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Gray whales (*Eschrichtius robustus*) in San Francisco Bay experience high mortality and have limited affiliation to known foraging groups

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Terrestrial and marine species are exhibiting distributional shifts due to climate change and resource availability. As food webs are impacted, some species have moved into areas of increased human activity, encountering anthropogenic hazards. A coastal marine species that undertakes a long migration between breeding and foraging ranges, the Eastern North Pacific (ENP) population of gray whales (*Eschrichtius robustus*) is especially vulnerable to changes. Subgroups of ENP gray whales, including the Pacific Coast Feeding Group and the (Puget) Sounders, have adapted to exploit alternative feeding grounds as prey availability declines in the Arctic. Novel to known migration phenology, gray whales have been observed seasonally since 2018 in San Francisco Bay (SF Bay), California. We evaluated subgroup identity and mortality of gray whales in SF Bay from 2018–2025 using photo-identification. Data were collected through vessel-based surveys, opportunistic effort, and community submissions. We identified 114 individual whales of which eight were matched to a subgroup, indicating gray whales utilizing SF Bay are not merely a range extension by foraging subgroups. Only four gray whales were resighted within SF Bay between years. Using photographs, 21 individuals were successfully matched to carcasses and a minimum mortality rate of 18% was determined. Blunt and/or sharp force trauma consistent with vessel strike was determined to be the cause of death for 30 of 70 carcasses, and for nine of 11 matched animals where a cause of death was determined. Sounder and PCFG matched whales were more likely to survive SF Bay than ENP individuals, though minimum length of stay did not influence mortality. This work confirms that gray whales entering SF Bay are highly susceptible to vessel strike mortality and highlights a crucial need to identify and implement adaptive management strategies to mitigate injuries and mortality as whales continue to utilize novel habitat.

KEYWORDS
anthropogenic impact, climate change, coastal ecosystem management, gray whale (Eschrichtius robustus), mortality, photo-identification, San Francisco Bay, vessel strike

1 Introduction

As global climates change, distributions of terrestrial and marine species across trophic levels are shifting in response (Dahms and Killen, 2023; Goncharov et al., 2023; MacLean and Beissinger, 2017). This is especially evident for species with ice-associated prey in the Arctic, which is warming faster than mid-latitude habitats (Crain et al., 2009; Lunn et al., 2016). As animals change their distributions, behavior, and migratory routes to take advantage of shifts in available habitat and prey, they may inadvertently increase overlap with human activity (Heemskerk et al., 2020; Meyer-Gutbrod et al., 2018; Santora et al., 2020). Progression of global climate change will continue to exacerbate areas of existing human-animal overlap and cause widespread species distribution shifts, which may result in further negative impacts to already vulnerable populations (Meyer-Gutbrod et al., 2018; Noel et al., 2022; Peters et al., 2022). The nearshore coast is a particularly vulnerable habitat. Negative impacts on coastal species are amplified by the pressure of increased human presence, associated direct mortality from vessel traffic and fisheries entanglement, and the interaction of multiple stressors including overharvesting, habitat loss, pollution, invasive species, disease, acoustic disturbance, freshwater incursion, and sea level rise (Cloern and Jassby, 2012; Crain et al., 2009; Hildebrand et al., 2025; Thrush et al., 2008; Rudebusch et al., 2020). An example of a species affected both by climate change and coastal threat amplification is the North Atlantic right whale (*Eubalaena glacialis*), which quickly shifted its range north following changes in distribution of preferred copepod prey (Greene et al., 2013; Meyer-Gutbrod and Greene, 2018; Meyer-Gutbrod et al., 2018). This range shift was followed by increased vessel strike mortality and entanglement rates for the already endangered species, as individuals entered an area with fewer protective measures in place for them (Baumgartner et al., 2017; Meyer-Gutbrod and Greene, 2018; Pirotta et al., 2025). Despite frequent mitigation efforts, the interaction of threats from human presence and global climate change make coastal ecosystems and the species that rely on them particularly vulnerable.

Eastern North Pacific (ENP) gray whales (*Eschrichtius robustus*) are a near-coastal population that feed primarily on amphipod species in the Arctic. These animals undergo one of the longest migrations of any mammal, a 15, 000-20, 000 km roundtrip, to utilize the warm lagoons in Baja California, Mexico for calving and capitalize on the Arctic's rich resources for feeding (Swartz, 2018; Urbán et al., 2021). This coastal migration phenology and life history strategy exposes them to impacts of climate change and associated overlap with humans. Their long migration is energetically expensive, and individuals rely on fat stores to sustain them through the year, as it is considered unusual for gray whales to feed during migration (Rice and Wolman, 1971; Swartz, 2018). Some individuals have adapted to forage in habitats south of the traditional Arctic feeding grounds, consuming unique prey such as ghost shrimp, herring roe, and other amphipod species (Calambokidis et al., 2019, 2024; Harris et al., 2022; Weitkamp et al., 1992). These individuals belong to a few established foraging subgroups with consistent members, including the Pacific Coast Feeding Group and the North Puget Sound whales or "Sounders". Both of these foraging groups are small (totaling ~212 and <20 individuals, respectively) and individuals using these habitats are known through photo-identification (Calambokidis et al., 2019; Harris et al., 2022; Weitkamp et al., 1992).

In recent years, ENP gray whales have experienced a dramatic decline in body condition and increased mortality following prolonged thermal anomalies in the North Pacific which favored less lipid-rich invertebrate prey (Moore et al., 2022; Raverty et al., 2024; Stewart et al., 2023). From 2019 - 2023, The National Oceanic and Atmospheric Administration (NOAA) declared an unusual mortality event (UME) for the population and recorded a decline of 46% over the event, though more recent estimates suggest a further decline post-UME. In 2025, the population estimate and calf count stand have reached some of the lowest levels on record, declining over 50% since the population's peak in 2016 (Eguchi et al., 2025; Stewart et al., 2023). Ecological regime shifts and Arctic warming contribute to population fluctuations in this species due to their reliance on productive feeding grounds. A previous gray whale UME (1999 - 2000) also followed a marine thermal anomaly, the 1997–1998 El Niño-Southern Oscillation. The cause of mortality was not determined but was assumed to be associated with malnutrition (Eguchi et al., 2025; Gulland et al., 2005; Stewart et al., 2023; Torres et al., 2022). Though the ENP gray whale population declined by an approximately equal proportion over each UME, a marked contrast between the two was that calf numbers have continued to fall following the official closure of the more recent event (Eguchi et al., 2025). Though gray whales have historically exhibited boom-bust cycles driven by Arctic climate fluctuations, the more recent decline and ongoing poor calf productivity appears to be exacerbated by continued climate perturbation (Stewart et al., 2023). Negative impacts of these changing conditions are also reflected in population declines affecting other high latitude species including seabirds and pinnipeds (Barratclough et al., 2023; Divoky et al., 2024; Shaikh et al., 2025; Stewart et al., 2023).

