Marine Mammal Science

ARTICLE OPEN ACCESS

Killer Whales in the Central Tropical Pacific: Occurrence, Resightings, Morphology, and Acoustics

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Received: 2 December 2025 | **Revised:** 23 April 2026 | **Accepted:** 25 April 2026

Keywords: acoustics | killer whales | morphology | movements | photo-identification

ABSTRACT

Compared to their well-studied coastal temperate counterparts, killer whales (*Orcinus orca*) in tropical-subtropical and oceanic areas are under-documented. We used sighting, photo-identification, and acoustic data of killer whales in the central tropical Pacific (CTP), collected from multiple platforms between 2002 and 2023, to assess their temporal and spatial distribution, group dynamics and behavior, movements, pigmentation and dorsal fin morphology, and vocalizations. Killer whales were rarely encountered but occur year-round in the CTP, primarily in waters deeper than 1000 m. Photo-identification of 113 individuals included multi-year resightings of individuals off the main Hawaiian Islands but found no matches to eastern tropical Pacific catalogs. CTP killer whales share characteristics with other tropical-subtropical killer whale populations including pigmentation and morphology, small group sizes (range: 1–12, Mdn = 5), and diverse prey choices (e.g., other cetaceans, bony fishes, and sharks). Acoustic recordings, collected during shipboard sightings, were dominated by echolocation clicks and high-frequency modulated whistles and provide the first detailed characterization of CTP killer whale vocalizations. This is the most expansive study of CTP killer whales to date, and it underscores the importance of continued collaboration between research groups and the local community in order to better understand rarely sighted species.

HAWAIIAN TRANSLATION

'A'ole palapala nui 'ia nā nai'a nui weliweli (*Orcinus orca*) ma nā wahi kai a me nā wahi kopikala-lalokopikala, inā ho'ohālike 'ia me nā lāhui i kilo nui 'ia ma nā kai kemepale. Ua ho'ohana mākou i ka 'ike 'ana, ka hō'oia ki'i, a me ka 'ikepili lohea o nā nai'a nui weliweli ma ka Pākīpika kopikala waena (CTP), a ua 'ohi 'ia mai nā kahua like 'ole mai ka makahiki 2002 a i ka makahiki 2023, i mea e kālailai aku ai i ko lākou ili pū'uo 'ana ma ka henua a me ke kaime, i ka hana a me ka lawena o ka pū'uo, i ka ne'e 'ana, i ke kālaikino o ke kualā a me ke kaukala 'ana, a me ka leo 'ana. Kaka'ikahi ka 'ike 'ana i nā nai'a nui weliweli, 'ike 'ia na'e ma ka makahiki ma ka CTP, keu ho'i ma ke kai i 'oi aku ka hohonu ma ka 1,000m. Hō'oia ki'i 'ia he 113 mea a 'ōkomo 'ia ka 'ike hou 'ia 'ana o nā mea ma nā makahiki i kai o ka pae'āina Hawai'i 'a'ole na'e i loa'a kekahi like ma nā wae'anona Pākīpika kopikala hikina. Like kekahi mau hi'ohi'ona o nā nai'a nui weliweli CTP me ko nā pū'uo nai'a nui weliweli ma kekahi mau wahi kopikala-lalokopikala, e la'a ho'i me ke kaukala 'ana a me ke kālaikino, nā pū'ulu li'ili'i (mai ka 1–12, ka 'awelike = 5), a me nā 'ano pio like 'ole, e la'a me nā māmala kai loa 'e a'e, na i'a iwiiwi, a me nā manō. Helu nui 'ia nā kani ana pīna'i a me nā hōkio kani ki'eki'e ma nā 'okileo lohea ma nā wā i 'ike 'ia mai ka moku aku, a 'o ia mau 'ikepili ka wehewehena mua o ke 'ano kiko'ī o ka leo 'ana o nā nai'a nui weliweli i loko o ka CTP. 'O kēia ke kālailaina piha loa o nā nai'a nui weliweli CTP a hiki i kēia, a he hō'ike i ke ko'iko'i o ka mālama mau 'ana i ka pilina ma waena o nā pū'ulu noi'i a me ke kaiāulu i mea e maopopo piha i kēia mau lāhui i 'ike kaka'ikahi 'ia.

1 | Introduction

Killer whales (*Orcinus* spp.) occur worldwide from the tropics to the poles but are found in higher densities at higher latitudes and in coastal waters that are typically more productive (Forney and Wade 2007). In the North Pacific Ocean, most of what is known about killer whales comes from extensive research in nearshore waters from California to Alaska where multiple ecotypes, recognized as separate subspecies, with overlapping distributions have been described (Bigg et al. 1987; Dahlheim et al. 2008; de Bruyn et al. 2013; Ford et al. 1998; Morin et al. 2024). Long-term studies have documented variations between these subspecies/ecotypes in their movements, foraging behavior and diet, acoustics, social structure, group size, morphology, and genetics (de Bruyn et al. 2013; Emmons et al. 2019; Morin et al. 2024; Moura et al. 2014). Recent genetic analyses, along with morphological and ecological evidence, were used to justify that the so-called "resident" and "transient" ecotypes within the eastern North Pacific (ENP) should be recognized as separate species (*Orcinus ater* and *Orcinus rectipinnus*, respectively) (Morin et al. 2024).

Killer whales in the tropics and subtropics of the North Pacific are less well known, but sightings and studies from the eastern tropical Pacific (ETP; from the southern Baja California Peninsula, Mexico, to northern Peru, including offshore waters) (Athayde et al. 2023; Olson and Gerrodette 2008; Ortega-Ortiz et al. 2023; Pitman et al. 2007; Testino et al. 2019; Vargas-Bravo et al. 2020) and within Hawaiian waters (Baird 2016; Baird et al. 2006) have revealed details on morphology, prey, and group size that resemble those of other tropical-subtropical killer whale populations (Bolaños-Jiménez et al. 2014, 2023; Kiszka et al. 2021; Pitman et al. 2003, 2015; Terrapon et al. 2021; Visser and Bonoccorso 2003; Visser et al. 2000, 2024; Weir et al. 2010). Vargas-Bravo et al. (2020) and Ortega-Ortiz et al. (2023) have suggested that killer whales within the waters of the Mexican central Pacific to Peru may be a completely different ecotype, and possibly a distinct tropical population or populations, than those found in the ENP based on "variations in seasonal-spatial distribution, group size structure, morphology, behavior, and trophic niche."

Killer whale sightings in Hawaiian waters are rare and some data suggest these animals are primarily pelagic and wide-ranging (Baird 2016; Baird et al. 2006). Individuals satellite tagged off Hawai'i Island in 2013 traveled more than 2000 km southwest of their tag deployment location and remained offshore for the duration of tracking (Baird 2016). With only a small number of biopsy samples collected from central tropical Pacific (CTP) killer whales, genetic analyses are not definitive in determining the relationship between CTP killer whales and those from the ETP or ENP. CTP killer whales encountered within the Hawaiian exclusive economic zone (EEZ) and off Palmyra Atoll (1000 km south of Hawai'i) share haplotypes with killer whales sampled off Mexico (Morin et al. 2015), as well as a mammal-eating type known from the Gulf of Alaska and another known from coastal Alaska with a haplotype that differs by only one DNA base pair (Baird et al. 2006; Morin et al. 2010). Currently, the U.S. National Oceanic and Atmospheric Administration's (NOAA) National Marine Fisheries Service, under the Marine Mammal Protection Act, recognizes the Hawai'i stock of killer whales as those found within the EEZ surrounding the Hawaiian archipelago and surrounding international waters (Carretta et al. 2021). Abundance of the Hawai'i stock is estimated as 161 (CV = 1.06) individuals, which was determined from a 2017 line-transect survey within the EEZ (Bradford et al. 2021; Carretta et al. 2021).

This study expands on the research conducted by Baird et al. (2006) and Baird (2016) in Hawai'i to characterize CTP killer whales and provide new information on their temporal and spatial occurrence, group size, behavior, morphology, and acoustics. By synthesizing these aspects we can better understand and define their ecological niche and investigate their connectivity to killer whales in the ETP and broader North Pacific, which is a critical step for ensuring informed management and conservation.

2 | Methods

2.1 | Effort and Sightings

Data on killer whales in the CTP were collected from various sources that included research surveys aboard ships and small boats that also collected effort data, as well as opportunistic sightings by tour operators and citizen scientists. Between 2002 and 2023, shipboard systematic line-transect surveys were conducted by NOAA Fisheries primarily for the purpose of estimating the density and abundance of cetaceans within U.S. EEZs. Visual data were collected following standard line-transect methodology (Buckland et al. 2001; Barlow 2006; Bradford et al. 2021). If time and conditions allowed, groups were approached for the collection of photos and biopsy samples from the ship. Group composition (age class and sex of individuals) was sometimes noted in the record. During some sightings, a small boat was launched to more easily approach animals for photo-identification, biopsy sampling, and satellite tag deployment. Satellite tags (Wildlife Computers; Redmond, WA, USA) were remotely deployed following the methods described by Baird et al. (2024). Acoustic monitoring and recording were conducted during all ship surveys using a towed hydrophone array.

Cascadia Research Collective (CRC) conducted nonsystematic small-boat surveys for cetaceans around the main Hawaiian Islands between 2002 and 2023. The survey area and effort expanded over the years, as did some methods of data collection, but surveys generally included three to seven individuals that scanned 360° around the vessel with unaided eye (Baird et al. 2024). Some of the data collected included the vessel's trackline (GPS), cetacean sighting locations (latitude/longitude), group size estimates, photographs for individual identification, and biopsy samples; satellite tags (Wildlife Computers) were deployed on some species (see Baird et al. 2024 for full details on data collection).

The Pacific Islands Fisheries Science Center (PIFSC) conducted nonsystematic small-boat surveys for cetaceans off Palmyra

Atoll in 2009–2011 in collaboration with Scripps Institute of Oceanography (SIO). In 2022, PIFSC participated in the Palmyra Bluewater Research project, which was a multi-organization, multi-species project led by The Nature Conservancy (TNC) to assess the impact of marine protected areas on species and ecosystems and included small-boat surveys for cetaceans around the atoll (Gilmour et al. 2022). During all of the Palmyra surveys, three to five individuals scanned 360° around the vessel with unaided eye. Some of the data collected included the vessel's trackline (GPS), cetacean sighting locations (latitude/longitude), group size estimates, photographs for individual identification, and biopsy samples when possible.

Within the main Hawaiian Islands, between 2006 and 2023, opportunistic sightings of killer whales were also made by captains, naturalists, and crew aboard commercial dolphin and whale watching vessels, as well as citizen scientists, and photos or videos were shared with CRC. The island off which each sighting occurred was identified and, in some cases, the location (latitude/longitude or description) was collected, but no effort data were collected. Additional sightings, by commercial operators working with CRC, were directed by satellite tag transmissions, but no effort data were collected. In 2008, an adult male killer whale stranded on Kaua'i, and photos and tissue samples were collected (Baird 2016).

The distance from shore and location depth of the killer whale sightings with recorded latitude/longitude were determined within ArcGIS Pro 3.1 (ESRI Inc.; 2023) and using bathymetry data from the GEBCO 2024 Grid (GEBCO Compilation Group; 2024).[1] Survey effort by depth and distance from shore was determined by first generating points along ship and small-boat survey tracklines every 100 m to standardize across surveys and tracks. Depth contour polygons were created in 1000 m increments from the GEBCO data. Distance polygons were created around islands at 25, 50, 100, 200, 300, and 400 km. Effort was summarized by percentage of total survey track points that fell within each depth and shore distance range.

