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Received: 19 January 2021 | Accepted: 22 July 2021

Running head: BAIRD ET AL.

ARTICLE

Site fidelity, spatial use, and behavior of dwarf sperm whales in Hawaiian waters: using small-boat surveys, photo-identification, and unmanned aerial systems to study a difficult-to-study species

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This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as doi: [10.1111/mms.12861](https://doi.org/10.1111/mms.12861)

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Abstract

Dwarf sperm whales (*Kogia sima*) have been studied rarely at sea. We used photo-identification, boat- and drone-based behavioral observations, and citizen science photo contributions to examine site fidelity, spatial use, and behavior in Hawai'i. Sighting rates were highest in island slope (500-1,000 m) waters. Over 40% of photo-identified individuals were linked by association in the same social network. More than half of the very distinctive individuals were seen more than once, and 28.5% were seen in multiple years, with one individual seen 14 times over a 15-year span. Resighted individuals and those in the main cluster of the social network were found in significantly shallower water than individuals that were not resighted or that were in isolated clusters. Distances between resighting locations suggest small home ranges. This suggests an insular slope-dwelling population that overlaps with an offshore population. Evidence of unsuccessful predatory attempts by large sharks was recorded on four individuals, and linear wounds consistent with interactions with line fisheries were documented on three individuals. Surface and subsurface behavior recorded by drone revealed vigilance behavior likely to minimize predation risk. Lessons learned from this study can be applied elsewhere to increase knowledge of this poorly known and

difficult-to-study species.

KEYWORDS

citizen science, fishery interactions, Hawai'i, home range,
Kogiidae, predation, shark, social interactions, UAS, vigilance

1 | INTRODUCTION

Although there are several species of beaked whales (family Ziphiidae) about which virtually nothing is known, as a family the Kogiidae may arguably be the least known of the nine extant families of odontocetes. Two species are currently recognized, the dwarf (*Kogia sima*) and pygmy (*K. breviceps*) sperm whale, although a third species may exist (Chivers et al., 2005), awaiting further genetic or morphological analyses. While both recognized species are widely distributed, they are rarely the subject of studies at sea, for good reason—both have a well-deserved reputation for being difficult to study. They live primarily in slope and offshore waters, and so are infrequently encountered in near-shore surveys (Kiszka & Braulik, 2020). They are hard to spot even when they are present: Barlow (2015) notes that in Beaufort 2 sea conditions the probability of sighting *Kogia* during large vessel surveys drops to less than 10% of their sighting probability in Beaufort 0 conditions, and by Beaufort 3, with scattered whitecaps, they are almost impossible to detect. Once spotted, resighting individuals or groups is difficult given their small size, low surfacing profile, lack of a visible blow, and typically slow surfacing speed that rarely creates a splash that can serve as a cue for detection. They are likely often missed even when they are in an area, as they may

dive for extended periods, perhaps as long as 43 min (Breese & Tershey, 1993). Even when they are seen, many authors have noted that dwarf and pygmy sperm whales are difficult to approach or may avoid vessels (e.g., Würsig et al., 1998), and they are typically far too difficult to approach closely enough for biopsy sampling or tagging.¹ Difficulty in discriminating between the two species at sea without photographs or good sighting conditions has further limited knowledge. They are widely reported to be difficult to tell apart given overlapping morphology, although this is more of an issue with juveniles and calves (Barros & Duffield, 2003). While they can be detected using passive acoustic monitoring, it is not yet possible to discriminate between the two species acoustically (Hildebrand et al., 2019), and their ranges broadly overlap (McAlpine, 2018). These factors have greatly limited studies of free-ranging individuals, to say the least. If not for the fact that they strand fairly frequently throughout much of the world (Caldwell & Caldwell, 1989; McAlpine, 2018; Willis & Baird, 1998), we would know virtually nothing about these species.

That said, dwarf sperm whales have been the subject of direct study at sea in both the Bahamas and Hawai'i (Baird, 2005, 2016; Dunphy-Daly et al., 2008). Around the main Hawaiian

¹ To our knowledge, free-swimming individuals of these species have never been remotely biopsied or tagged.

Islands, dwarf sperm whales have been irregularly encountered during a long-term multi-species study of odontocetes (Baird, 2016; Baird et al., 2013). During these encounters, efforts have been made to photo-identify all individuals present and record information on group size, behavior, and other group attributes. In addition to photos obtained from this directed research, contributions of photos from other researchers and citizen scientists around the main Hawaiian Islands have been made available. In mid-2018 we added unmanned aerial systems (UAS or drones) to our tool set for studying this species, providing additional insights into behavior and into the best ways to further study this species. Here we present the results of this research, based on survey effort from 2000 through mid-2020. Multi-year resighting information provides evidence of site fidelity, and information on spatial use and resightings suggests a resident population inhabiting the island slopes, as well as an offshore population. We document evidence of individuals surviving attacks from large sharks, most likely either tiger (*Galeocerdo cuvier*) or white (*Carcharodon carcharias*) sharks, as well as evidence of fisheries interactions. We also describe behavior visible from the drone in the context of vigilance in response to predation risk (Lima & Dill, 1990). Additionally, we provide practical suggestions

for studying this species in the field, in order to aid other researchers who may have the opportunity to work with dwarf sperm whales in the wild. Although our sample size of encounters and identifications is relatively small, this represents the most comprehensive study published to date on live dwarf sperm whales world-wide. Additionally, both dwarf and pygmy sperm whales have been involved in stranding events associated with high-intensity naval mid-frequency active sonar use (Baird, 2016; Hohn et al., 2006; Simmonds & Lopez-Jurado, 1991), so our results may have implications for understanding the consequences of such exposure for populations of this species.

2 | METHODS

2.1 | Field methods

General methods have been previously reported (Baird, 2016; Baird et al., 2013) and are only briefly summarized here. Surveys were undertaken with small vessels with three to seven observers scanning 180 degrees around the research vessel, transiting at ~15-20 km/hr. Surveys were undertaken from February 2000 through June 2020, with survey efforts spread throughout the main Hawaiian Islands, typically during field projects of several weeks in duration off one or more island areas (i.e., Kaua'i and Ni'ihau, O'ahu, Maui Nui [including the islands of Lāna'i, Moloka'i, Maui, and Kaho'olawe], Hawai'i

Island) each year. Depth and spatial extent of survey coverage varied by project depending on the island area surveyed and the primary purpose of each field effort, but attempts were made to maximize the spatial extent of survey effort while remaining in areas with relatively calm (i.e., Beaufort 2 or less) sea conditions. Efforts were made to minimize spatial bias in sampling effort, working in offshore areas when sea conditions allowed, and covering as broad a range of depths and habitats as possible, although survey efforts were concentrated off the leeward (west and southwest) sides of the islands.

All groups of odontocetes were approached for species identification. Dwarf sperm whales were distinguished from pygmy sperm whales in the field and later confirmed after reviewing photos. Features used to discriminate species were the relatively large size of the dorsal fin in relation to the amount of back visible, and the relatively small head when the apex of the melon was visible. Information was recorded for start and end GPS location and behavior, group size, and reason for ending the encounter (e.g., group lost, group not approachable, all individuals identified). Starting in 2006 we began recording the group envelope, i.e., the spatial extent of the group in two dimensions. Field crew trained periodically in distance estimation on the water using laser range finders to

improve the accuracy of group envelope estimates. For every encounter one or more photographers would attempt to obtain photographs of all individuals present. Dwarf sperm whale individuals are often widely spaced (separated by up to a couple hundred meters) and at the surface at the same time, while also being difficult to visually detect even at distances of a couple hundred meters. To maximize the likelihood of obtaining photographs of all individuals present, one person (usually the vessel driver) would call out surfacings and relative bearings of individuals and direct one or more photographers to obtain photos of specific individuals. During prolonged (i.e., more than a few minutes) encounters with dwarf sperm whales, waypoints were taken on the GPS close to the area where animals dove and the vessel would remain relatively close to the waypoint location while animals were on a longer dive (e.g., >5 min). Information was recorded on how straight the travel track was when three or more waypoints were obtained. For a subset of prolonged encounters, durations of long dives (i.e., dives of approximately 1 min or more) were recorded. Durations were recorded to the second for some dives, but only to the nearest minute for others, depending on the ease of keeping track of specific individuals present given available crew, the group size, sea conditions, and the distance between the vessel and

the individual(s). Sloughed skin, prey, and fecal samples were collected on an ad hoc basis.

2.2 | Photo-identification, association patterns, and spatial use

Photographs were available from 74 of our encounters, 10 sightings from another researcher (D. McSweeney, Wild Whale Research Foundation) taken opportunistically off Hawai'i Island (between 2004 and 2010), 22 citizen science encounters (six off O'ahu and 16 off Hawai'i Island), and from six strandings (provided by K. West, University of Hawai'i). Citizen science photos were contributed by tour operators and private boaters as part of a larger multispecies effort incorporating citizen science in studying cetaceans in Hawaiian waters.² All photographs obtained, regardless of source, were sorted within encounters by individual, and photos were then matched between encounters to identify resightings. Each unique individual was assigned an identification number (HIKs###), and the best photograph from each encounter was graded both for photo quality (PQ: 1 poor, 2 fair, 3 good, 4 excellent) and individual distinctiveness (Dist: 1 not, 2 slightly, 3 distinctive, 4 very distinctive), following protocols outlined by Baird et al. (2008). Individuals were broadly classified as adults, subadults

² <https://www.cascadiaresearch.org/communityscience>

and dependents (juveniles, calves, and neonates), based on relative size in photographs, and for neonates based on the presence of fetal folds or a bent dorsal fin. An individual was considered a subadult in the limited cases where a slightly smaller individual surfaced next to a known adult, allowing for comparison of relative size. Calves and juveniles were distinguished, when possible, by whether they were obviously less than half the size of an adult (calves) or slightly larger (juveniles). Dependents were also typically in close proximity to an adult in all photographs. Sex of adult-sized individuals was classified as female if neonates, calves, or juveniles were documented in close attendance in one or more encounters. Sex was classified as likely male if the individuals were adult sized and there were multiple encounters over two or more years with no juveniles or calves in close attendance, as previous studies have indicated that this species may calve at intervals of one or two years (Plön, 2004). The oldest documented age for a dwarf sperm whale is only 22 years (Plön, 2004), so it is unlikely females have an extended postreproductive phase where they might be classified as males due to the lack of calves in attendance. Photographs were assessed for ancillary information, including evidence of individuals surviving attacks from large sharks, entanglements in fishing gear, or vessel

strikes, following established protocols (Baird et al., 2015; Moore & Barco, 2013).

