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ARTICLE

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Long-term associations of common bottlenose dolphins with a fish farm in Hawai‘i and impacts on other protected species

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Abstract

The global expansion of mariculture offers numerous potential benefits but may also pose a threat to wildlife populations. There is currently only one commercial finfish mariculture facility in Hawai‘i, a nearshore kanpachi (*Seriola rivoliana*) farm off the west coast of Hawai‘i Island. This farm lies within the range of several resident odontocete species, and almost daily common bottlenose dolphin (*Tursiops truncatus*) associations with the farm have been reported since 2007. We analyzed photographs of 35 bottlenose dolphin groups at the farm sighted between 2008 and 2021 in the context of 20 years of survey effort and extensive community science contributions from Hawai‘i Island. Thirty-six bottlenose dolphins were identified associated with the farm, representing almost one-quarter of the estimated total population size. The discovery rate of new individuals at the farm indicates this is a conservative estimate of the total number of individuals associating with the farm, and social network analysis suggests that associations may continue to spread within the population. We also found a high frequency of farm associated bottlenose dolphins showing aggression towards several other species of dolphins, demonstrating impacts to multiple protected species.

KEYWORDS
aquaculture, behavior, interspecific aggression, mariculture, social network, *Stenella longirostris*, *Tursiops truncatus*

Hawaiian

Nui nā papaha o ka loaʻa ʻana i mau waiwai ma o ka hoʻomōhala honua ʻana i ka hana lawaiʻa, a pēlā nō ka papaha o ka weliweli o nā pūʻuo kai. Hoʻokahi wale nō wahi pāʻoihana lawaiʻa o Hawaiʻi, he loko kāhala (*Seriola rivoliana*) ma ke kai pāpaʻu ma ke kapakai komohana o ka mokupuni ʻo Hawaiʻi. Aia nō ia loko ma kahi o kekahi mau lāhui naiʻa, a helu ʻia kekahi mau kūkaʻi me nā naiʻa nuku poko (*Tursiops truncatus*) i kēlā me kēia lā ma ka loko mai ka makahiki 2007. Ua kālailai ʻia he kanakolukūmālima mau kiʻi o nā pūʻulu naiʻa nuku poko i ʻike ʻia ma ka loko mai ka makahiki 2008 a 2021, ma o nā anamanaʻo o iwakālua mau makahiki a me ka hana nui o ke kaiāulu akeakamai o ka mokupuni ʻo Hawaiʻi. Hōʻoia ʻia ka pilina o nā naiʻa nuku poko he kanakolukūmāono me ka loko, he hapahā paha o ka pūʻuo koho huinanui. ʻO kēia ana ʻana i ka ʻike ʻana i mau mea hou ma ka loko, he koho makaʻala i ka huinanui o nā mea e pili ana me ka loko, a wahi a ke ana pilina, e mau ana nō paha kēia ʻano pilina i waena o ka pūʻuo holoʻokoʻa. Ua ʻike pū mākou, ʻoi aʻe ka nui o ka hana mākonā o kēia mau naiʻa pili i ka loko i nā ʻano naiʻa ʻē aʻe ʻaʻohe o lākou pili i ka loko, he hōʻike ia i nā hopena o nā lāhui palekana.

1 | INTRODUCTION

Oceanic aquaculture, or mariculture, has grown substantially over the past few decades, driven by increased demand for fish from a global human population that is growing in both number and affluence (Garlock et al., 2020; Naylor et al., 2021). However, there are also numerous known environmental drawbacks to mariculture that must be taken into consideration, including potential nutrient loading around farms, increased risk of disease transmission to wild fish populations, depletion of some wild fish stocks for feed, risk of farmed species escaping into the environment, disruption of benthic communities, and potential impacts to other marine life attracted to or repelled by the farms, including odontocete cetaceans (Holmer, 2010; Krkošek et al., 2006; Tacon & Halwart, 2007; Würsig & Gailey, 2002).

While studies of mysticete interactions with mariculture primarily involve entanglements in gear (Callier et al., 2018; Young, 2015), observed odontocete responses to mariculture facilities have been more varied, usually based on the species being farmed. Shellfish farming has generally been suggested to displace odontocetes (Kemper et al., 2003; Markowitz et al., 2004; Ribeiro et al., 2007; Watson-Capps & Mann, 2005), though exceptions have been described (Díaz López & Methion, 2017). In contrast, finfish farming generally appears to attract odontocetes.

Common bottlenose dolphins (*Tursiops truncatus*, hereafter bottlenose dolphins) in the Gulf of Corinth in Greece exhibit a preference for areas in close proximity to fish farms, where they have been shown to opportunistically forage on aggregated fish populations attracted to the site by high nutrient concentrations and the farm structures (Bearzi et al., 2016; Bonizzoni et al., 2014, 2019). Similar findings emerged from a study in Port Lincoln, Australia, where it was found that both bottlenose dolphins and common dolphins (*Delphinus delphis*) were attracted to and feeding in the immediate vicinity of tuna feedlots (Kemper & Gibbs, 2001). Additionally, an ecosystem model of the inner Ionian Sea showed that mariculture expansion in the region had led to increases in the number of bottlenose dolphins observed in the area, which were presumably taking advantage of aggregated populations of wild fish near farms (Piroddi et al., 2011). Elsewhere, the expansion of a fish farm in the Gulf of Olbia off Sardinia is thought to have contributed to significant increases in bottlenose dolphin sighting rates in the area, and further investigation revealed that several individuals were showing high site fidelity to the area (Díaz López, 2017; Díaz López & Bernal Shirai, 2007; Díaz López et al., 2005). Unfortunately, attraction to fish farms can have fatal results; multiple odontocete entanglements in antipredator netting have been reported at fish farms in Australia, Tasmania, Chile, and Italy (Díaz López & Bernal Shirai, 2007; Espinosa-Miranda et al., 2020; Kemper & Gibbs, 2001; Kemper et al., 2003).