During the 1999–2000 UME, live gray whales entered the SF Bay and seemed to stay for increased lengths of time with a consequent elevation in carcass numbers reported (Gulland et al., 2005). Sightings and strandings became scant again after 2001 and remained so until a marked increase in 2018 (California Academy of Sciences, 2025). Between 2010–2017 as few as four live gray whales were observed each year and only three dead animals were reported; however, boat-based surveys for humpback whales (*Megaptera novaeangliae*) in SF Bay in 2018 observed a marked increase in gray whale sightings (Markowitz et al., 2024; TMMC unpublished data). The increase in gray whale sightings and strandings in SF Bay that season prompted this study, which coincided with the most recent UME declared from 2019 - 2023.

In this study, we developed a photo-identification catalog of gray whales sighted in SF Bay from 2018 - 2023. We utilized this catalog to 1) determine average individual minimum length of stay and interannual resighting rate; 2) compare individuals present in SF Bay to other known foraging subgroups along the west coast of the United States; and 3) compare live individuals to documented mortalities within SF Bay and the adjacent area. We then examined

subgroup identity and minimum length of stay as variables that potentially impact an individual whale's mortality probability.

2 Methods

2.1 Study area

SF Bay (Figure 1) is the largest estuary system on the west coast of the United States with a central section of 115 km^2 connected to the Pacific Ocean via the Golden Gate Strait (Figure 1; Cloern and Jassby, 2012; Feyrer et al., 2015). Whale sightings were categorized as within SF Bay when east of the Golden Gate Bridge (37.8199° N, 122.4783° W) and when sighted within the Golden Gate Strait between the Golden Gate Bridge and Point Bonita (37.8156° N, 122.5295° W). All vessel traffic accessing major ports, including Oakland, Richmond, and San Francisco, must enter and exit through the Golden Gate Strait and traverse the central bay (Cope et al., 2020). Additionally, high-speed ferries, tour vessels, and large numbers of recreational watercraft frequent the entire bay but are most prevalent in the central bay (Rudebusch et al., 2020).

2.2 Data sources

Dedicated vessel-based surveys for photo-identification were initiated in 2023, conducted aboard a 7.6 m (25') rigid-hull inflatable boat. Data collection software *Mysticetus* (Mysticetus, 2025) was used to record effort, conditions such as swell and Beaufort sea state, and collect sighting information including time, GPS location, group size, behavior, and photograph frame numbers (Harwood and Joynt, 2009). Photographs were taken with

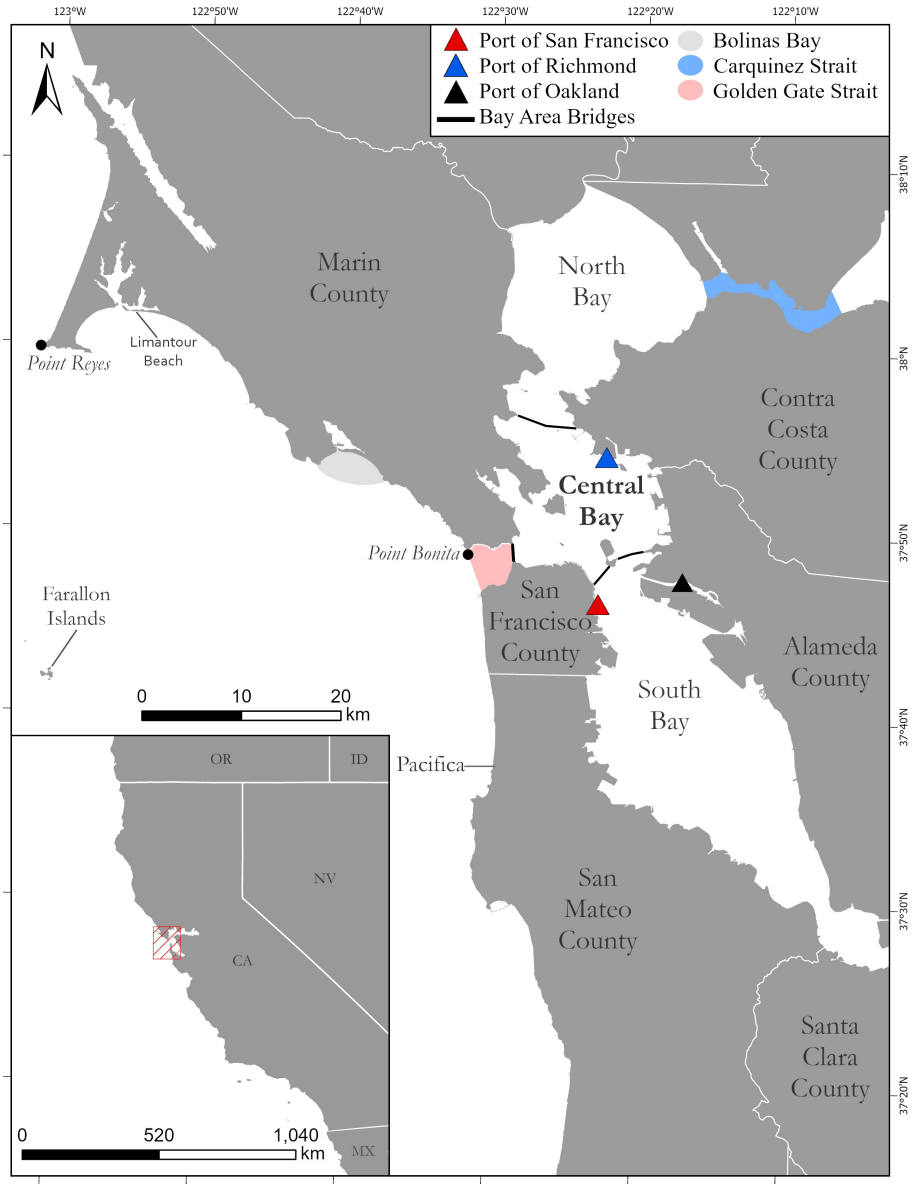

FIGURE 1
Study area map showing sections of San Francisco Bay, nearby water bodies, and coastal landmarks mentioned in the text.

a DSLR camera equipped with a 100-400mm zoom lens. Surveys did not follow a pre-determined route or transect. Instead, surveys utilized the most recent reports of whale sightings to plan a route intended to maximize gray whale encounters for photo-identification purposes (Weller et al., 1999). SF Bay effort was focused from the start of February through the end of June, totaling 54 dedicated cetacean surveys from 2023-2025. An additional 14 offshore surveys during the same time frame included effort in SF Bay (TMMC unpublished data). Most dedicated surveys covered the central section of SF Bay, though occasional efforts were made in the south and north sections of the bay (Figure 1). Survey effort was comparable from 2023 to 2024 but increased in 2025 reflecting an increased volume of gray whale sighting reports (TMMC unpublished data). Reports of sightings were received from community scientists through the TMMC's website form, U.S. Coast Guard's Vessel Traffic Service on marine radio, whale watch vessel operators, personal communication with local residents, and the mobile application WhaleAlert (International Fund for Animal Welfare, 2025).