2.2 | Photo-Identification and Social Network

Photos from ship and small-boat surveys were primarily taken using digital SLR cameras and telephoto lenses except for the 2002 Hawaiian Islands Cetacean and Ecosystem Assessment Survey (HICEAS) when cameras with print film were used and photos were digitally scanned. Images from opportunistic sightings came from digital photo and video cameras and included some aerial (drone) and underwater footage. For creating the CTP killer whale photo-identification catalog, all images were processed following CRC protocols (Baird et al. 2024). Distinctiveness ratings for each individual were based on notches and tears in the dorsal fin and the ridge of the back behind the dorsal fin, although when available eye patch and saddle patch pigmentation were also used in individual identification. The resulting CTP catalog (excluding nondistinctive individuals with only poor-quality photos) was used to look for matches within two existing killer whale photo-identification catalogs from the ETP totaling 810 individuals[2] (195 individuals from Olson and Gerrodette 2008).

Sex was assigned to a small number of individuals based on genetic sexing from collected biopsy samples. In addition, adult males were identified by their tall erect fins and adult females were identified as those with an associated calf. Age class was assigned to other individuals based on their size relative to other group members within the same image ("adult female sized," juvenile, calf). Calves were identified by their small size and close association with a known adult female or an "adult female sized" individual, while juveniles were identified by their intermediate size.

Given the relatively small number of individuals that were resighted, we did not undertake quantitative association or network analyses. We did create a social network (in Netdraw 2.176; Borgatti 2002) to illustrate linkages among individuals, and describe groupings of individuals within the network as components. While such components likely represent distinct social groups or clusters (see Mahaffy et al. 2023), sample sizes of resightings limit conclusive assessment. A network ID was assigned to each social component in chronological order using letters (A–BB).

2.3 | Genetic Sex Determination

Biopsy sampling was conducted during some sightings. Barnett RX-150 or Wildcat crossbows and projectile darts with Ceta-Dart (Copenhagen, Denmark) style tips (25 × 7 mm) were used to collect skin/blubber samples. Samples were frozen and sent to the Southwest Fishies Science Center's (SWFSC) Marine Mammal and Turtle Division for genetic sexing.

DNA was extracted from skin biopsies using the Machery-Nagel NucleoMag Tissue kit for DNA purification from cells and tissue (Item number: 744300.4). Extraction followed the manufacturer's protocol with one exception—Proteinase K tissue lysis was performed overnight at 37°C. Genetic sex was determined using a ZFX/ZFY 5′ exonuclease qPCR assay (Morin et al. 2005). DNA samples from stranded animals of known sex in the SWFSC Marine Mammal and Sea Turtle Research collection (SWFSC Lab IDs 67723 and 73709), one male and one female, were used as amplification positive controls.

2.4 | Morphological Characteristics

Photos of cataloged individuals were used to assess morphological characteristics of CTP killer whales in relation to other killer whale ecotypes within the North Pacific and populations in tropical-subtropical waters elsewhere. The eye patch shape, orientation, relative size, and position were characterized. The eye patches were categorized by shape (smooth, hooked, narrow front, hook & bump, multiple hook, bumps, jagged, rear variation) and variation within those shapes (1A-9C) (see figure 1 in Visser and Mäkeläinen 2000). For some individuals, images of both left and right eye patches were available and evaluated for symmetry. The orientation, relative length, and position of the eye patch were determined using images of individuals in which there was no or minimal horizontal- or vertical-axis parallax error (i.e., the

whale was parallel to the photographic plane and the dorsal fin was upright) (Bolaños-Jiménez et al. 2014; Durban and Parsons 2006; Evans et al. 1982; Visser and Mäkeläinen 2000). The orientation of the eye patch was assessed as parallel or angled relative to the long axis of the body (Evans et al. 1982; Visser and Mäkeläinen 2000). Following Bolaños-Jiménez et al. (2014), the relative length of the eye patch is reported as a proportion of the distance between the posterior edge of the blowhole and anterior insertion of the dorsal fin (Visser and Mäkeläinen 2000). The anterior and posterior insertions of the dorsal fin were determined using the method described in Durban and Parsons (2006) using ACDSee Photo Studio Professional 2019 software (ACD Systems International Inc.) (Figure S3). Measurements were made within Image-J software (Schneider et al. 2012). The position of the eye patch anterior margin was assessed relative to the blowhole and was recorded as anterior to, at, or posterior to the blowhole (Bolaños-Jiménez et al. 2014).

The presence/absence of a dorsal cape was assessed (Evans et al. 1982). Saddle patches were evaluated in images of individuals that were parallel to the photographic plane and not backlit, and only one side was used when there were both lefts and rights available, prioritizing the left side when possible following Mäkeläinen et al. (2025). The saddle patch was assessed qualitatively (when at least 80% was visible) for the presence (open) or absence (closed) of an intrusion of black pigmented skin (Evans et al. 1982; Baird and Stacey 1988), for shape (smooth, bump, horizontal notch, vertical notch, hook, not present/discernable) (Baird and Stacey 1988; Mäkeläinen et al. 2025; Sugarman 1984), and for the distinctiveness or clarity (faint, intermediate, or conspicuous) (Bolaños-Jiménez et al. 2014; Vargas-Bravo et al. 2020). Saddle patch size was characterized using the method developed by Mäkeläinen et al. (2025) in which the ratio of the saddle patch width (at its widest) to the dorsal fin base width (at its widest) determined if the saddle patch was narrow (<0.50), medium (0.50–0.70) or wide (>0.70). The distance between the anterior and posterior insertions of the dorsal fin was used for the base width.

The dorsal fin tip was categorized as pointed or round (Vargas-Bravo et al. 2020). Within ACDSee, the position of the dorsal fin tip was evaluated relative to the base of the dorsal fin using the categories of Bolaños-Jiménez et al. (2014): (i) forward of the anterior insertion, (ii) at the anterior insertion, (iii) between the anterior and posterior insertions, (iv) at the posterior insertion, or (v) beyond the posterior insertion of the dorsal fin (Bigg et al. 1987; Bolaños-Jiménez et al. 2014; Ford et al. 2000; Vargas-Bravo et al. 2020). Images with no or minimal parallax error along both the vertical and horizontal axes were used to determine the dorsal fin tip position.

In addition to permanent morphological characteristics, photos of the CTP killer whales were evaluated for the presence of cookiecutter shark (*Isistius* sp.) bite wounds and scars, remoras, skin conditions, and potential fisheries-related injuries or scarring (on the dorsal fin, body, and mouthline). Potential fisheries-related injuries were categorized following Harnish et al. (2024) as "consistent" or "potentially consistent" with a fisheries interaction.

2.5 | Acoustics

During PIFSC visual and passive acoustic shipboard surveys from 2010 to 2023 (Table S1), a hydrophone array was towed approximately 340 m behind the vessel. Hydrophones used during these surveys varied over the years. In 2013, data were collected with an ACP hydrophone (-174 ± 10 dB re: 1 V/uPa from 3 to 80 kHz) sampled at 192 kHz. During 2016–2023, data were collected with an HTI-96 (-144 ± 5 dB re: 1 V/uPa from 2 to 100 kHz) sampled at 500 kHz. The frequency response range of the hydrophones overlaps sufficiently for comparative analyses of the recorded killer whale repertoire.

Towed array data were processed using the click detector module (IIR Butterworth 2 kHz high pass filter) and whistle & moan detector within PAMGuard (v. 2.02.10a; Gillespie et al. 2026). Recordings were evaluated for the presence of echolocation clicks, pulsed calls, low-frequency whistles, and high-frequency modulated (HFM) whistles. The PAMGuard binary data of detected echolocation clicks and HFM whistles were analyzed in the open-source *PAMpal* package within R software (R Core Team 2024; Sakai 2020).

3 | Results

3.1 | Effort and Sightings

Between 2002 and 2023, the surveys from all ship and small-boat effort covered a total of 284,410 km of on-effort trackline over 2213 days within January–December (Tables S1, S3 and S4, Figures 1 and S1). There was a total of 23 killer whale sightings during these surveys, four of which were directed by other sources including radio calls from other vessels, satellite tag transmissions, and an acoustic detection (Table S2, Figures 1 and S1). The sighting rate across all surveys was 0.07 killer whale sightings per 1000 km surveyed when directed sightings are excluded. For detailed information about effort and sightings by survey type, see Appendix S1 in the Supporting Information.

Between 2006 and 2023, there were 22 opportunistic sightings, two directed sightings (from satellite tag transmissions), and one stranding throughout the main Hawaiian Islands (Table S2). No effort data were collected, but sighting locations (latitude/longitude) were recorded during five sightings.

Across all effort and locations, there were 47 killer whale sightings and one stranding between 2002 and 2023 (Table S2). Photos for individual identification were collected during 41 sightings (including the stranding), biopsy samples were collected during eight sightings (including the stranding), satellite tags were deployed during three sightings, and acoustic recordings were made during five ship sightings (Table S2, Figure 1).

Most killer whale sightings were within the Hawai'i EEZ (89.6%; $n=43$) and around the main Hawaiian Islands (75.0%; $n=36$) where most of the effort was, but others were in the northwestern Hawaiian Islands (Papahānaumokuākea Marine National Monument) ($n=6$), Palmyra ($n=3$), Johnston ($n=1$), and in international waters ($n=2$) (Figures 1 and S1). After removing

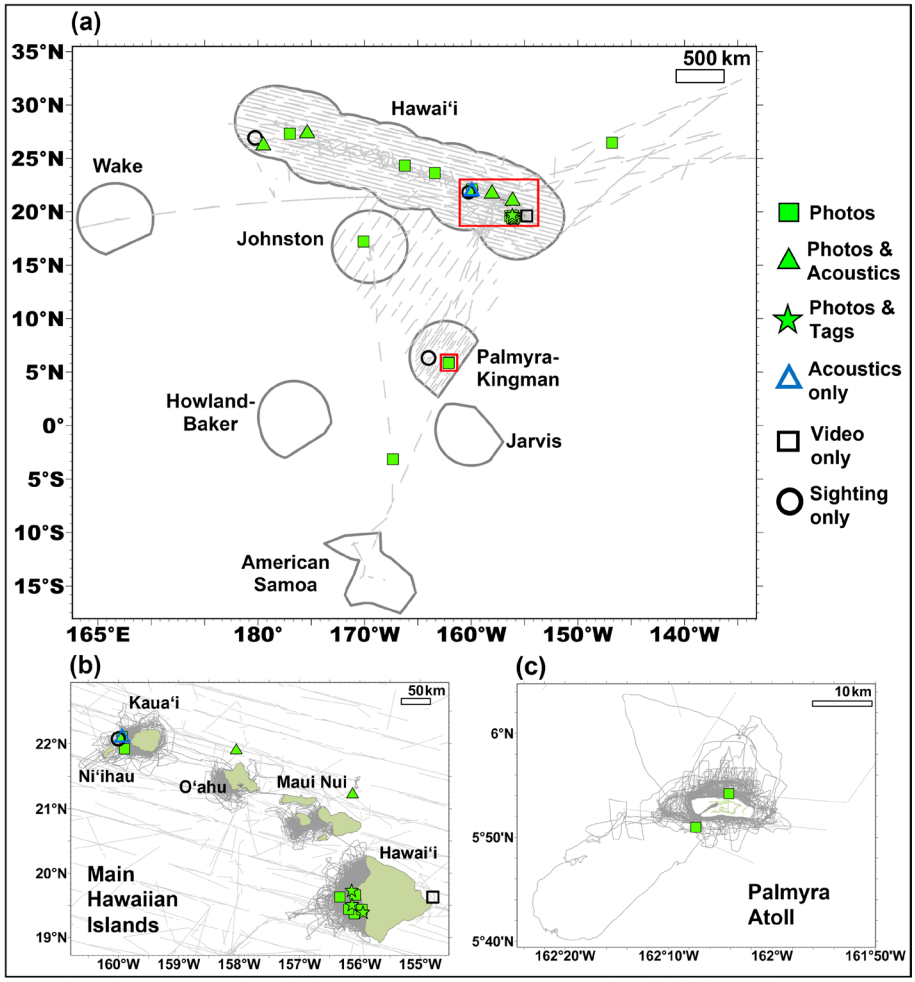

FIGURE 1 | Survey tracklines and killer whale sightings for which latitude/longitude were recorded ($n = 28$) within the central tropical Pacific (CTP) from 2002 to 2023. Different symbols represent the data collected during the sightings. (a) All locations within the CTP including the U.S. exclusive economic zones of Hawai'i, Wake, Johnston, Palmyra-Kingman, Howland-Baker, Jarvis, and American Samoa, and international waters. Red boxes designate the areas pictured in panels (b) and (c). (b) Around the main Hawaiian Islands. (c) Around Palmyra Atoll. Survey details are listed in Tables S1, S3, S4 and sighting details are listed in Table S2.

