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RESEARCH ARTICLE

WILEY

New urban habitat for endangered humpback whales: San Francisco Bay

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Abstract

1. As populations of large whales recover from whaling, species that forage and breed in coastal waters, including the humpback whale (*Megaptera novaeangliae*), increasingly overlap with human activities. This represents a potential hazard in locations worldwide subject to intensive vessel traffic, including New York, Panama City and Brisbane.
2. Historically, humpback whales were not considered part of San Francisco Bay's fauna, except for a few 'lost' whales that wandered into the estuary.
3. An unprecedented influx of humpback whales into highly urbanized San Francisco Bay began in 2016. Research efforts in 2016–2018 from vessels and shore resulted in 496 photo-identification records plus 319 visual sightings. Sixty-one individuals were photo-identified, of which 80% ($n = 49$) used the bay on multiple days (range = 2 to 39), and 34% ($n = 21$) were resighted in successive years.
4. Whales photographed in San Francisco Bay were found to belong to distinct population segments listed as endangered and threatened under the U.S. Endangered Species Act.
5. Whales moved in and out of the bay seasonally (April–November). Habitat use patterns indicated movements farther into San Francisco Bay correlated positively with high tides.
6. Humpback whales were visually observed lunge feeding on northern anchovy (*Engraulis mordax*) at the surface. Analysis of dive patterns by three tagged whales confirmed subsurface feeding when surface feeding was not apparent.
7. The use of San Francisco Bay and adjacent waters by recovering populations of humpback whales exacerbates the potential for collisions with vessels, entanglement in fishing gear, and harassment by recreational vessels. The most pressing conservation concern is the risk of ship strikes, observed where humpback whales occur near active seaports.

KEYWORDS

cetacean foraging, distinct population segment, endangered, estuary, Golden Gate, humpback whale, photo-identification, San Francisco Bay, ship strike

1 | INTRODUCTION

1.1 | Whales in the marine urban environment

Large whales have been the beneficiaries of legal protections from directed hunts, yet many recovering populations suffer from an increasing overlap with human activities. Repeated exposure to intense near-shore commerce leads to cumulative stressors that disrupt the behaviour of cetaceans and threaten their health and survivorship (Piwetz, 2019; Williams et al., 2014). The North Atlantic right whale (*Eubalaena glacialis*) has been dubbed 'the urban whale' because it inhabits the industrialized waters adjacent to eastern North America (Kraus & Rolland, 2009). The term might equally apply to other species, particularly the humpback whale (*Megaptera novaeangliae*), which has increased in abundance and now occurs regularly in the vicinity of active seaports, including New York, USA (Brown et al., 2019), Panama City, Panama (Guzman et al., 2013), and Brisbane, Australia (Mayaud et al., 2022).

Marine shorelines have always been prime locations for human settlement. Anthropogenic impacts, especially to sensitive areas such as estuaries, stem from the overexploitation of fishery resources, pollutants, shoreline development and habitat destruction. The result is significant long-term degradation of many estuarine ecosystems (Cloern et al., 2016; Lotze et al., 2006). Yet estuarine recoveries are documented (Lotze et al., 2011), and in certain places, marine mammals manage to co-exist with large-scale coastal development (Chilvers et al., 2005).

1.2 | The San Francisco Bay estuary

San Francisco Bay, California, is the most extensively modified estuary in the United States, ringed by a human population exceeding 7 million (Cloern & Jassby, 2012; Nichols et al., 1986). Beginning with the mid-19th century gold rush, its biological communities were severely disturbed by the effects of rapid urbanization, such as water pollution, wetland fill, construction and river sedimentation and diversion (Luoma & Cloern, 1982). The dominance of exotic organisms gave the bay a reputation for being the most invaded estuary in the world (Cohen & Carlton, 1998). Investments in restoration efforts began to reverse previous declines and led to more positive ecological indicators, including in fish populations (San Francisco Estuary Partnership, 2019). Improved habitat is credited with the reoccupation of the bay ecosystem by harbour porpoise (*Phocoena phocoena*) after decades of absence (Stern et al., 2017). This study reports a recent surge in the use of San Francisco Bay by humpback whales.

1.3 | Historical records of humpback whales in San Francisco Bay

Although humpback whales inhabited California's coastal waters historically, the species was not considered part of San Francisco Bay's fauna. A competent 19th-century observer, Charles Scammon, did not mention them in the bay, though he reported other marine mammals there (Scammon, 1874). In the 20th century, notwithstanding their reduced population due to hunting across the North Pacific and in northern California (Clapham et al., 1997; Ivashchenko et al., 2013), humpbacks continued to occur off San Francisco. By mid-century, the last commercial whalers in California operated out of Point San Pablo on the shore of San Francisco Bay, taking 841 humpbacks locally offshore from 1956–1965 (Rice, 1978) before the hunt was banned (IWC, 1967). The most notable exceptions to the absence of humpback whales within the bay involved 'lost' individuals, such as 'Humphrey' in 1985 and 1990 and the mother-calf pair 'Delta' and 'Dawn' in 2007, which travelled through the bay delta to reach the inland Sacramento River (Gulland et al., 2008). The only other large whale seen in San Francisco Bay is the gray whale (*Eschrichtius robustus*), some of which may visit from February to June during their northbound migration (Markowitz et al., 2022).

1.4 | Current status of humpback whales in the Eastern North Pacific Ocean

Despite their rarity within San Francisco Bay prior to recent years, humpback whales are commonly observed along the northern California coast from spring through fall. The species shows strong site fidelity to mid-latitude feeding areas (Calambokidis et al., 2008), and the federally managed California/Oregon/Washington stock returns annually (Carretta et al., 2018). The population size of the California-Oregon feeding group has increased over the past three decades and may be levelling off at approximately 2400 (Calambokidis et al., 2017). North Pacific humpback whales (*M. n. kuzira*; Jackson et al., 2014) are also structured by their low-latitude winter breeding areas in distinct population segments (DPSs). The group that forages off California is comprised almost exclusively of members from Mexico and the Central America DPSs (Calambokidis et al., 2000; Calambokidis et al., 2017). The Mexico DPS consists of an estimated 3477 whales that breed along the Pacific coast of mainland Mexico, the Baja California Peninsula and Revillagigedos Islands (Bettridge et al., 2015; Curtis et al., 2022; Martien et al., 2021; Wade et al., 2016). The smaller Central America DPS has a population of approximately 1500 (Curtis et al., 2022; Taylor et al., 2021), with recent data suggesting humpback whales breeding in southern Mexico are also members of the Central America DPS (Martínez-Loustalot et al., 2022). Although the humpback whale is considered a species of least concern globally (Cooke, 2018), the United States lists the Central America DPS as an endangered population under the Endangered Species Act and the Mexico DPS as threatened (U.S. Federal Register, 2016).

