females and calves). Given the duration of the study, for each cluster we used age class at the most recent sighting of each individual in order to include as many individuals as possible. Thus, it should be noted that we do not describe the age structure of each cluster at a particular point in time, since some individuals were born or died part way through the study, or were otherwise not seen in recent years. Four age classes were assigned following the methodology of Kratofil et al. (2022), which used the entire sighting history of the animal and considered several factors: (1) the amount of scarring on the dorsal fin or body (assuming scars accumulate with age, heavily marked animals are more likely to be older), (2) size relative to known adults when photographed in the same photo, and (3) repeated association with an adult presumed or known (from parentage, see Martien et al. 2019) to be the mother. Individuals were considered calves if they were seen in close, consistent association with the presumed mother and were estimated to be less than half her total length. Calves were assumed to be less than 3 yr of age. Juveniles were seen in association with the presumed mother but were at least half of her length. Juveniles were estimated to be 3–6 yr old for females and 3–9 yr for males. Subadults were often but not always seen traveling in loose association with the presumed mother and were slightly smaller in length. Subadults were estimated to be 6–9 yr for females and 9–14 yr for males. All other individuals were assumed to be adults. For comparisons, we pooled subadults, juveniles, and calves due to uncertainty in age class estimates associated with some younger individuals. Sex was determined genetically (see Martien et al. 2014) for 141 individuals. For 27 adults for which genetic sex was not available, sex was determined through a combination of life history information (such as calf presence for adult females) and morphology (such as head shape and presence of a leading-edge hump on the dorsal fin in adult males) visible in photos (see Kratofil et al. 2022).

We also reassessed the genetic differentiation between clusters reported by Martien et al. (2014, 2019) to determine whether the patterns of differentiation they observed were robust to the updated social cluster assignments. We re-stratified the mitochondrial haplotype and nuclear microsatellite data presented by Martien et al. (2014) based on the results of the best clustering method on the restricted dataset. As in the study by Martien et al. (2014), biopsied individuals were incorporated in this assessment regardless of the number of times seen or whether they were distinctive. In addition, we included haplotype data for 55 individuals that were sequenced subsequent to the study by Martien et al. (2014). Biopsied individuals that were not included in the restricted dataset were assigned to clusters based on analysis of the complete dataset. Sequencing methods were identical to those used by Martien et al. (2014). We used the 'strataG' package (Archer et al. 2017) in R v. 4.2.0 (R Core Team 2022) to calculate Φ_{ST} for the mitochondrial data and both F_{ST} and F'_{ST} for the nuclear data, and assessed statistical significance in both datasets using a χ^2 permutation test with 1000 permutations.

R code used in association and community assortativity analyses and figure generation is included in the Supplement at www.int-res.com/articles/suppl/n051p249_supp.pdf and is available on the CRC Git-

Hub page (https://github.com/cascadiaresearch/FKW-Social-Clusters-2023/).

3. RESULTS

Between 1999 and 2021, false killer whales from the main Hawaiian Islands insular population were photographed on 416 days, resulting in 3429 identifications of 349 individuals from 230 933 photos. When restricted to group encounters with at least 1 individual meeting our minimum photo quality and distinctiveness criteria (i.e. the relaxed dataset), there were group encounters on 382 days, with 2915 identifications of 292 individuals. Of these, identifications were obtained predominantly by CRC (1196), Wild Side Specialty Tours (366), PWF (286), Wild Whale Research Foundation (213), Hawai'i Whale Research Foundation (152), and NMFS (141), with the remaining 561 identifications contributed by 66 different organizations and individuals. Encounters took place throughout the islands, but over 99 % of sightings and photographic identifications were obtained from O'ahu, Maui Nui, and Hawai'i Island (Fig. 2A). The number of identifications available varied considerably by year (Fig. 2B). The median number of individuals identified per group was 5 (range: 1–47). Individual sighting histories varied dramatically; the number of days individuals were observed ranged from 1 to 62 (mean = 9.7, SD = 10.6), and individuals were seen over periods ranging from less than a year to the entire study period (23 yr). Restricting analyses to individuals seen on 5 or more days (i.e. the restricted dataset) resulted in 2639 identifications of 174 individuals from 376 group encounters.

3.1. Community (cluster) assignments

Maximum likelihood methods applied to the restricted dataset indicated a well-differentiated society (*S* = 1.149, SE = 0.023), and results from the correlation coefficient indicated that the data were moderately representative of true associations (r = 0.569, SE = 0.024). The 6 community assignment functions generated 4 to 6 (mode = 4) clusters, with modularity ranging from 0.578 to 0.605, and r_{com} (community assortativity) ranging from 0.913 to 0.968 (Table 2). The 3 community assignment algorithms that had the highest modularity and r_{com} values (Louvain, Fast-greedy, and Walktrap in decreasing order) produced identical results in terms of number (4) and composition of clusters: 62 individuals in Cluster 1, 15 individuals in Cluster 2, 60 individuals in Cluster 3 (which included the individuals from Cluster 5 identified by Baird et al. 2019), and 37 individuals in Cluster 4 (Table 2, Fig. 3A). Cluster membership between the current study and the clusters identified by Baird et al. (2012) showed little change from Clusters 1, 2, and 3. Of the 4 peripheral clusters identified by Baird et al. (2012), 2 were absorbed into Cluster 3, and 2 were combined to form Cluster 4 in the current study.

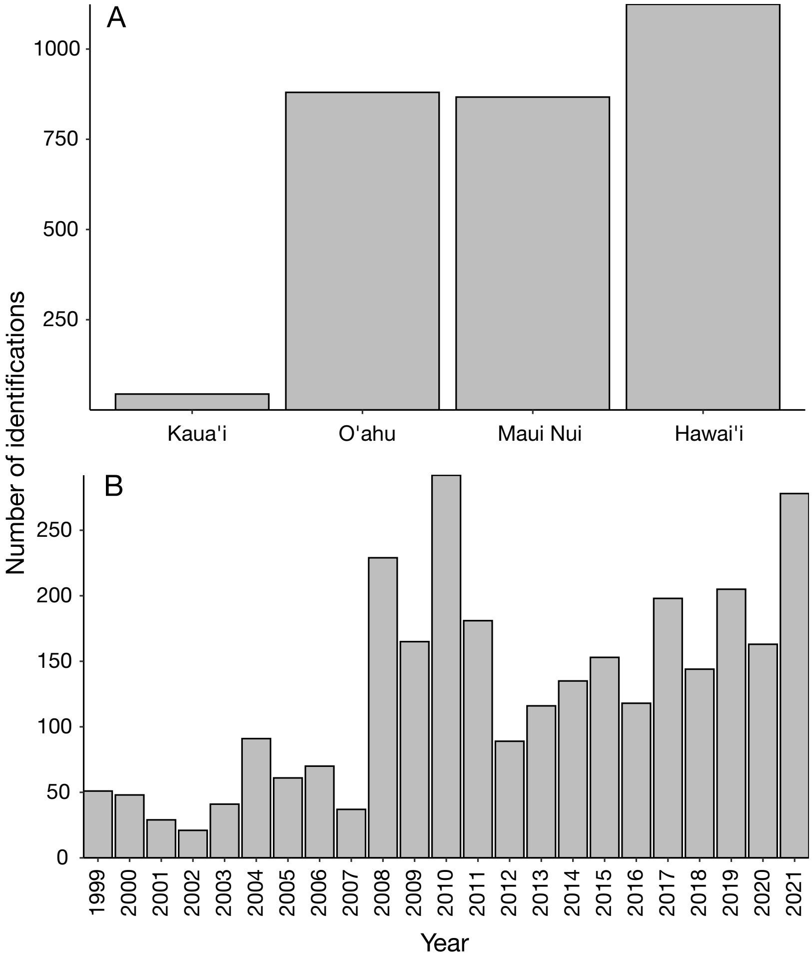

Fig. 2. Breakdown of photographic identifications (including within-year re-sightings) (A) by island area and (B) by year, restricted to individuals that were considered at least slightly distinctive with fair or better photo quality (i.e. the relaxed dataset)