Association analyses of photo-identified individuals were undertaken in SOCPROG 2.4 (Whitehead, 2008), and social network metrics were calculated and illustrated in Netdraw 2.158 (Borgatti, 2002). Analyses were undertaken with varying levels of restrictions on photo quality (e.g., no restrictions, PQ2+) and distinctiveness (e.g., no restrictions, Dist2+). Sighting histories of those seen over periods of 5 years or more were examined on a case-by-case basis to assess age and sex of associates.

We processed sighting locations and 5 min effort locations of the research vessel with R v.4.0.2 (R Core Team, 2020) to determine seafloor depths and distance from shore, using R packages *raster* (Hijmans, 2020) and *sf* (Pebesma, 2018), respectively. The Hawaiian Island 50-meter Bathymetry and Topography Grids (<https://www.soest.hawaii.edu/HMRG/Multibeam/grids.php>) were used for depth determination. For comparisons of sighting rates among island areas, only on-effort data in >350 m water depth with sea conditions of Beaufort 2 or less were used.

Sighting depths and distances from shore were compared for individuals that were seen on only a single occasion versus

those seen on two or more occasions. Distances between all possible pairs of locations both within island-areas and among all islands were calculated for all encounters where identification photos and latitude and longitude were available. To control for pseudoreplication, when more than one individual was identified from a particular encounter, that encounter location was only used once in the calculations. Combinations of encounters were generated using the *combinations* function within the *gtools* package (Warnes et al., 2020). Distances were calculated to account for intervening land masses (i.e., minimum distance required for an animal to travel between points), using the *raster* (Hijmans, 2020) and *fasterize* (Ross, 2020) packages. Distances between all encounter combinations for each individual sighted on two or more occasions were also calculated. Data were tested for normality and comparisons used nonparametric tests if data were nonnormally distributed.

2.3 | UAS operations

Starting in October 2019, when certain species (e.g., *Kogia* spp., beaked whales) were sighted, the drone pilot would immediately begin readying the drone for flight while the vessel continued in the general direction of the sighted group. When the drone was ready to deploy (typically less than one minute after the sighting was first made) the vessel would slow, and

the drone would be launched. A DJI Mavic 2 Pro was used for drone operations. This model has a built-in camera mounted to a three-axis stabilized gimbal that records MP4 video at a resolution of 3,840 × 2,160 pixels and a bit rate of 100 Mbps. A PolarPro polarizer filter was used to reduce surface glare. The drone was wrapped in a blue sky-colored vinyl to reduce possible disturbance due to its visual presence. Live telemetry (e.g., altitude, battery life) and 1,080 pixels 30 Hz live video was monitored using the DJI Go 4 app on an Apple iPhone 11 Pro Max mounted to the remote controller. The aircraft was operated by a U.S. Federal Aviation Administration (FAA) Part 107 licensed remote pilot.

Drones were generally flown over animals at an altitude of 30 m or greater, with descents to 15 m to allow for collection of detailed images, or to ~2-3 m for an attempt to collect a breath sample. At times the drone was flown at an estimated radial distance of 15 or 30 m to allow for collection of video or images from an angle. Once the drone was in the air, the research vessel would continue towards the sighted group, although when within a couple of hundred meters would slow to approach at speeds less than ~4 km/hr. The drone pilot provided a running commentary to photographers and the vessel driver regarding the number and behavior of animals visible subsurface.

When animals appeared to be surfacing, this information would be passed on to the vessel driver to allow positioning of the research vessel relative to where the animals were likely to surface (under the drone) in order to facilitate photo-identification. In general, the drone was piloted to keep the first individual detected in sight and at times was moved higher in altitude at the direction of on-board crew when other individuals were not visible to the drone pilot. This would allow for simultaneously monitoring multiple individuals that were more widely spaced.

Drone video was processed using DashWare 1.9.1 (GoPro, San Mateo, CA) to overlay flight telemetry and a compass wheel to aid in analysis. Video files were reviewed to record specific behavioral events (e.g., breaths) and states (e.g., logging, subsurface swimming), to assess relative body sizes of the individuals present as well as horizontal speeds and travel paths, and to record interactions among individuals.

3 | RESULTS

3.1 | Encounters, group size, and behavior

From February 2000 through June 2020, we surveyed approximately 136,681 km over 1,327 vessel days (8,343 hr). The majority of effort was off Hawai'i Island, which also had the greatest proportion of effort in suitable conditions (Beaufort 0, 1, or

2) for sighting dwarf sperm whales (Table 1). Off Hawai'i Island there was survey effort in suitable depths (>350 m) and conditions in all months of the year, although with the least amount of effort (3.7%) in winter (January-March) and the most (38.2%) in fall (October-December). In total we had 112 sightings (3.5% of all odontocete sightings) of either dwarf sperm whales (94 sightings, 3.0% of all odontocete sightings), pygmy sperm whales (8 sightings), or unidentified *Kogia* (10 sightings). At no point were other species of cetaceans associated with any of the groups. For sightings that were identified to the species-level, given the relative proportion of dwarf sperm whales (92.1% of identified kogiids) it is likely that most of the unidentified *Kogia* were also dwarf sperm whales. Dwarf sperm whales were encountered in depths ranging from 352 to 4,737 m (median = 879 m), and at distances from shore ranging from 0.73 to 40.23 km (median = 3.80 km). Pygmy sperm whales were encountered in significantly greater depths (Mann-Whitney *U*-test, $p = .002$; median = 2,627 m, range = 659-4,084 m) and at significantly greater distances from shore (Mann-Whitney *U*-test $p = .001$; median = 14.68 km, range = 7.43-32.78 km). Sightings of pygmy sperm whales and those not identified to species were not considered in additional analyses. The closest point of approach of the research vessel

during most encounters ranged from 40 to 100 m, with only a few encounters involving approaches to within 10-20 m, limiting observations of animals subsurface. Dwarf sperm whale sightings occurred off all the main island areas (Figures 1 and S1), but sighting rates were more than three times as high off Hawai'i Island than off Kaua'i/Ni'ihau (Table 1). Off Hawai'i Island dwarf sperm whales represented 4.0% of all odontocete encounters, tied for the sixth-most frequently encountered species of the 18 species encountered. Sightings were distributed along the entire west coast of Hawai'i Island (Figure 1).

Based on the distribution of search effort by depth, sighting rates were higher than expected in depths of 500-1,000 m, and lower than expected in both shallower and deeper waters (Figure 2). Encounter durations ranged from less than a minute (when the animal(s) dove and were not seen again) to 1 hr and 33 min (median = 16.2 min). The majority of encounters ($n = 56$, 60.0%) ended when the group was lost, although the probability of losing the group was higher (70.3%) when sea conditions were a Beaufort 2 or greater, compared to a Beaufort 0 or 1 (52.6%). The proportion of groups that were lost also varied by group size: 80% of lone individuals were lost, groups of two to four were lost 56.4% of the time, and groups of five or greater were

lost 35.7% of the time. Groups of two or more often included dependents or subadults, and thus it is possible these groups were easier to resight as dive durations may have been shorter than for lone adults (see dive duration information below). Group size increased with encounter duration (regression, $p < .001$, $r^2 = 0.22$), which likely reflects both the greater likelihood of losing very small groups and that longer encounters allow for a more accurate estimation of group size. Some encounters ($n = 17$, 18.1%) were deliberately ended after all individuals were thought to have been photographed for individual identification, including the two encounters for which drone operations were undertaken. Groups were also left ($n = 15$, 16.0%) with only some individuals photographed or because individuals showed an avoidance reaction and were not likely to be approachable ($n = 5$).

Dwarf sperm whale group sizes ranged from 1 to 8 (median = 2, $M = 2.78$, $SD = 1.70$), although lone individuals were the most-frequently encountered, representing 26.6% of all encounters (Figure 3). Groups could be widely dispersed. Pairs of individuals ranged from <3 m apart to an estimated 350 m apart (median = 12.5 m, $n = 20$). For groups of three or more, group envelopes ranged from 3 × 4 m to 300 × 800 m (median = 20 m × 190 m, $n = 40$), although all of the groups with individuals

an estimated 400 m apart or greater ($n = 9$) were of four or more individuals, and may have represented two independent groups that were visible at one time. There were only four encounters with neonates present (two in March 2006 of the same mother-neonate pair seen three days apart, one in October 2008, and one in October 2009). Group size in three of the cases was two individuals and in the remaining sighting was four individuals. Depths of the four encounters with neonates were relatively shallow – 352 m, 361 m, 565 m, and 744 m.

Long dive durations varied based on the age composition of groups (Figure 4), although the differences were not significant (Kruskal-Wallis one-way ANOVA, $p = .34$). Five long dive durations were recorded for the mother/neonate pairs that ranged from 2 min 0 s to 4 min 46 sec (median 2 min 11 s). Long dive durations recorded from eight encounters with one or more females and juveniles or calves ranged from 57 s to 9 min (median = 4 min, $n = 29$). Long dive durations recorded from 13 encounters that involved only adults and large subadults ranged from 1 to 22 min (median = 5 min, $n = 28$; Figure 4).