The marine waters adjacent to San Francisco Bay, the Gulf of the Farallones, have been identified as part of a Biologically Important Area for feeding humpback whales (Calambokidis et al., 2015), with critical habitat designated inshore along the 15-m isobath extending east to the Golden Gate Bridge (U.S. Federal Register, 2021). Prey in this area includes both krill and fish (Wright et al., 2016), particularly euphausiids (*Thysanoessa spinifera*), Pacific sardines (*Sardinops sagax*), Pacific herring (*Clupea pallasii*) and northern anchovy (*Engraulis mordax*) (Pyle & Gilbert, 1996).

1.5 | Research objectives

Beginning in 2016, humpback whales were observed moving inshore from Gulf waters to feed in areas with more congested vessel traffic, including San Francisco Bay (Figure 1). A dedicated year-round cetacean monitoring effort underway from 2010 using the Golden Gate Bridge as a primary platform yielded no humpback whale sightings prior to 2016, despite sightings of thousands of small cetaceans (porpoises and dolphins) documented in San Francisco Bay during the same time span (Keener et al., 2018; Stern et al., 2017). The unexpected influx of humpback whales prompted this field study to document humpback whale abundance, spatiotemporal use of San Francisco Bay habitat, foraging behaviour and connections to breeding populations. To address these objectives, a multiplatform approach was utilized to collect information on humpback whale locations, behaviour and identity from research vessels, whale tour vessels, shore stations and the Golden Gate Bridge. Understanding the whales' seasonality and movement patterns can help inform management to ensure the safety of migratory whales foraging in a highly urbanized waterway.

2 | METHODS

Data collection focused on the first 3 years (2016–2018) of humpback whale activity in San Francisco Bay and included whale sighting rates, photo-identification of individuals, location of whales within the bay, surface behaviour and detailed information on individual movements and dive patterns from tag deployments.

2.1 | Study area

San Francisco Bay is the U.S. West Coast's largest estuary, draining a 163,000 km^2 watershed through the Golden Gate into the Pacific Ocean (Cloern & Jassby, 2012; Feyrer et al., 2007). The bay has mixed semi-diurnal tides (Conomos et al., 1985), with currents approaching 5 kn. It is among the deepest estuarine outlets (reaching 100-m depth) in the world (Barnard et al., 2006). The Golden Gate is a 4.5-km-long strait that connects the adjacent Pacific Ocean waters (Gulf of the Farallones) with the bay (U.S. Coast Pilot, 2022). The Golden Gate Bridge (37° 49′ N, 122° 29′ W) spans the strait at its narrowest width (1.6 km) and deepest point (113 m). Observation efforts in San Francisco Bay focused on the strait west of the Golden Gate Bridge and the central bay east of the bridge (Figure 3). The strait's area is 5 km^2, while the main section of the central bay is much larger, approximately 115 km^2. San Francisco Bay is a major commercial shipping destination where vessels access six of California's seaports via the bay (Cope et al., 2020).

2.2 | Research platforms and monitoring effort

Research platforms included small survey vessels, whale watching tour vessels, shore-based monitoring stations and the Golden Gate Bridge. Vessels focused their effort in both the central bay and strait, while shore stations were located primarily on bluffs overlooking the strait. The pedestrian sidewalk of the bridge, 70 m above sea level, provided unobstructed views east into the central bay. The bridge is an efficient non-invasive photography platform for cetacean research (Stern et al., 2017), although visibility was occasionally hampered by low-lying fog, prevalent during summer months. From 2016–2018, humpback whales were documented during a total of 2028 h of research effort on 522 days from vessels (189 days in 2016, 149 days in 2017, 184 days in 2018), 352 h on 201 days from the Golden Gate Bridge (64 days in 2016, 78 days in 2017, 59 days in 2018) and 158 h on 132 days from shore stations (22 days in 2016, 73 days in 2017, 37 days in 2018). Sighting effort occurred year-round from the Golden Gate Bridge, with 41 days of effort in winter (December–February), 51 days in spring (March–May), 63 days in summer (June–August) and 46 days in autumn (September–November). Sighting effort for vessels and shore stations was seasonal, April through November. Research from vessels was conducted on 60 days in spring, 257 days in summer and 205 days in autumn; research from shore stations was conducted on 60 days in spring, 52 days in summer and 20 days in autumn.

The terms ‘sighting’, ‘count’, ‘observation’ and ‘record’ denoted a single data record of an individual whale, or multiple whales seen simultaneously. Whale sightings were divided into two types: photo-documented sightings of identified individuals (photo-IDs) and sightings of unidentified whales, with or without photographs (visual counts).

2.3 | Photo-identification

High-resolution photographs were collected using digital SLR cameras with telephoto lenses. Images were also sourced from

FIGURE 1 Humpback whales in San Francisco Bay: (top) lunge feeding under the Golden Gate Bridge; (bottom) in urban vessel traffic within the bay. Photos by T. Markowitz (top) and W. Keener (bottom) pursuant to National Marine Fisheries Service ESA/MMPA Permit No. 21678.

wildlife tour boat naturalists, citizen scientists and members of the public. Typically, a minimum of one tour vessel searched for local whales an average of 5 days per week throughout the entire spring to autumn season. All citizen scientists (non-specialist volunteers, *sensu* Bruce et al., 2014) were trained or personally vetted by a member of the research team (authors). Opportunistic visual sightings by the public, when not supported by photographs, were only accepted if the observer was contacted by a research team member and the whale species could be reliably determined. Contributions to the entire San Francisco Bay Area dataset of 815 sightings were made by the research team (48%, $n = 393$), whale watch naturalists (29%, $n = 235$), citizen scientists (17%, $n = 141$) and members of the public (6%, $n = 46$). Observers trained in cetacean photo-identification techniques (authors, whale watch naturalists and citizen scientists) were thus responsible for documenting 94% of all photo-identified whale sightings. Data reliability can be a concern when using citizen scientists, but photographs are verifiable and fluke matching was conducted only by the research team. Most of the 496 photo-documented sightings were collected from vessels (64%, $n = 319$), with the remainder from the Golden Gate Bridge (24%, $n = 121$), shore 11%, $n = 55$) or air ($n = 1$ news helicopter).

2.4 | Habitat use and behaviour

Data collected included date, time, actual or estimated GPS coordinates, group size, age class (life stage: adult, subadult, calf) and behaviour. Sex determination was not attempted, other than inferred female when accompanied by a dependent calf. Mother–calf pairs were identified due to clear contrast in sizes, consistent close proximity and synchronous movements. Surface behaviour was categorized into one of five predominant behavioural states (Markowitz et al., 2004; Pearson et al., 2017; Shane, 1990; Silber, 1986; Wells et al., 1999): travelling (linear movement), milling (non-linear movement with surfacing at different headings), resting (logging at the surface), feeding (lunging behaviour accompanied by distension of throat pleats) or surface active (breaching, tail slapping, pectoral fin slapping).