Beyond changes in odontocete distribution and the risk of entanglement, more complex unintended consequences can also result from fish farm presence. For example, changes in the distribution of bottlenose dolphins near farms in the Gulf of Corinth may be heightening the risk of exposure to pollution for these animals, as some of the farms are located near industrial areas (Bonizzoni et al., 2014). It has also been suggested that harmful algae blooms induced by excess nutrients in the water surrounding farms could pose a threat to cetaceans (Kemper et al., 2003). Fish farms are also known to affect the behavior of odontocetes in potentially detrimental ways. Differences in behavior and social structure among associated bottlenose dolphins were noted at a fish farm in the Gulf of Olbia; dolphins used unique feeding strategies to capture fish from the farm, and social associations between animals were weaker when dolphins were feeding at versus off the farm (Díaz López 2006; Díaz López & Bernal Shirai, 2008). The strength of social associations between bottlenose dolphins has been shown elsewhere to affect survival rates, especially for calves (Frère et al., 2010; Stanton & Mann, 2012). Additionally, there is a risk that changes in the distribution of species around mariculture facilities could result in the aggregation of multiple predator species. Multiple predator species occupying a small area where they may be competing for access to the same resources (e.g., escaped fish or aggregated surrounding fish) could lead to territoriality and aggression. Similar situations have resulted at locations where wildlife are regularly provisioned as part of tourism activities; for example, provisioning of stingrays and primates has led to aggregations of individuals, many of whom displayed increased aggression towards conspecifics (Newsome et al., 2004; Wrangham, 1974). While not proven, the aggregation of multiple predator species has also been suggested as a potential explanation for interspecific aggression in bottlenose dolphins in waters near aquaculture facilities in the western Mediterranean (Crespo-Picazo et al., 2021).

Here, we present the results from an analysis of bottlenose dolphin encounters at a fish farm off Hawai'i Island in the context of almost 20 years of effort and community science contributions in the area, and explore both the direct and indirect consequences of the farm's presence. First, we describe individual patterns of bottlenose dolphin association with the farm using long-term photo-ID data, exploring which individuals are associating with the farm, and the duration and frequency of these associations. We also construct a discovery curve to assess whether new individuals are continuing to become associated with the farm over time. Second, we use social network analysis to explore the population-level impacts of association with the farm, including how the behavior may be spreading across the population. We also use standardized lagged association rates (SLARs) to examine how enduring associations are, and test whether encounter location (i.e., at the farm versus not at the farm) is correlated with group size to explore the impact of farm association on social relationships between dolphins. The use of long-term data in all of these approaches allows us to assess the relative impacts of association with the farm in the wider context of the population as a whole. Finally, we describe some of the behaviors documented among farm associated bottlenose dolphins, including behaviors that are likely reinforcing associations with the farm, as well as several cases of interspecific aggression that we believe are linked to the farm's presence, and that may have ramifications for other odontocete species.

2 | METHODS

2.1 | History of the farm and description of overlapping odontocete populations

As of January 2023 there is only a single commercial finfish mariculture facility in Hawai‘i, though a mariculture facility producing Pacific threadfin (*Polydactylus sexfilis*), also known as moi, was in operation off O‘ahu between 2001 and 2011, and an aquaculture development research site is located approximately 10 km offshore of Hawai‘i Island (Sims, 2020; Tummons & Dawson, 2014). The currently operational commercial farm is operated by Blue Ocean Mariculture (BOM) off the west coast of Hawai‘i Island and produces kanpachi (*Seriola rivoliana*), also known as kampachi, kahala, Almaco Jack, or Hawaiian yellowtail. The farm currently uses five anchored, fully enclosed SeaStation cages that can be raised or lowered within the water column and has the capacity to produce over 400,000 kg of fish/year (Seafood Watch, 2020). Each cage has a volume of 8,000 m^3, with a single large steel rim that sits around a central steel spar, helping to suspend copper-alloy mesh netting across a series of spokelines that extend from the tips of the central spar to the rim (Seafood Watch, 2020; Sims, 2013). The cages also have access gates through which divers can enter and exit to remove dead fish or perform maintenance (Sims, 2013). The site is ~750 m offshore of Makako Bay, and is positioned above a bare sandy bottom in ~60 m depth with an adjacent stretch of coral reef just south of Unualoha Point. The farm sits within the known range of endangered Hawaiian monk seals (*Neomonachus schauinslandi*), as well as resident populations of four species of odontocetes: endangered main Hawaiian Islands insular false killer whales (*Pseudorca crassidens*), spinner dolphins (*Stenella longirostris*), pantropical spotted dolphins (*S. attenuata*), and bottlenose dolphins (Baird, 2016). Three of these resident odontocete species (bottlenose dolphins, spinner dolphins, and pantropical spotted dolphins) have recognized Hawai‘i Island stocks (Carretta et al., 2021), and are vulnerable to localized threats. Of these, spinner dolphin stocks are in apparent decline (Tyne et al., 2014), which has made them a high priority species for conservation efforts in recent years. Makako Bay is known as a traditional resting area for spinner dolphins (Tyne et al., 2018), and pantropical spotted dolphins sometimes join spinner dolphins in these resting bays. In contrast to spinner dolphins, a recent study showed that the abundance of the Hawai‘i Island bottlenose dolphin stock appears to be relatively stable and in the low 100 s (the 2018 abundance estimate was 136 individuals, 95% CI [61, 303]; Van Cise et al., 2021). Bottlenose dolphins off Hawai‘i Island have high levels of site fidelity and genetic differentiation from other populations in the Hawaiian Islands (Baird et al., 2009; Martien et al., 2011). False killer whales from the endangered main Hawaiian Islands population have occasionally been documented near the farm (Cascadia Research Collective, unpublished data; Colin J. Cornforth, personal communication, September 2016; Sims, 2013), and bottlenose dolphins have been regularly documented there since October 2006 (Sims, 2013).