Table 2. Comparison of community assignment algorithms for the study population of false killer whales, restricted to individuals seen on at least 5 days between 1999 and 2021 and that are at least slightly distinctive with fair or better quality photographs (n = 174). Community assortativity (r_{com}) was calculated with 1000 bootstraps. Cluster names shown with number of individuals per cluster represent names previously applied to this population (see Baird et al. 2019)

Algorithm	Clusters	Modularity (Q)	r_{com}	Individuals per cluster			
				Cluster 1	Cluster 2	Cluster 3/5	Cluster 4
Cluster_louvain()	4	0.605	0.968	62	15	60	37
Fastgreedy.community()	4	0.605	0.961	62	15	60	37
Walktrap.community()	4	0.605	0.944	62	15	60	37
Label.propagation.community()	4	0.600	0.949	64	14	59	37
Leading.eigenvector.community()	5	0.578	0.925	66	7, 6[a]	58	37
Edge.betweenness.community()	6	0.581	0.913	62	11, 1[a]	61, 1[a]	38

[a] Indicates a situation where the algorithm identified 2 clusters, both of which correspond to the same historical cluster

Although there was minor variation in cluster assignments for the other 3 clustering methods, all indicated the presence of 3 social clusters which are consistent with previously identified Clusters 1, 3 (combined with the previously identified Cluster 5), and 4 (Table 2). Additionally, all but one community assignment algorithm identified the previously identified Cluster 2, with the remaining algorithm (Leading Eigenvector, which had the lowest modularity value) splitting Cluster 2 into 2 separate clusters (Table 2). A comparison of cluster number and membership between the restricted, relaxed, and complete datasets indicated that clusters were robust to change. Only one individual, a male, switched cluster (from Cluster 3 to Cluster 1) when restrictions were relaxed and/or removed, and one new cluster of 5 individuals (all of which were seen once in 2002 and were associated with individuals from Cluster 2) was identified in the complete dataset (Table A1). Three of the 5 individuals from this new cluster were younger animals (calves and juveniles) that were either not distinctive or slightly distinctive and had poor or fair quality photos; the 2 remaining individuals were considered very distinctive adults with fair or good quality photos. Cluster 2 had the lowest number of sightings and identifications of any cluster (Table 3), increasing the length of time between sightings and, consequently, the likelihood of missing a match due to mark change, particularly in younger individuals. The uncertainty around this new cluster (rarely seen individuals and poor-quality data) is a good example of why the restricted dataset was used in most analyses.

The distribution of clusters in bootstrap replicates for the 3 top-ranking algorithms was similar, with the vast majority of bootstraps indicating 4 clusters (Fig. 4). A Mantel test indicated that within-cluster

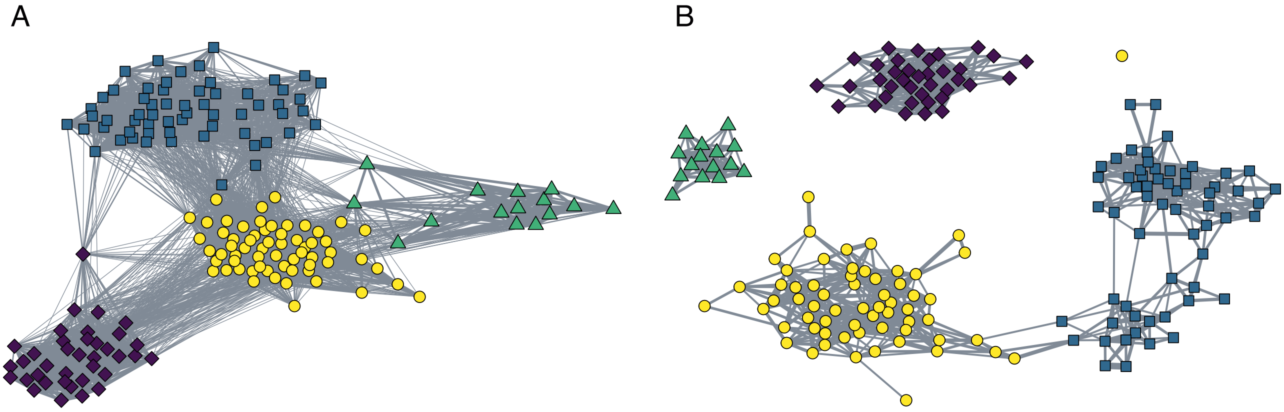

Fig. 3. Weighted social network diagrams generated using the Louvain algorithm with node color and shape indicating social clusters: Cluster 1 = yellow circles, Cluster 2 = green triangles, Cluster 3 (including individuals previously considered part of Cluster 5) = blue squares, Cluster 4 = purple diamonds. Note that Fastgreedy and Walktrap algorithms produced identical cluster assignments. (A) All individuals (1999–2021) considered slightly distinctive or above with fair or better photo quality sampled on 5 or more days for all associations (i.e. the restricted dataset). (B) Associations with a half-weight index ≥0.3

Table 3. Association values, measured as a half-weight index (HWI), for false killer whale clusters generated with the Louvain, Fastgreedy, and Walktrap algorithms. Data restricted to individuals seen on at least 5 days between 1999 and 2021 and that are at least slightly distinctive with fair or better photo quality (i.e. the restricted dataset, n = 174). Historical cluster refers to cluster assignments published in Baird et al. (2019)

Cluster	Historical cluster(s)	Individuals	Mean HWI (SD)	Sum of assoc. (SD)	Maximum HWI (SD)	Sampling days	Identifications	Proportion of individuals identified per group
Overall	1, 2, 3, 4, 5	174	0.06 (0.02)	11.43 (3.68)	0.6 (0.13)	376	2639	0.039
C1	1	62	0.19 (0.06)	12.88 (3.74)	0.59 (0.12)	221	1528	0.108
C2	2	15	0.36 (0.06)	5.99 (0.9)	0.64 (0.13)	32	95	0.199
C3	3, 5	60	0.15 (0.05)	10.08 (2.85)	0.6 (0.15)	108	651	0.099
C4	4	37	0.26 (0.07)	10.27 (2.41)	0.58 (0.11)	77	365	0.126
Within			0.21 (0.08)	10.77 (3.58)	0.59 (0.13)			
Between			0.01 (0.01)	1.17 (1.33)	0.15 (0.11)			

associations were significantly greater than those between clusters (*t* = 76.081, r = 0.698, p < 0.001). Within-cluster associations ranged widely among all clusters, with average dyadic association indices ranging from 0.15 to 0.36 (mean = 0.21, SD = 0.08), and maximum association indices ranging from 0.58 to 0.64 (mean = 0.59, SD = 0.13). Within-cluster association metrics were generally higher for Cluster 2 (Table 3). Probability plots for the 3 top-ranking algorithms (which had identical cluster assignments) indicated that individuals in Cluster 2 were most likely to be assigned to alternative clusters (primarily Cluster 1 and 3) in bootstrap replicates (Fig. 5). This likely reflects that the number of sampling days and number of identifications were lowest for Cluster 2 (32 sampling days and 95 identifications, Table 3). Encounters and identifications available for each social cluster varied among the islands (Fig. 6). While Cluster 1 was seen off all islands, Cluster 2 was seen primarily off Hawai‘i Island, Cluster 3 was seen primarily off O‘ahu and Hawai‘i Island, and Cluster 4 was seen primarily off Maui Nui.