Effort was not standardized until 2023, so images taken prior to that time were opportunistic. Photographs from community science and opportunistic efforts have proven useful for many studies, particularly with nearshore or coastal marine mammals (Ballance, 2018; Markowitz et al., 2024). TMMC's website public report form was used for the submission of incidental cetacean sightings, including photographs when available. The form included reporter contact information, date, time, and location, as well as an option for community scientists to submit photographs and notes. Photographs received through this source were used with the permission of the submitter and were uploaded to a centralized photograph database. Although not all photographs submitted by members of the public were of sufficient quality for photo-identification, in most cases they enabled species confirmation and aided in decisions for locations to conduct surveys. Additional photographs were collected through opportunistic research surveys (2018 - 2022), shore spotting, during on-water necropsy responses, and from local whale-watch naturalists and captains. All reported sightings with associated photographs were examined by the same process, regardless of source.

All whale necropsies and sampling were conducted under authorization by the National Marine Fisheries Service through Stranding Agreements issued to the California Academy of Sciences (CAS) and TMMC. Necropsy data and information on carcasses was made available through sharing of NOAA Large Whale Necropsy forms maintained by both the CAS Ornithology and Mammalogy department and TMMC's Pathology department. All demographic information and necropsy results were determined by experienced veterinary pathologists and reviewed by NOAA.

2.3 Photo-identification catalog

We compiled a photo-identification catalog utilizing opportunistic whale-watch, and community science photographs from 2018-2022, and images collected during dedicated efforts from 2023-2025. Each sighting was examined and the best photographs of each body area were given a unique alphanumeric code when determined to be a unique individual not previously sighted. Photographs of sufficient quality to allow photo-identification included those with visible distinct features of the individual, primarily the left or right flank, dorsal area, or fluke (Calambokidis et al., 2002a). Photographs of insufficient quality for identification were kept in the database, and the associated sightings were recorded and labeled "indeterminable". Individuals were determined to be unique based on scarring, mottling, depigmentation, and the dorsal hump shape and profile of the "knuckles", dorsal prominences of the peduncular vertebrae (Calambokidis et al., 2002a, 2002; Schwarz et al., 2022; Weller et al., 1999). Yearly catalogs were maintained in which each individual was assigned a year-specific provisional code (example: TMMC-2025-7) before comparing them at the end of the season to the provisional catalog in order to determine interannual resightings and assign new individuals permanent codes (example: TMMC-01-120). In several instances individual whales had fluke photographs only, rendering them insufficient for the primary catalog. These individuals were given a provisional code (example: TMMC-P1-3) and excluded from the primary catalog. The number of days elapsed from an individual's first photographed sighting to its most recent photographed sighting were considered its minimum length of stay. This is considered a minimum given the whale may have been present in SF Bay prior to being photographed and remained after its last known sighting. It is also possible, however, for whales to have exited and re-entered SF Bay between their first and last known sightings.

2.4 Subgroup and carcass comparisons

Once the primary catalog was complete, SF Bay whales were compared to the PCFG subgroup individuals by utilizing the open-source online catalog maintained by Cascadia Research Collective (CRC; Cascadia Research Collective, 2025). Eight individuals (~2%) of this subgroup were not compared in this study due to data-sharing restrictions. CRC also provided images of individuals that belong to the Sounders subgroup, as well as whales photographed passing through the Salish Sea. When an SF Bay whale was matched to any individual with an identification code and sighting history compiled by CRC, data from this study was shared for CRC's records. For purposes of this study, subgroup members of the PCFG, Sounders, and whales seen in the Salish Sea were considered to have a "subgroup identity".

Images of live whales in the primary SF Bay catalog and those with only provisional codes were compared to photographs of gray whale carcasses from the same time period (2018 - 2025). Photo-identification studies of other species have examined carcasses when possible, though cetacean skin sloughs off quickly after death (Koivuniemi et al., 2016; McGuire et al., 2021; Moore et al., 2020; Wells et al., 2015). Carcass photographs were taken by TMMC's pathology team and the CAS Ornithology and Mammalogy team. Carcasses from 2018–2025 were included in this study if the skin (epidermis or dermis) was visible, and if they were located within 60 km north or south of SF Bay (measured from the Golden Gate Bridge). One case that met these criteria was excluded because it was a previously known live whale from Los Angeles Harbor (Alisa

Schulman-Janiger personal communication 5 March 2025) which did not enter SF Bay; another case was excluded because its death date occurred before any live gray whales were photographed in SF Bay.

Carcass images were compared to all whales in the primary catalog that had a last known sighting date prior to carcass discovery. In many instances, insufficient skin remained on the carcass to allow a comparison to potential matches. For each carcass and potential live whale match, we evaluated whether the two would be comparable based on the area of skin present on the carcass and the area of skin photographed on that live individual. Carcasses were labeled "suitable" for matching if they were able to be compared to more than 60% of their potential live whale matches. Additional carcass information was collated for this study including the date first reported, date photographed, recumbency position, and if the carcass was photographed on land or only while floating. To reduce the chance of false matches, carcasses were confirmed to match a live individual when there were three or more matching marks on the same body area (Figure 2). A whale's "mortality window" was calculated as the number of days from the most recent live sighting date to the day before the initial carcass report. This time span includes the most recent sighting date to account for the possibility that a whale died the same day it was seen alive. It does not include the carcass report date, due to the fact that a whale takes time to bloat and refloat after death, so found carcasses are unlikely to have died on the day they are reported (Moore et al., 2020).

2.5 Analysis

All statistical analyses were conducted in R (R Studio Version 2025.05.1 + 513). To assess whether live whales' minimum lengths of stay differed among years with standardized effort (2023, 2024, and 2025), we used a linear mixed-effects model fitted with a Gaussian error distribution using the lme4 package in R (Bates et al., 2015). Year was included as a fixed effect and individual whale code as a random intercept to account for repeated observations of the same individuals across years. *Post-hoc* tests between years were conducted after a significant year effect. Due to limited sample size, Fisher's exact tests were used to determine if there were significant differences in age class or sex for the overall dataset and matched deceased whales between UME years (2019-2023) and non-UME years (2018, 2024-2025).

A multinomial mixed-effects logistic regression model was run using the package mclogit (Elff, 2022), to assess the influence of minimum length of stay and subgroup identity on mortality. Year was included as a random effect in the model to account for effort differences between years and potential data loss from the COVID-19 pandemic. Mortality was not treated as a binomial response, but instead a response variable with the following three potential outcomes: yes, no, or unknown. Mortality was only selected as no for individuals that were photographed outside of SF Bay after their last known sighting within SF Bay. Whales were considered to have an unknown fate if they were not resighted in or outside of SF Bay after their last known sighting nor matched to any carcass.