three resights of photo-identified groups that occurred within the same month of the same year and off the same island (see Section 3.3), the 45 remaining sightings occurred between January and November with more occurring in July ($n = 9$) and August ($n = 8$) than in other months (Table S2, Figures 2 and S1). Around the main Hawaiian Islands, sightings occurred in all months except December (Figure S1b). More than a third of the main Hawaiian Island sightings were off Hawai'i Island (36.1%; $n = 13$) and occurred in eight of the 12 months (all except February, March, October, and December) (Table S2, Figures 1 and S1).

The latitude/longitude were recorded for 28 killer whale sightings (Tables S2 and S5, Figure 1). Killer whales were found 1–1183 km from shore (Mdn = 22 km; $\bar{x} = 106$ km, SD = 231) and in depths that ranged 422–5408 m (Mdn = 2933; $\bar{x} = 3071$, SD = 1579) (Table S5). More than half of the sightings (53.6%; $n = 15$) were within 24 km from shore and most (89.3%; $n = 25$) were in depths greater than 1000 m (Figures 3 and S2). In Hawaiian waters, killer whales were seen as close as 4 km from shore and in water depth as shallow as 728 m (Table S5).

Group sizes were estimated in the field during 23 sightings and ranged from 1 to 12 individuals (Mdn = 5.0; $\bar{x} = 5.4$, SD = 2.5). Adult male killer whales were identified in more than half of the sightings (52.1%; $n = 25$; Table S2). During most of those sightings, only one adult male was present; but during three sightings there were two, three, and four adult males.

Behavior was recorded during 25 sightings, which included confirmed or suspected predation events during 10 sightings within Hawaiian and Palmyra waters (Table S2). Species being chased, attacked, or killed included melon-headed whale (*Peponocephala electra*), common bottlenose dolphin (*Tursiops truncatus*), rough-toothed dolphin (*Steno bredanensis*), *Kogia* sp., a possible unidentified cetacean, tuna (*Thunnus* sp.), and unidentified fish including a "bait fish" species. Killer whales were also observed killing a bigeye thresher shark (*Alopias superciliosus*) off Hawai'i Island (Baird 2016). There was one instance of killer whales ramming an adult male short-finned pilot whale (*Globicephala macrorhynchus*), but there was no evidence the pilot whale was killed, and the observer did not classify it as a predation event. During one killer whale

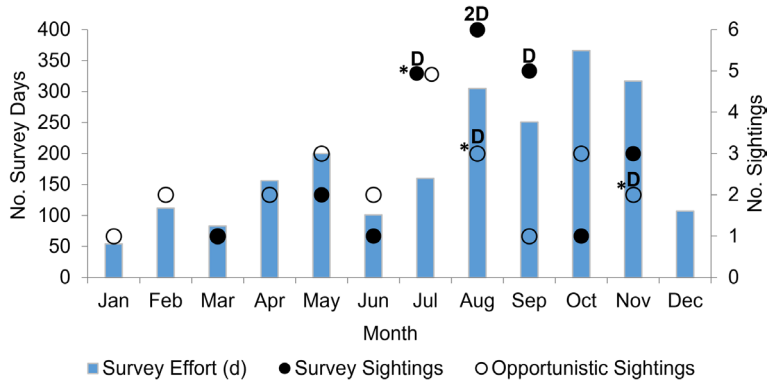

FIGURE 2 | Survey effort (days) and killer whale sightings within the central tropical Pacific. Opportunistic sightings had no associated effort data. The letter "D" above a symbol indicates that the vessel was directed to the group by an outside source (e.g., radio calls from another vessel, satellite tag transmissions, acoustic detection). An asterisk (*) next to a symbol indicates a resight of a group in the same month, year, and island location.

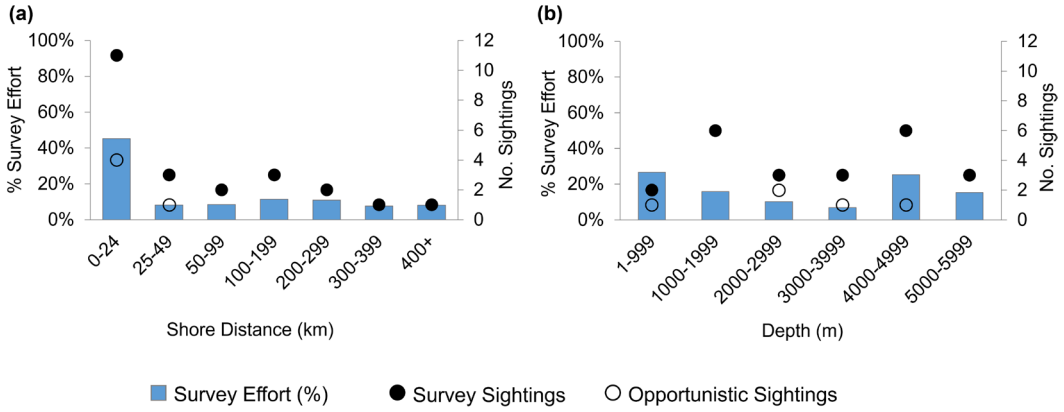

FIGURE 3 | Effort as a percent of survey track points (bars) and number of killer whale sightings (circles) within the central tropical Pacific by (a) distance from shore in kilometers and (b) depth in meters. Opportunistic sightings (open circles) had no associated effort.

sighting in 2006, in international waters of the central tropical South Pacific, short-finned pilot whales and unidentified dolphins were present, but there was no record of chasing or feeding attempts.

3.2 | Photo-Identification and Social Network

Photographs for individual identification were obtained from 38 group sightings (Table S2). With no restrictions for photo quality or distinctiveness, 161 identifications were obtained, representing 113 different individuals (Table S6). There are 21 components in the social network with two or more individuals, as well as seven individuals that are the only photo-identified killer whales from their sighted groups and do not link to any other component (Figure 4). Within the social network, individuals were seen on two or more occasions in four of the components (see Section 3.3). A quarter of the cataloged individuals (24.8%; $n = 28$) are considered distinctive or very distinctive (D3, D4) based on dorsal fin markings, and just under half of all cataloged individuals (45.1%; $n = 51$) have best photo qualities of good or excellent (Q3, Q4) (Table S6).

For the CTP catalog, genetic sexing was available for seven individuals within three social components and photos were used to determine their age class (five adult females, one juvenile male, one juvenile female) (Tables S2 and S6, Figure 4). In addition, an adult male (HIOo005) stranded on Kaua'i in 2008 and was genetically sexed from a tissue sample (Tables S2 and S6, Figure 4). Five biopsy samples were collected during sighting 2 in November 2002 (Table S2) and were genetically sexed (four males, one female), but no photos were collected during the sampling events and could not be associated with particular individuals within the photo-identification catalog. Photos of cataloged individuals were used to identify an additional 26 adult males within 20 components, two adult females with calves within two components, 43 "adult female sized" individuals within 22 components, 24 juveniles within 14 components, and three calves within three components. In addition, one individual (HIOo057) was classified as a calf when it was first seen in 2019 and then as a juvenile when resighted in 2023 (Table S6, Figure 4). Age class could not be determined for seven individuals within five components (Table S6, Figure 4). Overall, age class was estimated for 106 individuals, of which only four were calves (3.8%), and no neonates were documented.

3.3 | Individual Resightings

Of the 113 individuals in the photo-identification catalog, 19 (16.8%) were seen on two or more days (maximum of six), and

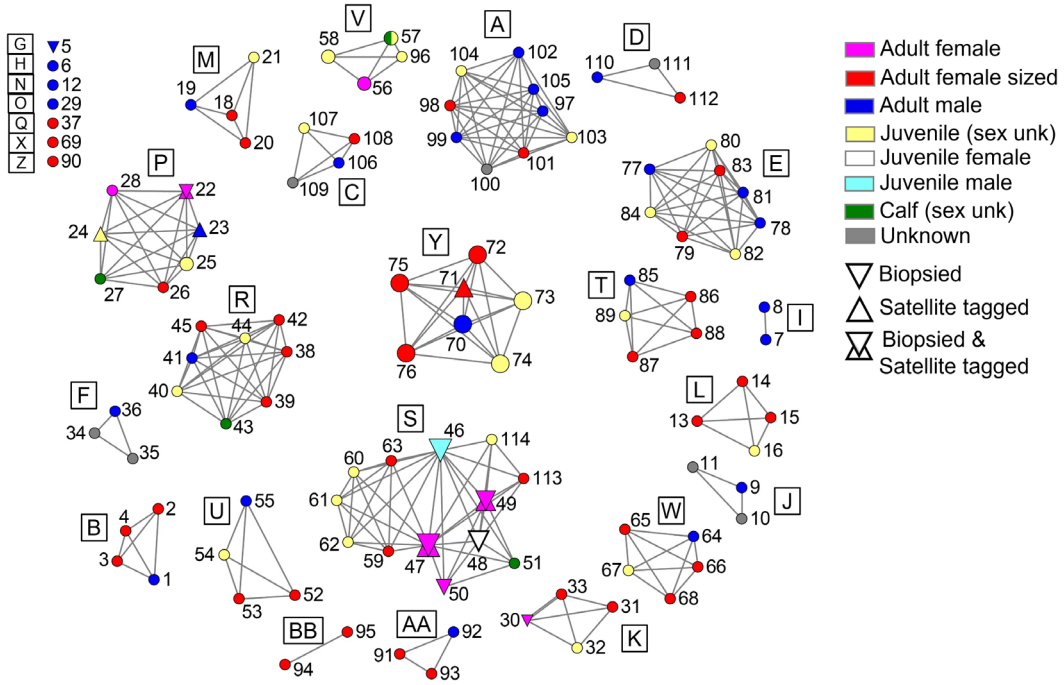

FIGURE 4 | Social network diagram of photo-identified killer whales in the central tropical Pacific. Letters represent the network IDs assigned to the social components in chronological sighting order. Numbers represent the catalog ID. Node color represents the age class and sex of the individual. Node shape denotes whether an individual was biopsy sampled, satellite tagged, both, or not. Node size represents sighting occurrence (larger nodes indicate more resights). See Tables S2 and S6 for details about the sightings and cataloged individuals.