The farm's net pens were deployed by Kona Blue Water Farms in February 2005, which dissolved in 2011 shortly after BOM acquired the lease for the farm (Wright, 2011). Kona Blue Water Farms documented instances of detrimental wildlife interactions, including provisioning of bottlenose dolphins in the first few years after the farm went in, the killing of a tiger shark (*Galeocerdo cuvier*) in 2005 by farm personnel, and a major fish escape caused by a Galapagos shark (*Carcharhinus galapagensis*) that bit through a net in 2009 (Baird, 2016; Seafood Watch, 2020; Sims, 2013). BOM took steps were taken to reduce predator interactions with the farm, including the use of predator-resistant netting materials and the prompt removal of dead fish, but the farm avoids the use of any proactive predator deterrents such as acoustic harassment devices or strobe lights (BOM, personal communication, September 2018 as cited in Seafood Watch, 2020). However, between 2011 and 2017, wildlife interactions were still the determined cause of 46% of fish escape events, and in 2017 a Hawaiian monk seal was found dead in one of the net pens, indicating that wildlife interactions with the farm remained an ongoing concern (Carretta et al., 2021; Seafood Watch, 2020). In March 2021 another monk seal was spotted swimming inside a net pen, although in this case the seal was detected in time for

BOM to open a panel and allow the seal to safely leave (Ann Garrett, personal communication, May 2022). In publicly released wildlife monitoring reports from 2016 to 2020, BOM disclosed that the immediate farm area was typically visited at least once a week by Hawaiian monk seals, and on an almost daily basis by bottlenose dolphins (BOM, 2016–2020).

2.2 | Data collection

Cascadia Research Collective (CRC) surveys were undertaken off Hawaiʻi Island every year from 2002 through 2021, with 17–73 survey days per year (median = 34 days). Survey efforts were focused on multiple odontocete species and attempted to cover as broad an area as possible along the west side of the island and far offshore (Baird et al., 2013), weather conditions permitting. Due to the specific goals of individual survey efforts, only limited time was spent in typical bottlenose dolphin habitat (i.e., <500 m bathymetric depth), and with only occasional passes by the farm, as many of the other, higher-priority species that were targeted during surveys are typically located in deeper water (Baird et al., 2013). During all encounters with odontocetes during CRC surveys, information was recorded on species present, group size, the general behavior of the group (e.g., traveling, milling, socializing, feeding, or resting), any unusual or noteworthy specific behaviors (e.g., predation events, interspecific harassment, association with the fish farm), and location, and photographs of animals were taken for individual identification. Additionally, biopsy samples were collected from some individual animals during CRC encounters using remote-sampling methods (i.e., crossbow or pole spear). Photographs and video of bottlenose dolphins off Hawaiʻi Island were also contributed by community scientists and obtained from social media, including both above- and below-water images. To aid in interpreting our results we also included information on interspecific interactions from CRC encounters with bottlenose dolphins elsewhere in the main Hawaiian Islands. Encounters involving aggressive interspecific interactions were primarily detailed based on analysis of photographs and video footage taken during encounters, and by notes taken during encounters by either research staff (CRC encounters) or community scientists.

All photographs of bottlenose dolphins were matched to a long-term catalog of individual bottlenose dolphins and assigned photograph quality and distinctiveness scores following established protocols (Baird et al., 2009). We identified encounters at or in close proximity to the farm based on GPS coordinates (not available for all encounters, especially those from community scientists), the presence of the fish cages in photographs, or provided sighting details, and noted the identities of individual bottlenose dolphins associated with the farm. Individuals were considered associated with the farm if they were sighted swimming in close proximity to (e.g., swimming between cages, or close enough that cages are clearly discernable in the photograph frame), or interacting with the cages (e.g., visibly investigating the cages, or attempting to remove fish). Sexes of some individuals were determined based on genetic analysis of biopsy samples (undertaken by the Southwest Fisheries Science Center following the protocols in Morin et al., 2005), by documentation with a calf in close attendance at any point in an animal's sighting history, or by morphology (e.g., presence of mammary slits or visible penis, relative distance of the urogenital slit from the anus). We noted identities of individual bottlenose dolphins involved in aggressive interspecific interactions in relation to whether these individuals have been documented at the farm at any point in their sighting history.

2.3 | Social network and group size analysis

Individuals that were considered not distinctive or that had poor quality photographs were not included in social network analyses, and analyses were restricted based on the total number of times an individual was seen (including sightings both at and away from the farm) as specified below to reduce any biases in metrics stemming from short sighting histories. All analyses used data from 2002 through 2021, unless otherwise specified. We considered individuals encountered together in the same group to be associated with one another. We processed association data in SOCPROG 2.9 (Whitehead, 2009), and used a half-weight index (HWI) to generate a social network (Whitehead & James, 2015). The association data processed by SOCPROG 2.9 was then imported into Netdraw 2.158 (Borgatti, 2002) and Gephi 0.9.2 (Bastian et al., 2009) to generate social network graphs.

To confirm that association data are an informative way to explore the social dynamics of the population, we first tested whether individuals in the population associated with others at random. To do this, we used a permutation test for preferred/avoided associations on a restricted dataset (all individuals seen at least twice) with 20,000 permutations (1,000 iterations per permutation) on groups within samples, where the sample period was set to one day, as described in Whitehead (2008). Then, to explore social relationships in the whole population in comparison to individuals encountered at the farm, we measured the network metrics of mean and maximum HWI (exploring the strength of associations across the network), mean strength (an alternative measure of the strength of associations that sums the association indices of each individual with all other individuals in the network), mean eigenvector centrality (a measure of the density of connections within the network, including both individuals and their associates) and mean clustering coefficient (another measure of the density of connections within the network, focusing solely on the associates of each individual) for all individuals seen at least twice. These metrics were then recalculated for farm associated dolphins and the rest of the sampled population separately. Using the restricted data set, a Mantel test (Schnell, 1985) was conducted to determine whether farm associated dolphins and all other individuals differed in association strength both within (e.g., farm associated dolphins to farm associated dolphins) and between (e.g., between farm associated dolphins and all other animals) these two groups, using 20,000 permutations.

