Marine Mammal Science

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ARTICLE

Variation in Social Structure Among Multiple Stocks of Island-Associated Common Bottlenose Dolphins (*Tursiops truncatus*) in Hawaiian Waters

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Keywords: association patterns | Delphinidae | habitat size | social networks | socioecology

ABSTRACT

The drivers of animal social structures remain poorly understood, particularly in species such as cetaceans that are wide-ranging and challenging to study. Understanding the factors shaping sociality can shed light on population ecology, gene flow, and information transmission. Here, we investigated variation in social structure among three independent island-associated stocks of common bottlenose dolphins (*Tursiops truncatus*) around the main Hawaiian Islands. We generated social networks for each stock using photo-identification data from 2002 to 2022. We calculated modularity, density, degree centralization, and betweenness centralization to assess network structure. We measured the stocks' available habitat and calculated their population densities. We also quantified association strength with the half-weight association index (HWI) and compared it within- and between-clusters, and by sex for each stock. HWIs revealed that within-cluster associations were much stronger than between-cluster in all stocks. Network modularity and HWI showed the lowest fragmentation into distinct clusters and the strongest associations in the smallest of the three habitats (Kaua‘i-Ni‘ihau). We found no conclusive evidence of sex differences in HWI. Our findings suggest that denser populations might drive social network fragmentation. Our study highlights the importance of further investigating the drivers of sociality.

HŌ‘ULU‘ MANA‘O

‘A‘ole maopopo le‘a nā mea e paipai ana i ka pili nohona holoholona, keu ho‘i ma nā lāhui koholā i noho i ‘ō a i ‘ane‘i a i pa‘akikī ko lākou kālailai ‘ia ‘ana. Ma o ka maopopo ‘ana i ia mau mea e pā ana i ka pilina, hiki nō paha ke mōakāka iki mai ka pū‘uo kālai kaiaola, ka ho‘oili ōewe, a me ka ho‘ōlapa ‘ike. Ua kolokolo mākou i ka ‘oko‘a ma ka pili nohona o ‘ekolu pū‘ulu nai‘a nuku poko (*Tursiops truncatus*) kū‘oko‘a pili i nā mokupuni a puni ka pae‘āina Hawai‘i. Ua ho‘okumu mākou i mau pūnaewele pilina no kēlā me kēia pūʻulu ma o ka ʻikepili hōʻoia kiʻi mai nā makahiki 2002–2022. Ua hoʻomaulia mākou i ka hoʻohui ʻana, ka paʻapū, ka nui o ka hoʻākoakoa ʻana, a me ka pilina o ka hoʻākoakoa ʻana i mea e kālailai aku ai i ka ʻōnaehana pūnaewele. Ua ana mākou i ka nui o ke kaianoho o nā pūʻulu a ua hoʻomaulia ʻia ka nui o ko lākou pūʻuo. Ua helu mākou i ka ikaika o ka pilina me ka papa kuhi o ka pilina hapa paona (HWI) a ua hoʻohālikelike ʻia i loko a i waena o nā pūʻulu, a ma ke keka o kēlā me kēia pūʻulu. Hōʻike ʻia ma nā HWIs, ʻoi loa aku ka ikaika o nā pilina i loko o nā pūʻulo ma mua o nā pilina ma waena o nā pūʻulu. No ka hoʻohui ʻana o ka pūnaewele a me ka HWI, ua hōʻike ʻia ka haʻahaʻa loa o ka ka hoʻohapa ʻana i nā ʻāhui kaʻawale a me ka ikaika loa o nā pilina ma ka liʻiliʻi loa o nā kainoho ʻekolu (Kauaʻi-Niʻihau). ʻAʻole i loaʻa iā mākou ka meheu paʻa no nā ʻokoʻa keka ma ka HWI. Ma o nā hua i loaʻa iā mākou, paipai nō paha nā pūʻuo nui i ka hoʻāpana ʻia ʻana o ka pūnaewele pilina. Kālele kā mākou kālailai i ke koʻikoʻi o ke kolokolo a noiʻi mau ʻana i nā mea e paipai ana i ka pili nohona.

1 | Introduction

Environmental features can constitute barriers to dispersal, leading animals to primarily associate with their neighbors and driving social network fragmentation (Farine and Sheldon 2016; He et al. 2019; Leu et al. 2016). In turn, network fragmentation can affect population-level reproductive patterns by influencing gene flow between communities (Armansin et al. 2020; Edenbrow et al. 2011). Social network structure can affect the transfer of information between and within social groups, creating cultural divergences that can further reinforce social structure within populations (Cantor and Whitehead 2013). Therefore, habitat availability and intrinsic characteristics of populations (e.g., density and reproductive rates) can play a major role in driving social and population structure, genetics, and evolution (Manel et al. 2003), as well as disease transmission (Guimarães Jr et al., 2007; Weiss et al. 2020; Powell et al. 2020).

In the marine environment, habitat heterogeneity can affect ranging patterns, social interactions, and population structure of highly mobile species, including odontocetes (Mann et al. 2000; Rosel et al. 2009). Anthropogenic impacts in marine ecosystems can also affect individual dispersal and social relationships within populations, acting similarly to habitat discontinuities (Ansmann et al. 2012; Greenfield et al. 2021; Visser et al. 2011). It has been hypothesized that most within-species variation in social structure is explained by the predictability of resources, particularly in delphinids (Gowans et al. 2007). Predictable resources should make individuals less reliant on cooperative foraging and social information, therefore increasing intra-species competition, leading to smaller groups and weaker individual associations (Foster et al. 2012; Levengood et al. 2022). Conversely, unpredictable resources should promote cooperative foraging group stability. Despite decades of research, delphinid socioecology is still poorly understood, with few studies having explored the effects of environmental factors on sociality (Gowans et al. 2007; Carnabuci et al. 2016).

