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# False killer whales and fisheries in Hawaiian waters: evidence from mouthline and dorsal fin injuries reveal ongoing and repeated interactions

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ABSTRACT: Monitoring bycatch in fisheries is essential for effective conservation and fisheries sustainability. False killer whales *Pseudorca crassidens* in Hawaiian waters are known to interact with both commercial and recreational fisheries, but limited observer coverage across Hawaiian fisheries obscures the ability to assess bycatch. We build upon previous work and assess occurrence of fisheries interactions through photographic evidence of dorsal fin and mouthline injuries for 3 false killer whale populations in Hawaiʻi. Photographs of injuries on dorsal fins and mouthlines collected between 1999–2021 were scored for consistency with fishery interactions ('not consistent', 'possibly consistent', 'consistent'). For individuals with both dorsal fin and mouthline photos available, the endangered main Hawaiian Islands (MHI) population had the highest rates of injuries consistent with fisheries interactions (28.7% of individuals), followed by the pelagic stock (11.7%), while no individuals from the Northwestern Hawaiian Islands population with both types of photos had fisheries-related injuries. Some individuals from the MHI population were documented with multiple fisheries-related injuries acquired on different occasions, indicating repeated interactions with fisheries. Individuals first began acquiring injuries consistent with fishery interactions at an estimated age of 2 yr. Females were more likely to have fisheries-related dorsal fin injuries than males, but rates of fisheries-related mouthline injuries were similar between the sexes. Injuries consistent with fisheries interactions were acquired throughout the study period, indicating that this is an ongoing issue, not a legacy of past fishery interactions. Our results suggest that efforts to reduce bycatch and begin monitoring of fisheries that overlap the range of the endangered MHI population are needed.

KEY WORDS: *Pseudorca crassidens* · False killer whale · Bycatch · Fisheries interaction · Hawaiʻi · Injuries · Age · Monitoring

HŌʻULUʻULU MANAʻO: He kūpono nō ka makaʻala ʻana aku i nā iʻa hopu ʻia ma ka ulia i mea e kūleʻa ai ka maluō a me ka paepae ʻane aku i nā kai lawaiʻa. ʻIke ʻia ka *Pseudorca crassidens* ma ke kai o Hawaiʻi ma ko lākou launa ʻana ma nā kai lawaiʻa kālepa me nā kai lawaiʻa leʻaleʻa pū kekahi. ʻO ka noiʻi i hana mua ʻia ke kahua no mākou a kālailai mākou i ka nui o nā hanana kai lawaiʻa ma o nā kiʻi o nā ʻeha ma ke kualā a me ka waha no nā pūʻuo ʻekolu o ka *P. crassidens* ma Hawaiʻi. Ana a hoʻohālikelike ʻia nā kiʻi o nā ʻeha kualā me nā ʻeha waha i ʻohi ʻia ma nā makahiki 1999–2021 no ka like me ka nui o nā hanana kai lawaiʻa (ʻʻaʻole like', 'like paha', 'like nō'). No nā mea me nā kiʻi o nā

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ʻeha ʻelua ma ke kualā a me ka waha, ʻo ka pūʻuo o ka Paeʻāina Hawaiʻi Nui (MHI) ka mea i nui kona pākēneka o nā ʻeha i kū i nā hanana kai lawaiʻa (28.7% o nā mea), a ma hope maila ka pūʻuo kūwaho (11.7%), a ʻaʻohe mea o ka pūʻuo Paeʻāina Hawaiʻi Noweke, me nā ʻano kiʻi ʻelua, i loaʻa i nā ʻeha hanana kai lawaiʻa. Paʻi kiʻi ʻia kekahi mau mea o ka pūʻuo MHI me kekahi mau ʻeha hanana kai lawaiʻa i loaʻa ma nā wā ʻokoʻa, he hōʻailona ia o nā hanana kai lawaiʻa he nui. Loaʻa mua paha ia mau ʻeha hanana kai lawaiʻa ma ka piha ʻana aʻe o nā makahiki he ʻelua iā lākou. ʻOi aku ka nui o ka papaha e loaʻa nā ʻeha kualā o ka hanana kai lawaiʻa i nā wāhine ma mua o nā kāne, like naʻe ka papaha o nā ʻeha waha o ka hanana kai lawaiʻa i nā keka ʻelua. Ma ka wā o ke kālailai, ua ʻano maʻa mau nā ʻeha hanana kai lawaiʻa i loaʻa a he hōʻailona nui ia i ke kūmau o kēia pilikia, ʻaʻole ia he hoʻoilina o nā hanana kai lawaiʻa o ke au i hala. Hōʻike mai kā mākou mau hua kālailai i ka pono e hoʻēmi i nā hopua ulia a e hoʻomaka i ka makaʻala i nā kai lawaiʻa e kaulapa i ke anapuni o ka pūʻuo ʻane halapohe MHI.

## 1. INTRODUCTION

Marine predator bycatch and depredation in commercial and recreational fisheries is a global issue, with consequences for both conservation and fisheries economics (Read 2008, Hamer et al. 2012, Lewison et al. 2014, Mitchell et al. 2018, Jog et al. 2022). Species with slow life histories (i.e. *K*-selected species) are particularly vulnerable, including a number of marine mammals (Davidson et al. 2012). Bycatch in fisheries has led to the decline of several marine mammal populations, and even the extinction of a river dolphin (baiji *Lipotes vexillifer*, Turvey et al. 2007). Thus, monitoring and assessing impacts of bycatch is critical to developing effective management efforts for these species (Wade et al. 2021).

Globally, false killer whales *Pseudorca crassidens* are listed as Near Threatened by the IUCN, due to a combination of bycatch in fisheries, directed takes in some areas, and susceptibility to population effects from bycatch and takes, given their slow life history (Baird 2018). In Hawaiian waters, false killer whales feed on a wide variety of both pelagic and reef-associated game fish, including ahi *Thunnus albacares*, aku *Katsuwonus pelamis*, mahimahi *Coryphaena hippurus*, monchong *Eumegistus illustrus*, uku *Aprion virescens*, kāhala *Seriola quinqueradiata*, and ulua aukea *Caranx ignobilis*, among others (Baird et al. 2008, 2023). All of these species are targeted by either commercial or recreational fisheries in Hawaiʻi, and false killer whales have been known to depredate catch from hook and line fisheries there since at least the early 1960s (Pryor 1975). Reports of depredation of tunas and billfish have been frequent but largely anecdotal in nature (Shallenberger 1981, Nitta & Henderson 1993), and actual documentation of depredation and bycatch in Hawaiian waters is limited, as only longline fisheries are required to use observers, and even then have limited coverage of the fishery as a whole (Forney et al. 2011). Observers in the Hawaiʻi-based longline fisheries document incidents of both protected species bycatch and depredation, and record details such as gear type and crew response (Forney et al. 2011). Observer coverage of the shallow-set longline fishery targeting swordfish *Xiphias gladius* reached 100% in 2004 and has been maintained at this level since then (Forney et al. 2011). Coverage of the deep-set longline fishery targeting bigeye tuna *T. obesus* reached 20% in 2001 and has fluctuated from 18% to 28% through 2023, but was reduced to 13.5% in 2024, with plans to reduce coverage again to 7% in 2025 (Forney et al. 2011, National Oceanic and Atmospheric Administration 2024). In the deep-set longline fishery, false killer whales are the most frequently recorded bycaught cetacean (Forney et al. 2011) and are thought to be responsible for the majority of depredation (Fader et al. 2021).

Around the main Hawaiian Islands (MHI), 3 overlapping populations of false killer whales have been recognized, based on a combination of association patterns of photo-identified individuals, genetics, and satellite-tagging (Baird et al. 2008, 2012, 2013, Martien et al. 2014, Bradford et al. 2015). An offshore population, referred to as the Hawaiʻi pelagic stock, ranges broadly inside and outside of the US exclusive economic zone (EEZ) surrounding the archipelago, and individuals occasionally come nearshore and pass through the islands (Anderson et al. 2020, Fader et al. 2021). This population overlaps with both US and international longline fisheries, as well as with nearshore fisheries. Two insular populations also exist, referred to as the Northwestern Hawaiian Islands (NWHI) stock and the MHI insular stock (Carretta et al. 2023). Groups from the NWHI population appear to spend most of their time in what is now the Papahānaumokuākea Marine National Monument (Baird et al. 2013, Kratofil et al. 2023a), and fishing effort has largely been excluded within the range of this population. Thus, individuals from this population have likely had limited interactions (i.e. depredation, hooking, or entanglement) with fisheries, at least in recent years.

Individuals from the MHI insular population, by contrast, overlap with a variety of commercial and recreational nearshore fisheries that target many of the same fish species that false killer whales feed on (Boggs & Ito 1993, Glazier 2007, McCoy et al. 2018, Baird et al. 2021). Prior to 1992, much of the US-based longline fishing effort was around the MHI (Boggs & Ito 1993, He et al. 1997), but in March 1992, longline fishing was excluded from an area around the MHI to reduce conflicts with nearshore fisheries. Today, by far the largest commercial gear type used around the MHI is trolling with lures, responsible for 74% of the days fished, based on State of Hawaiʻi commercial marine license data from 2007 through 2018 (Baird et al. 2021). However, other types of commercial fishing, i.e. trolling with bait, deep-sea handline, rod and reel, and palu-ahi, which is a traditional hook and line technique that utilizes a cloth bag of chum deployed at depth with a lead weight (Glazier 2007), were responsible for the highest levels of fishing effort in areas with the greatest potential for interactions between false killer whales and individual fishermen (Baird et al. 2021). Understanding of actual interactions or bycatch is limited, however, as there are no observer programs or other monitoring (e.g. electronic monitoring) in any of the nearshore fisheries around the Hawaiian Islands.

Several lines of evidence suggest the MHI insular population experienced a large decline in abundance between the late 1980s and the early 2000s (Baird 2009, Reeves et al. 2009, Oleson et al. 2010, Silva et al. 2013), and in 2012, this population was listed as endangered under the US Endangered Species Act (National Oceanic and Atmospheric Administration 2012). Based on recent analyses, the population again appears to be in decline, and in 2021 was estimated to number approximately 138 individuals (95% credible interval = 120–160, Badger et al. 2024). The factors that led the population to decline are unknown, but may include bycatch in fisheries, deleterious health effects due to high exposure to persistent organic pollutants, reduced prey availability, and deliberate killing (Baird 2009, Ylitalo et al. 2009, Oleson et al. 2010, Kratofil et al. 2020).