To explore the temporal dynamics of associations, we estimated the probability of individuals re-associating over time in farm associated versus nonfarm associated dolphins using SLARs for the two categories. We used only animals sighted at least three times to reduce potential bias stemming from limited sighting histories, and restrict sightings to a period after the farm had been established and bottlenose dolphins were known to be associating with it (after 2008). Standardized lagged association rates were chosen to account for incomplete documentation of all associations within the population (Bejder et al., 1998; Whitehead, 1995). We produced a SLAR curve representing association rates of nonfarm associated dolphins with every other animal in the population and a separate, equivalent curve for farm associated dolphins. Model-fitting was conducted on the SLARs to determine if they display differences in association stability. The tested models, in descending order of the long-term stability of associations, were “preferred companions,” “preferred companions and casual acquaintances,” “casual acquaintances,” and “two levels of casual acquaintances.” The model with the lowest QAIC value was selected as the best fit, with any models that fall within ΔQAIC $=$ 0–2 also considered strongly supported.

Group sizes, defined as the number of individuals present during an encounter, were not always provided for contributor encounters, so group size estimates were based solely on CRC encounters. We tested whether group sizes differed by encounter location (at the farm versus not at the farm) with a Mann–Whitney *U* test, as group sizes were not normally distributed.

2.4 | Code availability

All codes used for analysis and figure generation written in R v 4.2.1 (R Core Team, 2022) are available on GitHub at https://github.com/cascadiaresearch/Bottlenose-Dolphin-Fish-Farm-Associations-Code.

3 | RESULTS

CRC survey efforts covered 89,500 km of trackline off Hawaiʻi Island between 2002 and 2021, with approximately 10% of effort in habitat suitable for bottlenose dolphins (i.e., <500 m bathymetric depth), and 79 passes within 1 km of the farm site (Figure S1). During surveys, 2,289 groups of odontocetes were encountered, with only five of these encounters taking place at the farm, all with bottlenose dolphins. When community science contributor encounters were factored in, 56,082 photographs and 59.5 min of contributor video footage were obtained from 454 encounters with bottlenose dolphins off Hawaiʻi Island from 1986 to 2021, 35 of which were at the farm (Figure S1). From the 35 encounters at the farm, there were 97 identifications of 36 unique bottlenose dolphins, and the total number of individuals documented at the farm continued to increase over time (Figure 1, Table S1). Twenty-two of these individuals (61%) were seen at the farm on more than one occasion, and the mean number of times that individuals were sighted at the farm was 2.7 (range = 1–17, median = 2; Table S1). The animal encountered most frequently at the farm was an adult male (HITt0201) sighted 17 times there over 11 years. Of the 36 dolphins identified at the farm, sex was determined for 11 individuals; five males (three based on genetic analysis and two on morphology) and six females (two based on previous calf presence, two on genetic analysis and previous calf presence, and two on morphology). No mother/calf pairs were documented at the farm.

The social network revealed that all individuals encountered at the farm link to the main component of the Hawaiʻi Island social network (Figure 2). All farm associated dolphins were documented with other farm associated individuals at some point during their sighting history (Figure S2), but the farm associated individuals were also spread over a substantial portion of the social network and included extensive connections to nonfarm associated dolphins (Figure 2). Results from the permutation test for preferred/avoided associations for the whole population (Table S2) show that individuals appear to form short-term associations randomly, but display preferences for specific individuals when forming long-term associations, indicating that association data are a useful way to explore the population's social system. However, farm associated dolphins appear to form weaker social connections compared to the rest of the population (Table 1). Their lower mean eigenvector centrality suggests that farm associated dolphins have not only fewer connections, but that their associates are also not well connected within their social network. The lower average clustering coefficient of farm associated dolphins suggests that their social circles are more open compared to the rest of the

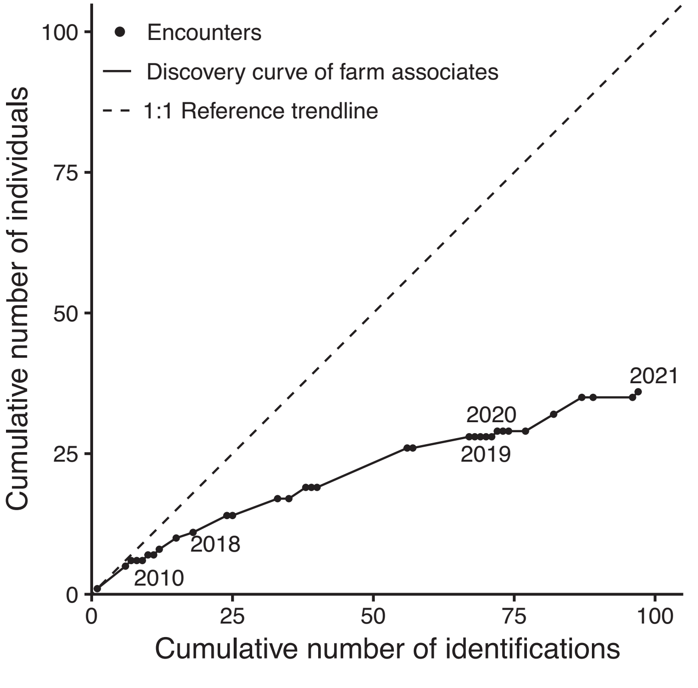

FIGURE 1 Discovery curve of all bottlenose dolphins (*Tursiops truncatus*) identified at the farm from 2008 to 2021, showing that the number of farm associated dolphins is continuing to increase. Year labels indicate the number of identifications and individuals at the start of the year specified.

network, with their associates in turn being less likely to be associated with each other. The Mantel test revealed that there are significant differences (matrix correlation = 0.1373; $t = 6.736$; $p < .0001$) in association rates within farm and nonfarm associated dolphins, as well as between the two classes, with the positive t-value indicating that farm associated dolphins tend to associate more with other farm associated dolphins, while nonfarm associated dolphins tend to associate more with other nonfarm associated dolphins. Despite limitations due to the difference in sample sizes, SLARs suggest that farm associated dolphins have a lower tendency to form long-term associations compared to nonfarm associated dolphins (Figure 3). Model-fitting on the SLAR curve for nonfarm associated dolphins found that the top-ranked model was of preferred companions and casual acquaintances, with no other models within ΔQAIC = 0–2, while the top ranked model for farm associated dolphins was of two levels of casual acquaintances, with no other models within ΔQAIC = 0–2 (Table 2).