Common bottlenose dolphins (*Tursiops truncatus*) are possibly the most studied cetacean in the world, particularly since coastal and estuarine populations are usually small, have a small home range, and individuals exhibit high residency (Wells and Scott 2018). However, this species exhibits a wide range of ecological and behavioral plasticity, whereby individuals and communities adapt their ranging patterns, movements, and trophic interactions in response to environmental variation. Thus, populations can display significant variation in habitat preferences, diets, and social structures (Connor et al. 2000). Resident populations mostly occur in shallow and productive coastal ecosystems where resources are relatively predictable in comparison to open-ocean environments. Within coastal ecosystems, the costs of within-group competition tend to outweigh the benefits of cooperative foraging and social information, leading to the formation of relatively small groups (Gowans et al. 2007). Most populations display fluid fission-fusion societies and changing both size and composition (Blasi and Boitani 2014; Díaz López 2020; Elliser and Herzing 2011; Frau et al. 2021) Within fluid fission-fusion societies, however, bottlenose dolphin populations display considerable intraspecific variation in social structure, and association patterns can vary considerably among individuals within communities (Eisfeld and Robinson 2004; Connor et al. 2000; Wells 2014).

The main Hawaiian Islands are oceanic islands in an oligotrophic environment, inhabited by several sympatric species of odontocetes (Baird 2016). Four demographically distinct populations of common bottlenose dolphins, generally referred to as stocks (as defined by the Marine Mammal Protection Act in the United States, 1972), have been identified in the archipelago (Baird et al. 2009; Carretta et al. 2021; Martien et al. 2012), primarily inhabiting waters less than 500 m deep. These stocks inhabit the coastal waters of Kauaʻi and Niʻihau, Oʻahu, the shallow waters of the islands of Maui Nui, and the coastal waters of Hawaiʻi Island (Baird et al. 2013).

Here, we aimed to assess the variation in social structure between three of these four stocks: Kauaʻi-Niʻihau, Maui Nui, and Hawaiʻi Island using social network analysis. The gene flow between these three stocks is limited, and they are considered demographically independent (Martien et al. 2012). As most data from Oʻahu are opportunistic (Harnish 2021; Van Cise et al. 2021), this stock was not included in the analysis. Suitable coastal habitats (< 500 m) for bottlenose dolphins are more available around Maui Nui and Hawaiʻi Island, whereas available habitat around the islands of Kauaʻi and Niʻihau is narrow. In 2018, the size of the Kauaʻi-Niʻihau stock was estimated to be 112 animals (SE = 27, range = 70–180), Oʻahu was estimated at 112 animals (SE = 19, range = 81–154), Maui Nui is estimated to have approximately 64 individuals (SE = 9.3, range = 48–85), and Hawaiʻi Island is estimated to have approximately 136 individuals (SE = 58, range = 61–303), the largest of the four stocks (Van Cise et al. 2021). Each stock differs in its distribution, abundance, and home range, providing an opportunity to assess whether habitat size affects fragmentation into distinct communities (He et al. 2019).

Comparing the social structure of multiple dolphin stocks in a shared environment can reveal how ecological variation shapes sociality, with implications for conservation, management, and understanding population dynamics. Here, we investigated the spatial variation in the social structure of bottlenose dolphins across three of the four stocks identified around the main Hawaiian Islands. We hypothesized that the Maui Nui and Hawaiʻi Island stocks would display higher network fragmentation into distinct communities (hereafter referred to as clusters for consistency with standard network theory terminology; He et al. 2019) compared to Kauaʻi-Niʻihau due to these differences in habitat availability. As spatially complex habitats have been associated with increased rates of association with animals sharing the same immediate vicinity in other species (Leu et al. 2016), associations were expected to be stronger among the Maui Nui and Hawaiʻi Island stocks than among the Kauaʻi-Niʻihau stock.

2 | Methods

2.1 | Data Collection

Standard photo-identification data (Baird et al. 2009) of common bottlenose dolphins were collected around all the main Hawaiian Islands during dedicated field efforts by Cascadia Research Collective (CRC), and specifically off Maui Nui by Pacific Whale Foundation (PWF), with survey effort between 2000 and 2020 (going as far back as 1996 for PWF). Details on sampling are presented in Baird et al. (2009, 2013, 2024) and Stack et al. (2020). Survey effort varies among island areas (see Kratofil et al. 2023). Off Hawaiʻi Island, our sampling was limited to the leeward (west) side of the island, due to environmental conditions on the windward (east) side preventing cetacean surveys with the small vessels available to us. Off Maui Nui, effort was concentrated between Maui, Lānaʻi, and Molokaʻi, and to the west of Lānaʻi. Off Niʻihau and Kauaʻi, surveys occurred off both east and west sides of the islands (Baird 2016). Therefore, at least for Maui and Hawaiʻi Island, our dataset is biased toward animals that can be regularly sighted on the leeward side of the islands. Effort track lines for CRC (years 2000–2020) and PWF (years 2010–2020) are provided in Supporting Information Figure A. The discovery curve of photo-identified individuals has leveled off for the Kauaʻi-Niʻihau and Maui Nui stocks, while Hawaiʻi Island's still has not reached a plateau, and therefore requires continued sampling (Harnish 2021; Van Cise et al. 2021). Thus, while social network analysis may provide very robust observations for the Kauaʻi-Niʻihau and Maui Nui stocks, there may be more room for error in Hawaiʻi Island social networks.