15 (13.3%) of those were seen in two or more years (maximum of four). One group of four individuals (HIOo022–HIOo025), that included one adult female, an adult male, and two juveniles, was originally seen off Hawai'i Island on 1 November 2013 (Tables S2 and S6; sighting 20, Figure 4). Satellite tags were deployed on three individuals (HIOo022–HIOo024), and the four individuals were relocated the next day, approximately 16 km away from their original sighting location (Tables S2 and S6; sighting 21), with three other individuals (an adult female and calf and an "adult female sized" individual). This group was observed feeding on a bigeye thresher shark (Baird 2016). As previously reported by Baird (2016), the tagged individuals moved offshore to the southwest and were 2000 km away from their tag deployment location, approximately a month later, when the final tag stopped transmitting.

The three other social components with individuals seen more than once were documented in multiple years, and some or all of the individuals were always together. One component ("S") includes five individuals (HIOo046–HIOo050) who were first seen off Hawai'i Island on 16 July 2016 and were resighted 19 km away on 21 July 2016 (Tables S2 and S6; sighting 27, 28, Figure 4). Biopsy samples were collected from all individuals, and the group included three adult females, one juvenile female, and one juvenile male. Satellite tags were deployed on two of the adult females (HIOo047, HIOo049). Over the following month, the tagged individuals moved over 1400 km north of their tag deployment location until the tags stopped transmitting in mid-August (PIFSC unpublished data). On 10 October 2016, four of the five individuals (HIOo046–HIOo049) were photographed off Moloka'i (Tables S2 and S6; sighting 29). It is possible that all five were present, but there was no effort to photograph all individuals and no group size estimates were made. In May 2017, all five individuals were resighted off the west side of Hawai'i Island and were accompanied by a new calf (Tables S2 and S6; sighting 31). In April 2020, two of the individuals (HIOo046, HIOo047) were seen off the west side of Hawai'i Island with five new individuals (HIOo059–HIOo063). In November 2023, four of the original group members (HIOo046–HIOo049) were resighted off O'ahu (Tables S2 and S6; sighting 47). There were two other individuals nearby, not closely associated with the four, that were photo-identified (HIOo113, HIOo114) and categorized as an "adult female sized" individual and a juvenile.

A second social component ("V") was first documented with three individuals (HIOo056–HIOo058, an adult female with a calf and a juvenile) off Hawai'i Island in May 2019 (Tables S2 and S6; sighting 34, Figure 4). These three individuals were resighted off O'ahu in November 2023 (Tables S2 and S6; sighting 48) accompanied by a juvenile (HIOo096), an adult male (not photographed but identified in the field by his dorsal fin), and another individual seen in the distance. During this sighting, an acoustic recording was collected from the towed hydrophone array (Table S2; acoustic ID 2401080).

A third social component ("Y") that includes seven individuals (HIOo070–HIOo076; an adult male, four "adult female sized" individuals, and two juveniles) was initially seen off Hawai'i Island in August 2021 (Tables S2 and S6; sighting 39, Figure 4). All seven were resighted off Hawai'i Island on 29 and 30 August 2022, and a satellite tag was deployed on one individual (HIOo071; Tables S2 and S6; sighting 42, 43, Figure 4). During these two encounters, this group was observed in an interaction with an adult male short-finned pilot whale (involving ramming the pilot whale but no evidence of killing or feeding on it),

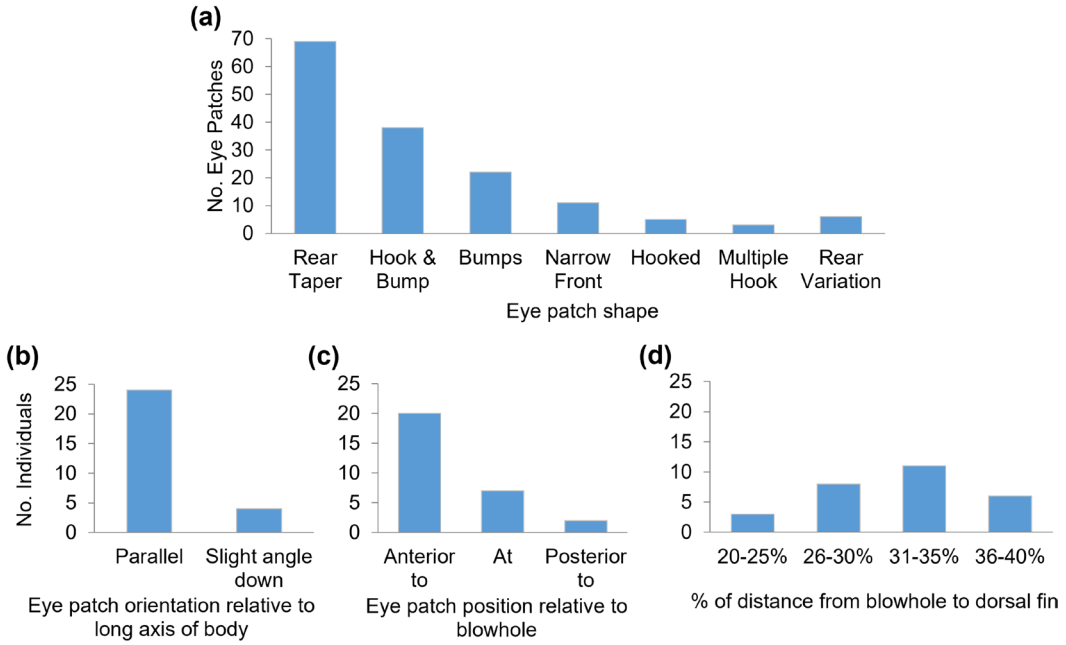

FIGURE 5 | Eye patch characteristics of central tropical Pacific killer whales. (a) Eye patch shape (see Figure S4 for example images). (b) Eye patch orientation relative to long-axis of the body. (c) Position of the anterior edge of the eye patch relative to the blowhole. (d) Eye patch length as a percent of the distance of the posterior edge of the blowhole to the anterior insertion of the dorsal fin. See text for sample sizes for each comparison.

and then attacking and killing a dwarf or pygmy sperm whale (*Kogia* sp). The group was resighted a week later off Hawai'i Island (Tables S2 and S6; sighting 44). All sighting locations were within 35 km of each other. The satellite tag transmitted for 1 month, during which HIOo071 generally remained near, or just offshore of, Hawai'i Island and Maui Nui (CRC unpublished data).

Comparisons of 87 individuals from the CTP catalog (excluding nondistinctive individuals with only poor quality photos) to those from the ETP yielded no matches.

3.4 | Morphological Characteristics

Shape was evaluated for 79 eye patches of 55 individuals from 15 social components. Six of the eight categories identified by Visser and Mäkeläinen (2000) are present in the CTP killer whales and include hook & bump (4D, 4B, 4A), bumps (6B, 6A, 6F, 6E, 6D), narrow front (3B, 3A), hooked (2B, 2A), and multiple hook (5A) in order of frequency of occurrence with six individuals also having a rear variation (9A–C) (Figures 5a and S4). Most (87.3%; $n = 69$) of the eye patches taper at the rear (Figures 5a and S4). There are left and right images available for 24 individuals and none have symmetrical eye patches, but the shape categories of the left and right eye patches on 14 of those individuals are the same. The orientation, relative size, and position of the eye patch were evaluated for 28 individuals from 11 social components. Most eye patches (85.7%; $n = 24$) have a parallel orientation relative to the long axis of the body, but four individuals from four different components have eye patches with a slight downward angle from front to back (Figure 5b). Most individuals (71.4%; $n = 20$) have eye patches with anterior edges forward of the blowhole and most eye patch lengths are 26%–35% of the blowhole to dorsal fin distance (67.9%; $n = 19$) (Figure 5c,d). For social components in which more than one individual was assessed, eye patch shape varies in eight of ten components, its position varies in three of seven components, and its relative size varies in six of seven components.

No killer whale within the CTP catalog has a visible dorsal cape. The shape, size, and distinctiveness/clarity of saddle patches were evaluated for 32 individuals from 10 social components. There are an additional two individuals from different social components for which the saddle patch is indiscernible even though the lighting and body orientation are good. All evaluated saddle patches are closed and have a smooth shape. The mean saddle patch/dorsal fin width ratio is 0.51 (range: 0.28–0.69). Nearly three-fifths (59.4%; $n = 19$) of the measured saddle patches are medium-sized, while the remainder are narrow (Figure 6a). More than half (53.1%; $n = 17$) of the saddle patches have an intermediate distinctiveness/clarity, while more than a third (34.4%; $n = 11$) are faint, and a little over a tenth (12.5%; $n = 4$) are conspicuous (Figure 6b). Saddle patches vary in size and distinctiveness/clarity between members within all eight social components for which there was more than one individual assessed.

The dorsal fin tip shape was evaluated for 104 individuals from 26 social components and more than half (57.7%; $n = 60$) are round, while the others have a rounded point (26.9%; $n = 28$) or point (8.7%; $n = 9$) (Figure 7a). Dorsal fin tip shape varies between members within 13 of 17 social components for which there was more than one individual assessed. The position of the dorsal fin tip relative to the base was evaluated for 45 individuals from 17 social components. Most of the dorsal fin tips (66.7%; $n = 30$) are beyond the posterior insertion of the dorsal fin base (category v), while less than a quarter (20.0%; $n = 9$) are between the anterior and posterior insertions (category iii), and the remaining fin tips (13.3%; $n = 6$) are at the posterior insertion

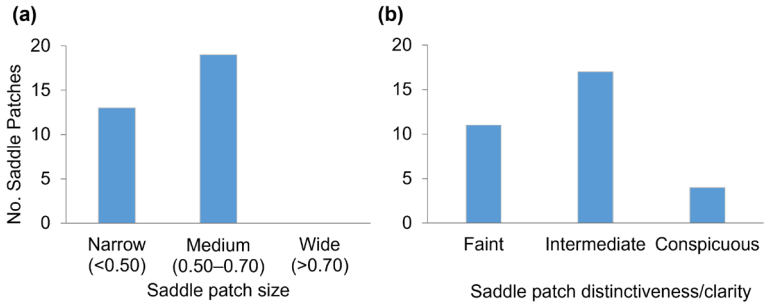

FIGURE 6 | Saddle patches of central tropical Pacific killer whales. Saddle patches of 32 individuals from 10 social components were evaluated. (a) Saddle patch size based on the ratio of saddle patch width to dorsal fin base width (narrow ≤ 0.50, medium = 0.50–0.70, wide ≥ 0.70). (b) Saddle patch distinctiveness/clarity (faint, intermediate, conspicuous). See Figure S5 for example images of saddle patch size and distinctiveness/clarity.