Within-cluster heterogeneity of associations was assessed by estimating social differentiation and mod-

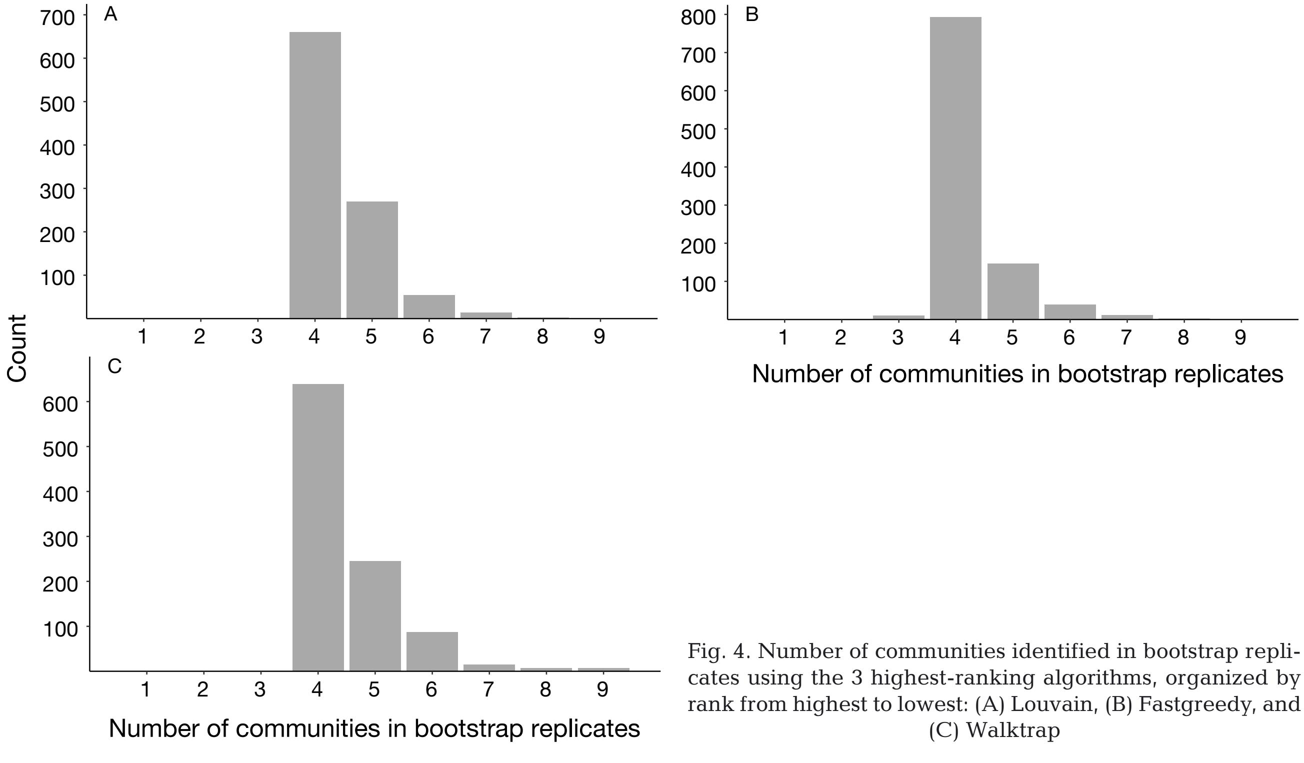

Fig. 4. Number of communities identified in bootstrap replicates using the 3 highest-ranking algorithms, organized by rank from highest to lowest: (A) Louvain, (B) Fastgreedy, and (C) Walktrap

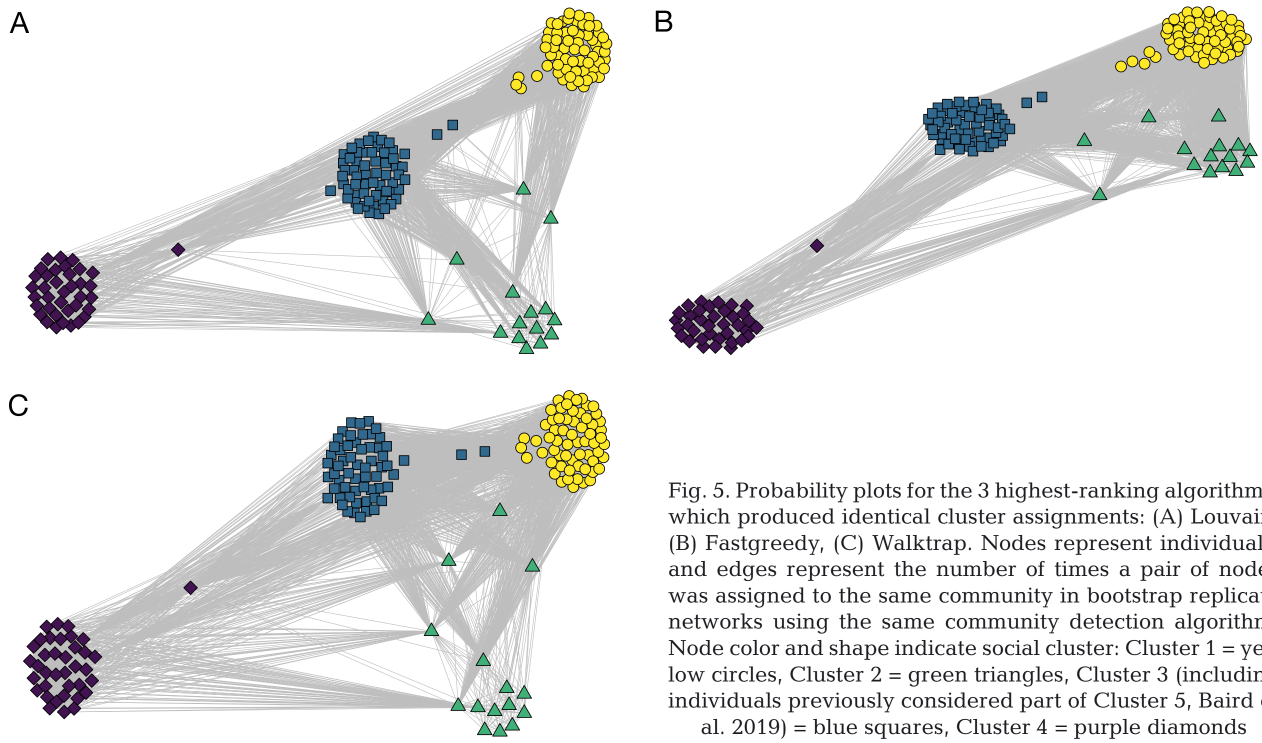

Fig. 5. Probability plots for the 3 highest-ranking algorithms, which produced identical cluster assignments: (A) Louvain, (B) Fastgreedy, (C) Walktrap. Nodes represent individuals, and edges represent the number of times a pair of nodes was assigned to the same community in bootstrap replicate networks using the same community detection algorithm. Node color and shape indicate social cluster: Cluster 1 = yellow circles, Cluster 2 = green triangles, Cluster 3 (including individuals previously considered part of Cluster 5, Baird et al. 2019) = blue squares, Cluster 4 = purple diamonds

ularity within each cluster. Modularity values did not support sub-clustering for any cluster (Table 4), suggesting further division was not warranted, although Cluster 3 ($Q = 0.262$) approached the threshold for community division. Associations were considered homogeneous ($S < 0.3$) for the 2 smaller clusters (Clusters 2 and 4), and the larger 2 (Clusters 1 and 3) showed moderate to high levels of social differentiation that were strongly correlated with true associations (Table 4). The high level of social differentiation estimated for the entire study population compared with the average ($S = 0.351$) of all within-cluster estimates indicates that much of the population-level heterogeneity in associations may be due to the presence of discrete clusters which vary in degree of heterogeneity (Table 4).