Mean group size for CRC encounters at the farm was 3.6 individuals ($n = 5$, range = 1–6, median = 4.0), compared to 9.5 individuals ($n = 128$, range = 1–60, median = 6.0) for encounters that did not take place at the farm.

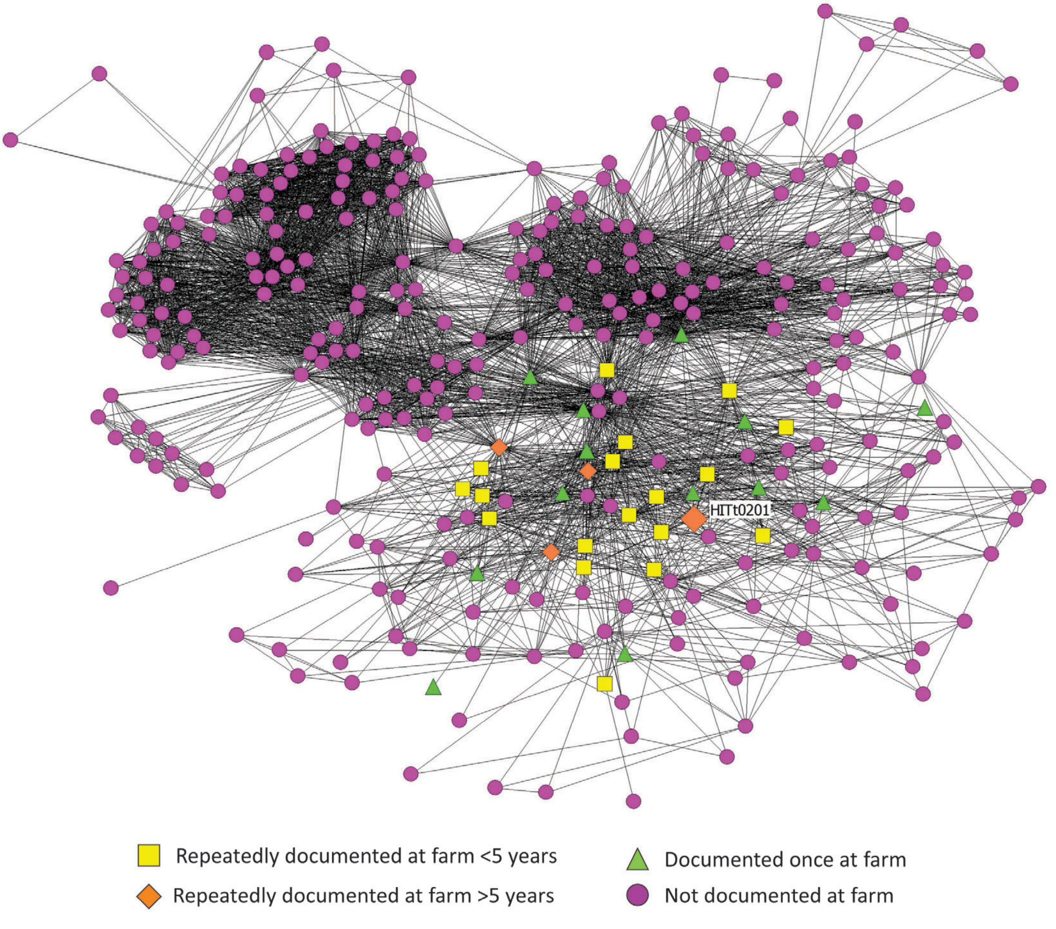

FIGURE 2 Main cluster of the unfiltered social network of common bottlenose dolphins (*Tursiops truncatus*) encountered off Hawai'i Island between 2002 and 2021, excluding pelagic groups and individuals encountered in isolation, and restricted to those considered at least slightly distinctive with fair or better quality photographs. This network shows that farm associated individuals are distributed throughout the network with extensive connections to nonfarm associated individuals, which may facilitate social transmission of the behavior of associating with the farm. The size of HITt0201's node has been increased to allow for ease of identification within the network, given this individual's repeated involvement in aggressive interspecific interactions and long-term association with the farm.

TABLE 1 Social network metrics for all common bottlenose dolphins (*Tursiops truncatus*) seen at least twice in encounters with good photograph quality and distinctiveness, showing that animals documented at the farm appear to form weaker social connections compared to the rest of the population.

Association	Number of individuals	Mean HWI	Maximum HWI	Mean strength	Mean eigenvector centrality	Mean clustering coefficient
Nonfarm associated dolphins	132	0.05 (0.04)	0.68 (0.24)	8.40 (5.81)	0.05 (0.07)	0.31 (0.15)
Farm associated dolphins	33	0.03 (0.02)	0.45 (0.11)	5.32 (2.86)	0.00 (0.01)	0.13 (0.05)
Whole population	165	0.05 (0.03)	0.64 (0.24)	7.79 (5.46)	0.04 (0.07)	0.27 (0.15)

Note: HWI = half-weight index. Standard deviation for the metrics is reported in parentheses.