2.5 | Tagging effort

To supplement visual observations and gain insights into humpback whale underwater behaviour and habitat use, suction-cup-attached, multi-sensor tags were deployed on three individuals within the study area on 23 July 2017 during the flood period of a single tidal cycle. Tags were deployed with a 5-m pole from the bow of a 6-m vessel and were subsequently recovered after detaching from the animals. The tags (Wildlife Computers TDR-10F; https://wildlifecomputers.com) were modified for attachment using four suction-cups (Customized Animal Tracking Solutions; https://cats.is) and sampled depth and 3D acceleration at 32 Hz, temperature and light-level at 1 Hz, as well as Fastloc® GPS when the animals surfaced. The duration of tag deployment ranged from 0.64 to 3.34 h (median = 2.37 h).

2.6 | Data analysis and statistics

Humpback whales using San Francisco Bay were initially photo-identified based on fluke ventral surface images, a standard photographic mark-recapture technique for this species (Barlow et al., 2011; Katona et al., 1979). Standard fluke images could not be obtained every time a whale was encountered, so other marks, such as dorsal fin shape, body scars or scratches, were used in some instances to provide consistent individual identifications (Franklin et al., 2020; Katona & Whitehead, 1981). These secondary marking were only used for intra-annual comparison and were always matched to fluke records of known individuals. Using the highest quality images available from each sighting, data were archived by a research team member experienced in pattern recognition and hand-compared against previously archived images from San Francisco Bay to detect resightings. Fluke images from San Francisco Bay were compared to the large North Pacific humpback whale catalogue maintained by Cascadia Research Collective (CRC), comprised of 5,538 unique individuals from 49,924 encounters gathered along the U.S. West Coast primarily from 1986 through 2018. This comparison effort was made using a combination of hand matching and automated algorithms and was supplemented by information available on Happywhale (www.happywhale.com; Cheeseman et al., 2022).

Photo-identifications were used to examine site fidelity (intra-annual and interannual resightings), document spatiotemporal variation in habitat use (including tidal patterns during daylight hours only) and confirm migration to low-latitude breeding areas. Because photo-documented sightings were associated with the most precise geographic coordinates, they were also used to map whale locations. The number of whales using San Francisco Bay was calculated as a minimum abundance by a direct count of known whales based on fluke images. Visual count data were not used for field identification of individual whales but were appropriate for assessing seasonality, monthly averages and establishing maximum daily numbers. No prey fish samples were collected, but high-quality photographs were reviewed by two research fisheries biologists at NOAA's Southwest Fisheries Science Center for species identification (Kevin Stierhoff and Andrew Thompson, pers. comms., August 2020).

Tag data were used to examine dive depths, times, surfacing locations and feeding lunges for focal whales. Raw tag data were processed using custom MATLAB (Mathworks, version 2017b) scripts to determine the animal's pitch, roll and speed (Cade et al., 2021; Johnson & Tyack, 2003). Feeding lunges were identified using stereotypical kinematic signatures from multiple sensors (e.g., the animal's depth, pitch, roll and speed; Cade et al., 2021; Goldbogen et al., 2006). GPS location data were filtered for unrealistic whale speeds (e.g., >6 m/s) using the ArgosFilter package (Version 0.62) in R (Version 3.5.1; https://www.r-project.org). Dives were identified as vertical excursions to depths greater than 10 m, and GPS locations were associated with the corresponding start time of the nearest dive. Processed tag data were downsampled to 1 Hz and analysed in R. Mean and standard deviation of water depth were calculated for each deployment as was the percent time the animal spent at depths <15 and <30 m. Number of dives per hour, maximum dive depth (mean and standard deviation) and dive duration (mean and range) were calculated for each individual. Feeding rates and feeding depth (mean and range) were assessed based on the identification of feeding lunges. For each GPS location, the bottom depth was extracted using a 10-m resolution digital elevation model (NOAA National Center for Environmental Information).

Microsoft Excel was used to calculate summary statistics (e.g., mean, median, harmonic mean, standard deviation and 95% CI) and produce data figures and tables. Statistical tests were performed in SPSS Statistics v25. Of all photo-identified sightings ($n = 496$), a subset limited to a maximum of a single sighting per day per individual whale ($n = 395$) was used to analyse resightings, behaviour and plot locations. Maps were created in ArcGIS Pro 2.3.3 software (ESRI; https://www.esri.com), using the Kernel Density tool to indicate high concentrations of whale sighting and feeding locations. A Minimum Bounding Geometry feature (Convex Hull) was used to output a Minimum Convex Polygon enclosing photo-identified whale sightings.

Mean depths, using the 10-m digital elevation model, were estimated for whale sightings based on the nearest 10-m isobath. Mean distance to shore was estimated for whale sightings based on the closest measured distance to the shoreline.

Tidal cycle correlations were based on tide heights in JTides v. 5.3 (www.arachnoid.com) using the San Francisco Bay station as the reference locality. Tidal periods were categorized as follows: The *low tide* period was defined as the time of low tide ± 1 h. The *high tide* period was defined as the time of high tide ± 1 h. The *flood tide* period was defined as the time between the end of the low tide period and the beginning of the high tide period. The *ebb tide* period was defined as the time between the end of the high tide period and the beginning of the low tide period. Sighting locations were binned by tidal state and displayed by kernel density. To test for significant differences in West (offshore) to East (inshore) distribution by tidal state, mean longitudinal values for the four tidal states were compared by ANOVA with Tukey post hoc pairwise comparisons (following tests confirming normality and homogeneity of variance).

3 | RESULTS

3.1 | Occurrence and seasonality

Humpback whales were observed in San Francisco Bay on 273 days from 2016 to 2018. They occurred seasonally from late April through mid-November. First and last sighting dates were similar between years, in contrast to interannual variability in the number of days whales were sighted, which ranged from 24% to 58% (Table 1). When whales were present ('whale days'), the average daily count (total whales/whale days) varied between years, from 3.5 whales per day in 2016 to 2.1 in 2018. For the entire study period, an average of three whales were sighted in San Francisco Bay when whales were present. The mean number of whales sighted per day varied significantly between years and seasons (ANOVA $P < 0.001$, $F_{year} = 8.51$, $F_{season} = 25.82$). Yearly averages ranged from 0.8 to 2.0 whales per day (Table 1), with monthly averages ranging from 0 to 5 whales per day (Figure 3). Across the 3-year study period, June and July were the peak months for humpback whale occurrences in San Francisco Bay based on the average number of sightings per day (Figure 2). Fewer whales were observed per day during autumn than in spring and summer.

Whale presence during each year was intermittent. Maximum consecutive whale days (longest streaks when whales were seen every day) was 8 days in 2016, 17 days in 2017 and 33 days in 2018. Consecutive days when no whales were observed in San Francisco Bay occurred multiple times each year. The first year had the longest gap, a span of 69 days when no whales were seen from 25 August to 1 November 2016. Whales were seen on only 24% of the days in that year, approximately half the number of whale days in 2017 and 2018 (Table 1). While whales were absent in San Francisco Bay on most days in 2016, that year also had the highest peak numbers of whales during the study. Maximum daily numbers reached 24 whales on 10 July 2016 in the strait west of the Golden Gate Bridge and 15 on 12 July 2016 in the central bay east of the bridge. The maximum daily number of whales observed in the bay was 10 in 2017 and 7 in 2018. These numbers ($n = 815$ total sightings) are conservative estimates based on photographs and visual counts of whale groups surfacing synchronously or in succession while spatially distributed.