Between-cluster associations among the 4 clusters identified were not uniform (Fig. 3A). Filtering out weak associations within the network by restricting associations to those with HWI ≥0.3 removed 74.3% of all links among individuals and all associations between Clusters 2 and 4 from the main network (Fig. 3B). After filtering, associations within Cluster 3 showed 2 smaller groups of individuals: one corresponding to Cluster 5 from Baird et al. (2019) and linking Cluster 1 to the rest of the Cluster 3, the other corresponding to historical Cluster 3 (Fig. 3). The visible partitioning of Cluster 3 supports within-cluster association heterogeneity (see above).

A comparison of membership of Cluster 1 using the restricted dataset from 2 time periods (1999–2010 versus 2011–2021) showed that 91% of Cluster 1 individuals (40 of 44 individuals) from the first time period that were also in the restricted dataset for the second time period were in Cluster 1 in both periods. Three individuals that were assigned to Cluster 1 in the first time period were assigned to Cluster 3 in the second, and 1 individual that was assigned to Cluster 2 in the first time period was assigned to Cluster 1 in the second.

3.2. Demographic and mitochondrial haplotype assessment by social cluster

Demographic assessment of clusters in the 1999–2021 restricted dataset revealed that all of the identified clusters contained similar mixes of known males and known females, and 3 of the 4 included all 4 age classes (Table 5). Cluster 2, the smallest of the clusters, contained only adults. This is likely due to our method of using the most recent age of individuals, combined with the small number of encounters available for Cluster 2, and thus a higher proportion of individuals not meeting the cutoff of 5 sighting days. When restrictions by the number of days seen were removed, the demographics of Cluster 2 were similar to the other 3 clusters (Table 6).

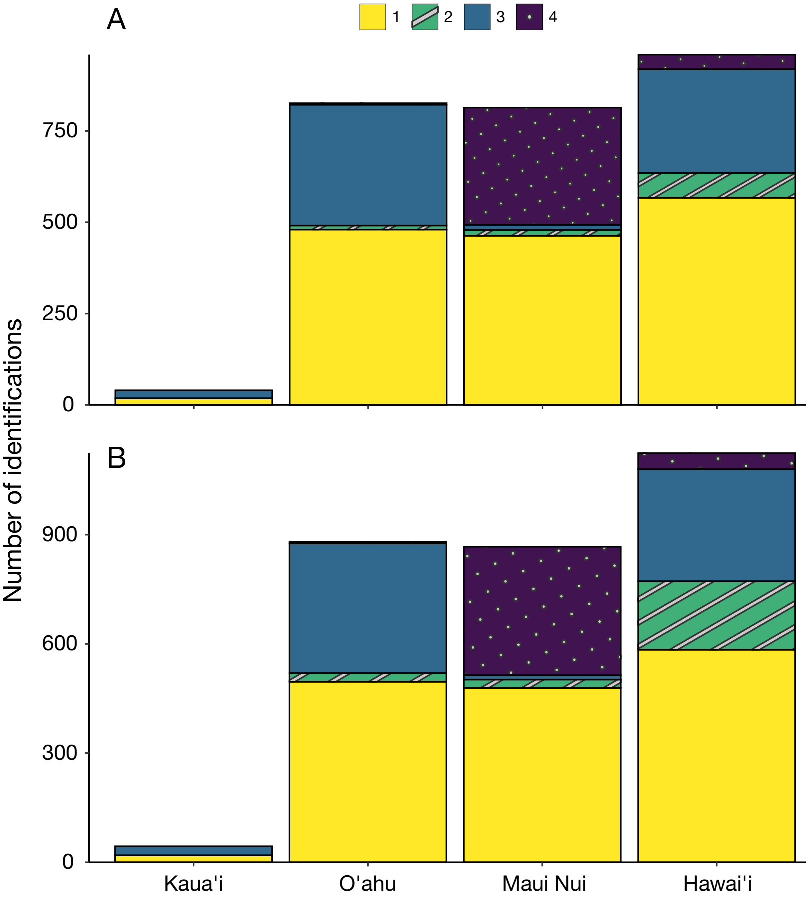

Fig. 6. Breakdown of identifications of each social cluster by island for clusters identified with the Louvain algorithm. (Fastgreedy and Walktrap algorithms produced identical cluster assignments.) Identifications only include individuals seen between 1999 and 2021 from (A) the restricted dataset and (B) the relaxed dataset; the latter is included to better reflect the spatial distribution of Cluster 2, given the relatively small number of individuals from that cluster seen on 5 or more days

The breakdown of mitochondrial haplotypes by cluster indicated that both haplotypes 1 and 2 (see Martien et al. 2014) were found both in Cluster 1 and Cluster 2, while only haplotype 1 was found in Cluster 3 and Cluster 4. No additional individuals with haplotype 5 (found in 1 individual from Cluster 2 by Martien et al. 2014) were found. This pattern persisted regardless of whether using the restricted dataset (i.e. only individuals seen on 5 or more days, Table 5) or the relaxed dataset (i.e. including all individuals with minimum photo quality and distinctiveness ratings regardless of the number of times seen, Table 6). The patterns of differentiation (Table 7) were comparable to that reported by Martien et al. (2019), with all pairs of clusters exhibiting low but significant differentiation in the nuclear dataset, and the clusters that include individuals with haplotype 2 (Clusters 1 and 2) exhibiting significant mitochondrial differentiation from those that do not (Clusters 3 and 4).

4. DISCUSSION

Analyses of associations over a 23 yr period indicate that false killer whales around the main Hawaiian Islands live in a strongly modular (Q = 0.605) and highly differentiated society ($S = 1.149$, SE = 0.023) composed of 4 distinct social clusters, with the majority of associations occurring within rather than between clusters. Of the 6 community detection algorithms used, 3 (Louvain, Fastgreedy, and Walktrap) all had the same highest modularity value and highest r_{com} values, and produced the same number and membership of clusters. Clusters were of mixed age and sex (Table 5), and our analysis of the 2 time periods for Cluster 1 demonstrated that individuals show long-term fidelity to their cluster. Our genetic analyses corroborate previous studies indicating limited dispersal of individuals between social clusters. Specifically, we found weak but statistically significant differentiation between all social clusters, as was the case in the analysis of Martien et al. (2019), suggesting limited dispersal between social clusters. We also found that haplotype 2

Table 4. Social differentiation (S) estimates and corresponding correlation coefficients (r) for false killer whales from the 1999–2021 restricted dataset (i.e. individuals seen on 5 or more days between 1999 and 2021 and considered slightly distinctive or above with fair or better photo quality, n = 174) and within social clusters constructed using the Louvain, Fastgreedy, and Walktrap algorithms. Within-cluster modularity (Q) was not significant for any cluster