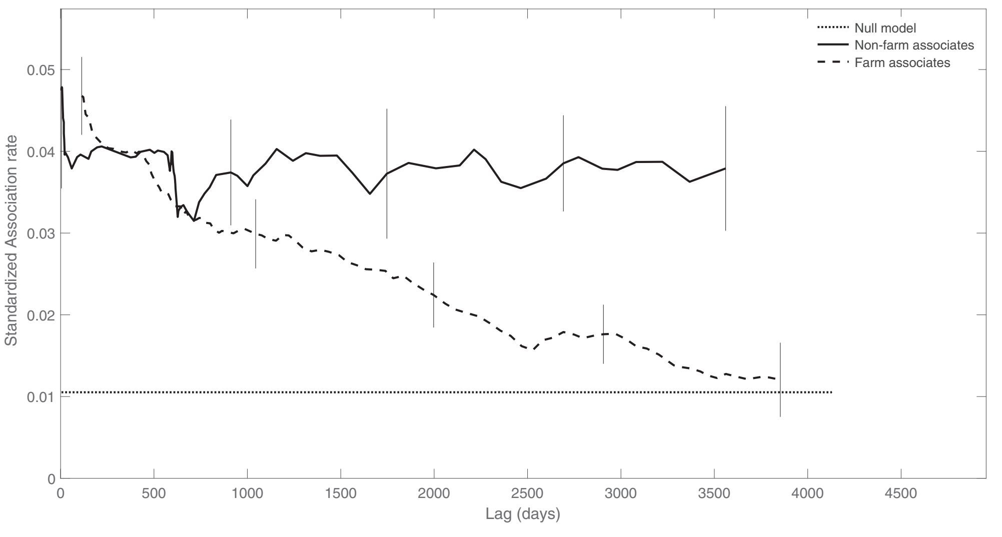

FIGURE 3 Standardized lagged association rates (SLAR) for farm associated and nonfarm associated common bottlenose dolphins (*Tursiops truncatus*) from 2008 to 2021 with all other animals in the social network, restricted to individuals considered at least somewhat distinctive, seen three or more times, and with fair or better quality photographs. The low SLAR of farm associated dolphins suggests that these individuals are less likely to form long-term social connections when compared to nonfarm associated dolphins. Vertical lines represent jackknife standard error bars. Individual lines represent rates of individuals reassociating (*y*-axis) over time expressed in number of days (*x*-axis). To aid the comparison of SLAR curves between farm associated dolphins and other animals, a null model for the whole population is provided. In the null model reassociation between pairs of individuals is completely random.

Differences in group size between encounter locations were not statistically significant (Mann–Whitney *U* test: $W = 181$, $p = .1005$).

During five of the encounters at the farm, dolphins were recorded consuming fish that closely resembled kanpachi, though species identity was not confirmed. In video footage from one of these encounters, an individual dolphin slowly approached a gate on one of the submerged cages, then suddenly jerked its body closer to the cages, spooking the fish near the netting, and causing them to push against the gate. This action caused the gate to lift slightly and allowed a single fish from inside the cage to escape, which was then rapidly captured by the dolphin (Video S1). This same action had been performed earlier in the encounter by the same animal, suggesting that the behavior was a deliberate attempt to remove fish from the net pens rather than a random action. In an additional

TABLE 2 Results of the model-fitting analysis on the SLAR of farm associated common bottlenose dolphins (*Tursiops truncatus*) and all other animals in the population (restricted to distinctive individuals seen in at least three encounters with good photograph quality), showing that farm associated dolphins have a lower tendency to form long-term social connections compared to nonfarm associated dolphins. The best-fitting model for each group, chosen as the one with the lowest quasi-Akaike Information criterion (QAIC), is reported in bold characters at the top, with remaining models ordered by increasing difference from the best-fitting model (ΔQAIC).

Farm association	Model	QAIC	ΔQAIC
Nonfarm associated dolphins $n = 65$	**Preferred companions and casual acquaintances**	**11,209.6971**	**0**
	Two levels of casual acquaintances	11,215.8384	6.1413
	Preferred companions	11,216.6627	6.9656
	Casual acquaintances	11,216.9935	7.2964
Farm associated dolphins $n = 30$	**Two levels of casual acquaintances**	**8,646.8633**	**0**
	Casual acquaintances	8,651.8314	4.9681
	Preferred companions and casual acquaintances	8,846.7492	199.8859
	Preferred companions	8,874.8857	228.0224

instance captured on video during December 2018, a dolphin blew air bubbles into the cage to frighten fish into escaping from a small hole in the netting (Currier, 2019; Tummons, 2021). During a sixth encounter it was noted that dolphins were feeding on what looked like escaped fish, though this behavior was not photographed.

Over the course of CRC field studies off all the main Hawaiian Islands, bottlenose dolphins were encountered 137 times off Hawai‘i Island, and 234 times off all other islands. Of these, mixed groups involving bottlenose dolphins and nine other species of cetacean were documented on 81 occasions (18 off Hawai‘i Island and 62 times off other islands; Table S3). No mixed groups involving bottlenose and spinner dolphins were documented during CRC surveys.

Interspecific aggression was directed towards other species of cetaceans in one of 18 CRC mixed-species encounters off Hawai‘i Island (with melon-headed whales, *Peponocephala electra*, in 2010) and four of 62 cases off other islands (two each with false killer whales and humpback whales, *Megaptera novaeangliae*). When incorporating community science encounters, a total of eight confirmed and one suspected aggressive interspecific interaction were directed towards other cetacean species off Hawai‘i Island, including the aforementioned melon-headed whales, as well as false killer whales, spinner dolphins, and pantropical spotted dolphins (see Table S4 for detailed narratives of each interaction). All the aggressive interspecific interactions except for the melon-headed whale interaction occurred between 2016 and 2021. Two of these interactions occurred at the kanpachi farm, and an additional two took place within 5 km of the farm. Six of the seven aggressive interactions where the identity of one or more bottlenose dolphins was known involved the repeat farm associated male dolphin HITt0201, and four of those cases also included other farm associated dolphins. Social media video footage captured on an unknown date in 2020 also showed HITt0201 attempting to steal a fish that closely resembled a kanpachi from a Hawaiian monk seal, although at no point in the footage did HITt0201 attempt to ram or bite the seal, and there is no indication that the interaction escalated to become aggressive. No additional documented community science encounters from other areas in the main Hawaiian Islands involved bottlenose dolphin aggressive interspecific interactions, despite photograph or video contributions from well over 1,000 encounters spanning almost 40 years.