3.2 | Photo-identification

A total of 496 photo-documented sightings resulted in 61 individually recognizable humpback whales, all identified previously or since outside of San Francisco Bay in the CRC catalogue. Ventral fluke patterns were used to add all 61 whales to the San Francisco Bay catalogue and make interannual reidentifications. In 2016, 17 whales were photo-identified, followed by 28 new whales in 2017 and 16 in 2018, continuing an upward trend in cumulative discoveries (Table 1). The 496 photo-identified sightings were documented by ventral

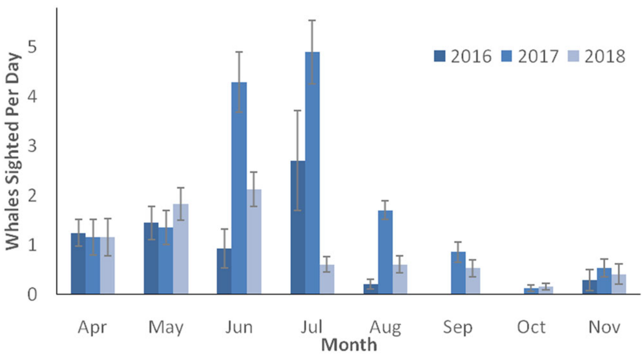

FIGURE 2 Monthly average numbers of humpback whales sighted per day in San Francisco Bay (mean ± 95% CI) are compared by year, based on all whale observations ($n = 815$). Mean values include days when no whales were sighted.

TABLE 1 Summary of humpback whale seasonal occurrences in San Francisco Bay ($n = 815$), 2016–2018.

Year	First sighting	Last sighting	Season length (days)	Days whales sighted	Total sightings	Whales/ day	Whales/ WD	IDs in Year	Cumulative IDs
2016	27 Apr	24 Nov	212	50 (24%)	111	0.8	3.5	17	17
2017	19 Apr	20 Nov	216	126 (58%)	383	2.0	3.4	41	45
2018	20 Apr	18 Nov	213	96 (45%)	321	1.0	2.1	30	61

Note: Total whale sightings, whales/day and whales/whale day (WD) are based on a maximum of 1 observation per whale per day.

flukes (68%, $n = 336$), dorsal flukes (15%, $n = 76$), dorsal fin shape (16%, $n = 79$), unique pigmentation (0.6%, $n = 3$) and prominent body scars (0.4%, $n = 2$). Other marks, for example, scratches on the dorsal surface of the flukes, were not permanent, but 84% ($n = 51$) of all photo-identified whales had sufficiently distinctive dorsal fins or marks on the dorsal flukes or lateral body to permit confident resightings during a single season. Such marks were used for 33% ($n = 135$) of intra-annual resightings ($n = 409$). All whales that were identified by markings on the body during every study year were reconciled to fluke identifications.

3.3 | Abundance, group size, age class, sex

The minimum abundance of humpback whales that used San Francisco Bay during the 3-year period was 61, equal to the number of individuals photographically identified. Group size, based on photo-identification sightings, averaged 2.3 whales, with a maximum of 10 on 21 June 2017. Of the 496 photo-documented sightings of whales, 46% ($n = 230$) were single animals, 25% ($n = 126$) were in pairs, and the rest were in groups of three or more (28%, $n = 140$).

A wide range of age groups used San Francisco Bay. Ages were known for nine whales, based on initial sightings when they were calves (outside San Francisco Bay). The two oldest animals were born in 1993, making them 23 and 24 years old when sighted in San Francisco Bay in 2016 and 2017, respectively. Using the earliest year seen anywhere as a minimum age, the average age of the animals seen in San Francisco Bay was 7 years. Both males and females used San Francisco Bay, with the sex of 12 of the 61 known from either genetic samples collected elsewhere ($n = 9$) or presumed based on exhibiting maternal care for their dependent calves ($n = 3$). Of the 12 whales of known sex, six were female and six were male. Four were known reproductive females, three based solely on their sightings outside San Francisco Bay. Two whales associated with dependent calves were observed in the bay. One whale (CRC-12420) was seen in 2016 and 2017 in small groups of two to six whales and returned on 5 June 2018 accompanied by a calf. On 22 July 2017, another whale (CRC-12560) was sighted in the bay with a calf.

3.4 | Low-latitude winter breeding areas

Almost all 61whales photo-identified in San Francisco Bay had been seen in other feeding areas along the U.S. West Coast; 60 (98%) were sighted at least once in the central California region from Monterey Bay north through the Gulf of the Farallones adjacent to San Francisco Bay, and 21 (34%) were seen in feeding areas further to the north or south. Fluke images also revealed that 48 (79%) of the identified whales using San Francisco Bay had been photographed in Mexico and Central America during the breeding season. Of these, photographic matches confirmed roughly one-third belonged to the endangered Central America DPS (35%, $n = 17$), and the rest belonged to the threatened Mexico DPS. Only one whale was identified from the Hawaii wintering area (a DPS not considered threatened or endangered under the U.S. Endangered Species Act) and that whale had an unusual sighting history including records also off Washington and British Columbia.

3.5 | Site fidelity

Resightings confirmed that photo-identified humpback whales used San Francisco Bay in successive years. Of 61 known whales, 34% ($n = 21$) were interannual visitors: six were present in all 3 years of the study period, and 15 occurred in 2 of 3 years. Of the 17 whales identified in 2016, 12 were re-sighted in 2017 or 2018. Forty whales (66%) were sighted in only a single season. Repeat sightings of known whales were frequent, with 80% ($n = 49$) seen on multiple days. The average number of days an individual whale was sighted was 6.5, with a median of 3 (harmonic mean 2.53). The average number of days between the first and last sightings of identified whales (based on 396 sightings, maximum of one observation per day per whale) showed little variation between years: 2016 = 52 ± 18.1, 2017 = 44 ± 6.5 and 2018 = 42.1 ± 8.6 (mean ± SD). The most frequently sighted whale, CRC-16056, was seen a total of 39 days during the 2017 and 2018 seasons. The most frequently sighted whale in a single season was CRC-17418, seen on 28 days in 2017. The whale sighted on the most successive days, CRC-15032, was recorded on 18 of 24 days beginning 22 May 2018. The maximum time between the first and last sighting was 883 days (2.4 years) for CRC-16154.

3.6 | Distribution

Humpback whale locations, based on photo-documented sightings, were distributed throughout the marine-influenced strait (east to the narrows at the Golden Gate Bridge area) continuing into the more estuarine-influenced central bay (Figure 3). The areal extent of humpback whales recorded visually in the bay was similar to that of the photo-identified whales, with two exceptions: the most northern sighting (Raccoon Strait, 29 April 2017) and the most southern/eastern sighting (off Pier 40, San Francisco, 20 July 2017; Figure 3). The latter location, 11.3 km from the Golden Gate Bridge, was the only humpback whale seen in the south bay (south of the San Francisco-Oakland Bay Bridge). The 2016–2018 locations of all 61 known whales, using a maximum of one observation per day per whale ($n = 396$), were plotted with a Minimum Convex Polygon indicating the whales' spatial footprint within the bay (Figure 3).