Start behavior was recorded for 89 encounters. Logging (i.e., remaining relatively motionless at the surface) was the most-frequently recorded start behavior (42 encounters; 44.6%). Travel was recorded as the start behavior in 23 encounters

(24.4%), and milling (i.e., nondirectional surfacing) or slow rolling was recorded as the start behavior in 22 encounters (23.4%). Both slow rolling and logging behavior were often observed in prolonged encounters. There were only three encounters where breaches or other aerial behaviors (e.g., leaping) were observed, all involving larger groups (3, 5, and 5 individuals). In one encounter, two breaches by one individual were observed, in another two different individuals appeared to breach once each, and in the third encounter an individual was observed leaping and defecating in air before entering the water headfirst. Individuals within groups were often asynchronous in their surfacings. This was most obvious when there were two or three pairs of individuals, with each pair representing an apparent adult and juvenile or calf (based on relative sizes). Individuals within a pair were generally synchronous within a few seconds of each other, but pairs would often be spaced up to a couple hundred meters apart and surfacing periods would either overlap only partially or not at all. Samples collected included sloughed skin ($n = 4$, collected in fluke prints and archived at the Southwest Fisheries Science Center), feces ($n = 1$), and suspected prey ($n = 1$, a squid tentacle found 30 m from an animal). The squid tentacle was identified as *Chiroteuthis* sp. c.f. *C. picteti* (W. A. Walker, personal communication, January

2021).

3.2 | Photo-identification, site fidelity, movements

Photographs from which individuals could be identified were available from 106 encounters with dwarf sperm whales as well as from six strandings of lone individuals. With no restrictions for photo quality or distinctiveness, 177 individuals were documented, and identifications were available from all months of the year. Considering only individuals that were at least slightly distinctive with fair or better-quality photos there were 101 individuals in the catalog. Five of the stranded individuals were at least slightly distinctive (one each from Kaua'i, O'ahu, and Hawai'i, and two from Maui)—none matched to any other individuals in the catalog.

A social network of the 96 nonstranded individuals (Figure 5) showed that 40 of the 96 (41.6%) were linked by association in the main cluster of the social network. Social network cohesion was low, with 13 individuals (32.5% of individuals in the main cluster) acting as cutpoints, i.e., locations in the network where groups of nodes are connected by a single individual. Similarly, only 15 individuals (37.5% of individuals in the main cluster) had betweenness centralities (i.e., the extent to which a node acts as a bridge between two nodes) greater than zero ($n = 40$, range 0.0–487.7; Table S1).

Of the 96 individuals, 30 were seen on more than one occasion (median = 2 occasions, maximum = 14), over spans ranging from 2 days to 14.9 years (median = 1.5 years). No individuals were documented moving among island areas, although the likelihood of documenting such movements was low, given the small number of individual identifications that were slightly distinctive or greater (including stranded individuals) from Lānaʻi or Maui ($n = 4$), Oʻahu ($n = 7$), or Kauaʻi/Niʻihau ($n = 4$). Although there were only five nonstranded individuals that were slightly distinctive or greater documented off Oʻahu, one (HIKs132) was seen in two different years (March 2016 and January 2017). All remaining re-sighted individuals were off Hawaiʻi Island. Of the 21 individuals seen for a span of more than one year, seven were classified as adult females based on the presence of juveniles or small calves in attendance, and four were classified as adult males due to repeated sightings (range 3-7) in two or more years with no juveniles or calves in attendance. Ten could not be categorized by sex due to a small number of sightings (range 2-4) or a short span of sightings.

While 30 of the 96 individuals (31.2%) were seen more than once, resighting rates varied by distinctiveness (Table 2). Restricted to very distinctive individuals with a best photo quality of fair or greater, 11 of 21 individuals (52.4%) were

seen more than once, and six of them were seen in more than one year. It should be noted that three of the 21 very distinctive individuals were documented off islands other than Hawai'i, where relatively few identifications were available. Of the 18 documented off Hawai'i Island, 10 (55.5%) were seen more than once, and half of those were seen in more than one year.

One very distinctive individual, HIKs020, was seen 14 times over a 14.9-year span, with sightings in 11 different years. The 14 sightings of this individual were in eight different months of the year (January, March, April, May, June, August, October, and November), suggesting that there is no seasonality to its presence. HIKs020 was seen in groups ranging from two to six individuals (median = 3), and it was documented with at least three different calves in close attendance, including a juvenile in January 2008, a neonate in October 2008, and a calf of undetermined size (due to photo quality) in October 2019. HIKs020 was documented with several nondistinctive individuals in intervening years, but it was not possible to conclusively determine if these were different individuals. Including nondistinctive individuals (which were calves, juveniles, or subadults), HIKs020 was documented associating with 15 different individuals over the 14 sightings. These 15 individuals included six individuals considered to be calves, juveniles or subadults

based on relative size, and nine adults. Of the nine adults, five were of unknown sex (i.e., with short sighting histories and no calves closely associated) and four were classified as adult males (i.e., with longer sighting histories and no calves closely associated). Considering individuals at least slightly distinctive, two repeated associations were documented for HIKs020, one with a likely adult male (HIKs035) documented together two days apart, and the other with a likely adult male (HIKs050) encountered in the same group 5 years apart. In the latter case both individuals had been seen separately in the intervening years.

Repeated associations were only documented for six other dyads, three over short periods (2, 2, and 10 days, the latter case likely a mother/offspring pair), one after 284 days (between an adult male and an adult of unknown sex), and two dyads seen together each after four years (1,471 and 1,481 days for the two pairs). These latter pairs included one likely adult male and an individual of unknown sex that was considered a subadult when first seen, and a likely adult male seen with another adult of unknown sex.

No latitude and longitude were available for one of the sightings of the individual resighted off O'ahu, so calculations of distances among resightings was restricted to Hawai'i Island

(Table 3). Distances between sighting locations for individuals that were resighted (grand $M = 15.2$ km, $SD = 15.5$ km, median = 10.3 km) were significantly less (Mann-Whitney U -test, $p < .001$) than the distance between all possible pairs of encounter locations off Hawai'i Island ($M = 33.7$ km, $SD = 26.2$ km, median = 28.4 km). The maximum distance between resightings of an individual was 77.0 km. Latitude and longitude were available for 11 of the 14 sightings of HIKs020 (Figure 6). The mean distance between the 54 possible combinations of sighting locations was only 6.1 km ($SD = 4.7$, median = 4.6, maximum = 19.7), suggesting a very restricted range.

For comparison of depths of sightings of individuals, data were restricted to those that were slightly distinctive or greater, with photo quality of fair or greater, and documented off Hawai'i Island. For this analysis there were 51 locations (from 43 individuals) available for individuals in isolated clusters, and 81 locations (from 41 individuals) available for individuals in the main cluster of the social network. A comparison of depths for individuals from the main cluster to individuals in isolated clusters showed that individuals in the main cluster were found in significantly shallower water ($M = 852$ m, $SD = 267$ m, median = 928 m, maximum = 1,505 m) than were those in isolated clusters ($M = 1,198$ m, $SD = 769$ m, median =

960 m, maximum = 3,876 m; Mann-Whitney *U*-test, $p = .041$; Figure 7). Assuming that there may be mixing between individuals from a putative resident insular population and an offshore population, we also compared depths of individuals seen only once compared to those seen multiple times. This comparison also found that individuals seen only once were found in significantly deeper water ($M = 1,178$ m, $SD = 723$ m, median = 960 m, maximum = 3,876 m) than were those seen on multiple occasions ($M = 843$ m, $SD = 319$ m, median = 885 m, maximum = 1,559; Mann-Whitney *U*-test, $p = .020$; Figure 7).

3.3 | Sources of injuries and markings

Wounds presumed to have been caused by large sharks were documented on four individuals (Figure 8), with wounds on the dorsal fin ($n = 2$), on the mid-back in front of the dorsal fin ($n = 1$), and on the caudal peduncle ($n = 1$). The individual with the wound on the caudal peduncle (HIKs088) had the largest wound (Figure 8a-c). The size of the wound was most consistent with an attack by a white shark or tiger shark C. G. Meyer, personal communication, January 2021), although it was not possible to confirm the shark species based on the condition of the wound. Based on the size of the individual relative to another (much smaller and nondistinctive) individual photographed next to it (presumed to be its calf), this individual was likely an adult

female. These individuals were photographed in October 2011, but HIKs088 has not been resighted subsequently.

Fresh and healed oval wounds from cookiecutter sharks (*Isistius* sp.) were frequently seen on individuals with good quality photos (Figure 9). Healed wounds had repigmented back to normal coloration in all cases where good quality photos were available. One juvenile was documented with a large slightly oblique rectangular cutaneous ulcer on the right side of the head (Figure 9c), with abrupt vertical to gently sloping margins. The wound extended from the mid-level of the rostrum caudally to approximately 2 cm behind the eye, and from the dorsolateral aspect of the melon to an estimated 2-3 cm below the level of the eye. The dorsal wound margin was slightly serrated, but there was no evidence of bites or rake marks in the adjoining tissues. Due to the abrupt and angulated margins, a ship strike with avulsion of the epidermis, conjunctiva and eyelids may be a possible cause (S. A. Raverty, personal communication, September 2020). The lesion was also similar to lesions seen on delphinids in Hawaiian waters associated with persistent remora (*Remora remora*) damage (R.W.B., unpublished observation). One adult-sized individual (Figure 9d) had numerous partially healed lesions on the dorsal and lateral surface of the head extending from at least the apex of the

melon to an estimated 20 cm caudal of the blowhole. It is possible that these lesions originated from contact with a hard substrate, for example if the animal were feeding benthically (W. A. Walker, personal communication, September 2020). This individual also had two partially healed wounds likely caused by cookiecutter sharks, as well as three healed parallel linear marks on the dorsal fin (Figure 9d) that were likely caused by an interaction with a larger odontocete (e.g., false killer whale, *Pseudorca crassidens*, or killer whale, *Orcinus orca*).