4 | DISCUSSION

Our study reveals the unintended consequences of a mariculture facility on protected species in Hawaiian waters, and illustrates the potential for such negative consequences on cetaceans elsewhere.

4.1 | Patterns of farm association

We identified 36 individual bottlenose dolphins at the farm, about one-quarter of the estimated Hawaiʻi Island resident population (Van Cise et al., 2021). Twenty-two of the dolphins seen at the farm were repeatedly documented there. Such long-term associations could lead to unknown consequences at a population level, especially if they alter social structure, as has been the case with bottlenose dolphins around other fish farm facilities (Díaz López & Bernal Shirai, 2008). Lagged association rates suggest that this may already be happening, as farm associated dolphins appear less likely to maintain long-term associations with one another, possibly because of decreased need for group cooperation while foraging at the farm (Figure 3). Weak social ties have been associated with decreased survival rates in other odontocete populations (Frère et al., 2010; Stanton & Mann, 2012), but the long-term impacts to survival within this population remain unclear.

Our results also suggest that there may be differences in group sizes for bottlenose dolphins at and away from the farm, as the mean group size of encounters at the farm was less than half the mean group size of encounters away from the farm. While the difference in group size by encounter location was not found to be statistically significant, the power to detect any differences was low given the small sample size for CRC encounters around the farm. Díaz López and Bernal Shirai (2008) found that dolphins in association with a fish farm off Sardinia had similar group sizes while feeding at versus away from the farm, and further research is needed to determine whether the apparent difference in group size at the kanpachi farm is real or just an artifact of sample size.

No mother/calf pairs were documented photographically at the farm and only a single sighting of a mother-calf pair at the farm has been reported, although they have been regularly documented in the population. This suggests that mothers with young calves are not regularly feeding around the farm, which may be a response either to aggression from other bottlenose dolphins, perceived dangers associated with the pens themselves, or to aggregated shark populations surrounding the farm. A 2010 telemetry study of sandbar (*Carcharhinus plumbeus*) and tiger shark movements in Hawaiʻi found that sandbar sharks showed fidelity to a now-removed mariculture installation off Oʻahu, while tiger sharks were transient visitors at the kanpachi farm (Papastamatiou et al., 2010). Local divers have also reaffirmed that multiple species of sharks are regularly present at the farm (Dylan Currier, personal communication, July 2021). Mother-calf pairs may be avoiding the farm to reduce the risk of predation by sharks, as calves are particularly vulnerable due to their small size. Similar avoidance of areas of high shark density by mother-calf pairs of Indo-Pacific bottlenose dolphins (*T. aduncus*) has been previously reported in Australia (Heithaus & Dill, 2002).

4.2 | Potential drivers of farm association

The rate at which new individuals have been documented at the farm (Figure 1) suggests that our sample represents only a portion of the total number of individuals associating with the farm, either due to continued recruitment to the farm, or inadequate effort to identify all farm associated individuals. While it is possible that changes in the availability of prey in the areas surrounding the farm are a driver behind the increasing number of individuals associating with the farm, there is little data available to substantiate this possibility. However, the close social connections and wide distribution of farm associated dolphins within the social network (Figure 2) do suggest that the habit of frequenting the fish farm might be spreading from the original individuals who first engaged in this behavior to their more proximate associates (Figure S2). Bottlenose dolphins are known to socially share information, with evidence suggesting cultural transmission of behaviors (King & Janik, 2015; Simões-Lopes et al., 2016). Given that the majority of individuals regularly seen at the fish farm occupy adjacent positions in the social network, there is reason to suspect that the habit of feeding at the farm might be gradually spreading to other individuals.

Instances of bottlenose dolphins at the farm feeding on fish that closely resemble kanpachi suggest that the dolphins are not primarily present only to predate on wild finfish attracted to the cages, but more likely have consistently returned to the cages to predate on the farmed kanpachi themselves. Bottlenose dolphins in Hawaiʻi consume a wide variety of reef and nearshore fish, likely including native kanpachi, and it is highly probable that the farm presents an appealing food source for nearby dolphins (Baird, 2016). Mariculture facilities are known to have an aggregative effect, with high nutrient concentrations, physical structure, and even the sounds of the facility attracting wild fish populations and their predators (Callier et al., 2018). However, there is also evidence that the farmed fish themselves are attracting bottlenose dolphins. Blue Ocean Mariculture has admitted to regular minor fish escapes, which the dolphins are known to take advantage of (BOM, 2016–2020; Seafood Watch, 2020; Sims, 2013). We have also presented evidence that dolphins have found direct ways to encourage fish to escape using different strategies. One dolphin encouraged fish to escape out of a submerged gate, and another used air bubbles to encourage fish to escape from a small hole in the cage netting (Video S1; Currier, 2019; Tummons, 2021). These troublesome behaviors reinforce associations with the farm and are problematic for the farm as well, which is losing valuable fish to escapes in these interactions. Additionally, frequent exposure to predators has been linked to increased stress levels in farmed fish, resulting in impacts such as immunosuppression and decreased growth rates that may pose further problems for the farm (Morris, 1996; Nash et al., 2000).

There are accounts that some staff during the farm's early years were feeding bottlenose dolphins (Baird, 2016). Though these activities were not sanctioned by the farm, they likely conditioned some dolphins to not only maintain associations with human activities, but to actively seek them out, as has been suggested at other fish farms where provisioning takes place (Díaz López, 2017; Kristy Long, personal communication, March 2021). Provisioning has been linked to decreased calf survival and reduced female reproductive success in Australian Indo-Pacific bottlenose dolphins, as well as long-term behavioral impacts that were sustained even after a reduction in provisioning (Foroughirad & Mann, 2013; Senigaglia et al., 2019). The farm may also be indirectly increasing fisheries interactions by attracting greater numbers of recreational fishermen to the area around the facility than might be otherwise expected. BOM has reported, and interviews with local fishers have reaffirmed that the areas around the farm have become a coveted spot for recreational fishermen targeting aggregated fish populations (Jessica Powell, personal communication, December 2021; Wong, 2022), raising the potential for detrimental interactions with bottlenose dolphins. Indirectly, increases in recreational fishing pressures on prey resources could further reinforce bottlenose dolphin associations with the farm if wild fish stocks become unreliable for the dolphins, as the farm would present a consistently available alternative food source. However, confirming this theory is impossible at present given the lack of available data about recreational fisheries effort or catches, as well as incomplete understanding of the diet of bottlenose dolphins in the area.