With no observer programs for fisheries around the MHI, evidence for fisheries interactions comes from indirect sources, including stranded animals and live individuals showing evidence of prior fishery interactions (e.g. Baird & Gorgone 2005, Kiszka et al. 2008, Moore & Barco 2013, Machernis et al. 2021). False killer whales are individually identified based on photographs of the dorsal fin and surrounding area (Baird et al. 2008). Baird & Gorgone (2005) documented dorsal fin disfigurements of 3 live animals, now known to be part of the MHI insular population, that were consistent with interactions with fishing gear. A more recent study used photos from 2000–2013 of all 3 recognized stocks and found that individuals from the MHI insular population had significantly higher rates of dorsal fin injuries that were consistent with fishery interactions than either the pelagic or NWHI populations (Baird et al. 2015). Additionally, the same study found that females have a higher rate of dorsal fin injuries consistent with fisheries interactions than males, and fisheries-related injury rates might vary by social cluster for the MHI population (Baird et al. 2015). Stack et al. (2019) reported bent dorsal fins in 2 out of 82 false killer whales documented off Maui, also thought to be from fisheries interactions.

Such injuries, typically to the leading edge of the dorsal fin, presumably originate when an animal is hooked in the mouth and struggles against the taut line, as is seen in observer video footage from the longline fishery (Pacific Islands Regional Office unpubl. data, see Baird & Gorgone 2005), although injuries to other areas of the body can also occur if an animal becomes entangled during the process. Presumably not all animals struggle in the same way after being hooked, and thus dorsal fin injuries are likely to represent only a subset of those individuals that survive hooking. Given that the majority of animals are likely hooked in the mouth, mouthline injuries caused by hooking may be a better representation of trends in hooking within and between populations, although head and mouth photos are often not available and frequently not matched to individual identifications.

Field efforts to photographically document false killer whales in Hawaiian waters have continued since the Baird et al. (2015) study, including research efforts by multiple independent groups and contributions from an increasing number of citizen scientists (Mahaffy et al. 2023). Additionally, new photos from 2000–2013 that were not originally included in the Baird et al. (2015) study have become available, so the current sample size of individual encounters available for assessment of fisheries-related injuries is roughly double that which was utilized in the earlier study. In recent years, particularly with the increased availability of fast high-resolution digital cameras, efforts have been made to obtain head (and thus mouthline) photos that are matched to individual identifications. Since the Baird et al. (2015) study, additional genetic samples are available to confirm the sex of more individuals in all 3 populations, and research examining the social structure of MHI false killer whales has revealed that there are 4 social clusters within that population (Mahaffy et al. 2023), as compared to the previously recognized 3 (Baird et al. 2012).

This study characterizes evidence of fisheries interactions among false killer whales in Hawaiian waters, using this expanded dataset of dorsal fin and mouthline photographs and updated knowledge of false killer whale social structure. We assess interaction rates by population, sex, and, for the MHI insular population, by social cluster. In addition to assessing variation in injury rates among clusters, we also examine association patterns of individuals with and without fisheries-related injuries, to see if injured individuals preferentially associate. We also use information on the estimated age of well-documented individuals (Kratofil et al. 2023b) to determine at what age individuals first begin interacting with (i.e. are hooked and subsequently injured by) fishing gear. Finally, we also determine whether the injuries observed are contemporary (i.e. from recent years), or a legacy of past interactions (e.g. from before the early 1990s, when longline fishing occurred closer to shore). Combined, these lines of investigation provide the best available data for interactions between MHI insular false killer whales and fisheries over the past 2 decades. We also provide suggestions for measures to reduce uncertainty and better understand the consequences of fishery interactions for these populations.

## 2. MATERIALS AND METHODS

Photographs of false killer whales available from 1999 to 2021 were used in this analysis (see Mahaffy et al. 2023). Following the protocol from Baird et al. (2008), encounters were sorted by individual and each individual was assigned a dorsal fin distinctiveness rating: 1 = not distinctive, 2 = slightly distinctive, 3 = distinctive, 4 = very distinctive. Each sighting was also assigned a photo quality score between 1 and 4 (1 = poor, 2 = fair, 3 = good, 4 = excellent), following Baird et al. (2008). Individual identification was conducted following the methods of Baird et al. (2008) and Mahaffy et al. (2023), using a combination of dorsal fin features (e.g. shape, notches) and body scars to identify and confirm matches. Identified individuals were each given a unique ID number (e.g. HIPc310) and were assigned to 1 of 3 stocks based on a combination of genetic results (Martien et al. 2014), location of sightings, satellite-tag data (see Bradford et al. 2015), and associations. Groups of individuals for which insufficient information was available to determine stock were classified as unknown. Individuals from the MHI insular stock were further assigned to 1 of 4 social clusters based on Mahaffy et al. (2023). When possible, the sex of individuals was identified using genetic analysis of biopsy samples (Morin et al. 2005, Chivers et al. 2010), by the presence of neonates or small calves in close proximity, or by morphology (e.g. head shape, leading edge dorsal fin hump, see Kratofil et al. 2023b). Age classes (calf [neonate to <3 yr], juvenile [⩾3 to <6 yr], sub-adult [⩾6 to <10 yr], or adult [10+ yr]) were assigned to each sighting of each MHI individual based on a number of factors, including relative body size, year first documented, and morphology (Kratofil et al. 2023b). All available lines of evidence were incorporated into the age estimates, including those derived from sightings occurring prior to 1999 or after 2021. Each individual was assigned an age class confidence rating following Kratofil et al. (2023b) ranging from 1 (low) to 5 (high). Only individuals with confidence ratings of 3 to 5 were used to assess the proportion of injuries among different age classes, but all available photos were used to identify when individuals that span multiple age classes first acquired injuries.

Dorsal fin and mouthline photos were examined for evidence of scarring or injuries following the protocol of Baird et al. (2015, 2017). Due to the large number of dorsal fin photos available, all photos were initially evaluated to identify sightings of individuals with damaged fins, for which representative photos of the injury, as well as photos pre-injury (when available), were compiled. When individuals had multiple separate instances of dorsal fin damage, representative photos were compiled for each unique injury, as well as photos pre-injury (when available). For mouthline assessments, all available photos for each individual from each sighting were compiled for assessment, as there were relatively few to assess. Details of mouthline injuries could easily be obscured by water or influenced by focus, and the majority of individuals had some form of scarring on the mouthline (whether from natural causes or fishery interactions) that merited assessment. For each sighting with mouthline photos available, the percentage of the mouthline visible for that sighting was estimated (e.g. 100% = entire view of both sides of mouthline, 50% = entire view of 1 side or portions of both sides of mouthline equating to 50% total). The compiled mouthlines for each sighting and dorsal fin photos of each potential injury were then independently scored by 4 reviewers as either 'consistent', 'possibly consistent', or 'not consistent' with a fisheries interaction. All reviewers had previous experience in photo-identification of false killer whales, as well as training in identifying injuries typical of fisheries interactions. A score was assigned to each potential dorsal fin injury, and to each sighting of the mouthline. If any reviewer felt they could not accurately assess a photo due to photo quality or other factors that obscured a clear view of the focal area, the reviewer scored the photo as 'undeterminable', and these photos of a particular individual were removed from consideration in the analysis regardless of the number of reviewers that scored the photo as 'undeterminable'.

Scarring and injuries to the dorsal fin considered consistent with fisheries interactions included deep notches to the leading edge of the dorsal fin, often seen with linear scarring extending from the notch along the side of the fin, and linear cuts into the dorsal fin, likely to have been caused by a monofilament line. Dorsal fin disfigurements also considered consistent with fisheries interactions include missing, collapsed, or bent dorsal fins (Baird & Gorgone 2005). Evidence of injuries on the mouthline considered consistent with fisheries interactions included lacerations along the mouthline, white scar tissue indicating major damage, or tissue loss (i.e. notches along the mouthline or in the gape). Additionally, though not factored into the dorsal fin or mouthline scores, reviewers noted any additional scarring from other areas of the body that may be indicative of a previous fisheries interaction, such as scarring on the peduncle or pectoral fins indicative of potential line wrap injuries.

Each of the ratings for both dorsal fin and mouthline injuries were converted to a numerical score of 3 ('consistent'), 2 ('possibly consistent'), or 1 ('not consistent'). Following protocol from Baird et al. (2015), we calculated the mean of the 4 reviewer scores for each individual's dorsal fin and mouthline scores. For individuals with mouthline photos that were seen multiple times, we used the highest mean score available from all sightings. Higher scores for mouthlines typically occurred with better-quality photos or when photos were available from both sides of the individual, and thus allowed for a more robust assessment of the cause of injuries. For all dorsal fins where no evidence of damage was noted during initial review (and for any dorsal fins not selected for review), an automatic mean highest score of 1 was assigned. This resulted in each individual having a single dorsal fin score, and each individual with mouthline photos of sufficient quality available also having a single mouthline score. We considered individuals with mean highest scores $\geqslant 2.5$ for either dorsal fins or mouthlines to have injuries consistent with a fisheries interaction, and those with mean highest scores $\geqslant 2$ but $<2.5$ to have injuries that were possibly consistent with a fisheries interaction.