3 Results

3.1 Photo-identification catalog

From 2018-2025, a total of 114 gray whales had photographs of sufficient quality to be determined as unique individuals and given

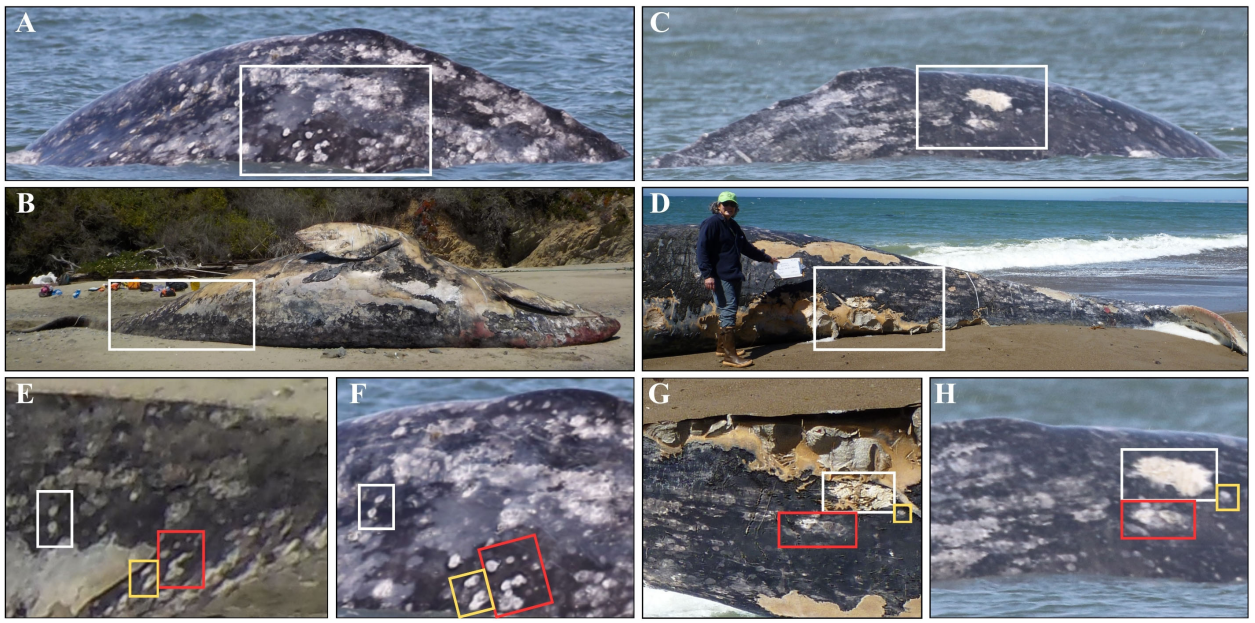

FIGURE 2
Carcass matching process using three marks. Images **(A)** (by R. Lane) and **(C)** (by J. Slaathaug) show the full area of skin visible on two live whales, and images **(B)** (TMMC) and **(D)** (CAS) show the skin visible on the respective carcasses, with the area of interest outlined in white. Images **(E–H)** show the area of interest zoomed in and rotated to match orientation. The three matching marks are outlined in colored boxes, white yellow and red.

identification codes for the primary catalog. Three individuals remain in the provisional catalog because their flukes were the only body areas clearly photographed, one in 2021, one in 2022, and one in 2025. The greatest number of new individuals were added to the catalog in 2025 (n=35). Across all years, only four individuals were interannually resighted in SF Bay (3.5%, Table 1). These individuals were all resighted in consecutive years except for one (TMMC-1-11). Only one individual was sighted in more than two years, and it was photographed within SF Bay yearly from 2022 to 2025 (TMMC-1-05). Individual minimum length of stay varied annually (Figure 3), with 2025 having the longest average stays of the comparable years 2023-2025. The longest minimum length of stay recorded was 75 days in 2023, followed by 67 days in 2025 and 22 days in 2024. The lowest minimum length of stay was one day, present in all years (Figure 3). The average minimum length of stay was 27.6 days for 2023 (n=17), 5 days for 2024 (n=6), and 24.2 days for 2025 (n=36). When removing the outliers of 75 days in 2023 and 22 days in 2024, the average narrowed to within 0.5 days for 2023 and 2025 at 24.7 and 24.2 days, respectively, and lowered to just 1.6 days for 2024. It is worthwhile to remove the outlier of 75 days for

TABLE 1 Gray whales photographed by year in SF Bay.

Year	Total individuals	PCFG	Sounders	Salish sea	Resighted
2018	6	–	–	1	–
2019	23	–	–	2	–
2020	7	–	–	2	1
2021	14	–	–	1	1
2022	11	2	–	–	–
2023	17	–	–	–	2
2024	6	–	–	1	1
2025	36	–	1	–	1

Number of total individual whales, number of the total who were known members of the Pacific Coast Feeding Group (PCFG), number of the total who were known individuals of the north Puget Sound whales (Sounders), number of the total who whales that were photographed in the Salish Sea one year but are not considered Sounders, and number of individuals within that year who had been sighted in SF Bay in a prior year.

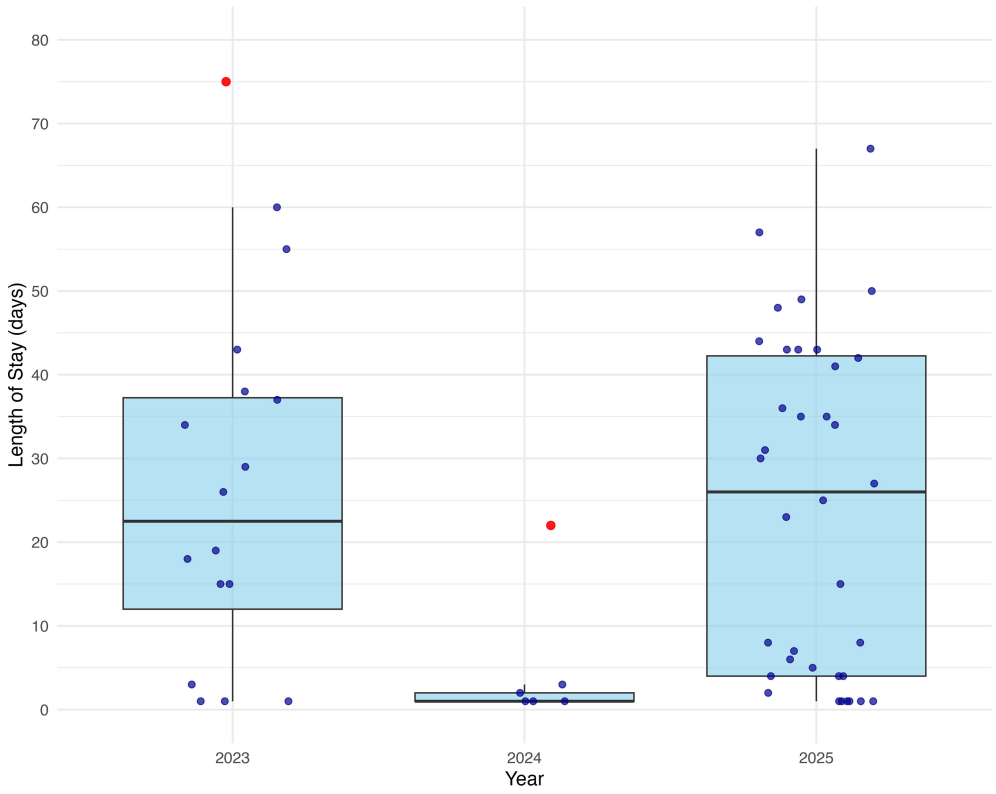

FIGURE 3
Minimum length of stay (days) for individual gray whales observed in San Francisco Bay across 2023–2025. Each point represents one individual's duration between first and last sighting within the respective year. Boxplots indicate the median, interquartile range, and outliers. Red points represent statistical outliers beyond 1.5× the interquartile range.

this comparison since that individual's mobility may have been limited by an injury, as detailed further in the discussion.