Cluster or population	S	SE	r	SE	Q
Entire population	1.149	0.023	0.569	0.024	0.605
Cluster 1	0.559	0.054	0.772	0.031	0.134
Cluster 2	0.000	0.309	0.000	0.424	0.123
Cluster 3	0.729	0.052	0.693	0.044	0.262
Cluster 4	0.117	0.1454	0.206	0.133	0.098
Cluster Mean	0.351				

Table 5. Demographic information by social cluster of false killer whales from the 1999–2021 restricted dataset (i.e. those considered slightly distinctive or above with fair or better photo quality that have been seen on 5 or more days, n = 174) identified using the Louvain, Fastgreedy, and Walktrap algorithms. Sex (M = male, F = female) was determined genetically, using morphology (for adult males), or by calf presence (for adult females). See Section 2.4 for additional details on sex and age determination. Non-adults (subadults, juveniles, calves) are combined here, as not all younger individuals could be unambiguously assigned to an age class. Mitochondrial haplotypes include 38 individuals sequenced subsequent to Martien et al. (2014)

Cluster	Males	Females	Unknown sex	Adults	Subadults, juveniles and calves	Haplotype 1 by sex	Haplotype 2 by sex
Cluster 1	19	28	15	47	15	11M, 9F	5M, 10F
Cluster 2	5	7	3	15	0	3M, 6F	2M
Cluster 3	18	26	16	45	15	15M, 23F	-
Cluster 4	11	15	11	27	10	9M, 14F	-
Total	53	75	46	134	40	38M, 52F	7M, 10F

Table 6. Demographic information by social cluster from the 1999–2021 relaxed dataset (i.e. those considered slightly distinctive or above with fair or better photo quality; n = 292). See Table 5 caption for details on sex and age determinations. Adults noted in parentheses are considered to be 'likely' adults. Mitochondrial haplotypes include 49 individuals sequenced subsequent to Martien et al. (2014)

Cluster	Males	Females	Unknown sex	Adults	Subadults, juveniles and calves	Haplotype 1 by sex	Haplotype 2 by sex
Cluster 1	19	28	26	48(4)	21	11M, 9F	5M, 10F
Cluster 2	13	27	35	47(3)	25	9M, 15F	4M, 7F
Cluster 3	25	30	34	55(4)	30	22M, 26F	–
Cluster 4	12	15	28	33(6)	16	10M, 14F	–
Total	69	99	124	183(17)	92	52M, 64F	9M, 17F

Table 7. Genetic differentiation between social clusters of false killer whales. For the mitochondrial analysis, 55 samples sequenced subsequent to the study by Martien et al. (2014) are included. n values represent sample sizes for the first (1) and second (2) cluster in each comparison. Clusters 3 and 4 were not compared in the mitochondrial analysis because they are both fixed for haplotype 1

Clusters	Mitochondrial DNA				Nuclear DNA				
compared	n1	n2	Φ_{ST}	χ^2 p-value	n1	n2	F_{ST}	F'_{ST}	χ^2 p-value
1 v. 2	35	36	−0.002	0.332	33	24	0.005	0.009	0.003
1 v. 3	35	43	0.441	<0.001	33	27	0.006	0.012	<0.001
1 v. 4	35	24	0.365	<0.001	33	8	0.008	0.016	0.01
2 v. 3	36	43	0.250	<0.001	24	27	0.006	0.013	0.002
2 v. 4	36	24	0.191	0.006	24	8	0.013	0.026	0.002
3 v. 4	43	24	–	–	27	8	0.012	0.024	0.046

is restricted to only 2 of the 4 clusters, indicating strong fidelity to natal social cluster (Martien et al. 2019). Strong social differentiation, high modularity, and/or long-term fidelity to groups has been reported in several other species of long-lived social odontocetes, including short-finned pilot whales *Globicephala macrorhynchus* (e.g. Mahaffy 2012, 2015, Alves et al. 2013), long-finned pilot whales *G. melas* (e.g. Wierucka et al. 2014, Augusto et al. 2017), pygmy killer whales *Feresa attenuata* (e.g. McSweeney et al. 2009), Risso's dolphins *Grampus griseus* (e.g. Hartman et al. 2008), and killer whales (e.g. Esteban et al. 2016, Ellis et al. 2017, Tavares et al. 2017). Although differences in methodology (e.g. how groups were defined) limit comparisons among studies, our results indicate that false killer whales around the main Hawaiian Islands live in longitudinally stable groups characteristic of these other long-lived social odontocetes.

Extensive data collected since the early 1970s from an endangered population of fish-eating killer whales in the eastern north Pacific (colloquially known as 'southern resident' killer whales) show that individuals live in a hierarchical matrilineal society where matrilines (one or more generations of females and their offspring) preferentially associate to form pods. These pods were defined by Bigg et al. (1990) as groups of individuals that spend more than half of their time traveling together. While the current study was not able to examine fine-scale associations due to the nature of the data (e.g. widely-distributed groups, incomplete sampling from opportunistic data), the clusters we have identified have a similar size, though with a lower mean association strength as the southern resident killer whale pods studied by Parsons et al. (2009), who used a definition of group similar to the one used in this study. Given that genetic data show that false killer whales in Hawai‘i exhibit natal group philopatry (Martien et al. 2019; our Table 5), a type of social structure shared by killer whales where neither male nor female offspring disperse from the natal group, and given the size of the clusters, it is likely that false killer whales also live in a hierarchically structured society. Additional research focused at the sub-group level (e.g. individuals with strong association values and/or traveling in close proximity) would demonstrate whether the clusters detected in our study correspond to related extended matrilines, as is seen in southern resident killer whales.

The median number of southern resident killer whale clusters (determined using a Bayesian mixture model) varied annually from 2 to 6, but when averaged across years was 4.03 ± 1.02, which is similar to the number of currently recognized pods (Parsons et al. 2009). Although the level of data for false killer whales around the main Hawaiian Islands is considered sparse for examining annual variations in cluster number or membership (Whitehead 2009), detailed studies of southern resident killer whale associations show that persistent social groups can also be dynamic over time (Parsons et al. 2009, Foster et al. 2012, Ellis et al. 2017). A comparison of the current false killer whale social clusters with historical clusters from Baird et al. (2012) revealed that individuals were consistently assigned to the same 3 main clusters (Table 3). This is not unexpected given the temporal overlap in the datasets, although the number of years included in the current study is twice as many as used by Baird et al. (2012). The fact that the membership of Cluster 1 was largely stable when our study was broken down into 2 time periods further supports the existence of stable associations and provides evidence of long-term fidelity to clusters. Three of the 44 individuals (1 male and 2 females) in Cluster 1 in the first time period were assigned to a different cluster in the second time period, and there are a number of possible reasons for this different assignment. For example, these individuals may have dispersed to a different cluster due to their particular social circumstances (e.g. if they had no surviving close relatives, similar to a case documented for southern resident killer whales) (Weiss et al. 2020). The difference in the number of social clusters reported in the current study compared to the earlier analysis is most likely due to our larger sample size and denser dataset (i.e. more identifications per year in recent years, see Fig. 2). Geographical variation in sampling effort (Fig. 1) and cluster-specific spatial use (Fig. 6) may also play a role in our refinement of social cluster numbers and membership. For example, Cluster 4 was first described by Baird et al. (2012) as a peripheral cluster considered to be part of Cluster 1 and was only formally recognized as a separate cluster by Baird et al. (2019), after sufficient survey effort had been undertaken off Lāna‘i, now considered a high-use area based on available satellite tag data (Baird et al. 2019). Although a relatively newly-described cluster, Cluster 4 was robust to clustering method, had the second-highest mean association of any cluster, and was only weakly associated with individuals outside the cluster (Table 3, Fig. 3).