Linear wounds or marks were documented on eight individuals (8.3% of the 96 individuals considered). Two of these involved amputations of the top of the dorsal fin. One individual had a vertical slice through the dorsal fin and the caudal portion of the fin bent laterally to the left (Figure 9e). This wound was consistent with either a line wrap or a propeller strike, and the individual also had a leading edge wound on the dorsal fin consistent with a line injury. One individual had multiple circumferential abrasions immediately behind the fin in addition to linear abrasions on the dorsal fin (Figure 9f), consistent with an interaction with a line fishery. One individual was documented with a deep indentation on the peduncle (Figure 9g, 9H) that was consistent with a line wrap injury. Four additional individuals had linear cuts into the leading edge of the dorsal

fin that were possibly consistent with line fishery interactions, although photo quality precluded conclusive determination of the cause of injuries.

3.4 | UAS operations

Drone operations were undertaken with two groups encountered in 2019 (October 28 and November 6). No reactions to the presence of the drone were noted in either encounter. Additional information from drone footage is provided in supplementary materials; highlighted here are observations relevant to using drones for study of this species, observations of social interactions, interbreath intervals, and swimming patterns. Between the two encounters, five different individuals were photo-identified, four in the first encounter and three in the second (two of the three in the second encounter were also present in the first). None of the five individuals had been previously identified, and thus no information was available from sighting histories that could be used to infer sex.

During the October 28 encounter, the total amount of time that one or more individuals were visible from the drone was 11 min and 25 s. One or more individuals were visible from the drone while subsurface, with no individuals visible at the surface, for a combined 10 min and 9 s (i.e., 89% of the total time that individuals were visible from the drone). Sloughed

skin was visible in the wake of an individual slow rolling on three different occasions.

While underwater, individuals generally exhibited a net forward motion, but rarely swam in a straight line for more than a few seconds. The path of motion over periods of 5-10 s was typically S-shaped, and the overall travel path was sinusoidal (Figure S2). Mean horizontal speed was 4.00 km/hr ($SD = 0.55$ km/hr). Over a 30 s period the individual might be traveling on an average bearing of 135° , but the bearing would fluctuate from $\sim 90^\circ$ to 180° , and back, repeatedly (Video S1). During subsurface swimming there were two cases where an individual stopped its forward motion, turned $\sim 180^\circ$, and then turned again back to its original course of travel. Three of the cases where logging was observed have footage available of the individual both before and after the logging period. In two of the three cases, individuals turned 100° and 135° from their prior course of travel prior to beginning logging. In the third case, the individual had been on a course of $140^\circ T$, turned (while remaining underwater) to $50^\circ T$, then turned 175° , slow rolled once, and then started logging while oriented towards $225^\circ T$. In the 1 or 2 s immediately prior to slow rolling, individuals were seen turning their head $10-30^\circ$ ($n = 4$) or turning their entire body from 20° to 60° ($n = 3$). Three of the five remaining cases

where slow rolling was documented and no head or body turning was documented involved a juvenile (HIKs166) engaged in social behavior with one of the adults. The other two cases where no turning was observed were surfacings five and four seconds after prior surfacings that did involve body turns.

For much of the time only a single individual was visible within the video frame, but three social interactions, with one individual (in all cases the juvenile HIKs166) approaching another, were documented. In the first case, HIKs166 approached HIKs167 from behind and below while both were swimming subsurface (Video S2). As the two individuals appeared to be about to come into contact, HIKs167 abruptly turned 130°, appearing to try to avoid HIKs166. HIKs166 followed HIKs167 in the turn for approximately 3 s, and then resumed the prior direction of travel. After 5 s, HIKs167 also resumed the prior direction of travel. Less than a minute later HIKs166 approached one of the other adults (HIKs168) while it was slowly surfacing just over a body length behind the third adult (HIKs165), which was logging at the surface. When HIKs166 was less than a body length from HIKs168, HIKs168 abruptly rolled laterally toward HIKs166 (Video S2). HIKs166 continued past HIKs168 and slowly approached HIKs165, which was logging at the surface. HIKs166 moved slowly closely underneath the caudal half of HIKs165, with

no obvious change in behavior of HIKs165, and then began logging next to HIKs165 less than a body length apart (see Figure 9g). All three individuals remained logging within one to two body lengths of each other for approximately 10 s before all dove, with HIKs166 closely following HIKs165, and remaining together while separating from HIKs168.

During the November 6 encounter, while subsurface with no individuals visible at the surface, one or more individuals were visible from the drone for a combined 21 min and 24 s (87% of the total time that the individuals were visible from the drone). Mean horizontal speed was 3.24 km/hr ($SD = 0.58$ km/hr), but the overall travel path was convoluted, with the start and end locations within a couple of hundred meters of each other (Figure S2). In the one or two seconds immediately prior to slow rolling individuals were seen turning their head 10° - 30° ($n = 6$) or turning their entire body from 20° to 60° ($n = 3$). One individual was seen turning its head once prior to logging. While underwater, individuals turned their heads four times, once apparently in response to surface ripples from a prior slow roll event. While the direction of travel generally remained constant, periodic turns while subsurface were observed. HIKs167 briefly turned to 90° T, then 225° T, then to 135° T before continuing on a course of 315° T for 38 s. Prior to surfacing

when starting a logging bout, HIKs167 turned to 45°T, then to 135°T, then turned 180° to surface on a heading of 315°T. Information on social interactions during the November 6 encounter are presented in supplementary materials.

For both encounters combined, interbreath intervals while individuals were logging ranged from 2 to 14 s (median = 6 s, $n = 64$). Interbreath intervals when individuals were slow rolling ranged from 4 s to 3 min 44 s (median = 15 s, $n = 39$), although it should be noted that this only includes confirmed periods where the animal remained visible for the entire period subsurface.

4 | DISCUSSION

Our photo-identification results demonstrate a relatively high degree of site fidelity for dwarf sperm whales off the island of Hawai'i. Despite a limited number of encounters and long periods between encounters, we documented high resighting rates of very distinctive individuals (55.5%), with half of those seen in more than one year. Six different individuals were documented over at least a 5-year time span, and one individual (HIKs020) was resighted 14 times over a 15-year period. For that individual, sightings were spread throughout the year, suggesting that at least some dwarf sperm whales may be resident year-round, or at least show no particular seasonal trend to their use of the

area. The average distance between re-sightings of individuals was less than half the average distance between all possible combinations of encounters off Hawai'i Island (Table 3), showing that even within our Hawai'i Island study area, individuals use a much smaller range than the overall distribution of dwarf sperm whale sightings (cf. Figures 1 and 6). The high number of sightings of HIKs020 (14 over a 15-year period) may reflect in part the proximity of its core range to Honokōhau Harbor (Figure 6), where most of our Hawai'i Island surveys originated. Given our sample size, we were not able to determine whether there were seasonal variations in habitat use, as documented by Dunphy-Daly et al. (2008) in the Bahamas, although for HIKs020 sighting records over six different months of the year were all in the range of 350-1,000 m (Figure 6).

There are sightings of this species both around the islands and in offshore Hawaiian waters (Baird, 2016; Bradford et al., 2021). Only a single stock of dwarf sperm whales is recognized in Hawaiian waters (Carretta et al., 2014), although Oleson et al. (2013) had proposed designating a (prospective) island-associated stock around Hawai'i Island, based on data available through 2012. Although our data set is sparse, given the inherent difficulties in detecting and working with dwarf sperm whales, we provide multiple lines of evidence supporting a small

resident population. Given the apparent susceptibility of this species to strand in relation to high-intensity military sonars (Baird, 2016; Hohn et al., 2006; Simmonds & Lopez-Jurado, 1991), this population warrants recognition and separate management from the much larger offshore population (Bradford et al., 2021), as suggested by Oleson et al. (2013). Whether there is interchange with the offshore population is unknown and would be difficult to determine given the inherent difficulties in obtaining genetic samples of this species. That said, we opportunistically collected sloughed skin samples from four different encounters. During drone operations, we observed sloughed skin in the water behind an individual on three different occasions. Future efforts to collect genetic samples from this species could be facilitated by the use of a drone to indicate when and where sampling (e.g., for eDNA) would be most effective.

Although this population of dwarf sperm whales is the only one for which such evidence of residency has been reported, residency to the slopes of Hawai'i Island has been documented for 10 other species of odontocetes, including both delphinids and beaked whales (Baird, 2016). For example, in Hawai'i there is evidence of a slope-dwelling population of Blainville's beaked whales (*Mesoplodon densirostris*) that overlaps with an

offshore population, with high resighting rates and shallower water distribution of the resident individuals (Baird, 2019; Baird et al., 2011; McSweeney et al., 2007). Similarly, for false killer whales (*Pseudorca crassidens*), both insular and pelagic populations with overlapping ranges have been recognized with additional evidence that these populations are reproductively isolated (Martien et al., 2014).

Whether resident populations occur off other islands within the main Hawaiian Islands is unclear, given the relative lack of identifications available, although the resighting of one individual off O'ahu in two different years suggests some level of site fidelity. Our sample size of photographs from Lāna'i and Kaua'i are small, limiting our ability to assess residency in those areas. However, when considering relative sighting rates by island area, Hawai'i Island and Maui Nui have similar sighting rates, while sighting rates off O'ahu and Kaua'i/Ni'ihau are much lower (Table 1). Off Kaua'i and Ni'ihau it is interesting to note the distribution of sightings in relation to search effort. Despite the majority of effort off the west side of Kaua'i, much of it overlapping with the area of the U.S. Navy's Pacific Missile Range Facility (PMRF), almost all sightings were off the eastern half of Kaua'i (Figure S1). Based on survey effort through 2015, Baird (2016) had previously

suggested that dwarf sperm whales were largely absent around PMRF due to the regular use of mid-frequency active sonar on the range. Additional effort off Kaua'i and Ni'ihau in subsequent years further supports a lack of use of that area (Figure S1).