Individuals sighted within the same group (animals traveling in the same direction and generally within several 100 m of each other) on the same day were considered associated (following the "gambit-of-the-group" approach; Croft et al. 2008; Syme et al. 2022; Whitehead and Dufault 1999). For each sighting of every individual, the best photograph was assigned a score between 1 and 4 for both quality and distinctiveness of the animal, following Baird et al. (2009). Distinctiveness scores were 1 for not distinctive animals, 2 for slightly distinctive, 3 for distinctive, and 4 for very distinctive individuals. Photograph quality was scored as 1 for poor, 2 for fair, 3 for good, and 4 for excellent. We restricted analyses to individuals considered at least slightly distinctive (score of 2) with fair (score of 2) or better photo qualities (Urian et al. 2015; Würsig and Jefferson 1992) to reduce the likelihood of mismatched individuals influencing the dataset. This can result in a bias against less marked individuals, particularly younger animals. Thus, the chance of nondistinctive animals being mismatched was considered too high to safely include in our analysis. We opted to reduce our sample to the most distinctive individuals. The sex of identified individuals was determined using multiple methods. Individuals sighted in close association with a calf (identified as such due to small size, lack of markings, and fetal folds for neonates) were assumed to be females. For individuals where photographs or videos with a clear view of the genital area were available, sex was determined via morphology (e.g., presence of mammary slits and/or placement of genital and anal slits). The sex of biopsied animals was also determined via genetic analyses (see Martien et al. 2012, for details), with analyses carried out at the Southwest Fisheries Science Center. Animals identified as calves (individuals about a third to half the size of a closely associated individual believed to be the mother, swimming in close proximity and often in echelon position) were not included in the analysis.

While there are considerable community science contributions of photographs available for all three stocks considered here (Harnish et al. 2023), we restricted analyses only to encounters by CRC and PWF, as efforts were made in both cases to obtain photos of all individuals present in encounters regardless of distinctiveness. Furthermore, both CRC and PWF kept records of survey effort. This also ensured that the co-occurrence of individuals within the same group would be determined through more consistent criteria, which is fundamental for comparing social networks (Castles et al. 2014). To further assess the power of our data, we calculated the $S^2 \times H$ index (where S is the stock's social differentiation, and H is the mean number of associations per individual) for each stock. $S^2 \times H$ indexes ≥ 5 are generally considered to be indicators of good power (Whitehead 2008).

2.2 | Social Network Structure Assessment

There is no agreed-upon standard on the appropriate minimum number of sightings needed for an animal to be included in social network analysis. However, it is generally understood that, while restrictions may cause data loss, including only individuals with extensive sighting histories will make social network analysis more accurate (Whitehead 2008). When Baird et al. (2009) first investigated bottlenose dolphin social structure in the main Hawaiian Islands, no restrictions were included. While more data are now available, resighting rates for bottlenose dolphins in the area remain low (Van Cise et al. 2021). Thus, we conducted two sets of network analyses with distinct restrictions.

Using the igraph package in R 4.2.2 (Csardi and Nepusz 2006; R Core Team 2022) and Gephi 0.10 (Bastian et al. 2009), an undirected social network was constructed for each stock, restricted to all animals seen at least twice. For each social network, the metrics of modularity, density (Whitehead 2008), betweenness centralization, and degree centralization

(Freeman 1978) were calculated. Modularity measures the extent to which a social network is fragmented into distinct communities (or clusters), and a modularity of 0.3 or higher indicates the presence of distinct social clusters within the network (Whitehead 2008). Network density is the proportion of observed associations between dyads over the total number of theoretically possible associations. It ranges between 0 and 1, with 1 meaning that every individual in the network is associated with every other individual in the network. Degree centralization represents the extent to which a social network is dominated by a few individuals with disproportionately more associates than everyone else. It ranges between 0 and 1, with a value of 0 indicating that all nodes have the same number of edges (i.e., a lattice network) and a value of 1 indicating that all nodes are connected only to a single central node (i.e., a star network). Betweenness centralization represents the extent to which a social network is reliant on a small number of individuals in order not to break apart into multiple disconnected networks, and ranges between 0 and 1. A value of 0 means that all nodes are equally important to the network's overall connectivity (lattice network), and a value of 1 means that a single node keeps all other nodes connected to each other (star network). As we were primarily interested in the overall structure of the social network, we decided to opt for a more relaxed set of restrictions, eliminating only those animals sighted only once.

Association patterns within each of the three stocks were also assessed using SOCPROG 2.9 (Whitehead 2009) and Gephi 0.10 (Bastian et al. 2009), restricting to individuals seen at least three times in the study period. For each network, a half-weight association index (HWI) was used to measure association strength (Whitehead 2008). We applied stricter restrictions on this dataset to ensure that HWIs would be calculated based on at least three sightings, therefore providing a more robust assessment of association strength. A permutation-based test for preferred/avoided association (permuting groups within samples) was performed on each social network to assess whether short- and long-term association patterns were significantly different from random, with a total of 30,000 permutations applied for each stock. Distinct clusters within each stock were identified through modularity-based cluster analysis (Newman 2006). A Mantel test (Schnell et al. 1985) was used to assess whether individuals were significantly more likely to associate with members of their own cluster, rather than with members of other clusters. Overall, within- and between-cluster mean, sum, and maximum HWIs were calculated for each stock. To our knowledge, this analysis cannot be conducted setting a minimum number of individuals per cluster. Therefore, some clusters would likely be comprised of only a few individuals. Using only those individuals whose sex was known, mean, sum, and maximum HWIs were also calculated for males, females, between-sex, male–male associations, and female–female associations in each stock.

We acknowledge that our restrictions may be considered lenient, thus making our analysis prone to bias due to our low resighting rates. However, we repeat the whole analysis on individuals from the three stocks sighted a minimum of five times (see Supporting Information). We then compared the results from this stricter analysis to assess the robustness of our conclusions.