3.2 Subgroup identity

A total of 503 whales from the PCFG, the Sounders, and the Salish Sea were compared to the primary catalog of 114 SF Bay individuals and the provisional catalog of three flukes (58, 851 whale to whale comparisons). Only 7% of whales photographed in SF Bay were members of a subgroup (n=8). Of the matches to external catalogs, the majority (n=5) were one-time visitors to the Salish Sea (Table 1). Notably, two of four whales resighted in SF Bay interannually were matched to one-time visitors of the Salish Sea.

Several individuals photographed in SF Bay (n=7) were also photographed in other local coastal areas in Northern California such as Pacifica, the Farallon Islands, or coastally north of SF Bay (including in Bolinas Bay and off Limantour beach; Figure 1). Two individuals seen in SF Bay, TMMC-1–05 and TMMC-1-06, were documented in Pacifica foraging on northern anchovies in June 2022 and photographed in SF Bay multiple times within the season, both before and after foraging in Pacifica (Webber et al., 2024). This confirms whales may enter and exit SF Bay multiple times within one year and are not always continuously resident in the bay from their first to last sighting.

3.3 Mortality

From 2018 - 2025, images from a total of 70 gray whale carcasses were examined, but only 45 had adequate skin remaining to compare to more than 60% their potential live whale matches. Of those with suitable skin, 21 were matched (46.7%). Out of 114 individuals in the primary catalog of SF Bay, 20 were matched to carcasses and an additional carcass was matched to the provisional catalog (18.2%). This is the minimum mortality rate of our live whale catalog, but it is likely that there are additional unconfirmed deaths; whales with unknown fate may represent additional potential mortality. Thirteen of the matched carcasses were found inside SF Bay, and the matched carcasses outside SF Bay were primarily located to the north (Supplementary Figure 1). Fourteen total whales were known to survive their time in SF Bay, and two individuals survived multiple years. All years except for 2021 had at least one instance of a surviving individual, with one in 2018, two in 2019, two in 2020, five in 2022, three in 2023, four in 2024, and one in 2025 (Figure 4).

The 70 deceased whales in this study did not significantly differ by sex (29 male, 38 female, three unknown) and were dominated by adult (n=42) and subadult (n=17) age classes as estimated by total length (Raverty et al., 2024; Rice and Wolman, 1971). Few dead calves were encountered during the study timeframe (n=3) and only one was examined in this study. One was excluded because it died prior to any photographs of live whales in the catalog, and the other was outside of the study's geographical range. As a subset of the total carcasses examined in this study, the 21 matched carcasses were composed of 14 males, six females, and one unknown sex, skewing opposite of the overall stranding trend. Two age classes were found among the 21 matched carcasses: adult (n=12) and subadult (n=9). Among the 21 matched, the cause of death could not be determined for 10 individuals due to lack of internal

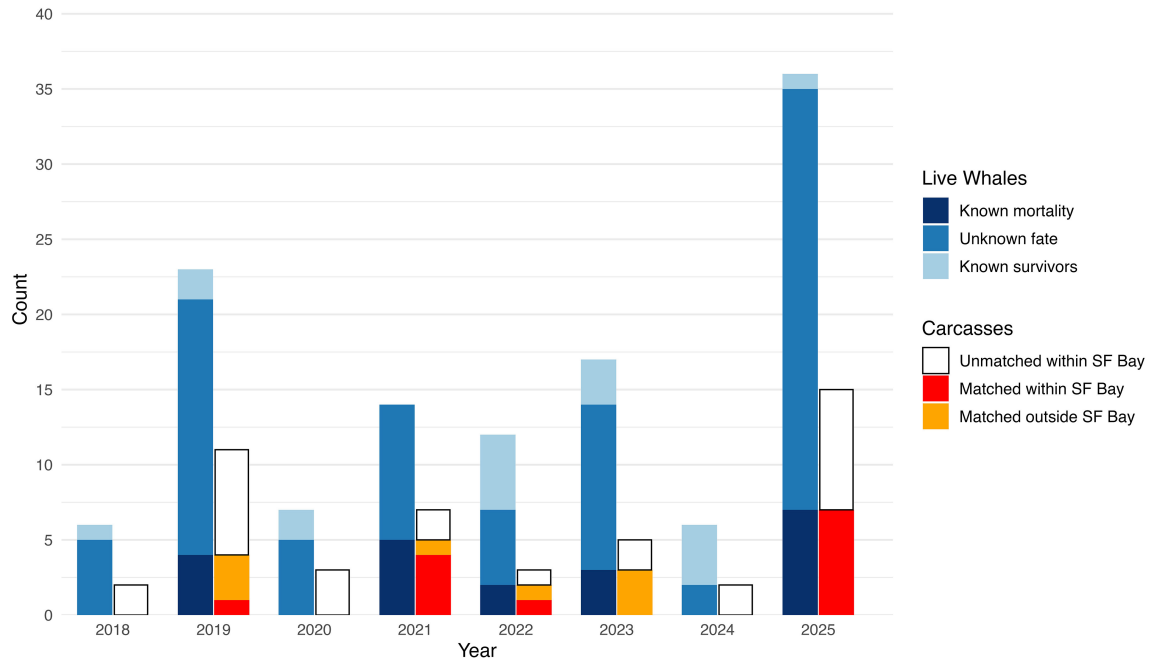

FIGURE 4
Annual counts of photo-identified live gray whales in SF Bay, compared with carcasses. Whales sighted afterwards outside of SF Bay are considered to have survived, shown here in light blue; whales with unknown fate are shown in blue and whales matched to carcasses are shown in dark blue. Carcasses recovered within SF Bay that were not matched to a live individual are shown in white; these represent potential additional mortality from the live whales with unknown fates. SF Bay carcasses successfully matched to a live whale are in red and carcasses found outside SF Bay that were matched to a live whale are in orange.

examination, recumbency position, or state of decomposition. Of the 11 individuals that had a determined or probable cause of death, most were blunt and/or sharp force trauma most likely due to vessel strikes (n=9), and the remaining were malnutrition (n=2). There were additional cases of vessel strike trauma, malnutrition, and entanglement-related mortality in the unmatched carcasses included in this study, but the majority had an undetermined cause of death, consistent with range-wide UME findings (Raverty et al., 2024).

The time elapsed between the last known live sighting and a carcass report (referred to as a "mortality window") ranged from two to 44 days, averaging 12.05 ± 2.28 days (Supplementary Table 1). The number of live observations of a whale before its death ranged from one to 11 unique days (average 3.3 days), and the minimum length of stay for individuals matched ranged from one to 75 days (average 15.86 days). Year had a marginally significant effect on minimum length of stay ($F_{2,\ 56} = 3.00$, $p = 0.058$). Mean minimum length of stay was significantly shorter in 2024 compared to 2023 ($\beta = -22.65 \pm 9.41$ SE, $t_{56} = -2.41$, $p = 0.020$), while minimum length of stay did not differ significantly between 2023 and 2025 ($\beta = -3.43 \pm 5.83$ SE, $t_{56} = -0.59$, $p = 0.56$).