Various restrictions were applied during analysis to reduce bias (Table 1). For most analyses, we consid-

Table 1. Summary of restrictions applied for different analyses of false killer whale dorsal fins and mouthlines. MHI: main Hawaiian Islands

| Analysis | Restrictions |
|---|---|
| Dorsal fin — Stock | 1999–2021, no 'undeterminable' scores, good or excellent photo quality, highest distinctiveness >1, individuals from known stocks |
| Dorsal fin — MHI cluster | 1999–2021, no 'undeterminable' scores, good or excellent photo quality, highest distinctiveness >1, individuals from the MHI stock |
| Dorsal fin — Sex | 1999–2021, no 'undeterminable' scores, good or excellent photo quality, highest distinctiveness >1, individuals of known sex |
| Dorsal fin — Age class | Only individuals seen in 1999 or later, individuals from the MHI stock, age class confidence ratings ⩾3 |
| Dorsal fin — Date injury occurred | None |
| Mouthline — Stock | 1999–2021, no 'undeterminable' scores, >50% of mouthline visible, highest distinctiveness >1, individuals from known stocks |
| Mouthline — MHI cluster | 1999–2021, no 'undeterminable' scores, >50% of mouthline visible, highest distinctiveness >1, individuals from the MHI stock |
| Mouthline — Sex | 1999–2021, no 'undeterminable' scores, >50% of mouthline visible, highest distinctiveness >1, individuals of known sex |
| Mouthline — Age class | Only individuals seen in 1999 or later, individuals from the MHI stock, age class confidence ratings ⩾3 |
| Mouthline — Date injury occurred | None |

ered only individuals at least slightly distinctive at some point in their sighting history, in order to reduce the chance of mismatched identifications being included in the dataset. For the analyses of age class, non-distinctive individuals were included to minimize bias, as younger animals tend to be less distinctive. Additionally, age class analyses were restricted to individuals from the MHI stock, due to the limited sighting histories of most pelagic and NWHI animals. The dorsal fin analysis was also restricted to individuals with good or excellent photo quality (Table 1). For mouthline photos, all were considered except for those sightings with 1 or more 'undeterminable' scores, which resulted in the removal of that sighting for assessment. To reduce negative bias from partial views, the mouthline analysis was restricted to cases where ⩾50% of the entire mouthline was visible (i.e. ⩾1 entire side of the mouthline, or proportions of both sides equivalent to ⩾50% of the entire mouthline).

All statistical tests were performed in R v.4.2.1 (R Core Team 2022). To explore any potential confounding variables for dorsal fins, we assessed how the proportion of animals with consistent injuries varied between those individuals with photos of both or just one side of the dorsal fin, or with good versus excellent photo qualities, with a Fisher's exact test, using the fisher.test() function. For mouthlines, we evaluated how the proportion of the mouthline visible varied between stocks, social clusters, and sexes. Kruskal-Wallis ANOVAs were used to test for differences in proportion of the mouthline visible by stock and cluster, using the kruskal.test() function. A Mann-Whitney *U*-test was used to test for differences between sexes in the proportion of mouthline visible by ID, using the wilcox.test() function. We also evaluated whether there was a difference in the proportion of mouthline visible between individuals with and without injuries with a Mann-Whitney *U*-test. To test for differences in the frequency of fisheries interactions by stock, cluster membership, and sex, the proportion of individuals with injuries considered consistent with fisheries interactions were compared using a Fisher's exact test. All statistical tests were 2-tailed.

For individuals seen on >1 occasion, we examined the time series of dorsal fin and mouthline photos available for each individual to identify the narrowest possible time frame for when the injury occurred (e.g. between year X and year Y). The most recent encounter an individual was seen without an injury prior to the first encounter the injury was documented was used as the lower bracket of the time frame the injury may have been acquired. Temporal evaluation of photos to identify when injuries most likely occurred used all available photos, including those from before 1999, regardless of photo quality or proportion of mouthline visible. Given the increased certainty surrounding the age of individuals documented as calves, juveniles, and sub-adults, we were able to use the ages of these individuals to narrow down the time frame for when individuals documented with injuries as calves, juveniles, and sub-adults acquired injuries. For these individuals, if they had no other information (e.g. no mouthline photos) available to assess the earliest year the individual could have acquired an injury, and had a high confidence age estimate (confidence rating of 3 or higher), we chose the year the individual was estimated to be 1 yr old to bracket the time frame the injury or injuries may have been acquired (see Kratofil et al. 2023b), as we assume that animals <1 yr of age are unlikely to interact with fishing gear. To assess whether there was an interaction between sex and age class (i.e. adult or non-adult) for known-sex individuals, we determined the age class that fisheries-related injuries were first documented, or, when known, first acquired. Given the small sample size by class when broken down by sex, we pooled calves, juveniles, and sub-adults as non-adults. For individuals that were first documented with fisheries-related injuries as adults, we examined the time series (when available) to determine whether injuries were acquired as an adult, versus those that could have been acquired as a non-adult but were first detected as an adult.

To examine association patterns and visualize the distribution of individuals with injuries consistent with fisheries interactions within the social network, we undertook analyses in SOCPROG 2.9 (Whitehead 2009) using MATLAB (MathWorks 2016) following the methodology of Mahaffy et al. (2023). In brief, we used a half-weight index (HWI) of association data to generate a social network. Association data were imported into NetDraw 2.1568 (Borgatti 2002) to generate social network diagrams. All individuals from the MHI population are linked together in the same component of the social network, but for both the NWHI and pelagic populations, multiple components (i.e. groups of individuals linked by association but not linked to other groups) are present. We examined the prevalence of injuries consistent with fishery interactions among components for the NWHI and pelagic populations. To compare social relationships of individuals with and without fisheries-related injuries, we used network measures from the weighted network for *strength* (the weighted-network equivalent of 'degree' in a binary network that measures an individual's gregariousness), *eigenvector centrality* (how well connected an individual is within a network), and *clustering coefficient* (a useful measure of individual sociality, see Croft et al. 2004, Whitehead 2008). We used the maximum HWI to assess the strength and connectivity of dyadic associations across the network using all 3 measures.

We used a Mantel test (Mantel 1967, Schnell et al. 1985) to determine whether those with and without fisheries-related injuries differed in association strength, using 20 000 permutations. The Mantel test was restricted to individuals considered slightly distinctive or above with fair or better photo quality that were seen on ⩾5 days. Because of the latter restriction, only individuals from the MHI population were included in this analysis. We also performed a sensitivity analysis on the Mantel test results (using the same set of restrictions above) for Cluster 1, the cluster with the largest sample size of identifications (see Mahaffy et al. 2023) to determine whether results were also representative within clusters.

## 3. RESULTS

Photos were available from 512 false killer whale sightings between 1999 and 2021. After restrictions (Table 1), there were 504 individuals with suitable dorsal fin photos (274 MHI, 87 NWHI, 134 pelagic, 9 unknown) (Fig. 1A–C), and 201 individuals with suitable mouthline photos (154 MHI, 17 NWHI, 24 pelagic, 6 unknown) (Fig. 1D–F). Of the 504 individuals with dorsal fin photos, 217 were assessed to determine source of injury (Table 2). Though not factored into the dorsal fin or mouthline scores, 29 individuals also had other evidence of possible fisheries interactions, such as injuries to the peduncle or pectoral fins, of which only 3 had dorsal fin injuries, and only 1 (out of 16 with mouthline photos) had mouthline injuries considered consistent with fisheries interactions.

### 3.1. Dorsal fin injuries

Forty-five of the 504 individuals assessed (8.7%) had their mean highest dorsal score by ID ⩾2.5, i.e. they had injuries considered to be consistent with fisheries interactions (Fig. 1A–C, Table S1 in the Supplement at www.int-res.com/articles/suppl/n055p273_supp.pdf). An additional individual with a mean highest dorsal score = 2.5 was included in age and date of injury assessments, though it did not meet the restrictions for inclusion in the stock, cluster, or sex analyses (Table 1). We were able to narrow down the range of years when initial injuries occurred for 21 individuals: 15 individuals using sighting history (i.e. for those individuals first documented prior to injury acquisition), and 6 individuals first documented with injuries as calves, juveniles, or sub-adults (with an age confidence rating of ⩾3) by using the year the individual was estimated to be 1 yr old as the start of the range (Table S1). Seven of these 21 individuals had initial injuries occurring in the first half of our study period (1999–2010), 12 acquired injuries in the second half (2011–2021), and 2 may have occurred in either half (Table S1).

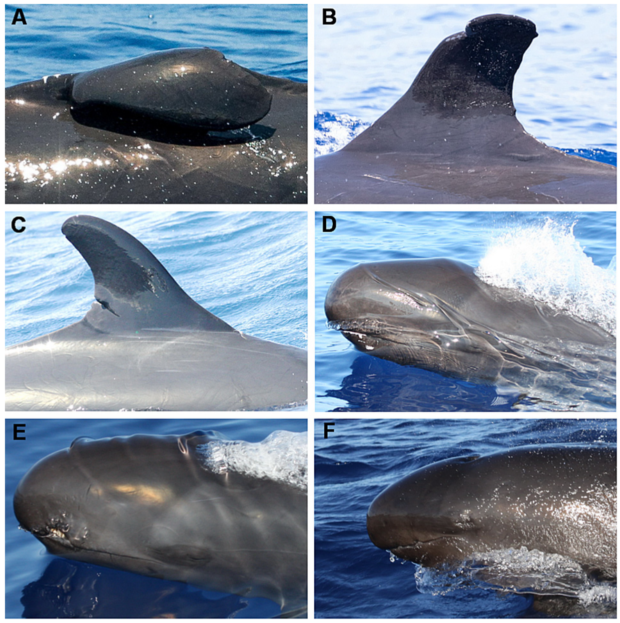


Fig. 1. Examples of injuries considered consistent with fishery interactions for individual false killer whales from the main Hawaiian Islands insular population. (A) Collapsed dorsal fin of HIPc186 with damage to the leading edge of the fin (photo: C. Babbitt). (B) Damage to the leading edge of the dorsal fin of HIPc264 (J. K. Lerma/Cascadia Research). (C) A narrow slice to the trailing edge of the dorsal fin of HIPc805, likely caused by an interaction with a monofilament line (Pacific Whale Foundation). (D) Depigmentation along the mouthline of HIPc230 (E. A. Weiss/Cascadia Research). (E) Large gap in the mouthline of HIPc339 with teeth visible (E. A. Weiss/Cascadia Research). (F) Multiple notches in the mouthline of HIPc356 (K. A. Wood/Cascadia Research)