2.3 | Habitat Availability Assessment

Sighting rates of common bottlenose dolphin around the main Hawaiian Islands are more than twice as high in areas with depths between 1 and 500 m compared to depths between 500 and 1000 m (Baird et al. 2013). We assessed sighting rates by depth range within our own sample and found a similar trend, with sighting rates highest in depths between 1 and 500 m (Supporting Information Figure B). Thus, primary bottlenose dolphin habitat was defined as waters between 1 m and 500 m of depth. Using the sf (Pebesma 2018), raster (Hijmans 2022), and ggspatial (Dunnington 2022) packages in R 4.2.2 (R Core Team 2022), a bathymetric map of the main Hawaiian Islands was generated using the University of Hawaiʻi SOEST Main Hawaiian Islands Multibeam Bathymetry and Backscatter Synthesis grid (https://www.soest.hawaii.edu/hmrg/multibeam/grids.php; Richards et al. 2019). An estimate of bottlenose dolphin habitat availability (1–500 m deep) off Kauaʻi-Niʻihau, Maui Nui, and Hawaiʻi Island was calculated with the marmap package (Pante et al. 2022). After obtaining the estimates of habitat size, we used the most recent (2018) stock size estimates from Van Cise et al. (2021) to calculate the apparent population densities (i.e., density in the area between the 1 m and 500 m depth contours) of the three stocks by dividing the point estimates of abundance by area.

3 | Results

3.1 | Data Available After Applying Restrictions

After restricting by distinctiveness and photograph quality, and removing all calves from the analysis, our sample was comprised of 874 sightings off Kauaʻi-Niʻihau (225 unique individuals), 1025 off Maui Nui (248 individuals), and 764 off Hawaiʻi Island (244 individuals). The resighting rates were relatively low. Within our whole sample, the mean number of sightings per individual was 3.7 (SD = 4.1). The mean resighting rate varied between stocks, being 2.3 for Kauaʻi-Niʻihau, 4.4 for Maui Nui, and 1.6 for Hawaiʻi Island. When removing all animals seen less than three times, the resighting rates were 6.3 for Kauaʻi-Niʻihau, 7.8 for Maui Nui, and 7.5 for Hawaiʻi Island. Social differentiation (S) was 0.94 for Kauaʻi-Niʻihau, 0.92 for Maui Nui, and 1.08 for Hawaiʻi Island. The mean number of associations per individual (H) was 92.78 for Kauaʻi-Niʻihau, 35.22 for Maui Nui, and 58.86 for Hawaiʻi Island. All $S^2 \times H$ were well above the 5 threshold (Kauaʻi-Niʻihau = 81.6; Maui Nui = 29.9; Hawaiʻi Island = 68.5), indicating strong power to detect preferred associations. The mean group size off Kauaʻi-Niʻihau was 10.6 (SD = 10.4) individuals, while the mean group size was 5.6 (SD = 5.2) off Maui Nui and 9 (SD = 8.8) off Hawaiʻi Island. After removing all individuals sighted only once, the sample included 142 animals for Kauaʻi-Niʻihau, 148 for Maui Nui, and 114 for Hawaiʻi Island (Supporting Information Tables A and B). Two individuals from Hawaiʻi Island had to be removed from the sample when calculating metrics as they were isolated nodes, disconnected from the social network, reducing the sample to 112 individuals. Within our sample, 118 animals off Kauaʻi-Niʻihau, 108 off Maui Nui, and 74 off Hawaiʻi Island were seen more than twice.

3.2 | Social Network Structure

Fragmentation into distinct clusters was the lowest for Kaua'i-Ni'ihau (modularity = 0.28) compared to the other two stocks (Maui Nui's modularity = 0.45; Hawai'i Island's modularity = 0.36; Table 1, Figure 1) and was also lowest in the analysis restricted to individuals seen five or more times (Supporting Information Table C). Maui Nui's value of betweenness centralization (0.15) was over twice as high as Hawai'i Island (0.06) and over three times higher than Kaua'i-Ni'ihau (0.04), indicating a higher reliance on a few individuals for the network not to break apart into separate, disconnected societies. Maui Nui also had the highest value of betweenness centralization (0.085) in the analysis restricted to individuals seen five or more times (Supporting Information Table C). The total number of associates per individual was more uniform in the Maui Nui stock compared to the other two, as indicated by the lower value of degree centralization (Kaua'i-Ni'ihau = 0.33; Maui Nui = 0.24; Hawai'i Island = 0.32), although this was not the case for the analysis restricted to individuals seen five or more times (Supporting Information Table C). Overall, the results of the sample of animals seen three or more times seem to agree with those from the sample of animals seen five or more, with the only exception being degree centralization.

In all three stocks, short-term associations were not significantly different from random, while long-term associations significantly differed from random (Table 2). This was indicated by the number of times the real SD (for long-term associations) and mean (for short-term associations) were higher than those of the permuted networks. The same was true when restricting to only animals seen a minimum of five times (Supporting Information Table D). Furthermore, the significant difference from random of the group size standard deviations indicates that, in all three stocks, some individuals tend to form larger groups than others. Again, this too remained the case when restricting to a minimum number of resightings of 5 (Supporting Information Table D). Only four clusters were identified in Kaua'i-Ni'ihau (one including a single individual). In Maui Nui, 14 clusters were identified, seven of which included three or fewer individuals. Hawai'i Island had six clusters, two of which were comprised of a single individual, while another cluster included over 40% of the sample. Mantel tests show that individuals were more likely to associate with members of their own cluster than members of other clusters in all three stocks (Figure 2), as indicated by the positive t values (Supporting Information Table E). Modularity-based cluster analysis operates by dividing the social network in a manner that maximizes the value of modularity (Newman 2004). While still providing a good overall estimate of HWI variation between- and within-cluster, our assessment was inevitably biased by the smaller clusters generated by the analysis. Overall association strength varied considerably between stocks, but within-cluster associations were always stronger than between-cluster associations (Table 3). While the within-cluster HWI was over four times the value of between-cluster HWI for Kaua'i-Ni'ihau (0.28–0.06), it was almost 13 times higher for Hawai'i Island (0.27–0.02) and 10 times higher off Maui Nui (0.2–0.02). Kaua'i-Ni'ihau displayed the highest HWIs overall (0.14), followed by Hawai'i Island (0.09) and Maui Nui (0.04). The number of individuals of known sex was small. We identified 18 males and 29 females in Kaua'i-Ni'ihau, 5 males and 19 females in Maui Nui, and 13 males and 17 females in Hawai'i. Males appeared to display stronger