Dwarf and pygmy sperm whales feed primarily on cephalopods, most of which are found deep in the water column (Ross, 1979; Staudinger et al., 2014). Although we recovered one squid tentacle from the vicinity of dwarf sperm whales, we have witnessed no behaviors at the surface indicative of feeding or chasing prey. This suggests that in Hawai'i, at least during the day, dwarf sperm whales likely do not regularly feed near the surface. Given their diet and presumed deep-water feeding habits they likely do not depredate catch in many fisheries, although there are records of bycatch of one or both species (Arbelo et al., 2013). Bycatch recorded in pelagic and artisanal gill nets (Carretta et al., 2017; Jiménez et al., 2018; Zerbini & Kotas, 1998) likely reflects animals accidentally encountering nets, but hook and line fisheries bycatch has also been recorded, which may reflect depredation of bait or catch. In the Hawai'i-based deep set longline fishery for tuna there is a 2014 record of a pygmy sperm whale being hooked in the mouth (Bradford & Forney, 2017), likely representing a case of depredation of bait. There is also a 1947 record of a reported pygmy sperm

whale being hooked on a hand line that was baited with “aku” (likely skipjack tuna, *Katsuwonus pelamis*, off Maui (Edmonson, 1948). This was prior to recognition of two species in the genus and this individual was reported with four teeth in the upper jaw (Young, 1947), indicating that the individual may have been a dwarf sperm whale. Linear wounds documented on live individuals in our study (Figure 9) also suggest that dwarf sperm whales in nearshore Hawaiian waters likely interact with one or more fisheries. The ika-shibi fishery involves the use of squid as bait, and fishing is undertaken primarily at night (Glazier et al., 2009). We suspect that this may be one of the fisheries where dwarf sperm whales may depredate bait, occasionally resulting in line injuries if individuals struggle against a taut line (Baird et al., 2015). Effort in this fishery does occur within our study area off Hawai‘i Island (Hawai‘i Division of Aquatic Resources, unpublished data) so such interactions may have occurred in the area, although there has been an overall decline in effort in this fishery (Glazier, 2007).

Evidence of vessel collisions with pygmy sperm whales have also been previously reported (McAlpine et al., 1997; Sylvestre, 1988); one dwarf sperm whale in our study was documented with a wound on the dorsal fin that was consistent with either a

propeller strike or a line wrap (Figure 9e). The behavior of frequently logging at the surface could put individuals at risk of vessel collision, although their reported reactions to vessels (Würsig et al., 1998) would suggest collisions are likely infrequent.

Individuals were documented with a wide variety of other types of wounds and injuries that were not related to anthropogenic interactions, including bite wounds from large and small sharks, as well as abrasions and lesions from other causes. Determining the cause of lesions is difficult without having an animal in hand, but scarring on the head of one individual was consistent with foraging on the bottom (Figure 9d), similar to head scars observed on benthic feeding Baird's beaked whales (*Berardius bairdii*) off Japan (W. A. Walker, personal communication, January 2021). Another individual had a large ulcer on the head, similar to damage caused by remoras documented for spinner dolphins (*Stenella logirostris*), pantropical spotted dolphins (*S. attenuata*), and common bottlenose dolphins (*Tursiops truncatus*) in Hawai'i (Baird, 2016). We had no sightings of dwarf sperm whales with remoras visible on the body. However, with the exception of the two encounters where we obtained drone footage, we were rarely close enough to document remoras, which typically stay low on the body

of cetaceans. Healed and fresh cookiecutter shark bites were commonly observed and sometime resulted in holes completely through the dorsal fin (Figure 9b). However, it is possible that some of the holes though the fin originated from gunshot wounds. Although they are not easy to approach, their behavior of logging at the surface for extended periods would increase the likelihood of being hit, and there are reports of fishermen shooting cetaceans off Hawai'i Island (Baird, 2016; Shallenberger, 1981; Tummons, 1997) and elsewhere in the main Hawaiian Islands (Harnish et al., 2019). There are records of a shooting of a pygmy sperm whale off California (Carretta et al., 2014) and a dwarf sperm whale off the southeast United States (Würsig, 2017).

Four individuals were documented with wounds from attacks by large sharks, suggesting that shark predation may occur regularly with this species. Both tiger and white sharks may be found in our study area off Hawai'i Island, although white sharks are likely there only during winter and spring months (Jorgensen et al., 2010; Meyer et al., 2018). While wounds for three of the individuals were largely healed, the wounds on the fourth individual were only partially healed and were extensive enough that they may have later resulted in the death of the individual. In all four cases, wounds were centered on the

dorsal surface of the animals, suggesting that individual dwarf sperm whales may roll to present their less vulnerable dorsal surface in response to an imminent attack by a shark, as has been suggested for other Hawaiian odontocetes that show evidence of at least occasionally surviving attacks by large sharks (e.g., melon-headed whales (*Peponocephala electra*) and pygmy killer whales (*Feresa attenuata*; Baird, 2016). It should be noted, however, that only dorsal photos are available from our study, so it is possible that individuals exhibited signs of shark attacks on the ventral surface that were not visible to us. Predation on dwarf sperm whales by killer whales and large sharks has been previously documented on a couple of occasions (Dunn & Claridge, 2014; Dunphy-Daly et al., 2008; Long & Jones, 1996)—our work demonstrates that such predation may occur fairly regularly, and at least on occasion individuals may survive such attacks.

Predation risk may influence behavior in a variety of ways. Drone footage showed that individuals appeared to be constantly vigilant for potential predators, regularly turning the head side to side before surfacing. In some cases, individual dwarf sperm whales did a complete 180° turn, appearing to check for potential predators following behind, similar to the behavior of Soviet submarines when “clearing the baffles” (Clancy, 1984;

Sontag & Drew, 1998), or loggerhead turtles (*Caretta caretta*) in areas where shark predation is high (Heithaus, 2013).

Our results clearly demonstrate the value of using both individual photo-identification and drones with this species. Our experience working with this species and being able to stay with an increasing proportion of groups until all individuals have been photo-identified, rather than losing the groups after the individuals dive, provides some practical suggestions for working with this species. For a species that is as difficult to get close to as a dwarf sperm whale, the resolution of images obtained for individual identification is critically important. In the early days of our work (prior to 2003), we relied on film cameras, but even with the switch to digital in 2003, both the size of the sensor (originally ~6 megapixel, now ~20 megapixel) and the quality of the lens has played a role in our ability to obtain photos of sufficient quality to identify individuals. Given the difficulty in getting close to this species, studies involving individual identification will greatly benefit from increases in the resolution of digital cameras and reduction in camera costs. We recommend that any efforts to photo-identify this species use camera systems with high resolution sensors and excellent ISO performance to allow for detection of marks from distant individuals. When encounters are short, as groups are

often lost quickly, having multiple photographers coordinating efforts to try to obtain photos of all individuals present has also played a key role, and we recommend such criteria be explicitly incorporated into research protocols to maximize the likelihood of obtaining photos of all group members.

Drone footage illustrated that individuals would often surface on a bearing different from their overall direction of travel (Video S1), which makes using surface cues (e.g., the direction an individual is pointing while at the surface) ineffective for determining direction of travel. While patience is clearly required, we have found that taking a GPS waypoint of where the animals went down, and remaining very close (i.e., within 20 m) until the animal(s) resurface is key to being able to prolong an encounter. On dives of <10 min, individuals tend not to move more than ~200 m. Even slight surface currents can move a boat far enough away from the dive location to preclude resighting the group. Repeating this approach after the animals have come back up (i.e., moving to the fluke prints of where the animal(s) dove and taking another waypoint, and measuring the distance and bearing from the original waypoint) allows for calculating approximate speed and direction of travel, increasing the likelihood of being able to track the group through subsequent surface/dive cycles. This is often critical,

as following groups over several dive cycles may be needed before the vessel is able to get close enough for photographers to obtain good quality identification photos. It should be noted however that travel paths are rarely straight (Figure S2). Using drone video feed in real time to maintain visual contact with individuals while they are subsurface also greatly increases the ability to follow groups for extended periods, increasing the likelihood of obtaining good quality identification photos of all individuals present. This is one clear benefit of using a drone with this species, in addition to the other types of information obtained from drone footage (e.g., behavioral observations, photogrammetry; Hartman et al., 2020).

Behavioral information obtained from the drone was valuable in a number of ways: documenting swimming behavior that may be related to vigilance for predators (as noted above), measuring interbreath intervals, and examining social interactions that are primarily occurring beneath the surface. Some prior examinations of dwarf and pygmy sperm whale interbreath intervals have focused only on long dive durations (e.g., Barlow, 1999), as observing breaths for a species that has no visible blow and often breathes while logging at the surface is problematic, to say the least. From the drone we were able to measure interbreath intervals for both logging and slow rolling

individuals. While these interbreath intervals are only for cases where animals do not go completely out of sight (i.e., deep in the water column), and thus exclude longer dives, they likely represent a good sample of interbreath intervals for animals that are near the surface. Our longer dive durations, recorded from the boat, are likely negatively biased, as individuals that dive for extended periods are typically lost, although the patterns observed do suggest that long dive durations vary based on the age composition of the group, with mothers with neonates having the shortest long dives.