In addition to the 5 individuals that were seen with amputated, collapsed, or bent dorsal fins prior to the start of the study (4 from the MHI insular population and 1 from the pelagic population), we were able to document full or partial dorsal fin collapse for 3 more individuals, all from the MHI insular population. One individual (HIPc310) was documented with a relatively recent (i.e. unhealed) fishing line injury at the anterior insertion of the dorsal fin in October 2016

Table 2. Summary of false killer whale–fishery interaction assessments by stock (and by cluster for the MHI population), using photos from 1999 through 2021. Numbers represent unique photo-identified individuals. Individuals considered not distinctive are not included. Dorsal fin numbers are restricted to individuals with good or better photo quality, and mouthlines are restricted to individuals with ⩾50% of the mouthline visible in ⩾1 sighting. MHI: main Hawaiian Islands; NWHI: Northwestern Hawaiian Islands

| Stock | MHI cluster | No. with dorsal fins assessed | No. (%) with dorsal fin injuries consistent with fishery interactions | No. (%) with dorsal fin injuries possibly consistent with fishery interactions | No. with mouthlines assessed | No. (%) with mouthline injuries consistent with fishery interactions | No. (%) with mouthline injuries possibly consistent with fishery interactions | No. with both dorsal fin and mouthline assessed | No. (%) with both or either type of injury considered consistent with fishery interactions, of those individuals with both areas assessed |
|---|---|---|---|---|---|---|---|---|---|
| MHI | All | 274 | 35 (12.8) | 37 (13.5) | 154 | 26 (16.9) | 17 (10.4) | 153 | 44 (28.7) |
| MHI | 1 | 69 | 9 (13.0) | 9 (13.0) | 40 | 5 (12.5) | 6 (15.0) | 40 | 10 (25.0) |
| MHI | 2 | 69 | 8 (11.6) | 10 (14.5) | 31 | 4 (12.9) | 0 (0.0) | 31 | 6 (19.4) |
| MHI | 3 | 86 | 15 (17.4) | 14 (16.3) | 55 | 12 (21.8) | 10 (18.2) | 55 | 21 (38.2) |
| MHI | 4 | 50 | 3 (6.0) | 4 (8.0) | 28 | 5 (17.9) | 1 (3.6) | 27 | 7 (25.9) |
| NWHI | – | 87 | 1 (1.1) | 1 (1.1) | 17 | 0 (0.0) | 3 (17.6) | 16 | 0 (0.0) |
| Pelagic | – | 134 | 7 (5.2) | 4 (3.0) | 24 | 3 (10.7) | 2 (7.1) | 17 | 2 (11.7) |
| Unknown | – | 9 | 2 (22.2) | 1 (11.1) | 6 | 1 (16.7) | 0 (0.0) | 1 | 0 (0.0) |
| All stocks | – | 504 | 45 (8.9) | 43 (8.5) | 201 | 30 (14.9) | 21 (10.4) | 187 | 46 (24.6) |

(Fig. 2A). The injury had partially resolved by 2017 (Fig. 2B,C), but was avulsed in 2021 (Fig. 2D,E). By February 2023, the dorsal fin of this individual had begun to collapse, apparently as a result of the injury (Fig. 2F). The dorsal fin of another individual (HIPc316) was partially severed at the base of the leading edge sometime between fall 1999 and July 2008. When resighted in 2008, the dorsal fin had lost some structural integrity from the injury to the leading edge and had started to collapse over to the left side. When this individual was last sighted in 2015, the fin had fully collapsed. A third individual (HIPc398) was documented with a healed leading-edge injury at the base of the fin when first seen in 2006. The individual was resighted in 2010 with 2 additional healed injuries higher up on the leading edge, 1 of which extended across the left side of the fin, causing the fin to bend to the left.

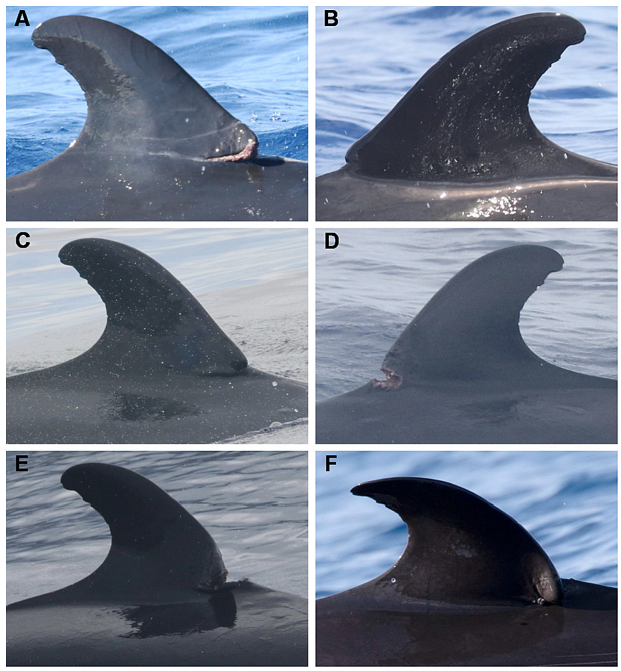


Fig. 2. Time series showing progression of wound healing and reinjury for false killer whale HIPc310 from Cluster 1 of the main Hawaiian Islands insular population. (A) Initial photo of injury (8 Oct 2016, A. M. Gorgone/Cascadia Research). (B) Left lateral view of healed injury (22 June 2020, A. M. Nix/Cascadia Research). (C) Right-side view of healed injury (2 Nov 2021, M. C. Hill/PIFSC). (D,E) Left and right-side views of reinjury (16 Nov 2021, E. Davis/Wild Side Specialty Tours). (F) View of the avulsed wound (10 Feb 2023, C. J. Cornforth/Captain Zodiac). Note the narrow longitudinal linear furrows dorsal to and parallel to the main injury across the leading edge of the fin and corresponding linear scar extending across the side of the fin when the initial injury was fresh (A). Smaller skin wounds such as these furrows or abrasions often appear cryptic after healing (F), and are difficult to identify or attribute to a specific cause

Evidence of repeated interactions with fisheries (from injuries to the dorsal fin acquired in separate years) was documented for 4 individuals from the MHI population, although this number is likely higher, as several individuals had additional injuries considered possibly consistent with fishery interactions. Five additional individuals, 4 from the MHI population and 1 from the pelagic population, were documented with multiple fishery-related injuries when first seen, making it unclear whether these injuries occurred during the same event or over several interactions: 4 individuals had multiple injuries to the leading edge of the fin, 1 had injuries to the leading and trailing edge of the fin, and 1 had injuries to the leading edge of the fin and was also missing the tip of the fin, all of which were considered consistent with fishery interactions.

Another 43 individuals (8.5%) had mean highest dorsal fin scores by ID ⩾2.0 but <2.5, meaning that they had injuries considered to be possibly consistent with fisheries interactions (Table S2). In all cases, ⩾1 reviewer scored the individual as consistent with fishery interactions. Injuries were similar to those considered consistent with fishery interactions but were more ambiguous in nature, and included notches and dents to the leading edge or top of the fin, fresh or healed smooth cuts to the leading or trailing edge (sometimes impacting the sidewall of the fin), and severed or partially severed dorsal fin tips. Dorsal fin consistency score was relatively robust to availability of photos of just 1 versus both sides of the dorsal fin (Table S3, Fisher's exact test, p = 1.000), but injuries were more likely to have a lower fishery consistency score if photo quality was good rather than excellent (Table S4, Fisher's exact test, p = 0.005).

The proportion of individuals with dorsal fin injuries consistent with fisheries interactions varied by stock (Fisher's exact test, p < 0.001): 12.8% of all MHI individuals, 5.2% of pelagic stock individuals, and 1.1% of NWHI stock individuals (Fig. 3A, Table 2, Table S1). Within clusters from the MHI stock, Cluster 3 had the highest rate (17.4%), almost 3 times the rate of Cluster 4 (6.0%), while Cluster 1 (13.0%) and Cluster 2 (11.6%) were intermediate, although these differences were not statistically significant (Fig. 3B, Table 2, Fisher's exact test, p = 0.281).

Of the 504 individuals whose dorsal fins were assessed, sex was known for 243 (149 females, 94 males). Of the 45 individuals with injuries considered consistent with fisheries interactions after restric-