The multinomial mixed-effects logistic regression revealed that subgroup was a significant predictor of mortality outcome. Specifically, individuals belonging to a subgroup (subgroup = Y) were significantly less likely to be classified as unknown (UNK) or dead (Y) compared to not dead (N) (UNK vs N: $\beta = -4.23 \pm 1.13$ SE, $z = -3.74$, $p < 0.001$; Y vs N: $\beta = -2.88 \pm 1.15$ SE, $z = -2.50$, $p = 0.0125$). Minimum length of stay was not a significant predictor in either mortality comparison ($p = 0.62$-0.74). Random effects by year showed negligible variance ($\sigma^2 \approx 0$), indicating minimal interannual variability in mortality outcomes. The model converged successfully after four Fisher scoring iterations (residual deviance = 180.3; n = 121 observations across eight years). Age and sex class of deceased individuals did not differ significantly between UME and non-UME years (Fisher's exact test, $p > 0.05$) for both the full carcass dataset and the subset matched to live whales.

4 Discussion

4.1 Photo-identification

We identified 114 gray whales in SF Bay using images of their flanks and an additional three individuals with fluke photos not associated with flanks. The number of individuals peaked in 2025 (n=36) with only one returning individual, followed by 2019 (n=23), notable due to the absence of standardized survey effort during that year. The fewest individuals were recorded in 2024 (n=6) and 2018 (n=6), comparable to 2020 (n=7), when opportunistic surveys and whale-watch reporting decreased due to the COVID-19 pandemic lockdown. The low resighting rate (3.5%) suggests that while a few whales may be returning to the bay yearly, most are not. By comparison, interannual resighting rates for the PCFG subgroup members are mostly above 50%, though it varies across the range (Calambokidis et al., 2017; Scordino et al., 2017). SF Bay survey coverage prior to 2023 was inconsistent, likely yielding minimum estimates of whales present. The apparent increase in individuals during 2023 and 2025 could reflect both improved survey effort and increase in overall presence, as heightened survey activity followed a spike in unsolicited community reports. The 2019 peak coincided with a rise in gray whale strandings across the migratory corridor (Raverty et al., 2024). This pattern supports the possibility that SF Bay use represents a conditional strategy, a habitat utilized more during a time of low resource availability on historic feeding grounds (Gross and Repka, 1998; Street et al., 2016).

Minimum length of stay varied significantly from 2023 to 2024, but did not vary from 2023 to 2025. It is important to note, however, that the 2024 sample size (n=6) was lower than in 2023 (n=17) or 2025 (n=36). Annual differences in individual counts (Table 1) and minimum length of stay between years (Figure 3) underscore the need to investigate potential drivers of gray whale habitat use in SF Bay. In years with a longer average minimum length of stay, there were still several individuals who were only photographed a single day in that season. This finding underscores individual variation in habitat use as seen in other areas (Hildebrand et al., 2025). Annual shifts in minimum length of stay may reflect environmental variation, prey availability, or nutritional state (Barlow et al., 2024; Bierlich et al., 2025; Calambokidis et al., 2024; Moore et al., 2022). In the ENP population, nutritionally stressed gray whales have been observed to enter and extend their stay in nearshore alternative foraging habitats such as Puget Sound, prompting recommendations for expanding Biologically Important Areas (Calambokidis et al., 2024). Body condition may be a factor influencing how long whales decide to remain in SF Bay to take advantage of local feeding opportunities or use the bay as a migratory stopover (Anderson et al., 2019; Soledade Lemos et al., 2020). Despite annual variation, our catalog reveals that multiple individuals were sighted seasonally in SF Bay since 2018. Further investigation into the behavior and body condition of individuals during their time in SF Bay could increase our understanding of drivers affecting annual variation in use of the bay.

4.2 Subgroup identity

The majority of whales in our live catalog did not have an established subgroup identity (93%, $n = 115$). The low match rate suggests that the whales entering SF Bay represent a new development in the migration phenology of the species or an emerging foraging subgroup. We hypothesize that these individuals, "Bay Grays", are seeking out new resources in response to changing environmental conditions (Pailthorp, 2021; Roberts et al., 2025; van Weelden et al., 2021). If prey availability and quality continue to decline in the Arctic, further adaptive foraging behavior along the migratory corridor is likely (Moore et al., 2022; Stewart et al., 2023; Webber et al., 2024). Gray whales can be flexible foragers, which may prove advantageous as climate change causes resource availability shifts (Hildebrand et al., 2021; Stewart et al., 2025; Webber et al., 2024). Other instances of atypical gray whale presence have been documented, including one gray whale observed opportunistically foraging in the North Atlantic after traveling from waters near Miami, Florida, and another

observed in Hawaiian waters (Baird et al., 2022; O'Brien et al., 2025). Local reports of foraging behavior along the northern California coastline (Mendocino and Sonoma counties) in 2016 and 2019 coincide with the timing of our observations of gray whales in SF Bay and along the Marin coastline, north of SF Bay (S. and T. Mercer personal communication 8 Oct 2025). Gray whales have been documented migrating by the Farallon Islands regularly, but occasionally appearing to remain resident throughout the summer and early fall (Pyle and Gilbert, 1996). We found no connection to the number or prevalence of "summering" gray whales at the Farallon Islands and the number of gray whales entering SF Bay each year of this study, though additional analysis and identification in future studies will prove critical to understanding the use of that habitat. Additional instances of foraging behavior in Pacifica after the anchovy influx of 2022 have occasionally been documented (Webber et al., 2024). Gray whale use of SF Bay, as well as the recent influx of humpback whales into the bay (Markowitz et al., 2024), may thus represent additional examples of an ongoing response by large whales to rapid environmental change. Future analysis of stomach content samples collected from stranded SF Bay whales may shed light on whether the bay is a feeding ground for these animals.

Whales with a subgroup identity were more likely to be resighted after occurring in SF Bay, due to their greater overlap with areas of consistent survey and photo-identification effort (Calambokidis et al., 2017; Lagerquist et al., 2019). Mortality and range assessments would be further improved by integrating additional datasets, such as photo-identification catalogs from the Baja lagoons (Gray Whale Research in Mexico, 2025). Expanding analyses with a larger dataset and employing open-source, AI-assisted photo-identification platforms (e.g., Happywhale, Flukebook) could enable comprehensive tracking across the full migratory range, potentially providing additional context or example of distribution shifts and identifying additional areas of high mortality (Blount et al., 2022; Cheeseman et al., 2022; Maglietta et al., 2022).