Our ability to interpret the social interactions observed (Video S2) is limited, given that these appear to be some of the only social interactions reported for this species and the sexes of the individuals involved is not known. That said, size differences among the individuals observed in our October 2019 encounter allow us to infer that the smaller individual moving among the three adult-sized individuals was a juvenile, which may suggest that it could be a recently weaned calf looking for opportunities to nurse, rather than a male approaching potential mates. The apparent avoidance reaction by two of the adult individuals present, and the lack of a reaction by the third, suggests that the third individual (HIKs165) may have been the mother of the juvenile. Obtaining future drone footage of known

sex (i.e., females that have been documented with small calves in attendance during their sighting history) or inferred sex (i.e., putative males based on long sighting histories with no calves in attendance) individuals will allow for a better understanding of the social dynamics of this species. Along with Cuvier's beaked whales (*Ziphius cavirostris*), dwarf sperm whales are tied for the second smallest average group size of the 18 species of odontocetes documented in Hawaiian waters, with only pygmy sperm whales having smaller average group sizes (Baird et al., 2013). Such small group sizes (Figure 3), combined with the limited information on the number of associates (Figure 5) and how infrequent repeat associations are all suggest that dwarf sperm whales live relatively solitary lives. Similarly, social network cohesion was tenuous, with the majority of individuals linked to the main cluster by a single individual (Figure 5), and a few individuals demonstrating particularly high betweenness centrality, which can be a useful measure of how information is disseminated within a network. Two individuals in particular, HIKs035, a suspected adult male and HIKs020, an adult female, were located near the center of the network cluster (Figure 5) and had both the highest number of associates and the highest betweenness centrality values. These individuals also acted as cut points in the network and were responsible for

maintaining overall network connectivity. Given the small population size and sparse network structure, such individuals may be an important part of the communication pathway in a species that is not highly social.

Our study is just the first glimpse into the behavior and social dynamics of this species in the wild, and we hope that in other areas where this species can be reliably found that increased efforts are made to study this representative of the family Kogiidae.

ACKNOWLEDGMENTS

Funding for surveys has come from a variety of sources, including grants from the Pacific Islands Fisheries Science Center, Southwest Fisheries Science Center, and Office of Naval Research, and contracts with the State of Hawai'i, Northwest Fisheries Science Center, and Commander, Pacific Fleet (through HDR Inc). We particularly acknowledge Office of Naval Research Award N00014-13-1-0648, our only funding specifically to work with dwarf sperm whales. A large number of individuals assisted with field work over the years, but we particularly thank Daniel Webster, Greg Schorr, Annie Douglas, Dan McSweeney, Colin Cornforth, Jessica Aschettino, Kim Wood, and Brittany Guenther. We thank Dan McSweeney, Chuck Babbitt, Colin Cornforth, Alli Craig, Tori Cullins, Landen Fletcher, Stacia Goecke, Shannon

Harrison, Paul Johnson, Laurie Montgomery, Georgia Struhsaker, Deron Verbeck, Alexa Vitek, Alicia Ward, Kristi West, and Kim Wood for providing photographs to our catalog. We thank Andy Read and William McLellan for examining photos for evidence of fisheries interactions, Jeremy Kiszka, Mike Heithaus, and Carl Meyer for input on shark bite wounds, and Stephen Raverty and Bill Walker for assessment of head lesions. Michaela Kratofil and Annette Harnish assisted with data processing and production of maps, and Samantha Norberg assisted with classification of behavior in drone footage. We thank Lynn Opritoiu, Karlina Merkens, Annette Harnish, Annie Douglas, and an anonymous reviewer for comments on earlier version of this manuscript.

ETHICS STATEMENT

Field operations were undertaken under NMFS Scientific Research Permits No. 731-1509, 731-1774, 15330 and 20605. The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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TABLE 1 Summary of survey effort and sightings of dwarf sperm whales by island area.

Island area	Total km	Total hr	# vessel days	% effort > 350 m depth < B3	# dwarf sperm whale sightings
Kaua'i/Ni'ihau	22,972	1,367	236	44.9	4
O'ahu	9,626	589	95	51.5	1
Maui Nui	14,680	1,029	172	13.8	3
Hawai'i	89,403	5,357	824	68.7	86

TABLE 2 Summary of resightings of photo-identified dwarf sperm whales by distinctiveness category with and without photo quality restrictions. Stranded individuals are not included in the totals.

Distinctiveness (when first documented)	No photo quality restrictions			Best photo quality fair or greater		
	# individuals	# (%) seen more than once	# seen multiple years	# individuals	# (%) seen more than once	# seen multiple years
Not distinctive	57	5 (8.8)	0	35	5 (14.2)	0
Slightly distinctive	47	10 (21.3)	7	40	10 (25.0)	7
Distinctive	44	9 (20.4)	8	35	9 (25.7)	8
Very distinctive	24	11 (45.8)	6	21	11 (52.4)	6
Total	172	35	21	131	35	21

TABLE 3 Distances between all possible pairs of encounters where individual dwarf sperm whales were photo-identified. All resighted individuals for which specific locations were available were from Hawai'i Island, and thus a comparison of individuals identified off Hawai'i Island is included for comparison. For the comparison of distances of resighted individuals, the grand mean/median values are shown.

	<i>M</i> distance (km)	<i>SD</i> distance (km)	Median distance (km)	Maximum distance (km)
All islands	92.6	141.8	36.5	555.0
Hawai'i-Hawai'i	33.7	26.2	28.4	132.0
Resighted individuals	15.2	15.5	10.3	77.0

FIGURE 1 Distribution of dwarf sperm whale sightings (dots) and survey effort (lines) off Hawai'i Island, including effort from April 2002 through June 2020. Effort in sea conditions of Beaufort 3 or greater is shown as light gray lines, while effort in Beaufort 0-2 is shown as dark gray (Kawaihae) harbors for departure of the research vessel are indicated.

FIGURE 2 Distribution of search effort (solid black) and dwarf sperm whale sightings (gray) by depth, including effort and sightings in Beaufort 0-2 conditions only from February 2000 through June 2020.

FIGURE 3 Distribution of group sizes of dwarf sperm whale sightings among the main Hawaiian Islands from directed research efforts ($n = 94$).

FIGURE 4 Box plot of long dive durations for groups of different age compositions. Groups composed only of adults or adults with one or more subadults present are pooled. Values in the "Adults/juvenile" category always include at least one adult and at least one juvenile or calf. Median values are represented by the middle horizontal line, with upper and lower box lines representing the 75th and 25th quartile, respectively. Vertical lines represent 1.5 times the interquartile range, and asterisks represent outliers.

FIGURE 5 Social network of photo-identified dwarf sperm whales from throughout the main Hawaiian Islands, with individuals represented by symbols and associations indicated by lines, excluding individuals with poor photo quality or that were considered not distinctive. Symbol shape and color indicate island (Kaua'i and Ni'ihau - light blue squares, O'ahu - green down triangles, Lāna'i - black up triangles, Hawai'i - red circles). No stranded individuals are included. Solitary nodes are not necessarily indicative of group size.

FIGURE 6 Sightings of dwarf sperm whale HIKs020 when latitude and longitude were available ($n = 11$). Depth contours shown are in meters. The location of the primary (Honokōhau) harbor for departure of the research vessel is indicated. Sightings shown here are from eight different years spanning 2004–2018, including sightings in six different months of the year.

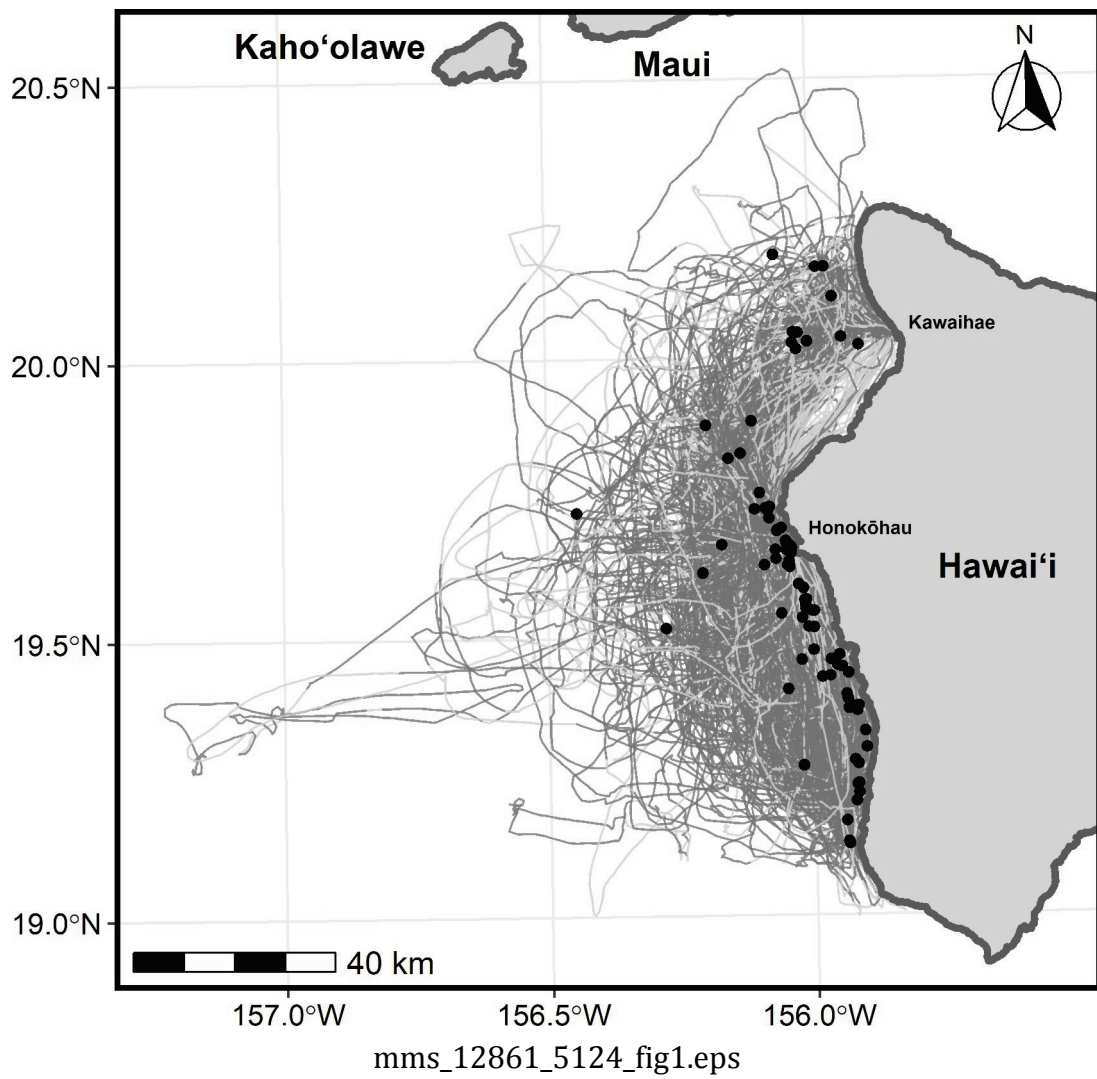
FIGURE 7 Depth at sighting locations of photo-identified dwarf sperm whales off Hawai'i Island, restricted to individuals that were considered at least slightly distinctive with fair or better quality photos. Top left: individuals in isolated clusters in the social network. Top right: individuals in the main cluster of the social network. Bottom left: individuals seen on only a single occasion. Bottom right: individuals seen