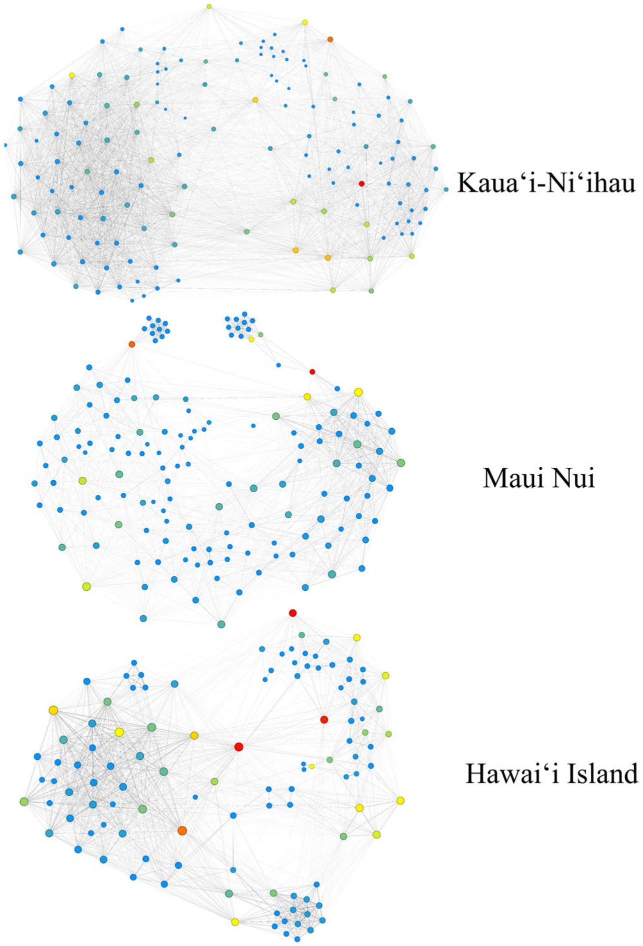

FIGURE 1 | Overall structure of the three common bottlenose dolphin stocks' social networks around the Main Hawaiian Islands. Node size increases with the number of associates (degree), while node color ranges on a blue-to-red spectrum with increasing betweenness centrality. Only adults seen at least twice are included in the networks.

TABLE 1 | Metrics calculated from the social networks of common bottlenose dolphins (*Tursiops truncatus*) seen at least twice in encounters with fair or better distinctiveness and photograph quality from dedicated field efforts.

Stock	*n*	Modularity	Density	Degree centralization	Betweenness centralization
Kaua'i-Ni'ihau	142	0.280	0.322	0.330	0.046
Maui Nui	148	0.448	0.129	0.238	0.153
Hawai'i Island	112	0.358	0.226	0.323	0.064

TABLE 2 | Results of permutation test for preferred/avoided associations. The tests assessed the number of times the test statistics from the real network were higher than those from the permuted networks. p values below $\alpha = 0.05$ indicated a statistically significant difference. Significant p values of the mean test statistic indicate that short-term associations are significantly different from random. Significant p values of *SD* and/or *CV* indicate that long-term associations are significantly different from random. Significant p values of group size *SD* indicate significant differences in gregariousness (some individuals have more associates than average) compared to permuted networks.

Stock	*n*	Test statistic	Real	Random mean	Real > random	*p*
Kauaʻi-Niʻihau	118	Mean	0.116	0.115	29,875/30,000	0.9958
		SD	0.179	0.165	30,000/30,000	< 0.0001
		CV	1.548	1.443	29,999/30,000	< 0.0001
		Group size SD	7.257	6.629	30,000/30,000	< 0.0001
Maui Nui	108	Mean	0.038	0.038	7926/30,000	0.2642
		SD	0.100	0.095	29,999/30,000	< 0.0001
		CV	2.622	2.494	29,999/30,000	< 0.0001
		Group size SD	2.741	2.601	29,999/30,000	< 0.0001
Hawaiʻi Island	74	Mean	0.093	0.093	2089/30,000	0.0696
		SD	0.175	0.166	30,000/30,000	< 0.0001
		CV	1.881	1.776	29,999/30,000	< 0.0001
		Group size SD	4.637	4.388	29,992/30,000	0.0003

associations than females off Kauaʻi-Niʻihau and Hawaiʻi (Supporting Information Figure D and Table F). Values for mixed-sex associations were variable (though within each other's standard deviation) between female-to-male and male-to-female associations due to the female sample size being larger than the male's, which affects the way SOCPROG calculates HWI (Whitehead 2009). Mixed-sex associations appeared to display intermediate HWIs, being slightly higher than female–female associations, but lower than male–male associations (Supporting Information Table F). Due to our small sample size, we opted to not pursue Mantel tests to corroborate our observations of sex-based HWI variation, as we do not believe they would yield reliable results.