3.7 | Habitat use

Humpback whales were not present inside San Francisco Bay throughout the season. Even the most frequently sighted individuals appeared to transit to and from bay habitat in a daily tidally dependent pattern. Whale counts were highest around high tide and

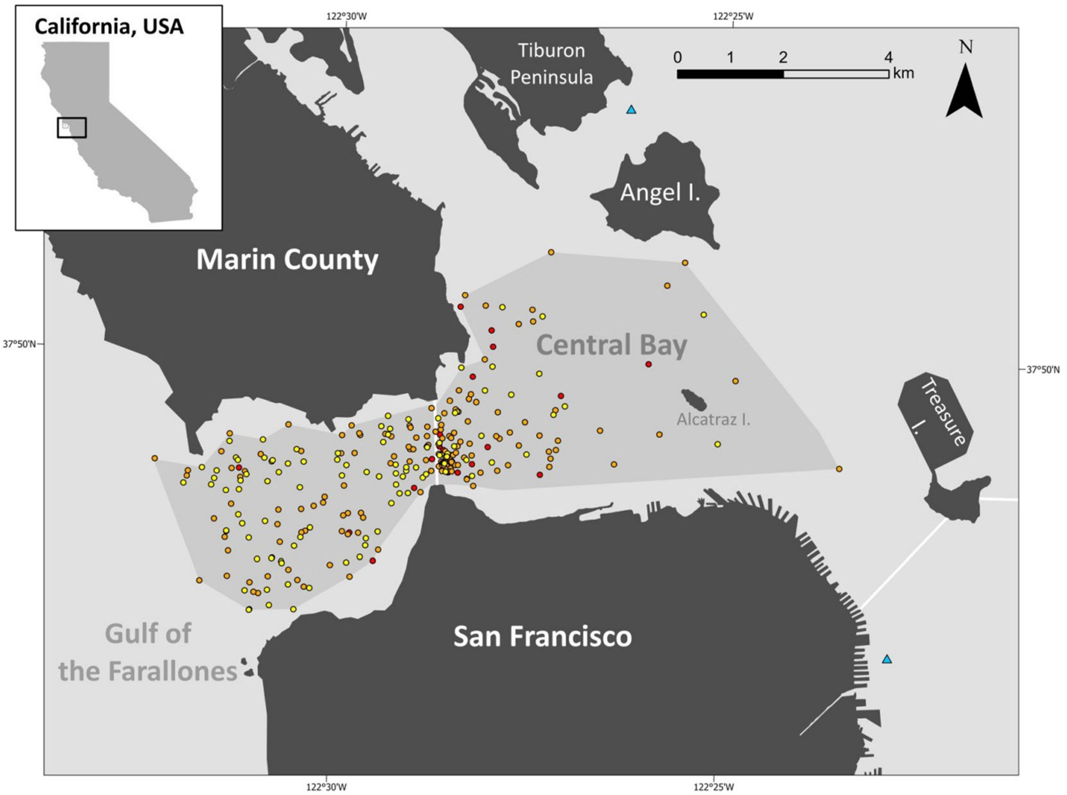

FIGURE 3 San Francisco Bay map with sightings and Minimum Convex Polygon for 61 photo-identified humpback whales ($n = 396$ sightings, maximum one observation/day/whale), plus outlier locations of visual sightings ($n = 2$, blue triangles). Red dots show locations of whales feeding at the surface; orange dots show milling (may include foraging); yellow dots are other behaviours. White lines represent major bridges.

lowest around low tide. Analyses of all 496 observed locations for the 61 known whales showed a significant shift based on tidal state (ANOVA, $F = 16.54$, $P < 0.0001$), with whales present farther west (towards the ocean end of the strait) at low tide and moving east towards the central bay with the flood current and high tide (Figure 4).

3.8 | Foraging behaviour

Predominant behavioural states of photo-identified whales ($n = 396$) included surface lunge feeding (14%, $n = 55$), milling (58%, $n = 228$), travelling (24%, $n = 96$) and other surface-active behaviours including breaching, pectoral fin slapping and tail slapping (2%, $n = 8$). No whales were observed resting (logging quietly at the surface), and behaviour was classified as unknown in 2% ($n = 9$) of observations. In 17 cases of milling, subsurface feeding was presumed based on other cues, such as seabirds following whales and diving on fish as the whales surfaced. Much surface behaviour categorized as milling may be related to foraging at depth (an interpretation supported by tag data). Surface lunge feeding was the only prey engulfment tactic visually observed, with some variation in lateral or vertical lunges. Whales usually foraged singly, but on two occasions a trio of whales in close proximity engaged in simultaneous coordinated lunge feeding. Small schooling fish photographed escaping surface lunge feeding bouts were identified by NOAA Fisheries experts as northern anchovy, the only prey documented.

Humpback whale habitat use in San Francisco Bay (water depth and distance from shore) varied significantly with behavioural state (ANOVA $F_{depth} = 3.27$, $P = 0.02$, $F_{distance} = 10.02$, $P < 0.0001$), with feeding occurring in the deepest water closest to shore. On average, feeding was observed within 500 m of shore at a depth of 57 m. Milling was observed at similar depths farther from shore. Travelling and surface-active behaviours (e.g., breaching and tail slapping) were observed in shallower water farther offshore. Examination of spatial distribution comparing foraging to non-foraging whales showed a focus of foraging activity near the narrows of the Golden Gate (Figure 3). While whale numbers in this area were highest at high tide, sighting locations at low tide showed a tendency for at least some foraging whales to remain in the bay, close to the narrows. Whales not foraging showed a broader distribution and were found farther from shore, particularly at low tide.

3.9 | Whale movements, dive patterns and subsurface feeding behaviour from tag data

Time at depth, diving and lunge feeding at depth for three whales tagged on 23 July 2017 are summarized in Table 2. Identification photographs were obtained for two of the whales, and fluke matches