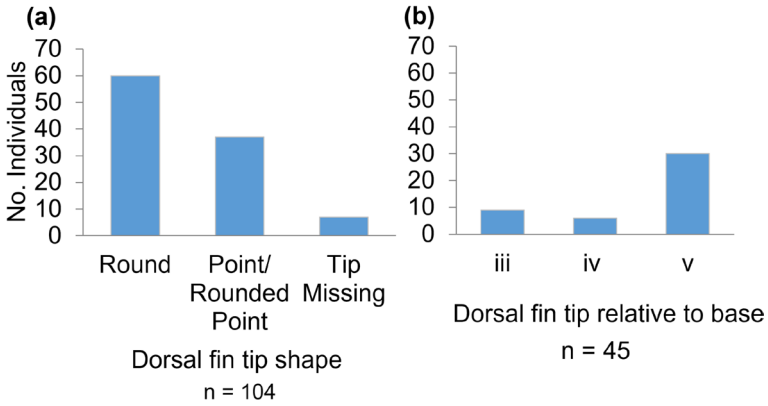

FIGURE 7 | Dorsal fins of central tropical Pacific killer whales. (a) Dorsal fin tip shapes were evaluated for 104 individuals from 26 social components (round, point/rounded point, tip missing). (b) Dorsal fin tip positions relative to the anterior and posterior insertions of the dorsal fin base were evaluated for 45 individuals from 17 social components (iii—between insertions, iv—at posterior insertion, v—beyond posterior insertion). See "Methods—2.4 Morphological Characteristics" for a description of all categories. See Figure S3 for a description of the method used to determine the anterior and posterior insertions of the dorsal fin base. See Figure S6 for example images of dorsal fin tip shapes and positions.

of the dorsal fin base (category iv) (Figure 7b). Relative dorsal fin tip positions vary between members within six of ten social components for which there was more than one individual assessed.

In addition to dorsal fin images, when available, images of the mouthline and body were assessed for potential fisheries-related scarring and other more ephemeral characteristics, such as cookiecutter shark wounds and scars, remoras, and skin conditions. Mouthline images were available for 18 individuals from 8 social components and were evaluated for potential hooking injuries. One individual, seen off Palmyra, has what looks like a stalked barnacle on its mouthline (the quality of the photograph makes it difficult to see clearly), which is consistent with a fisheries interaction (Figure S7a). As well, this individual has a scar on the leading edge of its dorsal fin, which is also consistent with a fisheries interaction (Figure S7b). Three other individuals, seen in Hawaiian waters, have scarring on the peduncle and body that are consistent with fisheries interactions, and one of those individuals has a dorsal fin tip amputation that is possibly consistent with a fisheries interaction (Figure S7c–e). Seventy-seven individuals from 23 social components have cookiecutter shark bite scars, 38 individuals from 18 components have open cookiecutter shark bite wounds in various stages of healing, 12 individuals from six components have remoras, and 12 individuals from seven components have unknown skin conditions, which in some cases resemble tattoo skin disease (Figure S8a–c).

3.5 | Acoustics

Killer whales were vocal during six of 10 sightings that occurred during PIFSC shipboard surveys between 2006 and 2023 (Table S2). Acoustic recordings from five of the sightings were included in the analysis.[3] No low-frequency whistles were detected. Pulsed calls were recorded during two sightings. Only a single pulsed call was recorded on 12 July 2016 off the north side of Maui (Table S2; sighting 26). A few standard two-part (buzz/call) pulsed calls were recorded on 16 September 2023 in the offshore waters of the Papahānaumokuākea Marine National Monument (Table S2, Figure S9; sighting 46).

All five acoustic encounters contain echolocation clicks, but instrument noise in 2013 prevented the extraction of the acoustic characteristics of the clicks. For the remaining acoustic encounters (2016–2023), the characteristics of the clicks ($n = 540$) and their median values (10th and 90th percentiles) include peak frequency: 16.8 kHz (8.4, 24.4), center frequency: 16.7 kHz (8.4, 24.3), −10 dB bandwidth: 7.6 kHz (5.4, 14.1), −10 dB lower end point: 12.5 kHz (4.6, 20.3), and duration: 155 μs (22, 781). Mean

spectra, averaged by event, are consistent between encounters (Figure S10).

HFM whistles were recorded during all five acoustic encounters and are structurally repetitive in nature within encounters (Figure 8). Median HFM whistle onset fundamental frequencies range between 23.1 and 24.8 kHz, except for one encounter (sighting 48) that is 39.4 kHz (Table S7, Figures 8e and 9a). All HFM whistles are down swept, and the median end fundamental frequencies range between 15.7 and 20.0 kHz for the first four encounters but are 26.2 kHz for sighting 48 (Table S7, Figures 8 and 9). HFM whistles have similar median durations (120–143 ms) for three acoustic encounters (sightings 17, 45, 48) while whistle durations from the two other encounters (sightings 26, 46) are longer (225 and 182 ms, respectively) (Table S7, Figures 8 and 9). Outliers for frequency characteristics indicate the presence of whistle production with harmonics (Figure 9).

The group of killer whales (social component V), recorded during sighting 48, was seen twice in Hawaiian waters. They were photographed off Hawai'i Island in May 2019 and then off O'ahu in November 2023 when the recording was made. There are no obvious morphological differences in the photo-identified individuals within this group compared to others within the catalog.

There was one acoustic encounter (sighting 17) during which there was a visually confirmed predation event (of a tuna). Killer whales produced echolocation clicks and HFM whistles during the encounter. During the 2006 ship sighting in the South Pacific, killer whales were observed near short-finned pilot whales and unidentified dolphins but were not pursuing them. The killer whales and short-finned pilot whales were vocal during the encounter, but the unidentified dolphins were silent.

4 | Discussion

This study represents the most extensive research on CTP killer whales, to date. Killer whale sightings are rare in Hawai'i and the surrounding CTP, but they occur throughout the year with no clear seasonal pattern. Killer whales were primarily documented in deep waters (> 1000 m) and relatively close to shore (within 24 km). Telemetry data demonstrate that individuals are wide-ranging, but photo-identification data show some degree of site fidelity. CTP killer whales are similar to other tropical-subtropical killer whales in their external morphology, diet, and

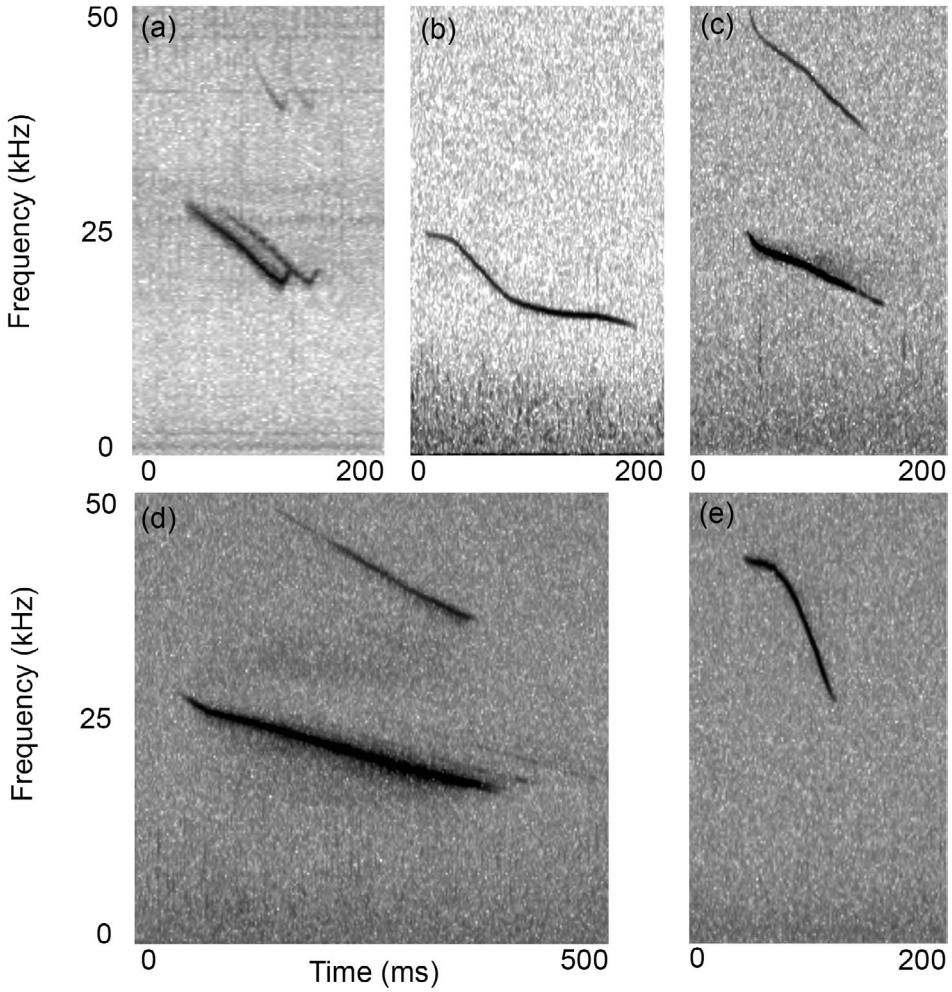

FIGURE 8 | Representative spectrograms of high frequency modulated (HFM) whistles from each killer whale acoustic encounter (1024-point FFT, 50% overlap). (a) Sighting 17–1303070. (b) Sighting 26–1604077. (c) Sighting 45–2303035. (d) Sighting 46–2303160. (e) Sighting 48–2401080. Harmonics are visible in panels a, c, and d. Acoustic encounters correspond to the acoustic recording IDs listed in Tables S2 and S7.

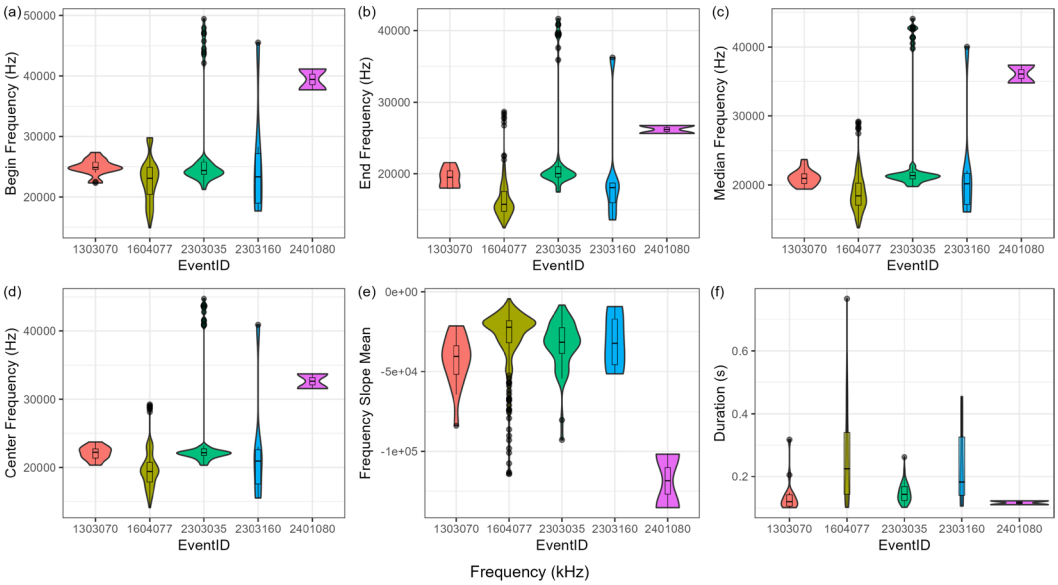

FIGURE 9 | Acoustic characteristics of high-frequency modulated (HFM) whistles recorded during five killer whale sightings during Pacific Islands Fisheries Science Center shipboard surveys (2013–2023). Outliers indicate the presence of harmonics. (a) Begin frequency (Hz). (b) End frequency (Hz). (c) Median frequency (Hz). (d) Center frequency (Hz). (e) Frequency slope mean. (f) Duration (s). Event IDs correspond to the acoustic recording IDs listed in Tables S2 and S7.

group sizes. Scarring and wounds on CTP killer whales show evidence of cookiecutter shark attacks and fisheries interactions. This study provides the first detailed characterization of killer whale vocalizations within the CTP. When killer whales are vocalizing, they regularly produce echolocation clicks and HFM whistles similar to those recorded in other North Pacific populations. The prevalence of HFM whistles in the absence of low frequency whistles and low occurrence of pulsed calls suggests CTP killer whales may at times use HFM whistles as a primary means of social communication.