4.3 Mortality

We matched 20 deceased gray whales to our primary live photo-identification catalog, and one additional carcass to a fluke-only individual. This represents, to our knowledge, the most successful effort to link live gray whales without artificial marks or tags to carcasses (Koivuniemi et al., 2016; McGuire et al., 2021; Wells et al., 2015). Necropsy response efforts were substantially expanded during the 2019–2023 UME compared to the 1999–2000 UME due to an increase in personnel and resources (Raverty et al., 2024). No significant difference was found in age class or sex of stranded animals between UME and non-UME years, consistent with range-wide research which included some of the carcasses evaluated in our study (Raverty et al., 2024). Most stranded individuals were adults or subadults, and no calves or juveniles were matched to carcasses. The only calf stranding within SF Bay during the study period coincided with an out-of-season sighting of a known presumed adult, though the carcass flanks could not be adequately compared given that it was floating in ventral recumbency. The discovery of the calf carcass in Carquinez Strait and the sighting of the presumed adult in the north bay were a day apart in November 2023. The live individual, TMMC-1-57, was photographed with a sub-lethal injury consistent with vessel interaction that was not present during its prior sighting. In addition to these out-of-season sightings, two sightings of unique individuals occurred after July, in August 2021 and December 2024, both photographed less than 0.5 km from the Golden Gate Bridge.

We report a minimum mortality rate of 18.2% for our live catalog. Although the known mortality rate is relatively high, it is likely underestimated. Cetacean carcasses are known to sink, and the buoyancy of a carcass depends on many factors including but not limited to nutritional condition of the animal, depth, salinity, temperature, and position in the water column when death occurred (Moore et al., 2020; Wells et al., 2015; Williams et al., 2011). Additionally, our matching technique utilizing three different unique marks to reduce the chance of false matches removed several potential matches that had only one or two marks but were unable to be confirmed with a third. The hypothesis that there may be additional carcasses that were live cataloged whales is supported by data from 2024, when two carcasses were unmatched and only two whales had an unknown fate (Figure 4). In years prior to dedicated photo-identification efforts, however, there was a greater probability that whales entering the bay were not photographed before they died.

Eight of the matched carcasses (38.1%) were found outside of SF Bay ranging from less than 1 km from the Golden Gate Bridge to 59 km (Supplementary Figure 1). Semi-diurnal tidal currents in SF Bay are strong (up to 3.4 knots) in the central bay and Golden Gate Strait, providing a mechanism whereby a whale that died in the bay could float out (Figure 5; Cloern and Jassby, 2012). This has been observed in several cases, though the floating carcass could not always be matched later to a beached carcass due to recumbency change, degradation or loss of skin, or lack of adequate photographs. SF Bay's heavy vessel traffic, urban shoreline, and multiple ways to report sightings likely increased our likelihood of finding gray whale carcasses and obtaining photographs while skin was still present post-mortem.

Of the 70 dead whales included in this study, 30 had evidence of blunt or sharp force trauma consistent with pre-mortem vessel strike. Forty-five carcasses in this study had full internal necropsies performed, and 27 of those had evidence of pre-mortem trauma consistent with suspect or probable vessel strike as the cause of death. In a range-wide review of gray whale UME necropsies from 2018-2021, seven out of 11 deaths by vessel strike took place in California, which is substantially more than any other state included in the study (Raverty et al., 2024). Typical challenges such as stranding location, recumbency position, and state of decomposition resulted in only 11 out of 21 matches being assigned a determined or probable cause of death. Of those with an assigned cause of death, nine were probable or suspected vessel strikes - a remarkably high proportion, even taking into account the limited sample size.

Several individuals identified in the live whale catalog had evidence of sub-lethal vessel interactions (Figure 6, Supplementary Figure 2). Two deceased individuals were photographed with sub-

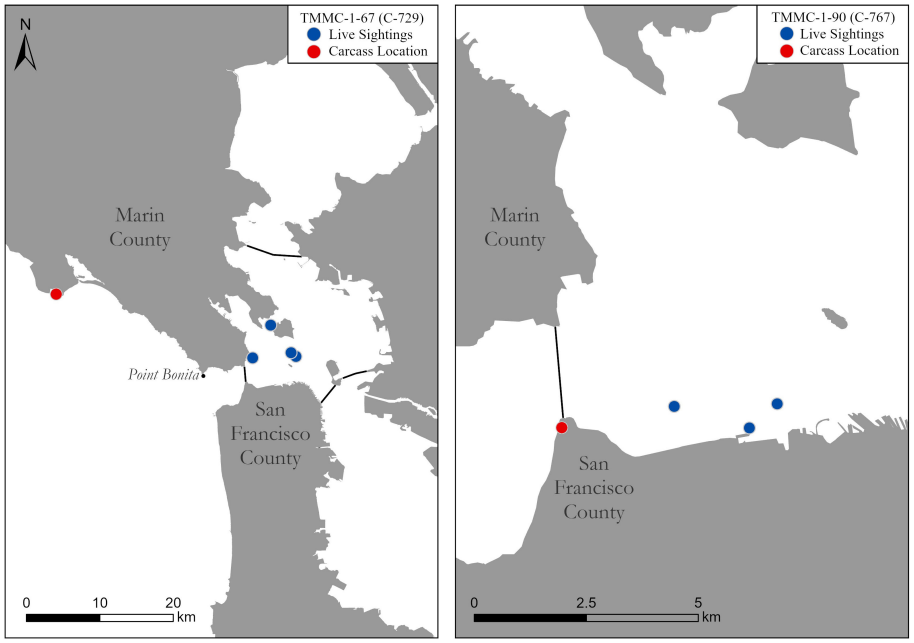

FIGURE 5
Two examples of carcasses matched to the live whale catalog with short "mortality windows." A carcass found outside SF Bay in 2023 (left, four-day mortality window) and inside SF Bay in 2025 (right, two-day mortality window).

lethal injuries prior to their deaths. In one case, a sub-lethal vessel strike may have caused a whale to remain in SF Bay (75 days) by limiting its mobility. This individual, TMMC-1-06, was initially matched to its carcass by the wound shape and confirmed by comparing marks on the skin remaining on the underside of its left flipper (Figure 6). Necropsy revealed that this individual had been the victim of an initial vessel strike across its dorsal flank, perpendicular to the spine, and later succumbed to a second pre-mortem vessel strike, as indicated by hemorrhaging and multiple fractures of its ribs, skull, and vertebrae (See Supplementary Material for details about this animal).

The low interannual resighting rate may partially reflect this high mortality, suggesting that some whales using SF Bay do not survive to return. This finding further supports that some whales with an unknown fate may have died in SF Bay and not been matched. Although the ENP gray whale population is not currently listed as endangered or threatened, it has declined by 52% since 2016 (Eguchi et al., 2025). Determined causes of death during the