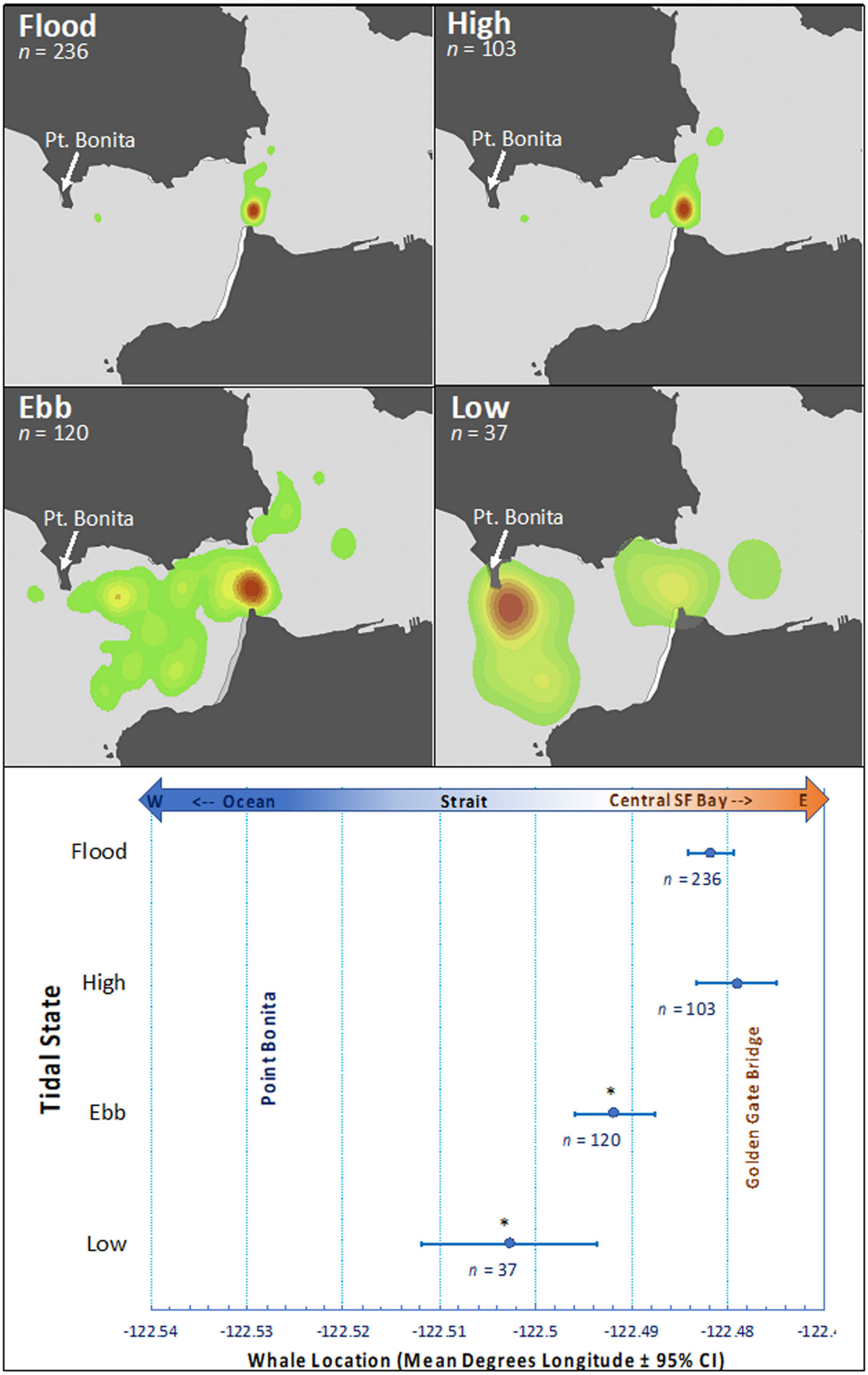

FIGURE 4 Tidal effect on photo-identified whale locations ($n = 496$) in San Francisco Bay. (Top) Kernel density maps of whales at flood, high, ebb and low tides. Dashed white line indicates the Golden Gate Bridge. (Bottom) Whale locations plotted by longitude (mean ± 95% CI) during four portions of the approximate 12-h tidal cycle. ANOVA $F = 16.54$, $P < 0.0001$. * Tukey post hoc.

TABLE 2 Summary of tag deployments and feeding dives for each humpback whale tagged in San Francisco Bay on 23 July 2017.

Tag deployment			Time at depth			Diving					Feeding			
								Duration (min)				Depth (m)		
Tag #	CRC #	Duration (h)	Depth (m) mean ± SD	% at <15 m	% at <30 m	Dives (per h)	Depth (m) mean ± SD	Min	Mean	Max	Lunges (per h)	Min	Mean	Max
11	UnID	0.64	8.2 ± 7.9	74.5%	100.0%	15.6	21.1 ± 5.3	0.9	1.8	3.5	3.1	19	23	27
12	11,696	3.34	15.2 ± 13.2	55.5%	81.3%	12.3	28.5 ± 11.1	0.8	3.2	5.7	4.5	14	28	32
14	17,495	2.37	19.7 ± 13.8	38.0%	65.0%	13.5	32.9 ± 7.8	0.6	3.3	5.7	4.6	27	30	36

confirmed they had spent multiple days in the area where they were tagged. CRC-11696 (Tag 12) was an adult identified 14 times since 2003, with all sightings in the central California region, including confirmed sightings in San Francisco Bay on 19 and 22 July 2017 a few days prior to tag deployment. CRC-17495 (Tag 14) was identified 13 times, including multiple times near the entrance to San Francisco Bay between 15 July and 9 August 2017.

Time at-depth analysis showed the average depth for the three tagged whales was 14.4 m. On average, they occurred in depths <15 m 56% of the time and at depths <30 m 82% of the time. The whales engaged in diving 12.3–15.6 times per hour, with mean dive durations ranging from 1.8 to 3.3 min, reaching a mean maximum depth per dive of 27.5 m (range 21.1–32.9 m; Table 2).

Although no surface feeding was observed, all three tagged whales engaged in subsurface feeding behaviour. All feeding lunges occurred at depths greater than 14 m (range 14–36 m). Bathymetric analysis showed feeding locations occurred at a mean seafloor depth of 55 m (range 23–108 m). Two of the tagged whales, CRC-11696 (Tag 12) and CRC-17495 (Tag 14), were travelling independently at the time they were tagged and fed separately before pairing (Figure 5, bottom). Subsequently, they fed in unison on one dive (their first feeding lunge within 10 s of each other) and remained tightly coupled during dives and surfacing series over the subsequent 30 min, although their feeding lunges (at depths of 30–34 m) did not exhibit a high degree of synchrony.

4 | DISCUSSION

4.1 | Seasonality, sighting rates and abundance of humpback whales in San Francisco Bay

Results verify the seasonal presence of multiple humpback whales in San Francisco Bay, a highly unusual location for the species prior to 2016. This unprecedented influx was not an anomaly as initially presumed but repeated from mid-April to mid-November in 2017 and 2018. Whale numbers varied by year, but intra-annual and interannual site fidelity was confirmed based on sightings of 61 photo-identified whales: 80% used the bay on multiple days (range = 2 to 39), and 34% were re-sighted in subsequent years. Whale abundance and habitat use showed seasonal variation with a higher number of whales sighted, and observed closest to shore, during spring and summer months, and fewer whales, observed farther offshore, in the fall. Counts and locations varied on a daily basis in response to tidal currents, showing a positive correlation with flood currents and high tides when the whales tended to travel east towards the central bay. The observed length of stay for any individual whale was less than a day, although no observations were made at night.