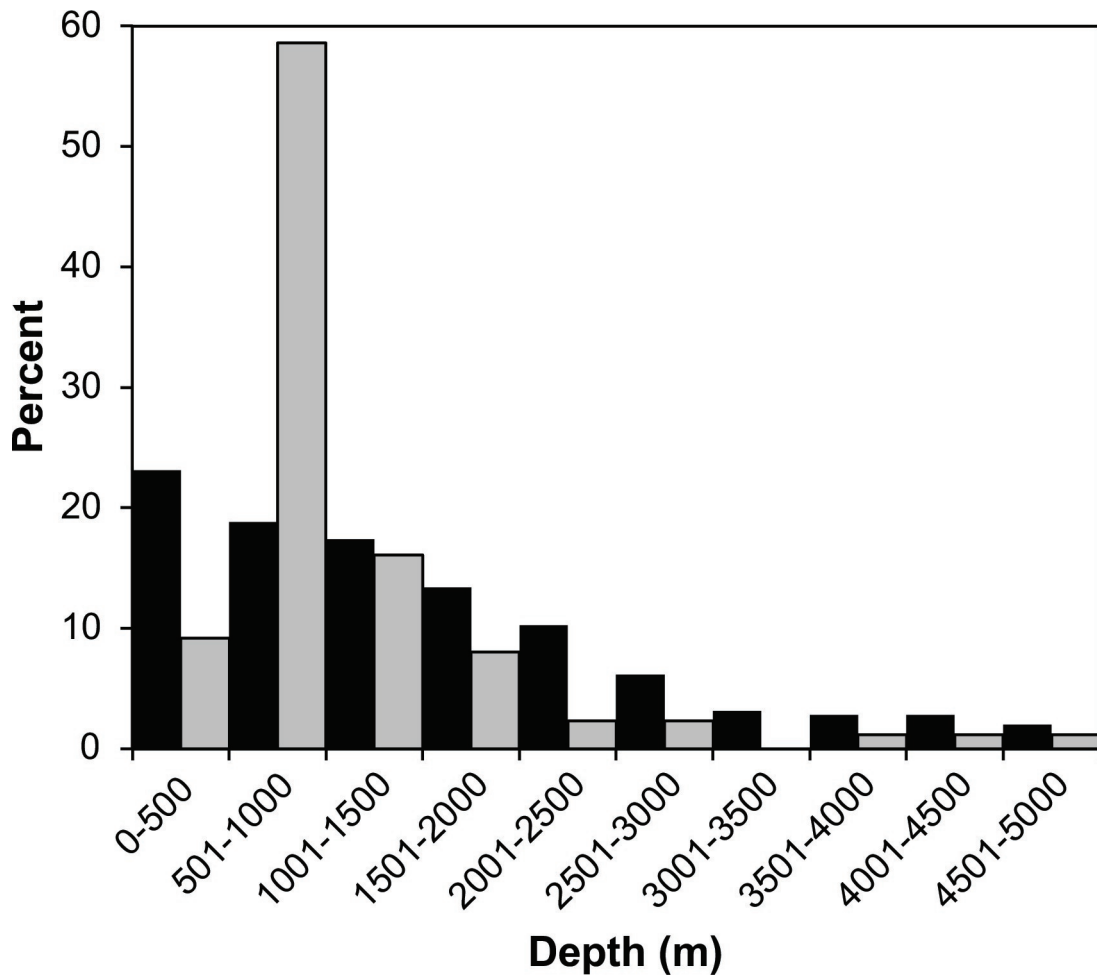
on multiple occasions. Median values are represented by the middle horizontal line, with upper and lower box lines representing the 75th and 25th quartile, respectively. Vertical lines represent 1.5 times the interquartile range, and asterisks represent outliers.

FIGURE 8 Examples of shark bite wounds (a-f) and other large markings of unknown origin (g-h) on individual dwarf sperm whales. (a-c) Three views of HIKs088, likely an adult female based on the presence of a small calf (b). Neither of these individuals have been resighted. (d) Partially healed shark bite wound on the mid back of HIKs050. (e) The wound on HIKs128 appears completely healed and is only visible with excellent quality photos. (f) Partially healed shark bite wound on the dorsal fin of HIKs139. (g) Large part of the dorsal fin missing on HIKs020. (h) Several wounds of unknown origin on the dorsal fin of HIKs113. Photos by J. M. Aschettino (a), R. W. Baird (b, c), D. J. McSweeney (d), B. K. Rone (e), A. Van Cise (h), D. L. Webster (g), K. A. Wood (f).

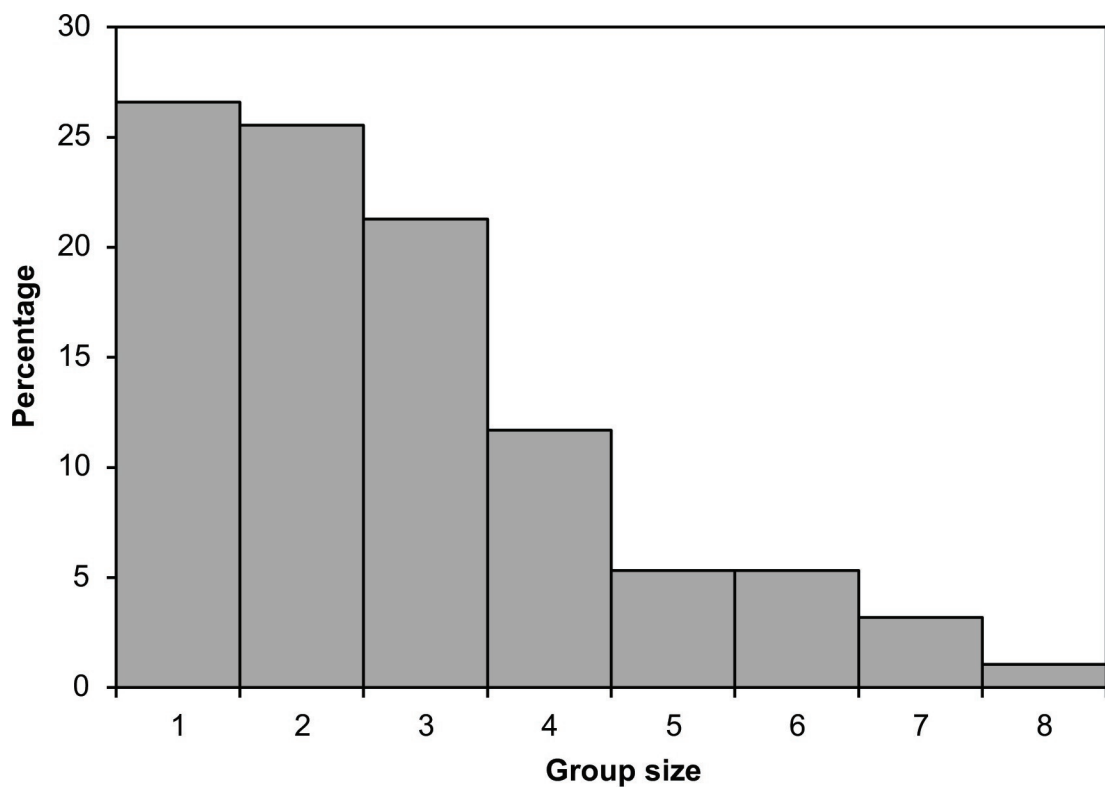
FIGURE 9 Examples of wounds of various origins on individual dwarf sperm whales. (a) HIKs121 with a fresh wound from a cookiecutter shark bite along the flank. (b) HIKs132 with a hole through the dorsal fin, likely caused by a cookiecutter shark

bite. (c) (foreground) with abrasion on the side of the head. D: HIKs095 with abrasions on top of head. (e) HIKs038 with linear cut through dorsal fin. (f) HIKs168 with line wrap and abrasions on dorsal fin. (g-h) HIKs165 (background in g) with indentation on caudal peduncle likely caused by a line wrap (HIKs166 is in the foreground). Photos by R. W. Baird (g), A. B. Douglas (e, f, h), J. K. Lerma (c), J. W. Ward (a), D. L. Webster (d), K. A. Wood (b).