3.3 | Habitat Availability and Stock Densities

The primary bottlenose dolphin habitat around Maui Nui is by far the largest, estimated at about 6798 km^2, followed by 2714 km^2 around Hawaiʻi Island. Habitat availability is the smallest around Kauaʻi-Niʻihau, estimated at 1374 km^2. The three stocks' primary habitats have different shapes, both when defining such habitat as waters within 500 m (Supporting Information Figure C) and when looking at a finer scale of waters within 250 m (Figure 3) of depth. The primary habitat around Kauaʻi-Niʻihau is concentrated along the coastlines of the two relatively small islands, with the shortest distance between the two areas of approximately 25–30 km. By comparison, the primary habitat around Maui Nui's is mostly located in the channels between the islandsand including Penguin Bank, extending west of Molokaʻi. Shallow waters off Hawaiʻi Island were thinly distributed along the coastline of the island. Such patterns were also evident when looking at the distribution of waters within 250 m of depth and between 500 m and 1000 m of depth (Figure 3). Based on the 2018 abundance estimates of the three stocks from Van Cise et al. (2021), the calculated population density of Kauaʻi-Niʻihau is ~0.081 individuals/km^2, Maui Nui's is 0.001 individuals/km^2, and the apparent population density for Hawaiʻi Island is 0.050 individuals/km^2.

4 | Discussion

Our results suggest differences in social network structure among three stocks of bottlenose dolphins around the main Hawaiian Islands. Kauaʻi-Niʻihau had the least fragmentation and the strongest associations. Maui Nui displayed both the highest social network fragmentation as well as the highest reliance on a small number of individuals to not break into separate social networks. Overall, Hawaiian common bottlenose dolphins seem to display similar association patterns to those of other populations around the globe, exhibiting relatively loose associations and social structures consistent with high rates of fission-fusion dynamics (Baird et al. 2009; Connor et al. 2000). Only long-term associations differed significantly from random. The observed differences in association strength between sexes do not appear to support the sex-based associations observed in some populations (Bouveroux and Mallefet 2010; Galezo et al. 2020; Connor et al. 2000; Mann and Cords 2014), although there are other bottlenose dolphin populations that are similar (Louis et al. 2018). However, the sample of individuals of known sex (Kauaʻi-Niʻihau: 18 males and 29 females out of 118 animals; Maui Nui: 5 males and 19 females out of 108 animals; Hawaiʻi Island: 13 males and 17 females out of 74 animals) was small, limiting interpretation of association patterns within and between sexes.

While sharing many similarities, there is clear evidence for some divergence in social structures between common bottlenose dolphin stocks in Hawaiʻi. Two stocks had modularity

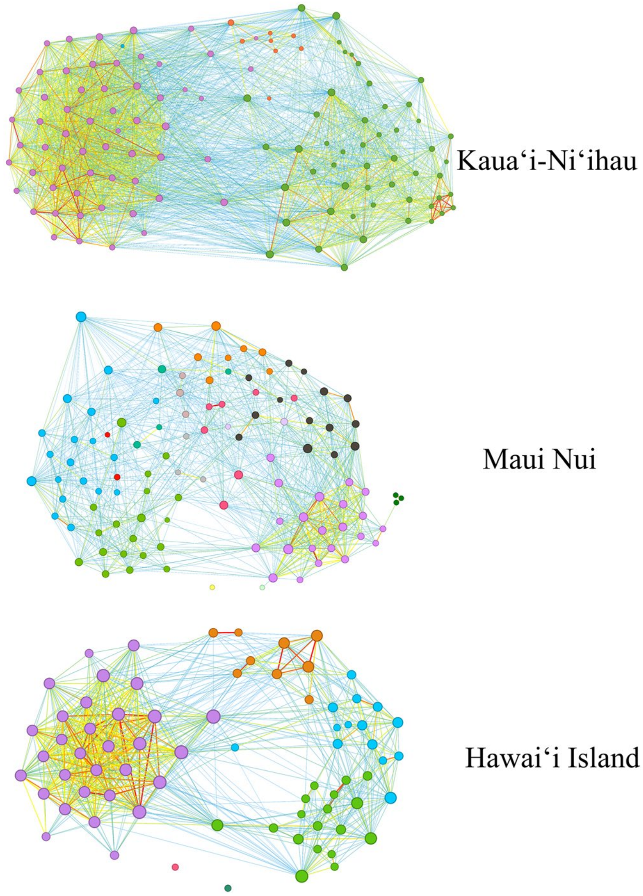

FIGURE 2 | Social networks of the three stocks of bottlenose dolphins around the main Hawaiian Islands highlighting social clusters and association strength. Node size increases with number of associates (degree), while node color represents the cluster the individual was assigned to. Edge color ranges on a spectrum from blue to red with increasing HWI. Networks are restricted to adults seen at least three times.

values beyond the 0.3 threshold (with Kauaʻi-Niʻihau's being extremely close to the value). However, the existence of distinct clusters (four in Kauaʻi-Niʻihau, 14 in Maui Nui, and six in Hawaiʻi Island) was corroborated by the results of the Mantel tests for all three stocks. The lower modularity (0.28) and higher network density (0.322) values of Kauaʻi-Niʻihau indicate that the stock presents a less fragmented network compared to Maui Nui and Hawaiʻi Island. This is likely due to habitat availability being by far the lowest (~1374 km^2) around Kauaʻi-Niʻihau. Association strength was also highest in the Kauaʻi-Niʻihau stock, possibly due to their smaller range increasing the probability of interactions between individuals within this stock. However, higher HWIs may reflect other factors, which we could not account for, such as predation risk, that might result in individuals from Kauaʻi-Niʻihau displaying stronger associations (Kelley et al. 2011). Resource availability can also affect social structure, with some species tending to form more and/or stronger associations when food is abundant and within-group competition is lower (Holekamp et al. 2012; Wolf et al. 2018). However, low prey predictability and/or abundance can also drive stronger associations among individuals, as cooperative foraging becomes more important (Gowans et al. 2007). Therefore, a possible driver for stronger associations in Kauaʻi-Niʻihau could be lower prey availability and/or predictability. However, there is not sufficient data on prey availability or predation risk around the main Hawaiian Islands to investigate their effects on social structure.