Killer whales were sighted in the CTP in most years of our study and in all months except for December (Figure 2), suggesting there is no obvious seasonal pattern to their occurrence. The apparent higher occurrence of killer whales within the CTP in July–September may be related to a greater presence of vessels on the water. More than half of the sightings in July were opportunistic, so it is difficult to assess whether this is directly related to effort. The higher sighting rate in August–September may be correlated with the increased effort in both ship and small-boat research surveys, but a higher sighting rate might be expected in October when all research survey effort was highest.

While there is no indication that there are resident groups of killer whales in Hawaiian waters, this study suggests that there is some degree of site fidelty with individuals returning to the same area within the same year and in multiple years. Most of the 113 individuals in the CTP catalog were seen only once, and all of the 19 individuals that were resighted were seen only around the main Hawaiian Islands. Data from satellite-tagged individuals within the photo-identification catalog demonstrate that their movements are wide-ranging (e.g., Baird 2016), but the full spatial extent of CTP killer whales is not known. The comparison of the CTP catalog to 810 individuals in the ETP yielded no matches, which suggests that there is little or no overlap between regions. However, only 24.8% ($n = 28$) of the CTP catalog individuals are considered distinctive or very distinctive and less than half (45.1%) of the catalog images are considered good or excellent quality. Future regional catalog comparisons should still be conducted.

The high occurrence of killer whale sightings in nearshore waters is likely related to the greater amount of small-boat effort close to shore (see Appendix S1). However, during ship surveys, the highest number of killer whale sightings relative to effort also occurred within 24 km of shore. The "island mass effect," which leads to upwelling, increased precipitation, and runoff in nearshore waters around the Hawaiian Islands, results in higher productivity and an increase in prey biomass that attracts predators (Doty and Oguri 1956; Gove et al. 2016). There are island-associated populations of 11 different species of odontocetes around the main Hawaiian Islands (Baird 2016; Baird et al. 2024; Kratofil et al. 2023), and the higher frequency of killer whale sightings within 24 km of shore may reflect overlap with these potential prey populations.

Killer whales observed in tropical and subtropical waters are described as generalist predators. They are known to feed on bony fishes, sharks, rays, cephalopods, turtles, birds, pinnipeds, dolphins, and large whales (Alava et al. 2013; Athayde et al. 2023; Baird 2016; Baird et al. 2006; Hanson and Walker 2014; Kiszka et al. 2021; Ortega-Ortiz et al. 2023; Pitman et al. 2003, 2007, 2015; Terrapon et al. 2021; Testino et al. 2019; Visser and Bonoccorso 2003; Weir et al. 2010; Whitt et al. 2015). It is likely that CTP killer whales are also generalist predators and take advantage of whatever prey they find, given that specializing on a particular prey could be less advantageous within the oligotrophic pelagic waters of the CTP (Baird et al. 2006). Predation or suspected predation was observed during 10 sightings and prey species included cetaceans (bottlenose and rough-toothed dolphin, melon-headed whale, and *Kogia* sp.), a bigeye thresher shark, and bony fish (*Thunnus* sp., unknown

"bait", and unknown other). Baird et al. (2006) documented additional prey of killer whales observed in Hawaiian waters that included humpback whale (*Megaptera novaeangliae*), pantropical spotted dolphin (*Stenella attenuata*), and octopus. Hanson and Walker (2014) noted that a female killer whale, stranded on Lāna'i in 2004, had only mesopelagic squid within her stomach. Although some groups in this study were resighted within the main Hawaiian Islands, observed predation or suspected predation events never involved the same group more than once. One possible exception was a group that was first seen on 29 August 2022 off Hawai'i Island in what was described as an "altercation" with an adult male pilot whale not thought to be a predation event. The following day, the same group was observed killing and eating a *Kogia* sp. Despite their proximity to shore, killer whale groups were primarily found in waters deeper than 1000 m, with the shallowest sighting around the main Hawaiian Islands of 728 m. Thus, regular overlap with, and predation on, Hawaiian monk seals (*Neomonachus schauinslandi*) seems unlikely, given they are benthic foragers and spend the majority of their time in shallow waters (Wilson et al. 2017).

Killer whale group sizes in the CTP ($\bar{x} = 5.4$) are similar to those previously reported in Hawai'i ($\bar{x} = 4.2$; Baird et al. 2006) and for other tropical-subtropical populations in the ETP, South Pacific, Caribbean, and South Atlantic ($\bar{x} = 3.2–6.0$; Bolaños-Jiménez et al. 2014; Denkinger et al. 2020; Hupman et al. 2015; Ortiz-Wolford et al. 2023; Vargas-Bravo et al. 2020; Visser et al. 2024; Wade and Gerrodette 1993; Weir et al. 2010). The composition of groups in the CTP is similar to what has been observed in the ETP (Vargas-Bravo et al. 2020), with variation between lone adult males and mixed groups of adults, "adult female sized" individuals, and juveniles. Fewer calves were observed within CTP killer whale groups ($n = 4$, 3.5% of photo-identified individuals) than what has been recorded in the ETP ($n = 8$, 32.0% of photo-identified individuals; Vargas-Bravo et al. 2020), likely reflecting the low productivity of the oligotrophic waters of the CTP. Adult male killer whales were present during half of the CTP sightings ($n = 24$) and constitute 23.0% of identified individuals ($n = 26$), which is lower than what has been observed in the ETP ($n = 7$, 38.9%; Denkinger et al. 2020).

The pigmentation of CTP killer whales is similar to other tropical-subtropical populations, including eye patches with a typical parallel orientation relative to the body (Barry et al. 2024; Bolaños-Jiménez et al. 2014; Vargas-Bravo et al. 2020; Visser and Mäkeläinen 2000; Visser et al. 2024; Weir et al. 2010). Four individuals have eye patches that are angled slightly backward, which has also been observed in the Caribbean, Gulf of Mexico, and ETP (Barry et al. 2024; Bolaños-Jiménez et al. 2014; Vargas-Bravo et al. 2020). The fact the angled eye patch is observed on single animals in four different social components within the CTP, that also contain individuals with parallel eye patches, suggests that it is an individual variation rather than a group-defining feature. As with killer whales in the Caribbean and ETP (Bolaños-Jiménez et al. 2014; Vargas-Bravo et al. 2020), most CTP eye patches are anterior to the blowhole. The most frequently occurring eye patch shapes are hook & bump and bumps, which is different than what has been observed in the ETP, Caribbean, and New Zealand where hooked eye shapes are most common (Bolaños-Jiménez et al. 2014; Vargas-Bravo et al. 2020; Visser and Mäkeläinen 2000). The eye patches of most CTP killer whales evaluated taper at the rear, which has not been noted in other studies. Eye patch shapes are individually variable and can be used along with the dorsal fin for photo-identification (Evans et al. 1982; Visser and Mäkeläinen 2000). The eye patches of CTP killer whales are not symmetrical, which emphasizes the need to collect both left- and right-side images in order to more readily use the eye patches to identify individuals.

Like other tropical-subtropical killer whales, CTP killer whales have no dorsal cape, as well as closed and smooth (or indiscernible) saddle patches that are narrower and less distinct than those of the temperate North Pacific ecotypes (Baird et al. 2006; Bolaños-Jiménez et al. 2014; Mäkeläinen et al. 2025; Olson and Gerrodette 2008; Vargas-Bravo et al. 2020; Weir et al. 2010). We found individual variability in the size and clarity/distinctiveness of saddle patches within social components. The size range of CTP killer whale saddle patches, based on the saddle patch width/dorsal fin base width ratio (0.28–0.69), is comparably broad to that of Hawai'i killer whales in the worldwide study by Mäkeläinen et al. (2025). However, the mean ratio in our study is higher (0.51) than that of Mäkeläinen et al. (2025) for Hawai'i killer whales (approximately 0.42), which may be related to their smaller sample size ($n = 5$). The mean size of CTP killer whale saddle patches is similar to those observed in other tropical-subtropical populations across the Pacific and Indian Oceans (Mäkeläinen et al. 2025).

We found that the dorsal fins of CTP killer whales most commonly have rounded tips, which is similar to those of ENP "offshore", ETP, and Caribbean killer whales (Bolaños-Jiménez et al. 2014; Ford et al. 2000; Vargas-Bravo et al. 2020). A difference is that in CTP killer whales, the dorsal fin tip is more commonly beyond the posterior insertion of the base (i.e., more falcate).

Recent methods used in assessing morphological characteristics have shown promise for distinguishing between killer whale ecotypes. Emmons et al. (2019) used elliptical Fourier analysis (EFA) to quantify the differences in dorsal fin, eye patch, and saddle patch shapes of killer whales within different ecotypes from the ENP and found that dorsal fin and eye patch shape could be used to discriminate between ecotypes. Hutchings et al. (2025) also used EFA to assess eye patch and dorsal fin variation in killer whales within Australian waters and found supporting evidence of both a tropical and temperate form. Ismail et al. (2025) used artificial intelligence machine learning methods to assess dorsal fins and saddle patches of killer whales in the Northwestern Pacific Ocean off Russia and were able to accurately distinguish between "resident" and "transient" killer whale ecotypes. With a larger sample size than what is available in the existing CTP dataset, it would be worthwhile to use EFA or an artificial intelligence approach to compare and quantify differences in eye and saddle patches and dorsal fins between CTP, ETP, and "offshore" killer whales in the Pacific, as well as the two recently described species (Morin et al. 2024).

Four individuals within the CTP photo-identification catalog, photographed in Palmyra and Hawaiian waters, have scarring

along the peduncle and on the dorsal fin that is consistent, or possibly consistent, with fisheries interactions. According to the 2022 National Marine Fisheries Service stock assessment report for the Hawai'i stock of killer whales, there have been no reports of interactions with nearshore fisheries (Carretta et al. 2023). Both international and U.S. commercial longline fisheries operate within the CTP. The U.S. longline fisheries that operate out of Hawai'i include a shallow-set fishery that primarily targets swordfish (*Xiphias gladius*) and a deep-set fishery that targets tuna. Between 2004 and 2018, during which there was 100% observer coverage on the shallow-set fishery and 18%–28% observer coverage on the deep-set fishery, there were no reports of hooked or entangled killer whales (Carretta et al. 2011, 2014, 2019). However, during that period there were multiple sightings of killer whales within 50 m (as close as 1 m) of longline gear.[4] In 1990, there was a report of a killer whale removing catch from a Hawai'i deep-set longline (Carretta et al. 2023; Dollar 1991). Although it may not be a regular occurrence, killer whales in the CTP may take advantage of "easy prey" when they encounter it on longlines, which could lead to entanglement and injury. Killer whale depredation of longline gear, entanglement, and hooking have been documented in Alaska, Australia, New Zealand, Brazil, the Gulf of Mexico, Indian Ocean, and the Faroe Islands (Luck et al. 2025).