Given that clusters have different high-use areas (Baird et al. 2012), the probability of sighting an individual a sufficient number of times to be included in our analyses may depend in part on its cluster membership. The relationship between cluster membership and capture probability is evident when comparing how the number of encounters and identifications differs among clusters (Table 3). Relatively fewer sightings of Cluster 2 and 4 suggest that there is less overlap between the area(s) where individuals in these clusters spend time and the areas surveyed. Such heterogeneity in capture probability introduces the possibility that additional individuals or even clusters exist in the population outside of areas commonly surveyed. While new individuals in the population are regularly documented, almost all are poorly marked young individuals (CRC unpubl. data). Given the extensive effort throughout the entire span of the main Hawaiian Islands (albeit with a leeward bias, Fig. 1), it is unlikely that entire clusters have been missed. Movement data from satellite-tagged individuals from all 4 clusters (Baird et al. 2019, CRC unpubl. data) show that individuals from all clusters move regularly among islands and often move back and forth from the leeward and windward sides of the islands (Baird 2016). This dynamic use of the waters surrounding the main Hawaiian Islands suggests that any false killer whales that are part of the resident population would periodically move through highly surveyed areas, regardless of preferred habitat. For example, despite extensive survey effort off the islands of Kauaʻi and Niʻihau, there have been relatively few sightings of individuals from this population (Figs. 1 & 6), suggesting that although that area is not particularly favored, it is used at least occasionally (Baird et al. 2012).

Overall, the social clusters produced using the 6 clustering algorithms were in strong agreement both with each other and with historical Clusters 1, 2, and 4 described by Baird et al. (2019), indicating that cluster assignments are persistent over time and robust to different clustering methodologies (Table 2). However, Clusters 3 and 5 from Baird et al. (2019) were combined into Cluster 3 using community assignment algorithms in this assessment (Table 3). In addition to increasing cluster membership, combining historical clusters into Cluster 3 resulted in the lowest mean association strength of any cluster, including Cluster 1, which had slightly more members (Table 3). In addition, Cluster 3 demonstrated the highest level of social differentiation of any cluster ($S = 0.729$, $r = 0.693$, Table 4), suggesting a high degree of heterogeneity among dyadic associations that may be indicative of within-cluster social partitioning. When removing weak ($HWI < 0.3$) associations from the population, Cluster 3 appeared largely to separate into 2 smaller groups that correspond to historical Cluster 3 and 5 (Fig. 3B). It is therefore possible that this group of individuals is either undergoing a fission event, as has been observed in killer whales (Parsons et al. 2009, Esteban et al. 2016), or that there are simply insufficient data to resolve the association patterns observed. Given its observed spatial use (Fig. 6), additional sampling of Cluster 3 off of Oʻahu or Hawaiʻi Island is warranted. Cluster 3 is 1 of 3 primary clusters first described by Baird et al. (2012) and has shown a preference for offshore waters off eastern Oʻahu and northwest Molokaʻi (Baird et al. 2019). While the preferred habitat for historical Cluster 3 partially overlaps with that of historical Cluster 5 (i.e. the waters of Oʻahu and NW Molokaʻi), an additional high-use area for Cluster 5 was also identified offshore of northeast Molokaʻi, indicating potential within-cluster variation in habitat preferences (Baird et al. 2019). Thus, while historical Clusters 3 and 5 have been combined into Cluster 3 in this study, within-cluster associations combined with heterogeneous movements of individuals within Cluster 3 observed from satellite tag data suggest that associations in this cluster may be more dynamic than in the other clusters and that cluster membership should be reviewed as more data are collected.

The length of the study (23 yr) combined with data collected from several disparate sources that varied by island area and year presented a unique set of challenges. Given the long timespan, the catalog likely includes many individuals that were born or that died part way through the study and thus were only sampled a few times. We considered dividing the data into smaller time periods for a more detailed analysis, which has been done for killer whales (e.g. Parsons et al. 2009, Ellis et al. 2017). However, unlike the studies by Parsons et al. (2009) and Ellis et al. (2017), the size of the study area in Hawaiʻi combined with a low sighting rate (Baird et al. 2013) resulted in a small number of identifications that varied substantially by year (Fig. 2). To minimize the influence of rarely seen individuals (such as those that were born or died during the study), we restricted the dataset to individuals seen on 5 or more days, and further restricted it to remove weak associations (Fig. 3B). We also set restrictions on photo quality and distinctiveness. Our comparison of the number of clusters and cluster membership generated from the complete, relaxed, and restricted datasets showed strong agreement across datasets (Table A1), suggesting that the results are robust to some forms of bias in the data (e.g. reduced photo quality, lower distinctiveness, and fewer encounters).

False killer whales in Hawaiʻi are upper trophic-level predators that consume a variety of large game fish such as yellowfin tuna *Thunnus albacares* and mahimahi *Coryphaena hippurus* (Baird 2016). Previous research on stable isotope and contaminant levels in the main Hawaiian Islands insular population found that both $\delta^{13}C$ levels and persistent organic pollutant (POP) concentrations varied according to social cluster (Kratofil et al. 2020), supporting previous findings from Baird et al. (2012, 2019) that spatial use varies by cluster and suggesting that diet composition may also differ by social cluster. While Kratofil et al. (2020) used 5 different clusters in their analyses, for both POP and $\delta^{13}C$ analyses, the sample breakdown by cluster was not influenced by our current results (i.e. Kratofil et al. 2020 did not compare results from Cluster 3 and the formerly recognized Cluster 5 for either analysis). Research on the impact of prey abundance on the stability and cohesiveness of killer whale social groups found that increased salmon abundance was positively correlated with association strength and with group size (Foster et al. 2012). The study found that while periods of low prey availability did not impact the stability of social groups, it increased the time animals spent foraging, limiting the amount of time that could be spent socializing. False killer whales in Hawai‘i hunt cooperatively and engage in prey sharing, which is thought to maintain and reaffirm social bonds among individuals (Baird 2016). Decreased prey abundance or availability may affect social group cohesion by leading to smaller groups that are more spread out, limiting social interactions and bonding opportunities, as has been seen in killer whales (Felleman et al. 1991, Parsons et al. 2009). However, we have insufficient information on cluster-specific dietary preferences to suggest that some clusters may be more influenced by this than others. The biomass and catch per unit effort (an indirect measure of abundance) of important, upper trophic level prey species such as yellowfin and bigeye tuna *T. obesus* has significantly declined in Hawaiian waters since the mid-1980s (Sibert et al. 2006, Polovina et al. 2009, Oleson et al. 2010), coinciding with a substantial decline in false killer whale group size, sighting rate, and overall abundance over that time period (Baird 2009, Reeves et al. 2009, Silva et al. 2013). While the extent of population decline is uncertain due to differences in survey methods among studies (e.g. aerial vs. shipboard or small vessel), the largest group observed in a 1989 aerial survey (470 individuals; Reeves et al. 2009) is almost 3 times greater than the population-wide estimate for the insular population of 167 animals (SE = 23) by Bradford et al. (2018). It is therefore possible that the population decline impacted how false killer whales in Hawai‘i associate today, as significant declines in the southern resident killer whale population have been accompanied by periods of more fluid associations within pods (Parsons et al. 2009). In addition, removal of socially important individuals (such as adult females with historical knowledge of foraging grounds) from the population can disproportionately affect social network cohesion and should be considered in management plans of vulnerable populations (Williams & Lusseau 2006).