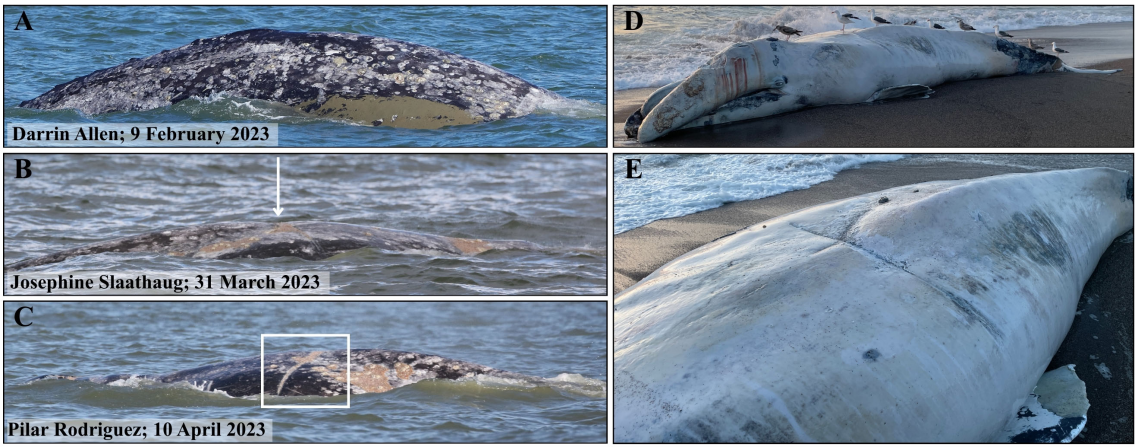

FIGURE 6
Gray whale pre-mortem injury. TMMC-1–06 in 2023 from initial sighting **(A)** to carcass **(D, E)**. **(A)** Silt or mud evident on the flank during the first SF Bay observation taken opportunistically. **(B)** First evidence of the injury on the flank indicated with a white arrow, and associated accumulation of epibiota. **(C)** View of the injury from the left flank, shown in the white box. **(D, E)** Carcass on Point Reyes National Seashore North Beach. The epidermis is missing due to decomposition but the linear indentation in the dermis over the caudal-dorsal thorax is evident. Taken 7 May 2023 by Matthew Enderle.

2019–2023 UME were primarily malnutrition (26%) and vessel strike (18%), though a cause of death could not be determined for nearly half of necropsied individuals (46%). A common denominator for all examined whales was suboptimal body condition (Raverty et al., 2024). Poor body condition during a UME may additionally impact whales' probability of vessel interaction, and should be investigated further. In this study, some necropsies were not performed due to resource shortages, lack of sites to safely tow and land carcasses, and in some cases the challenge of obtaining landowner permission to conduct a necropsy. Towing a floating carcass from the water for a necropsy likely improves the chances of matching by revealing more of the skin. Enhanced support for necropsy efforts and towing would greatly aid our understanding of sources and extent of mortality within the study area. The high prevalence of vessel interactions in SF Bay and the surrounding area could be mitigated by implementing adaptive management strategies that account for varied seasonal whale presence and distribution, such as dynamic speed restrictions, the use of onboard observers, and/or ferry route changes (Flynn and Calambokidis, 2019; Laist et al., 2014; Pirotta et al., 2025; Redfern et al., 2019; Reeves, 2022).

4.4 Predictors of mortality

We evaluated minimum length of stay and subgroup identity as predictors of mortality. Subgroup identity significantly influenced whether whales had unknown mortality or survived. This result, however, may be conflated by detection bias since subgroup whales had a small sample size (n=8) and were observed by other research groups, thus less likely to have unknown mortality classification. Additional future matching efforts in SF Bay and between subgroups could further clarify the significance. A potential explanation for differing mortality rates may be that subgroup whales have learned to reduce their risks based on prior experiences (Lima and Dill, 1990). Individuals who have ranged in areas with intense human activity may develop behaviors that help them avoid vessel interactions. The PCFG has been shown to have a high exposure level to traffic including ferries as well as commercial ships, varying among individuals based on their habitat use and site fidelity (Hildebrand et al., 2025; Lagerquist et al., 2019; Silber et al., 2021).

Surprisingly, we found no association between mortality and minimum length of stay. This is supported by our observations of some individuals entering and exiting the bay within the same season, perhaps alleviating their vessel strike risk as they are outside congested bay waters. To enter and exit the bay, however, they must pass through the Golden Gate Strait, which is a vessel traffic bottleneck (Markowitz et al., 2024; Rudebusch et al., 2020). Individual gray whales have been shown to use habitat in different ways, which is likely reflected here by some individuals remaining in the bay from their first to last sighting while others exit the bay for various periods (Hildebrand et al., 2025). Minimum length of stay may not be a metric sufficiently sensitive to capture these whale-to-whale differences in habitat use and the resulting differences in stress exposure or mortality risk. Further evaluation of the spatial ecology of individual whales in our study area may reveal different preferences and variation in corresponding risk.

5 Conclusion

As a coastal species that migrates thousands of kilometers to feed in the Arctic, gray whales are especially susceptible to overlapping threats which interact and magnify the potential for harm (Crain et al., 2009; Silber et al., 2021; Stimmelmayr and Gulland, 2020; Swartz, 2018). In response to climate change, gray whales have been observed exploiting new habitats, including SF Bay, resulting in increased overlap with human activities. This study reveals that a minimum of 114 unique individuals have utilized SF Bay as habitat since 2018, with only eight belonging to existing foraging subgroups, suggesting that additional individuals in the larger population are beginning to utilize this new habitat. The prevalence of vessel strike mortality and additional evidence of sub-lethal vessel interactions emphasize the crucial need for research and management to prioritize understanding and mitigating vessel interactions in SF Bay. Adaptive management strategies such as dynamic or presence-induced slow speed zones can be valuable in reducing vessel strike mortality (Allen and Garmestani, 2015; Holling et al., 1978; Laist et al., 2014; Reeves, 2022). Protecting this population along its migratory corridor as it contends with a changing environment will be critical for the species' ability to rebound from its current decline.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Figshare: https://doi.org/10.6084/m9.figshare.30643466.

Ethics statement

The animal study was approved by The Marine Mammal Center's Research and Institutional Animal Care and Use Committees. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

JS: Project administration, Validation, Investigation, Conceptualization, Data curation, Writing – review & editing, Methodology, Funding acquisition, Formal analysis, Writing – original draft, Software, Visualization, Resources. RL: Supervision, Resources, Conceptualization, Validation, Investigation, Data curation, Writing – review & editing, Funding acquisition, Writing – original draft, Formal analysis, Project administration, Visualization. WK: Funding acquisition, Resources, Data curation, Validation, Formal analysis, Conceptualization, Writing – review & editing, Supervision. AP: Supervision, Resources, Formal analysis,

Writing – review & editing, Investigation, Project administration, Methodology, Data curation, Validation, Conceptualization. MF: Resources, Writing – review & editing, Investigation, Validation, Supervision, Conceptualization. MW: Conceptualization, Validation, Supervision, Resources, Writing – review & editing, Funding acquisition, Investigation. AG: Data curation, Visualization, Validation, Writing – original draft, Writing – review & editing, Investigation. AW: Investigation, Validation, Writing – review & editing, Visualization, Data curation, Writing – original draft. JO: Writing – review & editing, Project administration, Supervision, Funding acquisition, Resources. PD: Investigation, Writing – review & editing, Supervision, Validation, Resources, Conceptualization, Project administration. JC: Writing – review & editing, Conceptualization, Project administration, Investigation, Methodology, Data curation, Resources. DC: Visualization, Resources, Conceptualization, Software, Funding acquisition, Project administration, Writing – review & editing, Supervision, Formal analysis, Writing – original draft, Validation, Methodology.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2026.1775666/full#supplementary-material

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