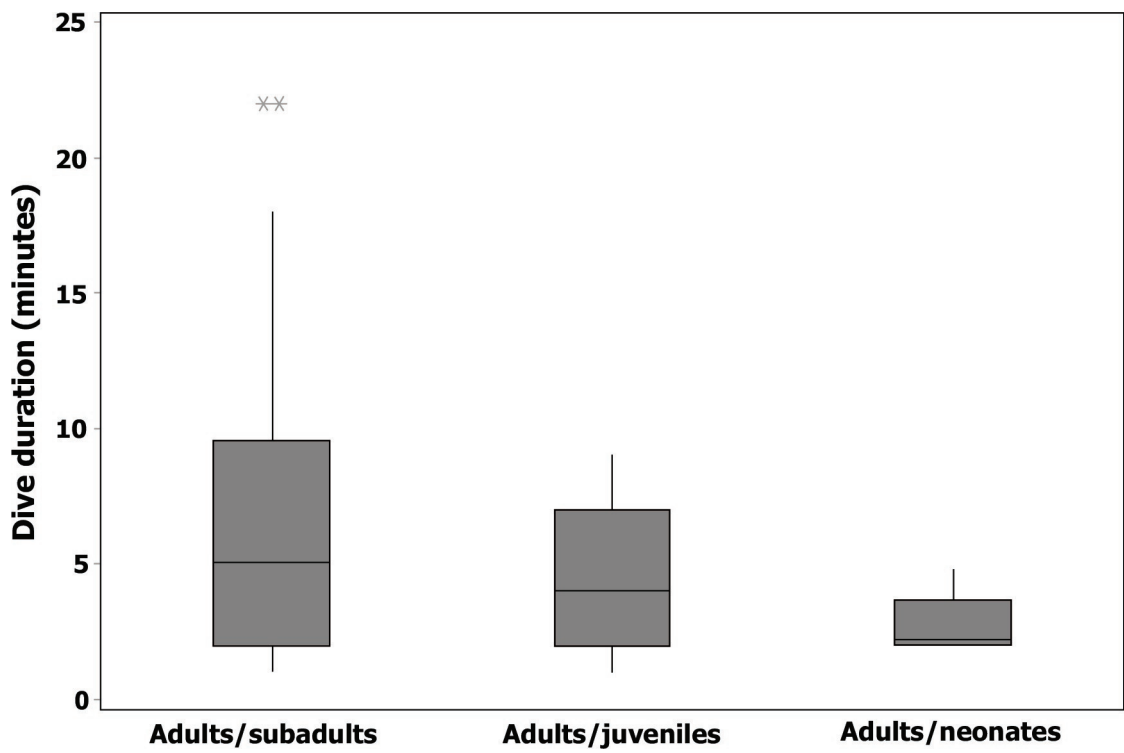




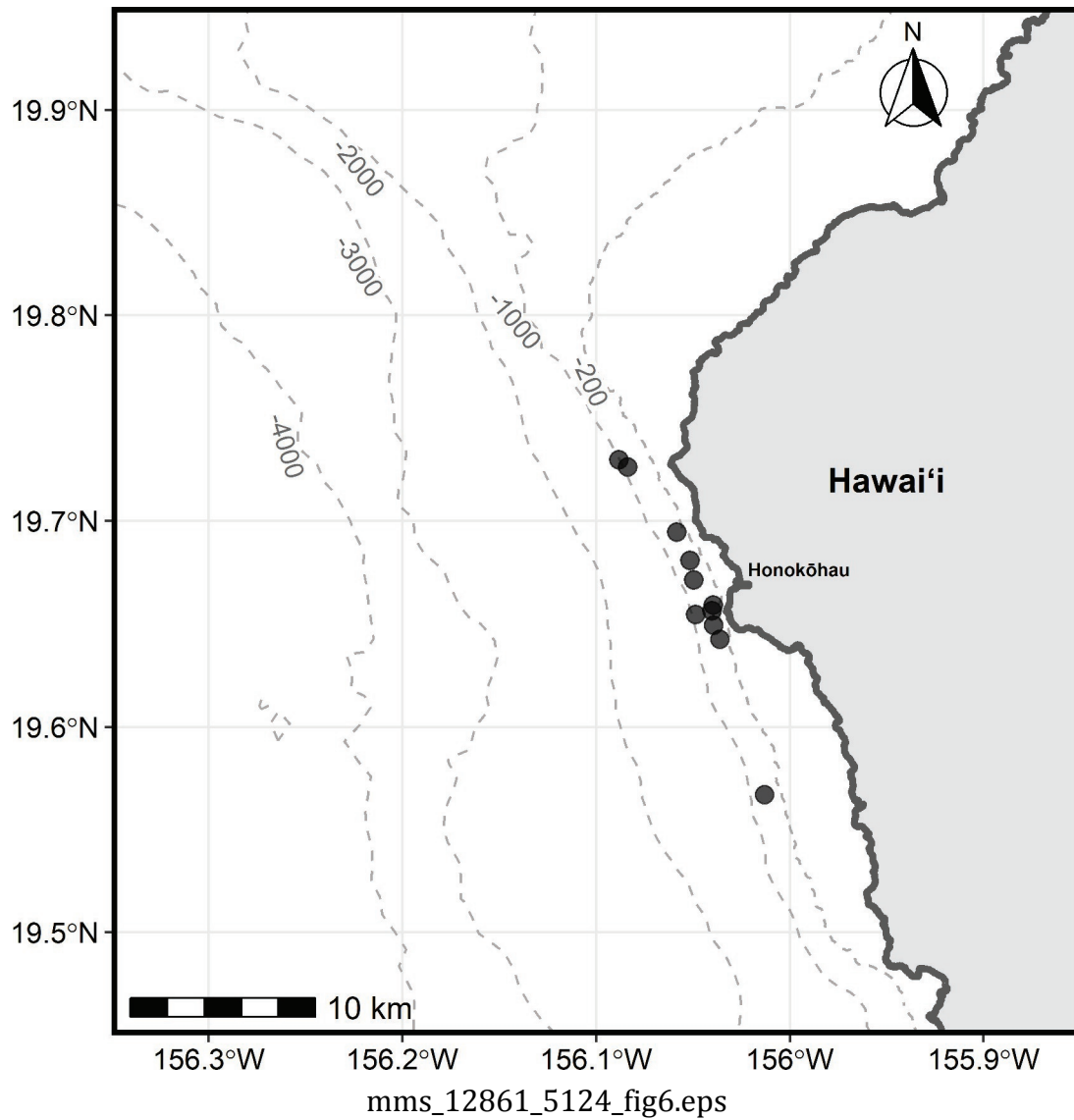
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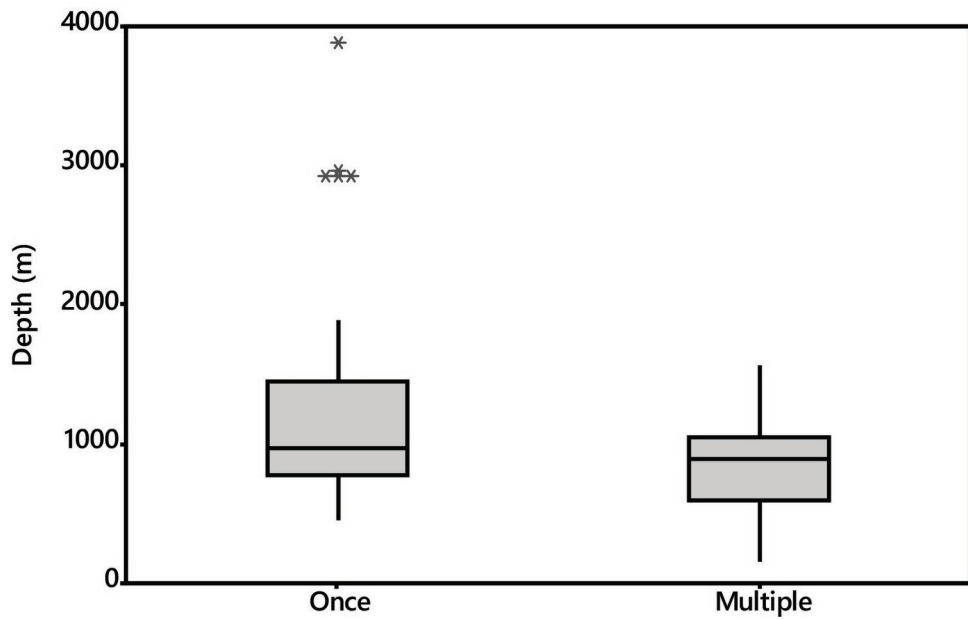
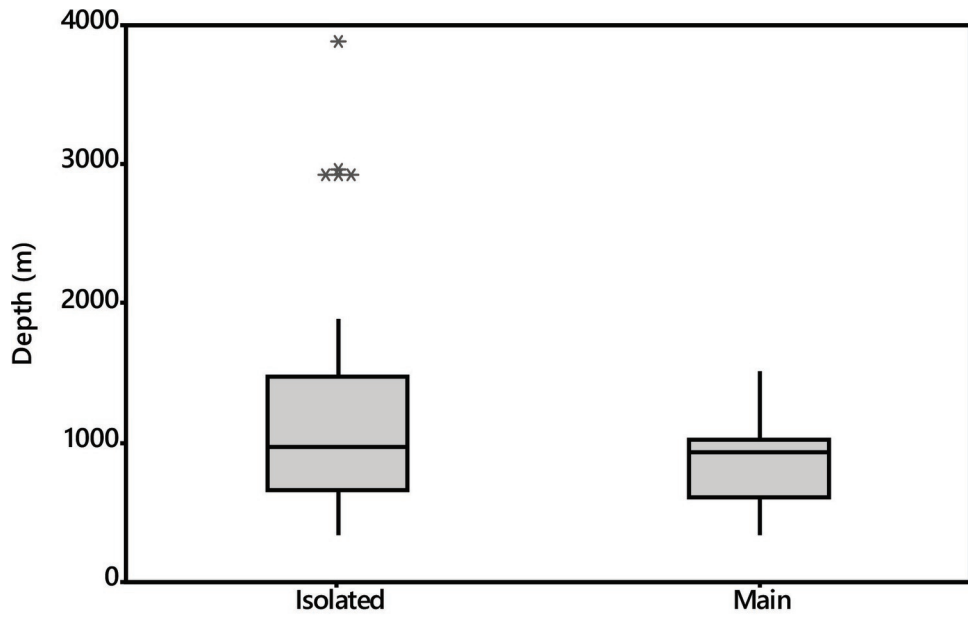


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