Our results demonstrate that the 4 social clusters of endangered false killer whales identified in this study have significant differences in association patterns, spatial use, and genetics, and this social structure should be considered when addressing management concerns for this population. Specifically, plans to mitigate human and fishery interactions should include evaluation of cluster-specific habitat preferences and spatial use, and long-term preferential associations should be considered for mark–recapture analyses and abundance estimation. Analyses of factors that may influence individuals differentially based on shared habitats (e.g. Baird et al. 2021) should use the 4 social clusters we have identified for this endangered population of false killer whales.

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LITERATURE CITED

Alves F, Quérouil S, Dinis A, Nicolau C and others (2013) Population structure of short-finned pilot whales in the oceanic archipelago of Madeira based on photo-identification and genetic analyses: implications for conservation. Aquat Conserv 23:758–776

Archer FI, Adams PE, Schneiders BB (2017) strataG: an R package for manipulating, summarizing and analysing population genetic data. Mol Ecol Resour 17:5–11

Augusto JF, Frasier TR, Whitehead H (2017) Characterizing alloparental care in the pilot whale (*Globicephala melas*) population that summers off Cape Breton, Nova Scotia, Canada. Mar Mamm Sci 33:440–456

Baird RW (2009) A review of false killer whales in Hawaiian waters: biology, status, and risk factors. Report prepared for the US Marine Mammal Commission under Order No. E40475499, Cascadia Research Collective, Olympia, WA

Baird RW (2016) The lives of Hawai‘i's dolphins and whales: natural history and conservation. University of Hawai‘i Press, Honolulu, HI

Baird RW, Dill LM (1995) Occurrence and behaviour of transient killer whales: seasonal and pod-specific variability, foraging behaviour and prey handling. Can J Zool 73: 1300–1311

Baird RW, Gorgone AM (2005) False killer whale dorsal fin disfigurements as a possible indicator of long-line fishery interactions in Hawaiian waters. Pac Sci 59:593–601

Baird RW, Whitehead H (2000) Social organization of mammal-eating killer whales: group stability and dispersal patterns. Can J Zool 78:2096–2105

Baird RW, Gorgone AM, McSweeney DJ, Webster DL and others (2008) False killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands: long-term site fidelity, inter-island movements, and association patterns. Mar Mamm Sci 24:591–612

Baird RW, Hanson MB, Schorr GS, Webster DL and others (2012) Range and primary habitats of Hawaiian insular false killer whales: informing determination of critical habitat. Endang Species Res 18:47–61

Baird RW, Webster DL, Aschettino JM, Schorr GS, McSweeney DJ (2013) Odontocete cetaceans around the main Hawaiian Islands: habitat use and relative abundance from small-boat sighting surveys. Aquat Mamm 39:253–269

Baird RW, Anderson DB, Kratofil MA, Webster DL, Mahaffy SD (2019) Cooperative conservation and long-term management of false killer whales in Hawai'i: geospatial analyses of fisheries and satellite tag data to understand fishery interactions. Report to the State of Hawai'i Board of Land and Natural Resources, under Contract No. 67703. Cascadia Research Collective, Olympia, WA

Baird RW, Anderson DB, Kratofil MA, Webster DL (2021) Bringing the right fishermen to the table: indices of overlap between endangered false killer whales and nearshore fisheries in Hawai'i. Biol Conserv 255:108975

Beck S, Kuningas S, Esteban R, Foote AD (2012) The influence of ecology on sociality in the killer whale (*Orcinus orca*). Behav Ecol 23:246–253

Bigg MA, Olesiuk PF, Ellis GM, Ford JKB, Balcomb KC (1990) Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Rep Int Whal Comm Spec Issue 12: 383–405

Blondel VD, Guillaume J, Lambiotte R, Lefebvre E (2008) Fast unfolding of communities in large networks. J Stat Mech 2008:P10008

Bradford AL, Forney KA, Oleson EM, Barlow J (2014) Accounting for subgroup structure in live-transect abundance estimates of false killer whales (*Pseudorca crassidens*) in Hawaiian waters. PLOS ONE 9:e90464

Bradford AL, Baird RW, Mahaffy SD, Gorgone AM and others (2018) Abundance estimates for management of endangered false killer whales in the main Hawaiian Islands. Endang Species Res 36:297–313

Bradford AL, Becker EA, Oleson EM, Forney KA, Moore JE, Barlow J (2020) Abundance estimates of false killer whales in Hawaiian waters and the broader central Pacific. NOAA Tech Memo NOAA-TM-NMFS-PIFSC-104

Brault S, Caswell H (1993) Pod-specific demography of killer whales (*Orcinus orca*). Ecology 74:1444–1454

Cairns SJ, Schwager SJ (1987) A comparison of association indexes. Anim Behav 35:1454–1469

Clauset A, Newman MEJ, Moore C (2004) Finding community structure in very large networks. Phys Rev E Stat Nonlin Soft Matter Phys 70:066111

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal Complex Syst 1695:1–9

Ellis S, Franks DW, Nattrass S, Cant MA and others (2017) Mortality risk and social network position in resident killer whales: sex differences and the importance of resource abundance. Proc R Soc B 284:20171313

Elliser CR, van der Linde K, MacIver K (2022) Adapting photo-identification methods to study poorly marked cetaceans: a case study for common dolphins and harbor porpoises. Mamm Biol 102:811–827

Esteban R, Verborgh P, Gauffier P, Giménez J, Foote AD, de Stephanis R (2016) Maternal kinship and fisheries interaction influence killer whale social structure. Behav Ecol Sociobiol 70:111–122

Farine D (2013) Animal social network inference and permutations for ecologists in R using asnipe. Methods Ecol Evol 4:1187–1194

Farine DR (2014) Measuring phenotypic assortment in animal social networks: weighted associations are more robust than binary edges. Anim Behav 89:141–153

Farine DR (2016) Assortnet: calculate the assortativity coefficient of weighted and binary networks. R package version 0.12. http://CRAN.R-project.org/package=assortnet

Felleman FL, Heimlich-Boran JR, Osborne RW (1991) The feeding ecology of killer whales (*Orcinus orca*) in the Pacific Northwest. In: Pryor K, Norris K (eds) Dolphin societies. Discoveries and puzzles. University of California Press, Berkeley, CA, p 113–147

Ferreira IM, Kasuya T, Marsh H, Best PB (2014) False killer whales (*Pseudorca crassidens*) from Japan and South Africa: differences in growth and reproduction. Mar Mamm Sci 30:64–84

Foster EA, Franks DW, Morrell LJ, Balcomb KC, Parsons KM, van Ginneken A, Croft DP (2012) Social network correlates of food availability in an endangered population of killer whales, *Orcinus orca.* J Anim Behav 83: 731–773

Girvan M, Newman ME (2002) Community structure in social and biological networks. Proc Natl Acad Sci USA 99:7821–7826

Hartman KL, Visser F, Hendriks AJ (2008) Social structure of Risso's dolphins (*Grampus griseus*) at the Azores: a stratified community based on highly associated social units. Can J Zool 86:294–306

Hinde RA (1976) Interactions, relationships and social structure. Man (Lond) 11:1–17