Remarkably, none of the many whales that entered San Francisco Bay over the 3-year study period became lost or travelled to the upper estuary/river system as had previous misoriented humpback whales. Whales travelling into the upper estuary or river in the past were easily sighted and as unusual events were widely reported by

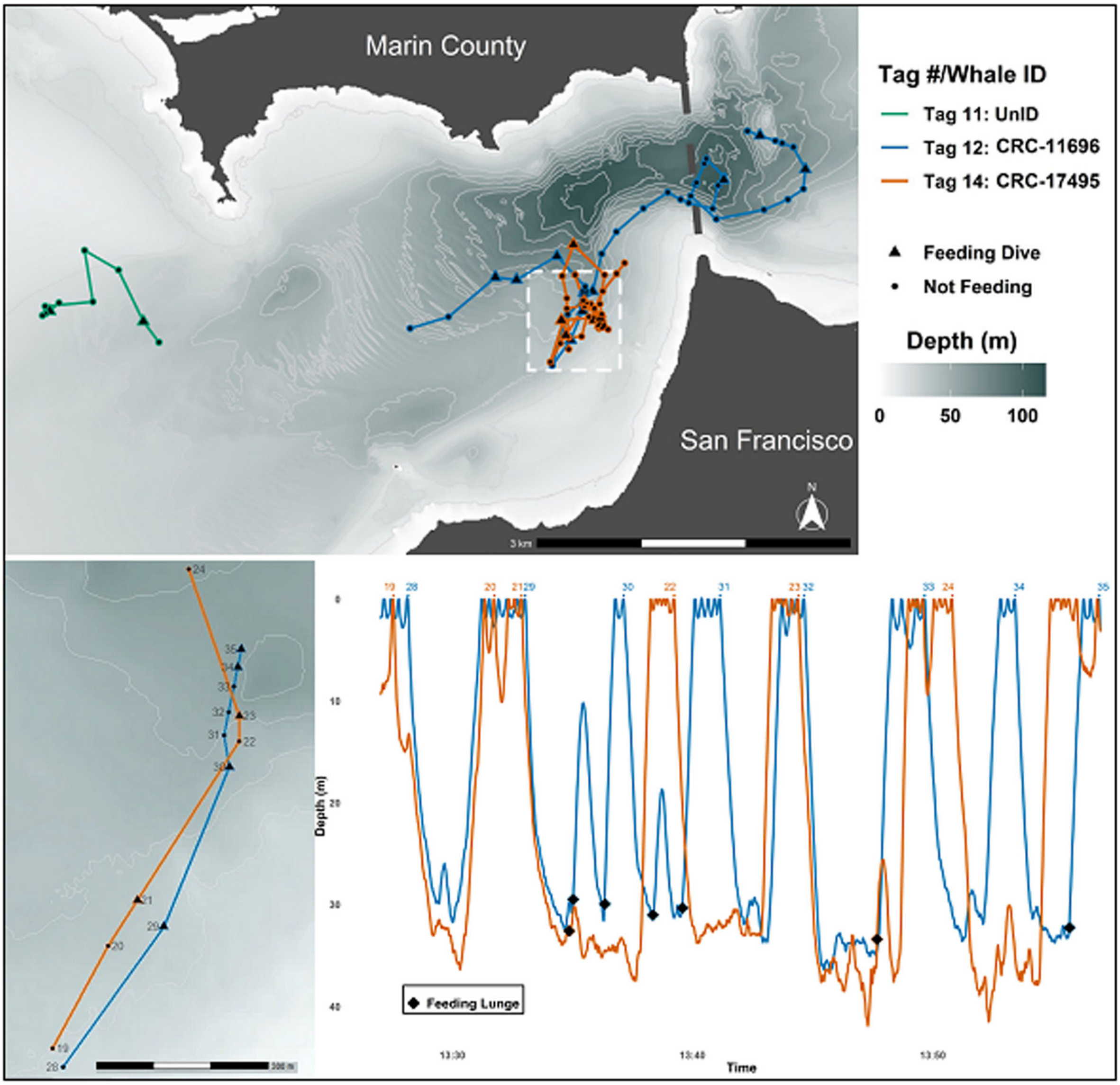

FIGURE 5 Location tracks for three humpback whales (including two photo-identified individuals) tagged in San Francisco Bay on 23 July 2017, with feeding dives indicated by triangles (top). Dive profiles for the two known whales during a portion of their overlapping track line (bottom left) show dive synchrony with feeding lunges at depths of 30–34 m for both whales (bottom right).

the media (Gulland et al., 2008). No whale appeared to suffer adverse health effects such as degraded skin condition from exposure to low salinity water, since the central bay receives marine water inflows from twice daily flood currents.

4.2 | San Francisco Bay habitat use and foraging ecology

The behaviours observed constitute the first documentation of feeding by humpback whales in San Francisco Bay. Lunge feeding was readily observed at the surface and tag dive data provided evidence of subsurface feeding lunges (Figure 5). Dive data provided only a limited picture of whale behaviour on a single day, but it did suggest that at least some of the surface behaviour categorized as milling likely indicates subsurface foraging and active feeding at depth. Surface feeding or milling was recorded for 71% of photo-identified sightings ($n = 283$ of 396 sightings).

Most feeding was seen near the Golden Gate narrows where a submarine slope descends to the deepest part of the bay. Predictable, tidally generated hydrodynamic processes on this gradient may lead to the concentration of zooplankton and fish. Whales engaged in feeding or milling in deep water closer to shore relative to other behavioural states. Frequent sightings near the narrows (Figure 3) contained about half ($n = 138$) of the whales sighted engaged in feeding or milling activity. Foraging whales were more likely than non-foraging whales to remain in this area independent of tidal state.

Two factors may be driving this feeding activity: recovery of humpback whale stocks and a shift in prey distribution. North Pacific humpback whales have increased in abundance following the cessation of commercial whaling (Barlow et al., 2011). Population recovery may be partly responsible for increased sightings of humpback whales in other areas in recent years, noteworthy in New York harbour (Brown et al., 2018), Boston harbour (Annear, 2018), the Salish Sea (Calambokidis et al., 2017) and Queensland, Australia (Noad et al., 2019). However, the Salish Sea and Australia examples are a return to areas occupied prior to the whales' extirpation, in contrast to San Francisco Bay where there is no history of foraging humpback whales.

One reason proposed for the robust recovery rate of depressed humpback populations is their foraging flexibility, specifically their ability to switch prey in response to environmental conditions (Fleming et al., 2015; Rockwood et al., 2020; Wright et al., 2016). The marine waters adjacent to San Francisco Bay are situated in a productive upwelling zone, the California Current Ecosystem, known for its high degree of variability (Ralston et al., 2015). Off California, the diet of humpback whales has been shown to alternate between krill during cool oceanic phases, when upwelling is strong, to schooling fish in times of warmer water with weak upwelling (Fleming et al., 2015). Preceding the influx of humpback whales into San Francisco Bay, California experienced an unusually powerful marine heatwave (Di Lorenzo & Mantua, 2016). Sea surface temperatures in the central California Current Ecosystem were persistently high from 2014–2016, leading to a decline in the availability of krill to which humpback whales responded by moving inshore to forage on fish in 2015–2016 (Calambokidis et al., 2017; Cheeseman et al., 2024; Santora et al., 2020).