The presence of cookiecutter shark bite scars and wounds on killer whales in the CTP is not surprising, given that cookiecutter sharks live in pelagic tropical and subtropical waters where sea surface temperatures are 18°C–26°C (Nakano and Tabuchi 1990) and are known to feed on cetaceans, including killer whales (Barry et al. 2024; Dwyer and Visser 2011) and many other species in Hawaiian waters (Baird 2016; Walker-Milne et al. 2025). As well, remoras (Family Echeneididae) live in tropical and subtropical waters and are known to associate with at least 20 cetacean species (Fertl and Landry 1999). Remoras were observed on two killer whales in the Gulf of California, Mexico (Guerrero-Ruiz and Urbán 2000), on a stranded killer whale in Venezuela (Bolaños-Jiménez et al. 2025), and were documented on more than 10% of the individuals identified in our study. The remoras photographed on CTP killer whales have a uniformly gray appearance (Figure S8b) like *Remora* sp., which makes them difficult to identify to species with photos alone (Fertl and Landry 1999). There are three *Remora* species (*R. brachyptera, R. osteochir, R. australis*) that are typically found in tropical offshore pelagic waters worldwide (Fertl and Landry 1999). *Remora australis* is called the "whalesucker" because it has only been identified on cetaceans (Fertl and Landry 1999).

The skin conditions visible on CTP killer whales are unidentified but on some individuals they resemble tattoo skin disease (Figure S8c), which is a poxvirus that has been identified in at least 21 cetacean species around the world (Van Bressem et al. 2022). Tattoo skin disease is not typically fatal for cetaceans, but is linked to the presence of chemical pollutants, poor health, and stress (Van Bressem et al. 2022). The male killer whale that stranded on Kaua'i in 2008 was found to have very high levels of pesticides and polychlorinated biphenyls (PCBs) in his tissues, including the highest levels of DDTs, PBCs, and mirex, among others, of any of the 16 species sampled (Bachman et al. 2014). Given that killer whales in the CTP feed on marine mammals and other species high in the food web, it is likely that other individuals have similarly high concentrations of contaminants, particularly males who cannot offload their contaminants. Another disease that may threaten CTP killer whales and can lead to death is cetacean morbillivirus, which has been identified in killer whales that stranded in Brazil and Washington State (Groch et al. 2020; Rowles et al. 2011), as well as in nine other cetacean species that have stranded in the Hawaiian Islands (Jacob et al. 2016; West et al. 2013, 2021). The level of threat from contaminants and disease in CTP killer whales cannot be easily assessed given their rare occurrence in nearshore waters and therefore the extremely rare stranding events. The collection of tissue samples from live killer whales, by remote biopsy, for the purpose of contaminant and pathogen analysis could be informative.

Killer whales produce whistles and pulsed calls for communication and echolocation clicks for foraging and navigation (Barrett-Lennard et al. 1996; Ford 1989). In addition, they occasionally produce HFM whistles, the purpose of which is unknown but has been suggested as short-range communication to prevent prey or competitors from detecting them or for longer-range prey detection or navigation (Andriolo et al. 2015; Filatova et al. 2012; Reyes Reyes et al. 2017; Samarra et al. 2010; Simonis et al. 2012). Echolocation clicks, pulsed calls, whistles, and HFM whistles have been identified and described for killer whales in the temperate North Pacific (Au et al. 2004; Filatova et al. 2012; Riesch et al. 2006; Simon et al. 2006; Simonis et al. 2012; Thomsen et al. 2001, 2002), but acoustic recordings from confirmed killer whale sightings in the tropical-subtropical North Pacific are rare (Jarvis et al. 2019; Pitman et al. 2007; Rankin et al. 2008; Simonis et al. 2012). The acoustic recordings made during PIFSC ship surveys in Hawai'i provide the first detailed descriptions of killer whale vocalizations from multiple groups seen in the CTP.

CTP killer whales produce broadband echolocation clicks with a mean peak frequency (16.6 kHz) that falls within the range of mean peak frequencies of the three ecotypes/subspecies within the temperate coastal eastern North Pacific (12–19 kHz) (Barrett-Lennard et al. 1996; Leu et al. 2022). Studies have found that Bigg's killer whales rarely produced echolocation clicks, which has been suggested as a hunting strategy to prevent their marine mammal prey, with sensitive hearing, from easily detecting them (Barrett-Lennard et al. 1996; Deecke et al. 2005; Leu et al. 2022). It is possible that tropical-subtropical killer whales use a similar strategy of stealth with reduced vocalization rates.

During SWFSC ship surveys within the eastern and central Pacific Ocean, killer whales were quiet during most sightings that occurred in tropical-subtropical waters, including those during HICEAS 2002 and PICEAS 2005[5] (Rankin et al. 2008) that are included in this study. It is possible that the killer whales were producing HFM whistles, but the equipment used during these early surveys was not designed to capture such high-frequency signals. During PIFSC ship surveys, four of 10 killer whale sightings had no acoustic detections. One of these sightings included suspected predation of an unknown fish species, but none included other marine mammals. It is possible that the killer whales were quiet because of the presence of the ship. It was noted during two other sightings that the animals were

avoiding the vessel. However, during the fourth sighting, individuals remained quiet as they approached the ship to bow ride. As well, there were three other sightings during which the killer whales were vocal and also avoided the vessel.

CTP killer whales were vocal during a single confirmed predation event of a tuna, as well as during a sighting with short-finned pilot whales and unidentified dolphins. Although there was no indication that the killer whales were hunting the others, the unidentified dolphins were quiet. Rankin et al. (2012) found that tropical dolphin groups were significantly less likely to vocalize when killer whales were nearby. Jarvis et al. (2019) documented vocalizing rough-toothed dolphins off Kaua'i going silent at the onset of killer whale HFM whistles. During a PIFSC ship survey in 2023, beaked whales were acoustically active and tracked overnight off Kaua'i in coordination with the U.S. Navy's Pacific Missile Range Facility. Just before dawn, killer whales were acoustically detected in the area, and the beaked whales stopped vocalizing. After sunrise, the killer whales were seen and continued producing echolocation clicks and HFM whistles, but the beaked whales were quiet and never seen. That night, there were no acoustic detections of either species. The lack of beaked whale detections indicated that they had either stopped foraging or left the area.

HFM whistles were recorded during all five PIFSC acoustic encounters with CTP killer whales. They generally have similar down-swept contours, frequency characteristics, and durations as those described for killer whales elsewhere in the North Pacific (Filatova et al. 2012; Jarvis et al. 2019; Simonis et al. 2012) and in the Gulf of Mexico (Barry et al. 2024). The frequency characteristics of the CTP HFM whistles, recorded during PIFSC surveys, are similar across encounters, with one exception (sighting 48). The median fundamental frequencies of the HFM whistles recorded during sighting 48 are quite a bit higher (downswept from 39 to 26 kHz) than those from the other encounters (downswept from 24 to 19 kHz), and the median duration is shorter (117 ms) than the others (120–225 ms). The frequency characteristics of the HFM whistles from sighting 48 are similar to those of the Type 2 HFM whistles (downswept from 37 to 32 kHz) that were recorded at the Southern California Bight (SCB) on a seafloor mounted recorder (Simonis et al. 2012), as well as those recorded on the U.S. Navy's Pacific Missle Range Facility off Kaua'i and the Southern California Offshore Range with downsweeps from above 32 kHz to approximately 16 kHz (Jarvis et al. 2019). However, the median duration of the HFM whistles from sighting 48 are more than twice that of the Type 2 whistles (56 ms). A comparison of morphological characteristics for the group recorded during sighting 48 indicates that there are no obvious differences from other killer whales within the CTP photo-identification catalog. The recordings made by Simonis et al. (2012) and Jarvis et al. (2019) were not associated with sightings or with photographs that could be used for similar comparison or determination of ecotype.

HFM whistles have been identified in killer whale populations in the North and South Atlantic, Gulf of Mexico, Antarctic, and North and South Pacific (Andriolo et al. 2015; Barry et al. 2024; Filatova et al. 2012; Reyes Reyes et al. 2017; Samarra et al. 2010; Simonis et al. 2012; Wellard et al. 2015). In the North Pacific, HFM whistles have been recorded in both coastal and offshore habitats and during confirmed sightings with "offshore" killer whales and other unidentified ecotypes (Filatova et al. 2012; Gassmann et al. 2013; Samarra et al. 2010; Simonis et al. 2012). The lack of detection of HFM whistles across all ecotypes/subspecies in the North Pacific may be related to the low sampling rates of the recordings, as noted in previous studies (Filatova et al. 2012; Simonis et al. 2012).

Although the exact purpose of HFM whistles is not known, for CTP killer whales recorded during PIFSC sightings, the lack of low-frequency whistles, low occurrence of pulsed calls, and prevalence of HFM whistles suggests that HFM whistles may, at times, be their primary means of within-group communication. The presence of the ship may have affected the killer whales' acoustic behavior, resulting in the reduction or cessation of the widely used social signals of other populations or ecotypes. The fact that all acoustic events included echolocation clicks does not rule out the use of HFM whistles for detection tasks. Additional acoustic recordings made during CTP killer whale sightings, in the presence of other marine mammals, would be informative for further assessing the killer whales' use of HFM whistles. In addition, analyses of unattended recordings of killer whales in the CTP may reveal their full acoustic repertoire.

This study provides new insights for understanding CTP killer whales through various methods including photo-identification, morphological assessment, and acoustic monitoring. Many aspects of their morphology and ecology documented in this study suggest that CTP killer whales represent a separate ecotype within the North Pacific that mirrors other tropical-subtropical populations around the world, including the ETP (Ortega-Ortiz et al. 2023; Vargas-Bravo et al. 2020). Whether CTP and ETP killer whales could be considered a connected population cannot be determined from this study because gaps exist due to data limitations and the rarity of sightings. This underscores the need for additional collaborative research efforts and continued contributions of local communities to address these gaps. Additional data collection and analyses are needed including biopsy sampling for genetics, stable isotopes, pathogens, and contaminants, satellite telemetry to understand the patterns and extent of CTP killer whales' movements, photo-identification data from the western tropical Pacific and continued comparisons to ETP catalogs, and analyses of existing acoustic data from bottom-mounted and drifting recorders in the CTP and the western tropical Pacific. Without addressing the knowledge gaps about their distribution, population size, and extent of threats, managing and conserving CTP killer whales will remain a challenge.

Author Contributions

Marie C. Hill: conceptualization, investigation, writing – original draft, methodology, writing – review and editing, data curation, validation, visualization, formal analysis, project administration. **Sabre D. Mahaffy:** investigation, writing – review and editing, methodology, validation, visualization, data curation, formal analysis. **Jennifer L. K. McCullough:** investigation, writing – original draft, methodology, validation, visualization, writing – review and editing, formal analysis, data curation. **Alaina Harmon:** investigation, writing – original draft, methodology, validation, writing – review and editing, data curation, formal analysis. **Robin W. Baird:** conceptualization, funding

acquisition, methodology, writing – review and editing, project administration, validation, investigation.