Our data have limitations that should be acknowledged. Survey effort off Kauaʻi–Niʻihau focused on deeper waters compared to other islands, while most surveys in Maui Nui were concentrated within shallow waters (Baird et al. 2024; Stack et al. 2020). Our ability to survey the windward side of the islands was also limited due to the small vessels used in field efforts (Baird 2016). Therefore, these differences have resulted in sampling biases. In addition, we did not incorporate mortality

TABLE 3 | Summary of mean, sum, and mean individual maximum HWI (standard deviation in parentheses) for each stock, showing the variation in association strength among bottlenose dolphins in the Main Hawaiian Islands. Only adults seen at least three times were included in this sample. Where the "Within-Cluster" row in the "Class" column is boldened, the Mantel test showed that the stock displayed significantly stronger within-cluster than between-cluster associations. Social differentiation and correlation of true and estimated HWI are included (standard error in parentheses).

Stock	*N*	Social differentiation estimate (SE)	Correlation of true and estimated HWI (SE)	Class	Mean HWI (SD)	Max HWI (SD)	Sum HWI (SD)
Kauaʻi-Niʻihau	118	0.94 (0.04)	0.61 (0.03)	Overall	0.14 (0.07)	0.66 (0.15)	16.82 (7.92)
				Within-cluster	0.28 (0.12)	0.65 (0.16)	12.66 (6.92)
				Between-cluster	0.06 (0.04)	0.31 (0.10)	4.16 (2.87)
Maui Nui	108	0.92 (0.04)	0.35 (0.02)	Overall	0.04 (0.02)	0.48 (0.20)	5.08 (2.65)
				Within-cluster	0.20 (0.12)	0.48 (0.20)	3.56 (2.32)
				Between-Cluster	0.02 (0.01)	0.23 (0.10)	1.52 (1.08)
Hawaiʻi Island	74	1.08 (0.04)	0.57 (0.03)	Overall	0.09 (0.06)	0.60 (0.19)	7.78 (4.74)
				Within-cluster	0.27 (0.14)	0.61 (0.16)	6.89 (4.82)
				Between-cluster	0.02 (0.02)	0.20 (0.12)	0.89 (0.88)

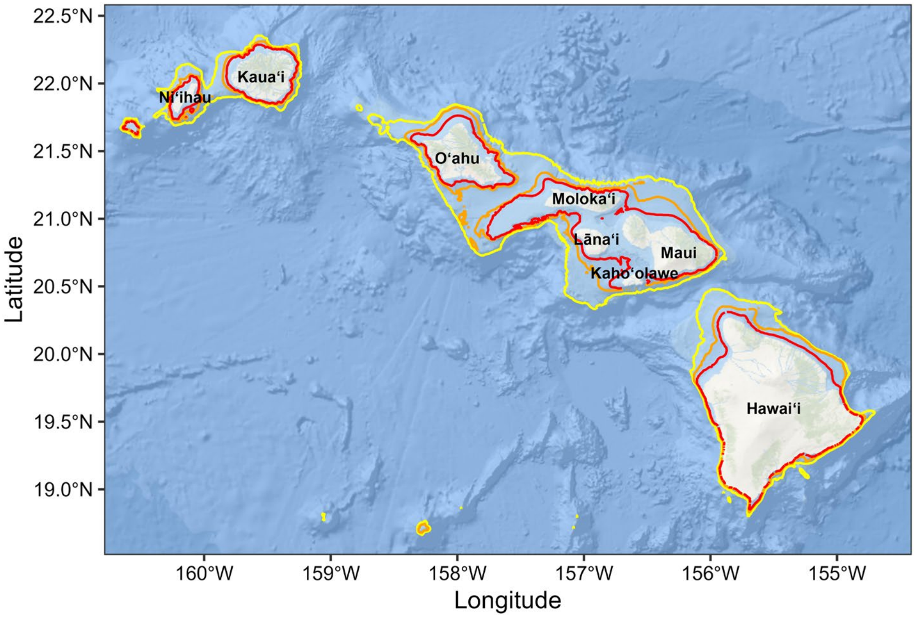

FIGURE 3 | Depth contours of the areas within 250 (red line), 500 (orange line), and 1000 m (yellow line) of depth in the Main Hawaiian Islands. Penguin Bank is the large shallow area to the southwest of Moloka'i.

estimates, immigration, and emigration in our social structure analyses. We also had no means to account for the potential bias of individuals reassociating after many years apart, since HWIs do not account for the time between encounters. This may have potentially caused short-term association patterns to not be significantly different from random. Due to the small percentage of individuals whose sex is known, we were unable to assess sex-biased dorsal fin distinctiveness, particularly since males tend to be more identifiable than females (Tolley et al. 1995; Rowe et al. 2009; James et al. 2022). Therefore, our results should be viewed as the analysis of a sample of the populations' social networks, rather than a comprehensive description of the three stocks' true societies. Furthermore, while we could estimate the availability of suitable habitat for bottlenose dolphins around the main Hawaiian Islands, we still have a limited understanding of fine-scale habitat use patterns for these dolphins.