Northern anchovy, a small, short-lived planktivorous schooling fish, were prey targeted by whales lunge feeding at the surface. The species is common, at times abundant, in the California Current Ecosystem and San Francisco Bay, where it is an important part of the forage fish community (Kimmerer, 2006; Thayer et al., 2017). Northern anchovy are strongly influenced by climate variability, and during a recent intense marine heatwave that peaked in 2015, their preferred cool-water habitat was compressed towards the coast (MacCall et al., 2016; Santora et al., 2020; Thayer et al., 2017). The total biomass of California's central stock of anchovy grew in 2016, increasing significantly by 2018 (Stierhoff et al., 2019; Zwolinski et al., 2017). An explanation for the sudden appearance of humpback whales in San Francisco Bay in 2016 is that the anchovy concentration there reached the threshold for efficient feeding. Thus, a localized food resource became dense enough to attract the whales (Piatt & Methven, 1992), vital at a time when krill had lost much of its favourable cold-water habitat offshore (Santora et al., 2020). It is plausible that by the time the heatwave abated, these whales had learned to navigate San Francisco Bay as a place to find food and revisited the bay in subsequent years (De Weerdt & Ramos, 2020). Intensive feeding by humpback whales may play a novel role in San Francisco Bay's trophic web through predation and nutrient transfer (Roman & McCarthy, 2010; Surma & Pitcher, 2015).

4.3 | Implications for conservation

The humpback whales using San Francisco Bay are of particular conservation interest because photo-identification matches confirmed most belonged to either the endangered Central America DPS or the threatened Mexico DPS. The most significant threats confronting these whales in their coastal feeding area are entanglement in fishing gear and vessel strikes. Recent shoreward shifts in humpback whale foraging areas due to climate events led to a record number of entanglements along the California coast (Ingman et al., 2021; Payne, 2022; Santora et al., 2020). Ships are a major source of human-caused mortality for humpback whales on the U.S. West Coast (Carretta et al., 2019). Due to a combination of whale feeding aggregations and traffic volume, risk is exceptionally high in the shipping lanes off San Francisco (Redfern et al., 2020; Rockwood et al., 2017). Large commercial vessels transiting to and from multiple ports within the bay include container ships, oil tankers, commuter ferries and sightseeing boats. As the whales follow food resources inshore, they enter a busy, urbanized bay habitat, where adverse interactions with vessels are likely to be exacerbated.

Two areas where humpback whales forage within San Francisco Bay are of special concern. The first is the narrowest section of the 1.6-km-wide Golden Gate strait. Large ship movements here are restricted to inbound and outbound lanes between the towers of the Golden Gate Bridge (1.2 km apart) and have little leeway. These lanes run through the highest densities of whale sightings and areas where whale foraging was found to be most commonly observed during this study (Figure 3). The second area of concern lies 5–6 km due east of the Golden Gate Bridge where the whales overlap with high-speed ferry routes. These commuter ferries are the fastest commercial vessels on the bay, regularly reaching 30 kn (Cope et al., 2020).

Ship strikes could have negative population-level consequences on humpback whales listed as threatened or endangered (Redfern et al., 2020). Fourteen humpback whales were reported struck by vessels between 2013 and 2017 on the U.S. West Coast (Carretta et al., 2019), but due to low detection rates, the actual number of strikes is likely much higher (Laist et al., 2001). Whales entering San Francisco Bay also experience elevated exposure to harassment by recreational boats and personal watercraft. Sub-lethal effects of harassment and human-caused noise include physiological and behavioural changes due to stress (Wright et al., 2007). Anthropogenic disturbances to cetaceans, particularly when repeated or intense (e.g., multiple boats in their vicinity), can lead to avoidance reactions and feeding interruptions (Bejder et al., 2006; Stamation et al., 2010). Although San Francisco Bay's ecosystem has benefitted from restoration efforts, chronic noise from large ships continues to degrade its acoustic habitat (Williams et al., 2014). Humpback whales have been shown to vocalize while foraging (D'Vincent et al., 1985), and acoustic interference from ship-generated noise may reduce the communication space of whales in San Francisco Bay (Clark et al., 2009). Whether the whales are negatively impacted or habituated to anthropogenic noise and 'tune out' the presence of the sound sources in this heavily used urban environment is unknown.

4.4 | Recommendations

Further research is necessary to understand the phenomenon of humpback whale occurrence in San Francisco Bay, particularly due to the risk of ship strike. Priority projects include tracking whales and ships in the bay using a shore-based theodolite and radar system to accurately plot the movements and interactions of whales and vessels. This work could be augmented by the installation of hydrophones providing acoustic data to improve the assessment of ship strike risks and provide background on the soundscape, important for resource management (Cope et al., 2020; Cope et al., 2021; Dransfield et al., 2014). Other research is underway in the adjacent Gulf of the Farallones where a hydrophone was anchored in 2022 capable of identifying humpback whale vocalizations (Baumgartner et al., 2019). This passive acoustic device, part of the 'Whale Safe' program (Benioff Ocean Initiative, 2023), provides a better year-round picture of whale presence near the entrance to San Francisco Bay. Additional passive acoustic monitoring within the bay could yield finer scale information on whale presence within this urbanized estuary.

Increased safeguards for humpback whales inside San Francisco Bay are appropriate and timely. Recently, the Gulf of the Farallones and the strait leading to the bay received federal designation as critical habitat for humpback whales, but it did not include central San Francisco Bay east of the Golden Gate Bridge (U.S. Federal Register, 2021). Additionally, government-sponsored voluntary ship speed reduction programs have been implemented by the local National Marine Sanctuary, but they do not cover San Francisco Bay waters. Sanctuary boundaries should be expanded east towards the bay, as has been proposed (U.S. Federal Register, 2012). Our findings support an extension of these measures that show promise to reduce the potential for lethal collisions (Conn & Silber, 2013; Rockwood et al., 2021). Other efforts should engage the public, as education is lacking for the recreational boating community not accustomed to encountering humpback whales in the bay. Responsible boating practices can reduce harassment and maximize the safety of people who encounter local whales (Williams et al., 2002). This study reports increased use of San Francisco Bay as foraging habitat by endangered and threatened humpback whales. While this recent change indicates both ecological and population recovery, increased whale-vessel overlap within this heavily trafficked estuary warrants further monitoring. This research can shed light on marine resource conservation issues and vessel traffic management in other busy ports around the world where whales confront an increased risk of vessel strikes.

AUTHOR CONTRIBUTIONS

Tim Markowitz: Conceptualization, formal analysis, investigation, writing—review and editing. **William Keener**: Conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft, review and editing. **Marc Webber**: Conceptualization, formal analysis, investigation, methodology, writing—review and editing. **Allison Payne**: Investigation, visualization, writing—review and editing. **Rebekah Lane**: Investigation, visualization, writing—review and editing. **James Fahlbusch**: Data curation, formal analysis, investigation, methodology, software, visualization, writing—review and editing. **John Calambokidis**: Data curation, formal analysis, investigation, methodology, resources, writing—review and editing. All authors approved the submitted version of the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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