Kratofil MA, Ylitalo GM, Mahaffy SD, West KL, Baird RW (2020) Life history and social structure as drivers of persistent organic pollutant levels and stable isotopes in Hawaiian false killer whales (*Pseudorca crassidens*). Sci Total Environ 733:138880

Kratofil MA, Mahaffy SD, Baird RW (2022) Photo-identification-based age estimation of false killer whales utilizing information on sex, relative size, markings, and morphology. IWC Meeting Document SC/68D/SM/04. International Whaling Commission, Impington

Mahaffy SD (2012) Site fidelity, associations and long-term bonds of short-finned pilot whales off the island of Hawai'i. MSc thesis, Portland State University, Portland, OR

Mahaffy SD, Baird RW, McSweeney DJ, Webster DL, Schorr GS (2015) High site fidelity, strong associations, and long-term bonds: short-finned pilot whales off the island of Hawai'i. Mar Mamm Sci 31:1427–1451

Martien KK, Chivers SJ, Baird RW, Archer FI and others (2014) Nuclear and mitochondrial patterns of population structure in North Pacific false killer whales (*Pseudorca crassidens*). J Hered 105:611–626

Martien KK, Taylor BL, Chivers SJ, Mahaffy SD, Gorgone AM, Baird RW (2019) Fidelity to natal social groups and mating both within and between social groups in an endangered false killer whale population. Endang Species Res 40:219–230

MATLAB (2016) version 9.1.0.441655 (R2016b). The MathWorks Inc., Natick, MA

McSweeney DJ, Baird RW, Mahaffy SD, Webster DL, Schorr GS (2009) Site fidelity and association patterns of a rare species: pygmy killer whales (*Feresa attenuata*) in the main Hawaiian Islands. Mar Mamm Sci 25:557–572

National Oceanic and Atmospheric Administration (2012) Endangered and threatened wildlife and plants: endangered status for the main Hawaiian Islands insular false killer whale distinct population segment. Fed Regist 77: 70915–70939

Newman MEJ (2004) Analysis of weighted networks. Phys Rev E Stat Nonlin Soft Matter Phys 70:056131

Newman MEJ (2006) Finding community structure in networks using the eigenvectors of matrices. Phys Rev E Stat Nonlin Soft Matter Phys 74:036104

Newman MEJ, Girvan M (2004) Finding and evaluating community structure in networks. Phys Rev E Stat Nonlin Soft Matter Phys 69:026113

Oleson EM, Boggs CH, Forney KA, Hanson MB and others (2010) Status review of Hawaiian insular false killer whales (*Pseudorca crassidens*) under the Endangered Species Act. NOAA Tech Memo NMFS-PIFSC

Olsen DW, Matkin CO, Andrews RD, Atkinson S (2018) Seasonal and pod-specific differences in core use areas by resident killer whales in the northern Gulf of Alaska. Deep Sea Res II 147:196–202

Parsons KM, Balcomb KC, Ford JKB, Durban JW (2009) The social dynamics of southern resident killer whales and conservation implications for this endangered population. Anim Behav 77:963–971

Photopoulou T, Ferreira IM, Best PB, Kasuya T, Marsh H (2017) Evidence for a postreproductive phase in female false killer whales *Pseudorca crassidens.* Front Zool 14: 30

Polovina JJ, Abecassis M, Howell EA, Woodworth P (2009) Increases in the relative abundance of mid-trophic level fishes concurrent with declines in apex predators in the subtropical North Pacific. Fish Bull 107:523–531

Pons P, Latapy M (2005) Computing communities in large networks using random walks. In: Yolum P, Güngör T, Gürgen F, Özturan C (eds) Computer and information sciences – ISCIS 2005. ISCIS 2005. Lecture notes in computer science, Vol 3733. Springer, Berlin, p 284–293

R Core Team (2022) R: a language and environment for statistical computing (version 3.6.0). R Foundation for Statistical Computing, Vienna

Raghavan UN, Albert R, Kumara S (2007) Near linear time algorithm to detect community structures in large-scale networks. Phys Rev E Stat Nonlin Soft Matter Phys 76: 036106

Reeves RR, Leatherwood S, Baird RW (2009) Evidence of a possible decline since 1989 in false killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands. Pac Sci 63: 253–261

Shizuka D, Farine DR (2016) Measuring the robustness of network community structure using assortativity. Anim Behav 112:237–246

Sibert J, Hampton J, Kleiber P, Maunder M (2006) Biomass, size, and trophic status of top predators in the Pacific Ocean. Science 314:1773–1776

Silva IF, Kaufman GD, Rankin RW, Maldini D (2013) Presence and distribution of Hawaiian false killer whales (*Pseudorca crassidens*) in Maui County waters: a historical perspective. Aquat Mamm 39:409–414

Stack SH, Currie JJ, McCordic JA, Olson GL (2019) Incidence of odontocetes with dorsal fin collapse in Maui Nui, Hawaii. Aquat Mamm 45:257–265

Tavares SB, Samarra FI, Miller PJ (2017) A multilevel society of herring-eating killer whales indicates adaptation to prey characteristics. Behav Ecol 28:500–514

Tixier P, Barbraud C, Pardo D, Gasco N, Duhamel G, Guinet C (2017) Demographic consequences of fisheries interaction within a killer whale (*Orcinus orca*) population. Mar Biol 164:170

Urian K, Gorgone A, Read A, Balmer B and others (2015) Recommendations for photo-identification methods used in capture–recapture models with cetaceans. Mar Mamm Sci 31:298–321

Weiss MN, Franks DW, Balcomb KC, Ellifrit DK, Silk MJ, Cant MA, Croft DP (2020) Modelling cetacean morbillivirus outbreaks in an endangered killer whale population. Biol Conserv 242:108398

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

Whitehead H (2008b) Precision and power in the analysis of social structure using associations. Anim Behav 75: 1093–1099

Whitehead H (2009) SOCPROG programs: analyzing animal social structures. Behav Ecol Sociobiol 63:765–778

Wierucka K, Verborgh P, Meade R, Colmant L and others (2014) Effects of a morbillivirus epizootic on long-finned pilot whales *Globicephala melas* in Spanish Mediterranean waters. Mar Ecol Prog Ser 502:1–10

Williams R, Lusseau D (2006) A killer whale social network is vulnerable to targeted removals. Biol Lett 2:497–500

Yang Z, Algesheimer R, Tessone CJ (2016) A comparative analysis of community detection algorithms on artificial networks. Sci Rep 6:30750

Ylitalo GM, Baird RW, Yanagida GY, Webster DL and others (2009) High levels of persistent organic pollutants measured in blubber of island-associated false killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands. Mar Pollut Bull 58:1932–1937

Appendix.

Table A1. Comparison of cluster number and membership between 1999–2021 datasets with different sets of restrictions. The restricted dataset refers to individuals considered slightly distinctive or above with fair or better photo quality that were seen on 5 or more days. The relaxed dataset refers to individuals considered slightly distinctive or above with fair or better photo quality with no restrictions on the number of days seen. The complete dataset refers to individuals with no restrictions on distinctiveness, photo quality, or the number of days seen. Clusters were generated in R using the Louvain algorithm in the R package 'igraph'

Restricted dataset (n = 174)	Relaxed dataset (n = 292)	Complete dataset[a] (n = 349)	Notes
Cluster 1	No change	No change	
Cluster 2	No change	No change	
Cluster 3	1 change	1 change	1 individual moved from C3 to C1
Cluster 4	No change	No change	

[a] Five individuals seen once formed their own cluster, but aligned most closely with Cluster 2

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