4.1 | Influence of Dolphin Densities and Habitat Availability

Our study suggests that Hawaiian bottlenose dolphin societies are more fragmented when their primary habitat is larger, though dyadic associations would not necessarily be any stronger than in smaller habitats. With regard to stock size, the smallest of the three (Maui Nui, ~64 animals in 2018) displays the highest fragmentation, while the second largest (Kaua'i-Ni'ihau, ~112) is the least fragmented. The largest stock (Hawai'i Island, ~136) displays intermediate levels of fragmentation. Thus, there appears to be no trend linking stock size to social network structure in common bottlenose dolphins in the main Hawaiian Islands. This may be due to individual bottlenose dolphins' tendency to use a very small range within their habitats (Van Cise et al. 2021). With regard to apparent population density, Maui Nui is the least dense (0.001 estimated number of individuals/km^2), Kaua'i-Ni'ihau is the densest stock (0.081 estimated number of individuals/km^2), and Hawai'i Island falls once again somewhere between the other two (0.05 estimated number of individuals/km^2). Therefore, our results do not suggest a relationship between stock density and social network structure. It is worth noting that the Maui Nui and likely Kaua'i-Ni'ihau stocks have been experiencing population declines, while Hawai'i Island appears to be stable (Van Cise et al. 2021). Thus, there also appears to be no trend linking population decline with social network structure, though such a trend may emerge with time and become evident in future studies. Habitat availability may affect bottlenose dolphin social structure in the main Hawaiian Islands, with fragmentation into clusters increasing with habitat size as observed in other species (He et al. 2019). However, other factors, including predation risk, prey availability, and anthropogenic impacts, may also influence the social structure of bottlenose dolphins. Habitat-driven social network clustering has been associated with diverging foraging specializations in other populations of common bottlenose dolphins, which in turn affect population-level genetics and reproductive patterns (Armansin et al. 2020; Kopps et al. 2014). Monitoring the patterns and changes of bottlenose dolphin social structure will therefore remain an important endeavor to understand their ecology and manage their stocks in the Main Hawaiian Islands.

4.2 | Management Implications

Human-caused disturbance can be perceived as a source of risk in a similar way to predation risk (i.e., the risk disturbance hypothesis; Frid and Dill 2002), and anthropogenic disturbance in the form of fisheries or vessel traffic could be perceived similarly to those caused by the presence of a predator (Frid and Dill 2002; La Manna et al. 2023). Hawai'i Island experiences more intense trolling and handlining fisheries (Baird et al. 2021), with evidence of other Hawaiian species interacting with them, such as rough-toothed dolphins (*Steno bredanensis*; Kuljis 1983) and false killer whales (*Pseudorca crassidens*; Baird and Gorgone 2005, Baird et al. 2015). In an Australian population of the closely related Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), high rates of fisheries interaction have been associated with increased social network fragmentation (Ansmann et al. 2012). Negative interactions with local fishermen have been documented in Hawaiian common bottlenose dolphins (Harnish et al. 2019), mostly associated with bait or catch depredation attempts (Nitta and Henderson 1993; Yuen 1977). Foraging around fishing vessels has been known to drive smaller group sizes than usual in other bottlenose dolphin populations (Bearzi et al. 1999) and may contribute to the higher modularity observed off Hawai‘i Island. However, it must be noted that the opposite trend was observed by Chilvers and Corkeron (2001) in dolphins living in Moreton Bay, Australia, where fishery interaction drove larger groups. As Maui Nui is also the stock most reliant on a few individuals to keep distinct clusters connected, management of this stock should pay special attention to any threats that may endanger these important social brokers. It is worth noting that the Kaua‘i-Ni‘ihau stock experiences a much higher exposure to acoustic disturbance from navy sonars, which have been known to affect the foraging behavior of other species (Miller et al. 2022). If sonar disturbance was to be perceived similarly to predation risk, it might explain Kaua‘i-Ni‘ihau's stronger HWIs and lower network fragmentation. Furthermore, social network fragmentation can affect the transmission of both information and disease across a society (Hirsch et al. 2013; Webster et al. 2013), with high modularity slowing the spread of both (Evans et al. 2021). Concerns about the transmission of detrimental behaviors, such as fish depredation from aquaculture operations, are growing in the main Hawaiian Islands (Harnish et al. 2023). Thus, continuous monitoring of Hawaiian bottlenose dolphins will remain important to manage these stocks in the future.

Author Contributions

Enrico Corsi: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing – original draft, writing – review and editing. **Robin W. Baird:** conceptualization, funding acquisition, investigation, project administration, supervision, writing – review and editing. **Annette E. Harnish:** data curation, writing – review and editing. **Antoinette M. Gorgone:** data curation, investigation, writing – review and editing. **Jens J. Currie:** data curation, investigation, writing – review and editing. **Stephanie H. Stack:** data curation, investigation, writing – review and editing. **Jeremy J. Kiszka:** conceptualization, funding acquisition, project administration, supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure A:** Field effort track lines for Cascadia Research Collective (CRC, red, 2000–2020) and Pacific Whale Foundation (PWF, yellow, 2010–2020). **Figure B:** Sighting rates per 100 h of effort by depth ranges off Kaua‘i and Ni‘ihau, Maui Nui and Hawai‘i Island between 2000 and 2022 (Cascadia Research Collective). **Figure C:** The Main Hawaiian Islands (500 m depth contour in red). **Figure D:** Social networks of the three Hawaiian stocks of common bottlenose dolphins considered in this study for each sex (male = blue, female = red, unknown = purple). Node size increases with number of associates (degree). Edge color ranges from blue to red with increasing HWIs. Networks are restricted to adults seen at least three times. **Table A:** Summary of data used after applying restrictions. **Table B:** Number of individuals seen at least twice for each common bottlenose dolphin stock in Hawaiian waters. **Table C:** Metrics calculated from the social networks for individuals seen at least five times. **Table D:** Results of permutation test for preferred/avoided associations on all animals seen at least five times. The tests assessed the number of times the test statistics from the real network were higher than those from the permuted networks. p values below $\alpha = 0.05$ indicated a statistically significant difference. Significant p values of the mean test statistic indicate that short-term associations are significantly different from random. Significant p values of SD and/or CV indicate that long-term associations are significantly different from random. Significant p values of group size SD indicate significant differences in gregariousness (some individuals have more associates than average) compared to permuted networks. **Table E:** Results of Mantel tests assessing whether individuals in the three stocks tend to associate with animals from their own social cluster (within-cluster associations) more than with animals from other social clusters (between-cluster associations). The tests include only adult animals seen at least three times. Positive t values indicate that animals tend to interact with members of their own clusters more than with members of other clusters. **Table F:** Mean, maximum, and sum HWI (standard deviation in brackets) for each common bottlenose dolphin stock for each sex. Only adults seen at least three times were included.