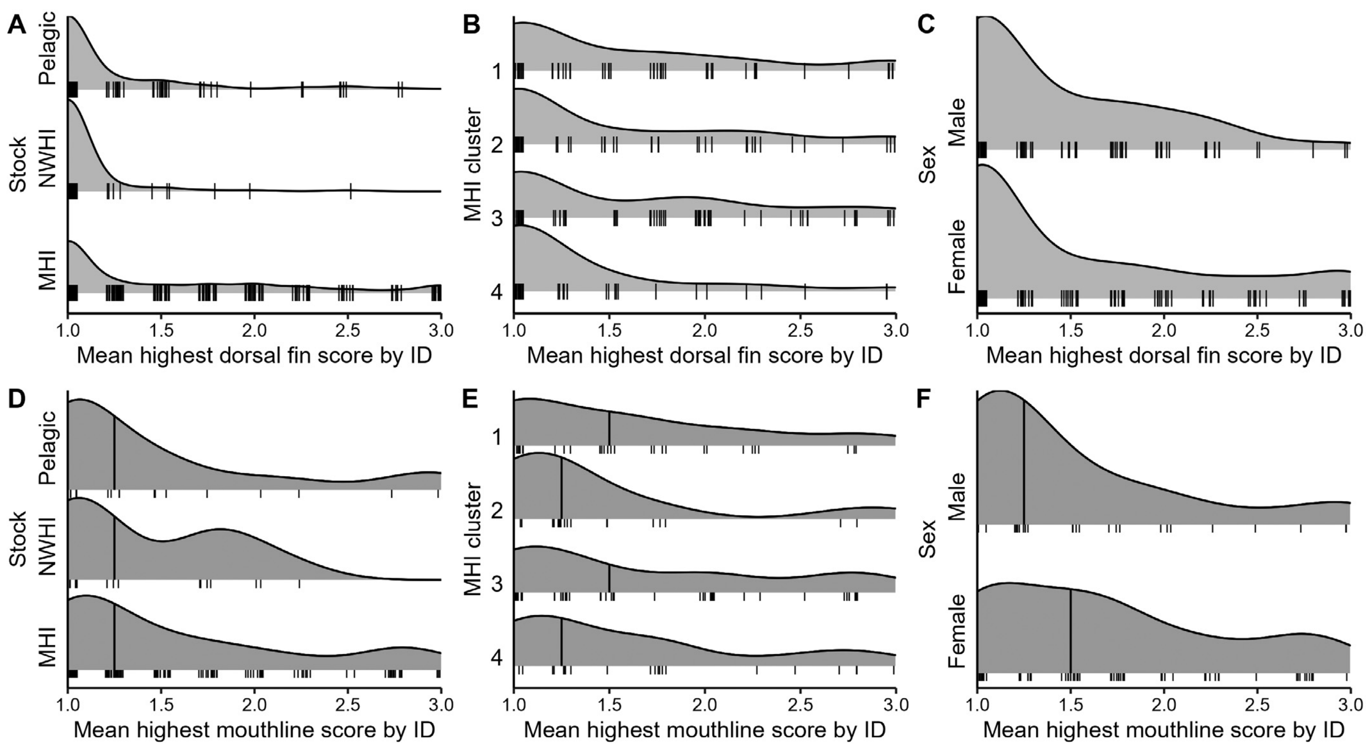


Fig. 3. Ridgeline plots illustrating the density of mean highest fisheries interaction scores (A–C: dorsal fin score; D–F: mouthline score) by ID vs. stock (A,D), cluster (B,E), and sex (C,F) for animals from known stocks. Each datapoint is indicated below the ridgelines with a vertical tick mark. The median mean highest fisheries interaction score by ID for each stock is indicated in (D–F) with a vertical line (A–C: note that the median is not visible for any stock, cluster, or sex with assessed dorsal fins, as the medians are all 1.0). MHI: main Hawaiian Islands; NWHI: Northwestern Hawaiian Islands

tions, 26 were female (17.4% of all females), 5 were male (5.3% of all males), and 14 were of unknown sex (5.3% of all individuals of unknown sex, Table S1). The proportion of individuals with dorsal fin injuries differed by sex for individuals of known sex, with a significantly higher proportion of females with dorsal fin injuries (Fig. 3C, Fisher's exact test, $p = 0.005$).

In total, 228 individuals from the MHI stock with dorsal fin photos were included in the age analyses (Table S5). Individuals considered not distinctive were included and all photo quality restrictions were dropped in order to ensure the inclusion of as many individuals as possible within each age class. Just over half of the individuals (n = 122, 53.5%) were documented in only 1 age class, though 106 individuals (46.5%) were documented across multiple age classes. However, because the age class analyses were restricted to those individuals with age class confidence ratings of ⩾3, only 20 individuals in this dataset had mean highest dorsal fin scores ⩾2.5. Generally, dorsal fin scores increased with age class, with the first injuries considered consistent with fisheries interactions appearing among calves (the earliest at a best estimated age of 2 yr), and becoming more frequent with increasing age class (Table 3). Individuals documented only as adults made up almost half of individuals with injuries considered consistent with fisheries interactions (n = 9, 45.0%). Among the individuals with injuries considered consistent with fisheries interactions that were documented across multiple age classes (n = 8), 4 were first documented with injuries as adults, 1 as a sub-adult, 1 as a juvenile, and 2 as calves. There appeared to be an interaction between sex and the age class for when fisheries-related dorsal fin injuries were first detected. For males, similar proportions of adults and non-adults had fisheries-consistent dorsal fin injuries first detected during these age classes (5.7% of pooled calves, juveniles and sub-adults, versus 4.2% of adults; Table S6). For females, 4.8% of pooled calves, juveniles, and sub-adults were known to have acquired fisheries-consistent dorsal fin injuries, while 16.9% of adults had injuries first detected as adults (Table S6). The majority of adult females with injuries first detected as adults (7 of 10, 70.0%) were documented as adults prior to injury acquisition, but 3 may have acquired injuries either as an adult or a non-adult, given their sighting histories. For males, 1 of the 2 with injuries first documented as an adult was known to have acquired the injury as an adult, but the other could have been acquired either as an adult or non-adult.

Table 3. Summary of dorsal fin results for individual false killer whales by age class, restricted to individuals with age class confidence of 3 or higher. Individuals documented across multiple age classes are counted for each class that they were seen in, thus the sum of individuals over all age classes is greater than the total number of individuals included in this analysis. A total of 288 unique individuals with dorsal fin photos were included in the age analysis, of which 20 were considered to have injuries consistent with fishery interactions

| Age class | No. scored | No. (%) with injuries consistent with fishery interactions | Range of ages (yr) when injuries first documented in this age class |
|---|---|---|---|
| Calf | 50 | 2 (4.0) | 2 |
| Juvenile | 91 | 5 (5.5) | 3 |
| Sub-adult | 98 | 5 (5.1) | 6–9 (median = 8) |
| Adult | 133 | 15 (11.3) | 10–40 (median = 22) |

### 3.2. Mouthline injuries

Overall, 30 of 201 individuals (15.4%) had mean highest mouthline scores by ID ⩾2.5, and thus were considered to have injuries consistent with fisheries interactions (Fig. 1D–F, Table S7). An additional individual with a mean highest mouthline score = 2.5 was included in age and date of injury assessments, but had a distinctiveness score that was too low for inclusion in the stock, cluster, or sex analyses (Table 1). Additionally, another 22 individuals (10.9%) had mean highest mouthline scores by ID ⩾2 but <2.5, meaning that they had injuries considered to be possibly consistent with fisheries interactions (Table S8). The proportion of mouthline visible by stock, MHI cluster, and sex were similar (Table S9). Individuals with injuries consistent with fishery interactions had a greater proportion of mouthline visible (median = 80%) than those with no injuries (median = 50%), although this was not statistically significant (Mann-Whitney *U*-test, $W = 3042.5$, $p = 0.079$).

For the majority of individuals with mouthline injuries consistent with fisheries interactions (27 out of 30, 90.0%), the injury was documented in the first mouthline photos of the injured region that were available, although we were able to narrow down the time frame of the injury for an additional 5 individuals that were calves, juveniles, or sub-adults when first seen (Table S7). Two of these injuries occurred in the first half of the study (1999–2010), 3 occurred in the second half (2011–2021), and the timing of the remaining 3 spanned the 2 periods. Injuries for 2 of the 3 from the second half were acquired sometime between 2018 and 2021 (Table S7).

The proportion of individuals with mouthline injuries consistent with fisheries interactions varied by stock—albeit not significantly (Fisher's exact test, p = 0.161)—with 16.9% of individuals from the MHI stock (26 of 154 individuals), 10.7% of individuals from the pelagic stock (3 of 24), and none from the NWHI stock (0 of 17 individuals, Fig. 3D, Table 2, Table S7). Within clusters from the MHI stock, there was less variability in the proportion of individuals with mouthline injuries consistent with fishery interactions: Cluster 1: 12.5%, Cluster 2:12.9%, Cluster 3: 21.8%, and Cluster 4: 17.9% (Fig. 3E, Table 2, Fisher's exact test, p = 0.628). Of the 201 individuals that were assessed, sex was known for 114 (73 females, 41 males). Females had a slightly higher proportion of individuals with injuries consistent with fishery interactions (13 of 72, 17.8%) than males, although this finding was not statistically significant (Fig. 3F, 5 of 41, 12.2% of all males, Fisher's exact test, p = 0.594).

A total of 188 individuals from the MHI stock with mouthline photos were included in the age analyses (Table S10), as individuals considered not distinctive were included, and all photo-quality restrictions were dropped in order to ensure that as many age classes as were available were assessed. Most individuals (n = 141, 75.0%) were only documented within 1 age class, with 47 (25.0%) documented across multiple age classes (e.g. from juvenile to sub-adult, sub-adult to adult). However, because the age class analyses were restricted to those individuals with age class confidence ratings of ≥3, only 14 individuals had highest mouthline scores ≥2.5. Injuries scored as consistent with fisheries interactions began to appear in the juvenile age class (the earliest at a best estimated age of 4 yr), and became more frequent with increasing age class (Table 4). Of the individuals documented across multiple age classes, 14.9% (7 of 47) were documented with injuries consistent with fishery interactions, the majority of which (5 out of 7, 71.4%) were first documented with injuries as sub-adults, with the remaining 2 first documented with injuries as a juvenile and as an adult. All other individuals included in the age analysis with mouthline injuries considered consistent with fisheries interactions (n = 7) were only documented as adults. The interaction between sex and age class that was apparent for dorsal fin injuries did not appear to occur for mouthline injuries: for both males and females, the proportion of individuals that had injuries first detected as adults (8.1% males, 7.8% females) was similar to the proportion of injuries known to have been acquired as calves, juveniles or sub-adults (males 11.8%, females 8.0%, Table S6). Three-quarters of the adult females (3 of 4) first documented with injuries as adults had not been seen as an adult pre-injury, so may have acquired them in a younger age class. For adult males with injuries first documented as adults, 1 (out of 3) was not seen as an adult pre-injury, so may have acquired the injuries in a younger age class.

### 3.3. Individuals with both dorsal fin and mouthline scoring

Dorsal fin and mouthline scores were both available for 187 individuals (Table 5). Overall, approximately two-thirds (63.7%) had the same scores for both dorsal fin and mouthline, largely driven by consensus on which dorsal fins and mouthlines did not have injuries considered to be consistent with fishery interactions. Six individuals had both dorsal fin and mouthline injuries considered to be consistent with fisheries interactions, out of the 25 individuals with consistent dorsal fin injuries and 27 individuals with consistent mouthline injuries that had both score types available (Table 5). However, the median percentage of mouthline visible for those individuals with dorsal fin injuries ranged from 50 to 55% (Table S11); thus, many of these individuals may also have had mouthline injuries that were not detectable with available photographs.