Acknowledgments

We would like to thank Jason Baker, Paula Olson, Ingrid Visser, and an anonymous reviewer for their reviews of the manuscript. We thank many individuals for assisting in the collection and contribution of data including Jay Barlow (SWFSC Chief Scientist); James Carretta (SWFSC); Erin Oleson, and Dave Johnston (PIFSC Chief Scientists & CRP Leads); Allan Ligon (satellite tagging, biopsy), Colin Cornforth (satellite tagging); Daniel Webster (satellite tagging, biopsy); Adam Ü (biopsy, photography); Mark Deakos, Jason Larese, and Kydd Pollock (2009–2011 Palmyra surveys); Colin Cornforth, Kydd Pollock, Carl Lobue, Robbie Schallert, and Alex Filous (Palmyra Bluewater Research Team); Amanda Bradford, Kym Yano, Laura McCue, Paula Olson, Suzanne Yin, and Russ Andrews (photographers); Shannon Rankin (acoustician), all cruise leaders, marine mammal observers, acousticians, NOAA officers and crew who participated in shipboard surveys, and citizen scientists (Chris Bane, A. Reinprecht, Masa Ushioda, H. Yocum, James Begeman, I. Blue, Megan Magennis, K. Chadick, Wendy Castillo, J. Kuni, Tabitha Pupuhi, K. Attix, Alicia Franco, Seth Conae, Jason Lafferty, D. Bock, C. Kauffman, Jim Ward). We thank Christian Ortega-Ortiz, Paula Olson, Tim Gerrodette and associated contributors for sharing their catalogs of ETP killer whales used for comparison in this study. All research surveys (and associated photography, biopsy sampling, and satellite tagging) were covered under National Marine Fisheries Service permits. Funding for ship and small-boat surveys was provided by various sources including NOAA (SWFSC & PIFSC), the U.S. Navy (ONR & PACFLT), Bureau of Ocean Energy Management, and The Nature Conservancy. We thank Ākeamakamae Kiyuna for the ʻŌlelo Hawaiʻi translation of the Abstract.

Funding

This work was supported by the Pacific Islands Fisheries Science Center, Southwest Fisheries Science Center, Office of Naval Research, U.S. Navy Pacific Fleet, Bureau of Ocean Energy Management, and The Nature Conservancy.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that supports the findings of this study are available in the Supporting Information of this article.

Endnotes

[1] GEBCO 2024 Grid (doi: 10.5285/1c44ce99-0a0d-5f4f-e063-7086abc0ea0f).

[2] This includes 615 individuals from a photo-identification catalog provided by Christian Ortega-Ortiz (Lazcano-Pacheco et al., in review. Morphological and ecological insights of the predominant ecotype of killer whales (*Orcinus orca*) in the Eastern Tropical Pacific).

[3] Killer whales were vocal during the 2006 sighting as documented in an unpublished report (Rankin, S. American Samoa-Hawai'i cetacean research survey: Passive acoustics survey report. 28 March 2006). Manual localization, in real-time by an experienced acoustician, was used to attribute pulsed calls to killer whales during the mixed species encounter (S. Rankin, personal communication). While the acoustician expressed confidence in real-time, the raw data are no longer available for re-examination and there remains some potential for misclassification of these calls. The frequency response of the array (500 Hz–25 kHz ± 10 dB) and the sampling rate of the recording (48 kHz) would have prevented direct comparison to the other recordings.

[4] Unpublished data provided by the Pacific Islands Regional Office, Honolulu, HI.

[5] There was a single acoustic detection of killer whales within the CTP during PICEAS 2005 but it was not associated with a sighting and was not analyzed for this study.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** mms70197-sup-0001-supinfo.docx. **Table S1:** Summary of ship surveys and killer whale sightings by the Pacific Islands Fisheries Science Center (PIFSC) and the Southwest Fisheries Science Center (SWFSC) within the central tropical Pacific (CTP) between 2002 and 2023. For surveys in which the ship(s) transited to and from California (CA), the on-effort days and distance are listed for the entire survey and for the study area within the CTP (see Figure 1a). Locations include the U.S. exclusive economic zones (EEZs) of Hawai'i (HI), Johnston (JA), Palmyra/Kingman (PA), American Samoa (AS), Wake, Guam, as well as sublocations within the Hawai'i EEZ (main Hawaiian Islands (MHI), Northwestern Hawaiian Islands (NWHI)—also referred to as the Papahānaumokuākea Marine National Monument (PMNM)), and the surrounding international waters (IW). *One killer whale sighting during the 2016 HI-TEC survey was initiated by Cascadia Research Collective. This sighting was excluded from the ship sighting rate calculation. **Table S2:** Details of killer whale sightings in the central tropical Pacific. Sighting numbers are listed in chronological order. The sighting number is followed by a letter to signify the type of sighting (*R* = research, RD = research directed, D = directed (no effort data), O = opportunistic). The source of sightings is listed by contributing organization (CRC = Cascadia Research Collective, PIFSC = Pacific

Islands Fisheries Science Center, PIRO = Pacific Islands Regional Office, SWFSC = Southwest Fisheries Science Center) or individual (first initial, last name) and for research sightings the specific survey, year, and sighting number associated with that survey is listed (see Tables S1, S3, and S4 for survey summaries). The Location was assigned either based on the latitude/longitude for research sightings or information provided by the contributors of opportunistic sightings (NWHI = northwestern Hawaiian Islands, IW = international waters). The best estimate for group size (Grp. Best Est.) is listed when an estimate was made in the field during the sighting. The No. photo-IDs is the observed number of identified individuals from the photo-identification (photo-ID) catalog, and the social network ID (NetID) is assigned as a letter. Individuals seen together (sometimes in multiple sightings) are part of the same social network component and share the same NetID (see Figure 4 and Table S6). The group composition includes adult males (AM), adult females (AF), "adult female sized" (AFS) individuals (possible sub-adult males), juveniles (J), calves (C) and unknown (U). Sex/age class was determined using photos (no lowercase letter), genetic sex (g), presence of a calf (c) or observations in the field (f). See "Methods—2.2 Photo-Identification and Social Network" for details on sex/age class determination. **Table S3:** Summary of small-boat surveys and killer whale sightings conducted by Cascadia Research Collective around the main Hawaiian Islands between 2002 and 2023. Maui Nui includes the islands of Molokaʻi, Maui, Lānaʻi, and Kohoʻolawe. Three killer whale sightings were directed from sources outside of the visual survey effort (e.g., satellite tag transmissions, acoustic detection, radio call). **Table S4:** Summary of small-boat surveys and killer whale sightings around Palmyra Atoll conducted by the Pacific Islands Fisheries Science Center (PIFSC) and Scripps Institute of Oceanography (SIO) in 2009–2011 and for the Palmyra Bluewater Research project, which was a multi-species study and multi-organization collaboration with The Nature Conservancy (TNC), PIFSC, Southwest Fisheries Science Center (SWFSC), San Jose State University (SJSU), Stanford University (SU), University of California, Santa Barbara (UCSB), National Geographic (NatGeo), University of Washington (UW), University of Hawaiʻi (UH), and the U.S. Fish and Wildlife Service (USFW) in 2022. **Table S5:** Depth (m) and distance from shore (km) of killer whale sightings in the central tropical Pacific for which latitude and longitude were recorded in the field. Records are listed in order by survey effort type. "Ship—directed" and "Small boat—directed" sightings are those in which the vessel was directed to the killer whale group by an outside source (e.g., satellite tag transmissions, acoustic detection, radio call). Associated effort data were collected with these sightings. The "Directed" sighting is one in which the vessel was directed to the killer whale group but no effort information was recorded and was therefore grouped with opportunistic sightings in Figures S1c and S2. Locations include the northwestern Hawaiian Islands (NWHI) and international waters (IW). **Table S6:** Central tropical Pacific killer whale photo-identified individuals ($n = 113$) listed in order by social network ID (NetID) and catalog ID. Summary includes the sightings during which they were photographed, the years and locations seen (NWHI-northwestern Hawaiian Islands, IW-international waters), their distinctiveness (D) rating (1-not distinctive, 2-slightly distinctive, 3-distinctive, 4-very distinctive), the highest image quality (Q) rating (1-poor, 2-fair, 3-good, 4-excellent), an indication if they were biopsy sampled (B), satellite tagged (T), or not (N), and their assigned age-class and sex. Adult males (AM) were assigned if they had a tall and erect fin. The age class of other individuals was determined by the size of the individual relative to others of within an image. (AFS-"adult female sized" (possible sub-adult male), J-juvenile, C-calf, U-unknown), The sex of one AM and nine non-AM individuals was determined by genetics (g) or the presence of an associated calf (c). See Table S2 for details of each sighting. **Table S7:** Acoustic characteristics of central tropical Pacific killer whale highfrequency modulated whistles by sighting number and acoustic encounter given as median values with 10th and 90th percentiles in parentheses. Acoustic encounters correspond to the acoustic recording IDs listed in Table S2. **Figure S1:** Survey effort (days) and killer whale sightings within the central tropical Pacific by effort type (ship, small boat, opportunistic) and month. (a) Ship survey effort (bars) and sightings (symbols) by location: U.S. exclusive economic zone (EEZ) or international waters (IW; NP—North Pacific, SP—South Pacific). There were no sightings (NA) within Wake or American Samoa EEZs. (b) Small-boat survey effort (bars) and sightings (symbols) by island location. There were no sightings (NA) off Oʻahu or Maui Nui. (c) Opportunistic and directed sightings in the main Hawaiian Islands. No effort was recorded. Notes: The letter "D" above a symbol indicates that the survey vessel was directed to the group by an outside source (see all panels). In panel (a), one sighting was directed by Cascadia Research Collective during ship surveys. An asterisk (*) next to a symbol indicates a resight of a group in the same month, year, and island location (see panels (a) and (c)). One regular (nondirected) sighting during a ship survey (panel (a)) was a resight. Both directed sightings in panel (c) were resights prompted by satellite tag transmissions. **Figure S2:** Effort as a percent of survey track points (bars) and number of killer whale sightings (symbols) within the central tropical Pacific by (a) distance from shore in kilometers and (b) depth in meters during ship surveys, small-boat surveys in Palmyra and the main Hawaiian Islands (MHI) and opportunistically in the MHI. There was no effort recorded for opportunistic sightings. Note: Opportunistic sightings include one sighting for which the vessel was directed to the killer whale group location by satellite tag transmissions but no associated effort data were recorded. **Figure S3:** Determination of the anterior and posterior insertions of the dorsal fin (white circles) following Durban and Parsons (2006). Defined as the mid-point of the curve between intersecting lines that follow the main axes of the dorsal fin and body (solid white lines). **Figure S4:** Examples of eye patch shapes of central tropical Pacific killer whales in order of frequency of occurrence (see Figure 5). (a) Hook & bump, (b) Bumps, (c) Narrow front, (d) Hooked, (e) Multiple hooks, (f) Rear variation. Note: Left side images showing rear taper observed in most (87%) eye patches. **Figure S5:** Example images of central tropical Pacific killer whale saddle patches showing the variation in size based on the ratio of saddle patch width (at its widest) to dorsal fin base width (at its widest) ((a) Narrow (< 0.50), (b) Medium (0.50–0.70), Note: no saddle patches are categorized as wide (> 0.70)) and distinctiveness/clarity ((c) Faint, (d) Intermediate, (e) Conspicuous). **Figure S6:** Example images of central tropical Pacific killer whale dorsal fins showing the variation in tip shape ((a) Round, (b) Point, (c) Tip missing) and the dorsal fin tip relative to its base ((d) iii—between insertions, (e) iv—at posterior insertion, (f) v—beyond posterior insertion). **Figure S7:** Central tropical Pacific killer whales with (a) mouthline, (b) dorsal fin, and (c–e) peduncle injuries consistent with fisheries interactions, and (e) a dorsal fin tip amputation possibly consistent with a fisheries interaction. The photo-identification catalog ID and location where the individual was seen is noted on the image. (NWHI—northwestern Hawaiian Islands). **Figure S8:** Central tropical Pacific killer whales with (a) cookiecutter wounds and scars, (b) remoras, and (c) an unknown skin condition resembling tattoo skin disease. **Figure S9:** Example pulsed call recorded during sighting 46 (acoustic encounter 2303160). **Figure S10:** Spectral averages of individual towed hydrophone array event data (gray lines) for killer whale echolocation signals with the mean overlaid (thick black line). (Plotted using R-packages *PAMpal* and *ggplot2* (Sakai 2020; Wickham 2016)).