4.3 | Interspecific aggression

As noted, aggression by bottlenose dolphins towards other cetaceans has been increasingly documented off Hawai'i Island in recent years. Interspecific aggression in itself is not surprising—bottlenose dolphins have a reputation for such behavior, and are known to regularly associate with other species in contexts ranging from cooperative foraging to frequently documented aggressive socio-sexual behaviors and infanticide (Cotter et al., 2012; Crespo-Picazo et al., 2021; Dunn et al., 2002; May-Collado, 2010; Methion & Díaz López, 2021; Patterson et al., 1998; Syme et al., 2021; Wedekin et al., 2004; Zaeschmar et al., 2013). However, the repeated documentation of aggressive encounters directed towards spinner dolphins off Hawai'i Island, many near the Makako Bay farm and involving farm associated dolphins, is particularly striking. These two species overlap throughout the main Hawaiian Islands yet rarely interact (Baird et al., 2009, 2013; Stack et al., 2020), and such aggressive interactions have only been reported, so far, off Hawai'i Island, despite over 20 years of widely distributed survey effort (e.g., Baird et al., 2013) and community science contributions from well over 1,000 encounters with bottlenose dolphins spanning almost 40 years throughout the main Hawaiian Islands. Two of the aggressive encounters took place at the farm itself, two additional encounters have taken place within 5 km of the farm, and all aggressive interactions have taken place after the farm was installed, despite substantial survey effort and dozens of community science contributions from the area previously (Figure S1). Additionally, six of the seven aggressive interactions where the bottlenose dolphins could be identified have involved farm associated animals, further demonstrating a link between the farm and the aggressive behaviors that so far have been undocumented elsewhere within the main Hawaiian Islands. While all but one of the confirmed aggressive interactions where the bottlenose could be identified involved HITt0201, other farm associated bottlenose dolphins were also involved in four aggressive interactions, suggesting that the trend of aggressive encounters near the farm cannot be fully explained by the aberrant behaviors of a single individual. We believe that the high frequency of aggressive interspecific interactions in this area is a direct consequence of the presence of the farm, which is altering both the behavior and distribution of bottlenose dolphins in ways that lead to conflict between species.

The fact that the aggressive interactions at the farm involved multiple combinations of species also indicates that the fish farm is affecting multiple populations. By bringing species into closer proximity to one another for longer periods of time than if the farm were absent, the farm is increasing the opportunities for interspecific interactions, including those that are aggressive. For example, observations (Tyne et al., 2018) and predictive habitat modelling (Thorne et al., 2012) have shown that nearby Makako Bay is an ideal resting habitat for spinner dolphins, who use shallow water areas during the daytime. The presence of the farm has brought bottlenose dolphins into closer regular association with nearby spinner dolphins than might be expected otherwise, apparently resulting in at least four instances of bottlenose dolphins harassing spinner dolphins. If the dolphins are attracted to the site due to the structure itself acting as a fish aggregating device, similar situations may result from the expansion of marine infrastructure in general, including the rapid expansion of offshore wind farms. Marine infrastructure is known to support aggregations of marine wildlife attracted to biofouling on the structures (Callier et al., 2018), including populations of marine mammals (Russell et al., 2014). Such aggregations could increase the potential for intra- and interspecific aggression stemming from territorial behaviors, and further research and monitoring is needed to explore the long-term consequences of marine infrastructure expansions on wildlife behavior.

Several surveys of Makako Bay by CRC and community scientists in 2021 and 2022 have found no spinner dolphins (Table S5), and tour operators have noted that spinner dolphins appear to have abandoned the bay in the last couple of years (Colin J. Cornforth, personal communication, April 2022; D. Perrine, personal observation). We suggest this abandonment of an important daytime resting area for this species is likely due in part to the increased presence of bottlenose dolphins because of the fish farm, though other factors such as extensive ecotourism or increased presence of sharks in the area may have also played a role. NOAA Fisheries prohibited swimming with spinner dolphins and otherwise approaching them within 50 yards (42 m) in October 2021, and all commercial activities directed towards spinner dolphins have declined as a result. Despite this, as of December 2022 spinner dolphins have not reoccupied the site. The large number of aggressive interspecific interactions that have been captured on camera near the farm and involving farm associated bottlenose dolphins strongly suggests that the presence of the fish farm is a much more significant driver in this particular circumstance. By altering the distribution of bottlenose dolphins, the farm has unintentionally altered the distribution of other species, a prime example of the unintended consequences that can stem from mariculture facilities.

4.4 | Conclusion

Given current human population trajectories, the rapid global expansion of mariculture seems unlikely to slow down. However, as we have demonstrated, placing mariculture facilities within the range of protected species carries with it a considerable risk of unintended consequences. The spectrum of these consequences ranges from changes in distribution and behavioral changes to more complex scenarios that include interspecific interactions and population-level effects. Further research into the long-term ecological impacts of mariculture to protected species is needed, as are the development of safe and effective mitigation strategies.

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AUTHOR CONTRIBUTIONS

Annette Harnish: Conceptualization; formal analysis; visualization; writing – original draft; writing – review and editing. **Robin Baird:** Conceptualization; data curation; funding acquisition; investigation; project administration; writing – original draft; writing – review and editing. **Enrico Corsi:** Formal analysis; methodology; visualization; writing – original draft; writing – review and editing. **Antoinette Gorgone:** Data curation; writing – review and editing. **Doug Perrine:** Investigation; writing – review and editing. **Alicia Franco:** Investigation; writing – review and editing. **Cynthia Hankins:** Investigation; writing – review and editing. **Emily Sepeta:** Investigation; writing – review and editing.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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