Of the 187 individuals with both types of scores, 46 (24.6%) had either or both a dorsal fin or mouthline injury that was considered to be consistent with fishery interactions. The proportions of individuals with injuries varied significantly by stock, with 28.7% of MHI individuals, 11.7% of pelagic stock individuals, and no NWHI indi-

Table 4. Summary of mouthline results for individual false killer whales by age class. Individuals documented across multiple age classes are counted for each class that they were seen in, thus the sum of individuals over all age classes is greater than the total number of individuals included in this analysis. A total of 188 unique individuals with mouthline photos were included in the age analysis, of which 14 were considered to have injuries consistent with fishery interactions. NA: not applicable

| Age class | No. scored | No. (%) with injuries consistent with fishery interactions | Range of ages (yr) when injuries first documented in this age class |
|---|---|---|---|
| Calf | 34 | 0 (0.0) | NA |
| Juvenile | 58 | 1 (1.7) | 4 |
| Sub-adult | 46 | 6 (13.0) | 6–9 (median = 9) |
| Adult | 104 | 11 (10.6) | 11–28 (median = 21) |

Table 5. Summary of scoring by ID for individual false killer whales that had both dorsal fin and mouthline scores, using photos from 1999 through 2021. Numbers presented are on an individual basis. Dorsal fins are restricted to sightings with good or better photo quality, and mouthlines are restricted to sightings with ≥50% of the mouthline visible

| | Total | No. (%) with consistent mouthline scores | No. (%) with possibly consistent mouthline scores | No. (%) with not-consistent mouthline scores |
|---|---|---|---|---|
| Total | 187 | 27 (14.4) | 21 (11.2) | 139 (74.3) |
| No. (%) with consistent dorsal fin scores | 25 (13.4) | 6 (3.2) | 5 (2.7) | 14 (7.5) |
| No. (%) with possibly consistent dorsal fin scores | 22 (11.8) | 6 (3.2) | 2 (1.1) | 14 (7.5) |
| No. (%) with not-consistent dorsal fin scores | 140 (74.9) | 15 (8.0) | 14 (7.5) | 111 (59.4) |

viduals with both score types available having an injury considered consistent with a fisheries interaction (Fisher's exact test, p = 0.010). Among MHI individuals, Cluster 3 had the greatest proportion of individuals with either or both injury types (38.2%), followed by Cluster 4 (25.9%), Cluster 1 (25.0%), and Cluster 2 (19.4%), though the proportion of individuals with injuries did not show statistically significant variation between clusters (Fisher's exact test, p = 0.274). Among the individuals with both score types of known sex (73 females, 43 males), the proportion of females with injuries (35.6%) was almost double the proportion of males with injuries (19.5%), although this was not statistically significant (Fisher's exact test, p = 0.060).

### 3.4. Association analyses

Individuals with injuries consistent with fishery interactions were found in the largest component of the NWHI population, in 7 of the 17 isolated components of pelagic stock false killer whales, and in 2 of 11 components of individuals from an unknown population (Fig. 4). Note, these unknown components range in size from 1 to 3 individuals, thus represent a small number of individuals overall (Fig. 4). Within the MHI population, association rates between individuals with evidence of fishery interactions were similar to those without evidence of fisheries interactions (matrix correlation = 0.0200, $t$ = 1.527, p = 0.146 [2-sided test]), although it should be noted that only ~56% of individuals with dorsal fin photos also have mouthline photos, and thus many individuals may have fisheries-related injuries that we did not detect. Additionally, the entire sighting history of those with fisheries-related injuries was utilized in the analyses, and thus may have included associations prior to acquiring the injuries. Mean maximum association strength and overall interaction rates (i.e. *strength* or gregariousness), connectivity (i.e. *eigenvector centrality*), and individual sociality (i.e. *clustering coefficient*) between those with and without fishery interactions were also similar (Table S12), suggesting that the behavior that resulted in fishery-related injuries did not affect the number of associates or strength of associations. A sensitivity analysis on individuals from Cluster 1 supported results for the MHI population (matrix correlation = −0.022, $t$ = −0.379, p = 0.747 [2-sided test]).

## 4. DISCUSSION

Our results showed that individuals from the endangered MHI population of false killer whales have higher rates of injuries consistent with fishery interactions than individuals from either the pelagic or NWHI stocks of false killer whales. This finding was consistent both for dorsal fin and mouthline injuries. In our earlier analysis of dorsal fin injuries of distinctive individuals and using an average score of >2.5 as the cutoff, 7.1% of individuals from the MHI stock, 1.3% of individuals from the pelagic stock, and 0% of individuals from the NWHI stock had injuries consistent with fisheries interactions (Baird et al. 2015). Rates of dorsal fin injuries consistent with fishery interactions in our current study, with much larger sample sizes for all 3 populations, are substantially higher (MHI: 12.8%, pelagic: 5.2%, NWHI: 1.1%). We are confident that the comparatively high rates of dorsal fin injuries are not a consequence of including scars from natural sources, such as failed shark or killer whale (*Orcinus* spp.) attacks. Both types of injury leave behind highly characteristic scarring (Heithaus 2001, Baird 2016, Corsi et al. 2021) that all reviewers in the present study were familiar with. Several individual false killer whales have scars that may be from killer whale attacks, but these are not definitive. Shark bite scars are rare among Hawaiian false

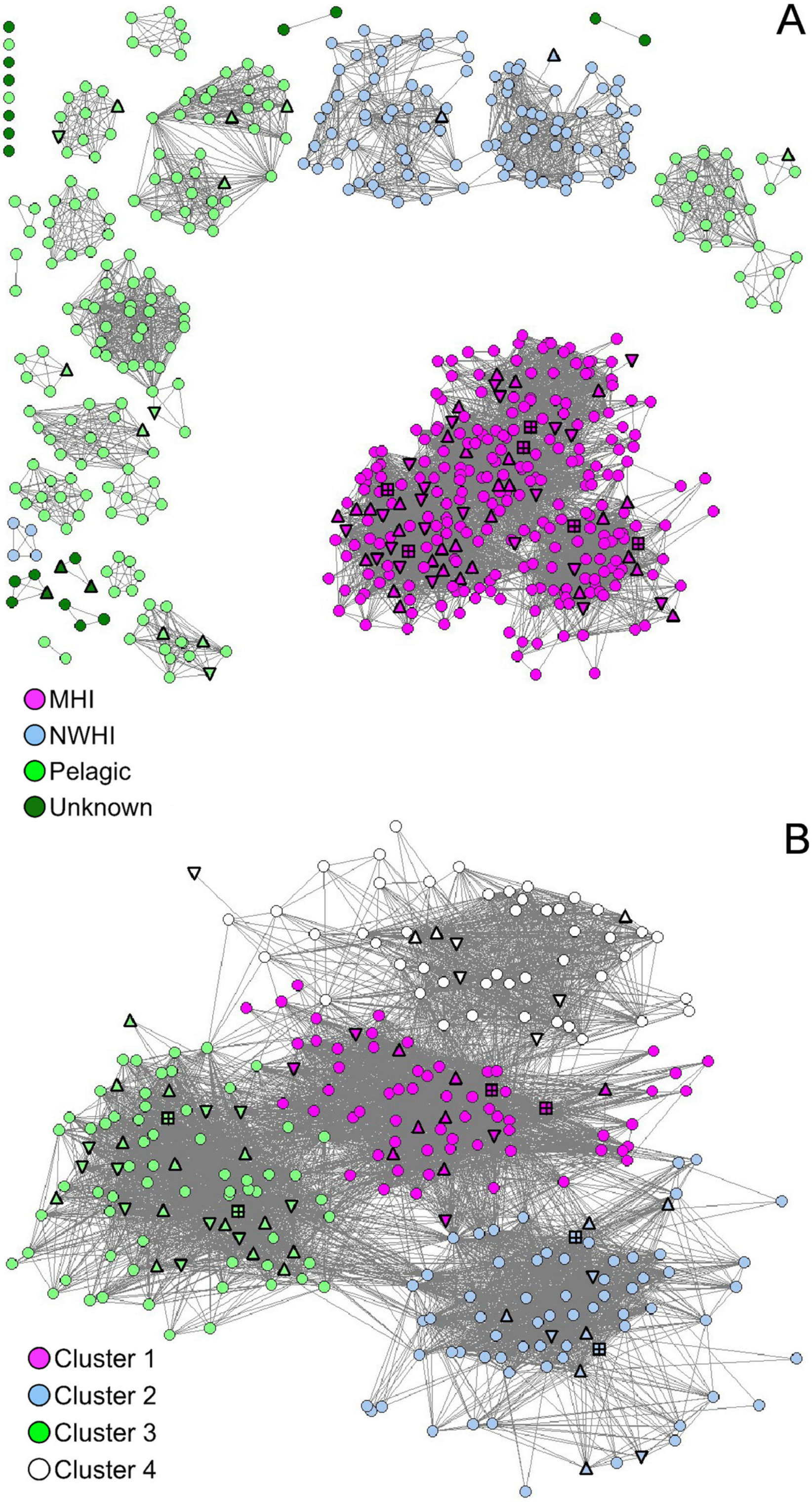


Fig. 4. False killer whale social networks for individuals sighted from 1999 through 2021 that were considered at least slightly distinctive with fair or better quality photos. Individuals with injuries consistent with fisheries interactions are indicated by symbol type (up triangles: dorsal fin; down triangles: mouthline; box: both dorsal fin and mouthline; circular: none). (A) All populations, color-coded by population. (B) MHI insular population, color-coded by cluster. MHI: main Hawaiian Islands; NWHI: Northwestern Hawaiian Islands

killer whales (~2% of individuals from the MHI population, Cascadia Research Collective unpubl. data). In addition, tiger sharks *Galeocerdo cuvier*, the most likely cause of shark bite scars, primarily use waters <200 m in depth (Meyer et al. 2018), while the false killer whale social cluster with the highest rates of fishery-related injuries (Cluster 3) primarily uses waters between 500 and 1000 m in depth (Baird et al. 2023).

In our current study, we expanded our analyses to include slightly distinctive individuals, which theoretically should have reduced the overall proportion of individuals in the population with evidence of injuries from fishery interactions, particularly since such injuries typically make an individual much more distinctive. Including slightly distinctive individuals does minimally increase the risk of mismatched individuals being included in the dataset. However, any inclusions of mismatched individuals would decrease the overall proportion of individuals with injuries considered consistent with fisheries interactions, as the mismatched individuals would likely lack distinctive scarring in the first place. Mismatches of individuals that undergo major mark changes (e.g. collapse of the dorsal fin) from fishery interactions might occasionally occur, and would similarly result in a decrease in the overall proportion of individuals with injuries considered consistent with fishery interactions, given the relatively small proportion of individuals with >1 independently-acquired injury. Our larger sample sizes provide a more robust assessment of trends in fisheries-related injuries among these 3 populations, and information that can be incorporated into future analyses of survival rates.

The higher rates of fishery-related injuries that we have documented reflect that fishery interactions are ongoing. This is also demonstrated through our temporal evaluation of when injuries occurred; when considering either dorsal fin or mouthline injuries, slightly more occurred in the second half of our study period (2011–2021) than during the first. Two individuals with mouthline injuries known to have been acquired in the second half of our study period acquired those injuries between 2018 and 2021, further demonstrating that fishery interactions are ongoing. Additionally, we found evidence of repeated fishery interactions for multiple individuals, showing that the behaviors that lead to interactions are regularly repeated and likely to continue in the future. Certain types of fisheries-related injuries, such as notches or slices on the dorsal fin, may even exacerbate the potential for re-injury, e.g. in the case that a line gets caught within a notch from a previous injury (Fig. 2).

### 4.1. Injuries by stock

Although the results are consistent with the Baird et al. (2015) study, the higher rates of fisheries-related injuries for the MHI stock than for the pelagic stock are unexpected, given that individuals from the pelagic population are known to regularly depredate bait and catch in the US pelagic longline fishery (Thode et al. 2016, Bayless et al. 2017, Fader et al. 2021), and the number estimated killed or seriously injured (i.e. an interaction that has a >50% chance of leading to mortality, National Marine Fisheries Service 2022) in the fishery has ranged from 12 to 69 individuals $yr^{-1}$ from 2008 through 2021 (Oleson et al. 2023). There are several possible reasons for this finding. First, it could be that individuals from the MHI population more regularly depredate fishing gear and are injured as a result. Evidence of repeated interactions with fisheries (from fisheries-related injuries to the dorsal fin acquired in separate years) for individuals from the MHI population suggests that interactions may be more frequent than previously thought. The fact that injury rates were relatively high in all 4 MHI clusters (Fig. 3B,E, Table 2), while many groups from the pelagic stock had no fisheries-related injuries (Fig. 4), could also reflect that not all social groups from the pelagic stock regularly interact with and depredate catch. This is somewhat supported by analyses of satellite-tag data from 3 different pelagic social groups in relation to logbook data from the US deep-set longline fishery, where only 1 of the 3 groups appeared to approach fishing vessels and sets of longline gear in the water (Anderson et al. 2020). Our photo-identification catalog includes the vast majority of individuals from the MHI population, but a relatively small proportion of those estimated to be in the pelagic population (Bradford et al. 2020); thus, our sample of photos from the latter population is less representative of the population as a whole, and there may be un-photographed social groups from the pelagic population that have much higher rates of fisheries-related injuries. Second, it is possible that mortality or serious injury may be higher in pelagic longline gear than in the typically lighter gear used in most nearshore fisheries, as suggested by Baird et al. (2015). Third, it is possible that pelagic false killer whales are more skilled at depredating bait or catch from gear, and thus less likely to be injured as a result. Related to this, it is possible that the differences in gear types and methods used in nearshore fisheries (i.e. predominantly trolling, with active gear towed) versus the high seas (i.e. longlining, with active gear soaking) could contribute to false killer whales' ability to avoid injuries during depredation. Finally, the more extensive sighting histories of individuals from the MHI population also likely contributes to the difference. Line injuries heal differently depending on the depth of the injury (Fig. 2). In the example shown in Fig. 2, a shallow fresh line injury is visible above a more profound leading-edge injury (Fig. 2A). By the time these injuries have fully healed and repigmented, the shallow line injury is barely visible (Fig. 2C,F). Since most wounds repigment in false killer whales, having photos of an individual from multiple encounters within or between years increases the likelihood of being able to detect injuries before they are completely healed, with information to assess the origin of the injury. The possible reasons for the differences among stocks are not mutually exclusive, and all may contribute to the higher rate of injuries for the MHI population. Continued efforts to obtain both mouthline and dorsal fin photos of sufficient quality from pelagic stock false killer whales are needed to reduce uncertainty and better understand the possible causes of this difference. Fisheries observers or crew on pelagic longline vessels that spend extensive time within the range of pelagic false killer whales represent a potentially valuable source of mouthline and dorsal fin photos from this population, both of bycaught animals and animals that happen to be passing within a short distance of the vessel. Obtaining photos from this source would be of long-term value for reducing uncertainty.

The relative lack of injuries consistent with fisheries interactions for the NWHI population (1.1% for dorsal fin injuries, 0% for mouthline injuries, albeit with a small sample size of mouthline photos) compared to the MHI population is as expected, given the relative levels of fishing effort in the core ranges of the 2 populations (Kittinger et al. 2010, Baird et al. 2021). This finding further reinforces our confidence in our scoring system as a reliable means of assessing fishery interactions. Prior to 1980, foreign longline fishing effort did occur around the NWHI (Yong & Wetherall 1980). Starting in October 1991, longline fishing was excluded within 50 nautical miles (92.6 km) of the NWHI to protect Hawaiian monk seals *Monachus schauinslandi*, and since June 2011, all commercial fishing for pelagic species (e.g. from trolling) and for bottomfish has been prohibited. The 2 populations do overlap off Kauaʻi and Niʻihau (Baird 2016, Kratofil et al. 2023a), but there is limited fishing effort there compared to elsewhere in the MHI (McCoy et al. 2018, Baird et al. 2021). Based on both sighting rates and satellite-tag data, that area is also not a high-use area for either population (Baird 2016), although information on space use is comparatively limited for the NWHI stock (Baird et al. 2013, Kratofil et al. 2023a). This is due to the fact that the MHI are more accessible for small-boat dedicated research efforts than the NWHI, which also contributes to the limited NWHI stock sightings overall and re-sightings of NWHI individuals in our study. Our sample of individuals from the NWHI population (87 with dorsal fins assessed) is relatively small compared to the most recent abundance estimate for the population (477 individuals, CV = 1.71, Bradford et al. 2020). Thus, it is possible that we have missed entire social groups with varying levels (either higher or lower) of fisheries-related injuries. The majority of biological research within the Papahānaumokuākea Marine National Monument is not focused on cetaceans, but other boat-based research efforts may serve as platforms of opportunity for obtaining photographs that could be used to assess the presence of injuries on individuals in this population. Continued efforts to expand satellite-tag datasets for this stock (Baird et al. 2013) will be particularly valuable for understanding how different social groups overlap with fisheries effort, in addition to dedicated large- or small-boat research efforts to photographically document this population.

As expected, since most hookings likely occur in the mouth and only a subset of individuals end up struggling in such a way that they would also acquire line injuries on the dorsal fin, we found higher proportions of individuals with mouthline than dorsal fin injuries for both the MHI insular and pelagic populations (e.g. 16.9% versus 12.8% for mouthline and dorsal fin injuries for the MHI insular population). This was not the case for NWHI stock individuals, but the sample size of individuals with mouthline photos (n = 17) was small relative to the total number of individuals with dorsal fin photos (n = 87). However, our estimates based on mouthline injuries are negatively biased, since mouthline injuries tend to be visible from only 1 side, and photographs of the entire mouthline are rarely available (the median percentage of mouthline visible for individuals considered in these analyses was only 60% for MHI and NWHI individuals, and 50% for pelagic stock individuals, Table S9). Attempting to obtain both left and right-side head photos in future research efforts will help reduce this bias, and the potential confounding effect it may have on analyses when individuals with injuries are incorrectly being treated as not having injuries. Additionally, it may be worth expanding analyses to include other areas of the body that are likely to bear injuries from fisheries interactions, such as the peduncle and pectoral fins. While we made note of instances where such injuries were readily visible, we did not systematically quantify them, partially due to limited availability of high-quality images of these areas. Collecting high-quality underwater video footage of animals will likely improve the availability of complete views of not only mouthlines, but also the pectoral fins, peduncle, and fluke.

### 4.2. Injuries by sex and age

Our analyses of sex bias in the likelihood of acquiring such injuries showed that females were significantly more likely to have fisheries-related dorsal fin injuries than males (17.4% versus 5.3%), accounting for the difference in the number of known females versus males. There was a similar trend for mouthline injuries (17.8% for females versus 12.2% for males), although this difference was not statistically significant. Interestingly, at least for dorsal fin injuries, there appears to be an interaction between age and sex. For males, similar proportions of adults and non-adults had acquired dorsal fin injuries consistent with fisheries interactions, which in itself is surprising, given the relative timespans of different life stages, and indicates higher injury rates than might be expected among non-adults if interactions were happening randomly throughout individuals' life spans. The same was true for males and females with mouthline injuries (Table S6). However, for females, the likelihood of acquiring dorsal fin injuries was much higher for adults (Table S6). False killer whales are sexually dimorphic as adults, with adult females being about 83–84% of the length of adult males (Ferreira et al. 2014). Baird et al. (2015) speculated that this larger size may allow adult males to break free from gear without struggling in a way that might lead to dorsal fin injuries. For our analyses, we considered individuals to be adults when they are sexually mature, at 10 yr of age, but false killer whales continue to grow until about 25 yr of age (Ferreira et al. 2014). Additionally, our analyses of the age at which individuals first acquire such injuries suggest that some males may be interacting with fishing gear at much younger ages (i.e. as sub-adults), well before sexually dimorphic body size differences would be apparent. Thus, it is unlikely that body size differences leading to a reduced likelihood of dorsal fin injuries for adult males is entirely responsible for this difference. Why the difference exists for dorsal fin injuries but not for mouthline injuries is unclear. As suggested by Baird et al. (2015), it is possible that the higher energetic needs of females that are pregnant or lactating may influence their likelihood of depredating catch. However, among some odontocete populations, adult males have been shown to have higher rates of interaction with fishing gear and anthropogenic markings than adult females, suggesting that such demographic trends are likely species- or potentially even population-specific (Powell & Wells 2011, Adimey et al. 2014, Feyrer et al. 2021). Among all stocks of Hawaiian false killer whales, sex is known for approximately half of the individuals, limiting our ability to examine how sex and age act in combination to affect the likelihood of interacting with fisheries. Confirming the sex of more individuals using genetic methods (Morin et al. 2005) would be of value in addressing these limitations. This information could also be utilized in future work to explore differences in foraging behavior and prey selection based on sex (e.g. Tennessen et al. 2023), which would ultimately help to understand the underlying drivers of fishery interactions.

Findings from the age analyses indicate that false killer whales begin interacting with fisheries at younger ages. The number of injuries detected in younger age classes far exceeds the number that would be expected if injuries were occurring randomly in relation to age, given the relative amount of time spent in each age class for both mouthline and dorsal fin injuries (4 out of 8 dorsal injuries, and 6 out of 7 mouthline injuries for animals sighted in multiple age classes were detected as non-adults). Social learning is an important part of many odontocete societies, including killer whales, where cultural transmission of foraging strategies and knowledge of hunting grounds is conferred to other members of the community by example and learned through imitation (Foote et al. 2016). False killer whales are known to engage in communal hunting and prey sharing, a behavior thought to reinforce cultural and social bonds among individuals by sharing knowledge of hunting strategies with younger members of the community (Baird 2016). Thus, cultural transmission of high-risk, high-reward behavior such as depredating catch off fishing lines is likely. False killer whale calves, which are slow to mature and require significant maternal investment, likely engage in prolonged social learning of hunting practices, watching adults before participating themselves. In observer data from the offshore longline fishery, smaller individuals are frequently recorded as hooked or entangled (Bradford & Forney 2016). While it is unknown how many younger animals are killed during interactions with fisheries, they are clearly exposed to and engage with fisheries from a young age. Over time, it is possible that the spread of depredation behaviors through the population may weaken social bonds between animals as reliance on cooperative hunting to capture prey declines in favor of depredating catch, as has been shown among common bottlenose dolphins *Tursiops truncatus* off Hawai‘i Island that were associating with a fish farm (Harnish et al. 2023). While our results do not currently suggest any weakening of social ties, it is difficult to confirm whether cultural transmission of depredation behaviors or changes in social structure are occurring using quantitative approaches (e.g. Hasenjager et al. 2020), as our knowledge of which individuals are interacting with fisheries is limited to only those individuals who have obtained easily visible external injuries from these interactions. Further, our knowledge of when these injuries occur is constrained by sampling effort, photo quality, and ability to obtain high-quality images of the injured area, particularly mouthlines. Future efforts to estimate the age structure of these populations (at the very least, the MHI stock) are imperative to understanding how serious injury and mortality of young individuals may impact overall population dynamics.

### 4.3. Limitations of this study

While the information on evidence of fisheries interactions through photographic methods, as documented here, is valuable for monitoring efforts, there are a number of limitations of such indirect methods. Most notably, not all individuals who interact with fisheries and survive may have clear evidence of such interactions that we are able to capture with photographs. Unlike some closely related species (e.g. pygmy killer whales *Feresa attenuata*, Baird 2016), external injuries on false killer whales typically repigment to the original skin color as they heal; thus, in order for a fishery interaction to be visible once fully healed, there must be some degree of permanent disfigurement or tissue loss (Fig. 2). This wound healing and repigmenting process obscures the origin of smaller, less invasive injuries, biasing the assessment of fishery interactions toward a narrow band of more profound interactions that are more likely to result in serious injury but not mortality. As noted in Section 3.1, fisheries-related injuries to the dorsal fin were more likely to be documented for individuals with excellent-quality photos (Table S4), yet our analyses also include those only with good-quality photos, thus our estimates of dorsal fin injury rates are likely negatively biased across all groups. Additionally, aspects of how data collection has changed over the study period limits our ability to draw firm conclusions about temporal trends in injury rates, particularly for mouthline injuries, as high-quality mouthline photos were more frequently available after the switch from film to digital cameras in the field in the early 2000s. More importantly, this methodology only represents individuals that survive fisheries interactions. Thus, while fisheries-related injuries may provide an indication of how widespread hooking is among the populations and how it varies by sex and social cluster, they do not directly address bycatch rates per se. Hook ingestion by bottlenose dolphins often leads to mortality, sometimes long after the hook was originally ingested (Wells et al. 2008). Similarly, an *in situ* study of how longline hooks behave within the soft and hard tissues of the mouth of stranded and deceased large odontocetes showed that certain hook types may cause severe soft-tissue damage and leave behind pieces of the hook within the tissues, and even result in fractures to the mandible (McLellan et al. 2015). However, there are only a small handful of stranded false killer whales that have been examined to identify fishery interactions post mortem (e.g. Baird et al. 2015), thus little information is available from that source as to how often hooking might lead to death among wild animals. The low retrieval rates of false killer whale carcasses in Hawaiʻi are likely due to a combination of ocean currents sweeping animals offshore, scavenging by sharks, and large areas of coastline that are inaccessible to humans (see Faerber & Baird 2010).

While beyond the scope of this study, information on which individuals are known to have evidence of prior fisheries interactions could be used to compare survival or reproduction of those with and without fisheries-related injuries. However, it is important to note that many individuals in the 'without evidence' category may have cryptic injuries that were not detected, due to a lack of or limited mouthline photos, or only good-quality (versus excellent-quality) dorsal fin photos. Such analyses should be undertaken as the sample size of high-quality photos increases for individuals from the endangered MHI population.

### 4.4. Monitoring and management implications

Additional strategies to supplement photographic monitoring include analysis of space use and movements from satellite-tagging in relation to fisheries, which has been informative for Hawaiian false killer whales (Anderson et al. 2020, Baird et al. 2021, Fader et al. 2021). However, without the precise locations of fishing vessels, inference from satellite-tagging methods is generally limited to broad scale overlap (e.g. Baird et al. 2021) and, for rarely encountered populations (e.g. pelagic, NWHI), only a small sample size of tagged animals are available to infer associations with fisheries (Anderson et al. 2020, Fader et al. 2021). Visual monitoring methods would be the most direct, informative approach for understanding how false killer whales interact with fishing gear and from which solutions can be more effectively developed. Observer monitoring programs are commonly implemented for monitoring marine mammal bycatch, although these are costly, and observer coverage is often limited to a small proportion of the actual operating fleet. Observers are placed on US longline vessels that operate within the range of the pelagic false killer whale stock; however, at the existing coverage (20% in recent years, but decreasing to 13.5% in 2024), information on the nature of interactions remains limited. Observer coverage over most of the range of the endangered MHI stock — the population with the highest rates of injuries consistent with fisheries interactions — is nonexistent, which creates a barrier to understanding the full extent of risk that fisheries pose to the declining population. Electronic monitoring programs have gained recent attention for their cost efficiency and ability to document depredation and bycatch across a broader proportion of the fleet (e.g. Kindt-Larsen et al. 2012, Monaghan et al. 2024). Given our results, some form of monitoring (observers and/or electronic monitoring) is warranted for nearshore fisheries that overlap with the endangered MHI false killer whale population. There are >1000 commercially licensed fishermen in Hawaiʻi, as well as a large number of non-commercial (i.e. recreational or subsistence) fishermen, and choosing how such monitoring should be allocated will be difficult. Baird et al. (2021) developed an index of overlap between false killer whales and commercial fishermen, using whale satellite-tag data and commercial marine license data for fishing effort, and identified areas where individual fishermen are likely to have higher interaction rates. Given likely limited monitoring resources, it would be prudent to monitor fisheries in areas where the interaction rates are likely to be highest. Additional areas to prioritize monitoring could potentially be identified by conducting surveys about depredation rates among fishermen. Such surveys should be framed so that they could yield valuable results for both false killer whale conservation efforts and the fishing community, to ensure buy-in. One possible avenue to achieve this is by centering questions on how depredation and marine mammal presence impacts fishing success depending on when and where fishing effort is being conducted. It is important to note, however, that many fishermen in Hawaiʻi acknowledge that discriminating between false killer whales and other 'blackfish' is difficult and species misidentification may often occur (Madge 2016).

Efforts to reduce bycatch in the Hawaiʻi-based longline fishery since 2013 have largely been ineffective, and depredation remains a continued threat to both the conservation of false killer whales and the economic interests of fishermen (Oleson et al. 2023). For the MHI insular population, fisheries-related efforts have been limited to outreach and education, providing information to help fishers discriminate between false killer whales and other similar species (i.e. pygmy killer whales, melon-headed whales *Peponocephala electra*, and short-finned pilot whales *Globicephala macrorhynchus*), and encouraging fishers to move out of the area when false killer whales are present. In spite of these efforts, we have demonstrated that fisheries interactions are ongoing for the endangered MHI population and a large proportion of the population appears to interact with fishing gear. Individuals begin to acquire fisheries-related injuries at young ages, and new injuries have continued to be documented across the past 20 yr, including repeated injuries for some individuals. We have also demonstrated that the impacts of bycatch are not evenly distributed between or even within stocks, which carries implications for population dynamics and should be taken into account by managers.

Continued resources should be dedicated to monitoring the impacts of fishery interactions among Hawaiian false killer whales, both through indirect studies such as the analysis presented here, and through direct monitoring via observer coverage or electronic monitoring. However, our results also suggest that direct efforts to reduce bycatch for the endangered MHI population are particularly needed. In the deep-set longline fishery, such measures have included gear changes (i.e. using 'weak' circle hooks and strong terminal gear) as well as handling guidelines, but these measures have been ineffective (Fader et al. 2021, Baird 2024). To add complexity to this issue, nearshore fisheries around the MHI involve a wide variety of hook and line fishing methods, and no single gear change could work across the various fisheries. Spatial management approaches such as 'move-on' strategies may contribute to a solution, but would still require the use of enforcement or initiatives to ensure compliance (Cox et al. 2007, Tixier et al. 2019, Fader et al. 2021). Novel targeted measures should be developed to either effectively reduce the rate of interactions or reduce the likelihood of injury or mortality, ideally through collaborative efforts with stakeholder communities.

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