Aquatic Mammals 2017, *43*(6), 691-702, DOI 10.1578/AM.43.6.2017.691

Return of Harbor Porpoises (*Phocoena phocoena*) to San Francisco Bay

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Abstract

Harbor porpoises (*Phocoena phocoena*) were rarely seen in San Francisco Bay prior to 2008 despite numerous marine mammal search efforts beginning in the 1970s. The species inhabited the bay historically before they were functionally extirpated by the early 1940s. Their disappearance correlated with increased anthropogenic disturbances such as dredging, shoreline construction, World War II military defenses, and environmental impacts from industrialization. After observing porpoises throughout the central San Francisco Bay from 2008 to 2010, we documented the porpoises' occurrence by means of a visual count from the Golden Gate Bridge. From 2011 to 2014, we spent 288 h counting porpoises from that unique platform, resulting in 2,698 porpoise group sightings recorded in all months of the year. Group size averaged 2.15, and the maximum group size was 16 animals. Calves comprised 10% of all porpoises sighted and were also seen throughout the year. Porpoises were observed on 96% of 169 survey days, and an average of 34.37 ± 29.19 were seen per day. Porpoises can now be seen in the central bay daily throughout the year. Stranding records for the bay reflected the general pattern of the porpoises' decades-long absence and their reappearance. Potential reasons for the porpoises' return include decreased water and noise pollution, improved water quality, and increased marine productivity that created conditions in the bay that were favorable for porpoises.

Key Words: San Francisco Bay, cetacean, extirpation, habitat reoccupation, recovery, recolonization, ecosystem resilience, harbor porpoises, *Phocoena phocoena*

†Deceased; see "In Memoriam" on page 703.

Introduction

Herein, we report an instance that counters the global trend of biodiversity loss in estuaries (Wolff, 2000; Lotze et al., 2006): harbor porpoises (*Phocoena phocoena*) have recently reoccupied central San Francisco Bay (SF Bay) after an absence of more than 60 y. This species has been known to recover habitat in other parts of its range, including the North Sea (Camphuysen, 2004), Germany's Weser River (Wenger & Koschinski, 2012), and farther north along the U.S. Pacific coast in Puget Sound where they returned to habitat abandoned decades earlier (Evenson et al., 2016; Jefferson et al., 2016).

Harbor porpoises are one of the smallest toothed whales, reaching adult lengths of 1.5 to 2.0 m and weights of 50 to 70 kg (Gaskin et al., 1974; Jefferson et al., 2015). They inhabit the cool coastal waters of the northern hemisphere and are common along the central and northern California coast (Allen et al., 2011). They tend to be inconspicuous, avoiding boats, keeping a low surface profile, and occurring in small groups (Jefferson et al., 2015). The species is listed as of "Least Concern" by the International Union for Conservation of Nature (Hammond et al., 2008) and is not listed under the U.S. Endangered Species Act. Harbor porpoises in the eastern North Pacific (*P. p. vomerina*) are divided into nine management stocks. The nonmigratory San Francisco–Russian River stock, which includes the Gulf of the Farallones adjacent to SF Bay, is estimated to have a stable population with no apparent trend of 9,886 animals (CV = 0.51) and an average group size of 1.75 based on National Oceanic and Atmospheric Administration (NOAA) aerial surveys from 2007 through 2011 over coastal waters that did not cover SF Bay (Forney et al., 2014). In this area, porpoises utilize relatively shallow (< 100 m) nearshore waters (Carretta et al., 2001) where they feed on a variety of small schooling fishes such as northern anchovy

(*Engraulis mordax*) and Pacific herring (*Clupea pallasii)* (Jones, 1981; Oliaro, 2013). Herring enter SF Bay during winter to spawn, while anchovy arrive during spring and summer and are the most abundant fish in the more saline parts of SF Bay such as the central bay (Kimmerer, 2006; Fish et al., 2012).

Historically, harbor porpoises were part of the SF Bay fauna as evidenced by the fact that their skeletal remains appear throughout the strata of an indigenous people's midden located on the bay's eastern shore, the Emeryville shellmound, dating from approximately 2,600 to 700 y ago (Broughton, 1999). Harbor porpoises were taken in the 19th-century SF Bay seine fishery (Scammon, 1874). By the beginning of the 20th century, they were reported as "formerly abundant" ("Save the Seals," 1906, p. 26), and Kofoid (1915) remarked that, "Porpoises (*Phocaena phocaena*) . . . still enter" SF Bay "occasionally" (p. 131). They were seen there until World War II (Benson, 1939-1942), but in the decades following the war, there were only sporadic live sightings and strandings, with only three live sight records during the 1970s and 1980s despite repeated searches (Huber et al., 1982). Over this time span, naturalists working on local whale-watch boats docked in SF Bay compiled approximately 1,000 harbor porpoise sightings of which only two were inside the bay (Szczepaniak, 1990).

Human-caused alterations and their cumulative impacts on the SF Bay ecosystem are among the multiple factors that probably drove harbor porpoises out of the bay. SF Bay is one of the most modified major estuaries in the United States (Nichols et al., 1986), with the human population around it now exceeding 7 million. Disturbance of the bay's biological communities began with the gold rush in the mid-19th century when hydraulic mining resulted in mercury contamination and massive downstream sedimentation (Chin et al., 2004). Rapid urbanization was accompanied by effluent pollution, wetland fill, river diversion, the spread of exotic organisms, the blasting of submerged rocks deemed navigation hazards, and major construction projects (Luoma & Cloern, 1982; Cohen & Carlton, 1998; Chin et al., 2004; San Francisco Estuary Partnership [SFEP], 2015).

The 1930s were a time of several large-scale projects in SF Bay such as the construction of the Golden Gate Bridge, the San Francisco–Oakland Bay Bridge, and the creation of the artificial 1.6 km^2 Treasure Island by dredge and fill (Goldman, 1969). The 1940s saw sharply increased vessel traffic, shipyard construction, and harbor fortification, including the planting of hundreds of floating mines at the entrance to the Golden Gate (Chin, 1994). Such sources of intense activity and noise likely would have disturbed the porpoises (Forney et al., 2017).

In particular, a World War II-era anti-submarine net may have physically and acoustically deterred harbor porpoises from entering SF Bay. The U.S. Navy deployed the net from August 1941 until August 1945 ("Schooner Tangles," 1941; "Golden Gate Sub Net," 1945). It stretched 5 km across the bay from San Francisco to Sausalito, Marin County (see Figure 1) and was buoyed at the surface and anchored to the bottom in depths up to 30 to 35 m (Chin, 1994). A gate in the net opened only for short durations to allow ship passage. Two types of netting were used: (1) to ensnare submarines and (2) to stop torpedoes. The submarine net was woven of steel cable approximately 2.5 cm thick into a mesh 1.2 m square. The torpedo net was formed by interlocking steel wire rings that varied between 30 to 40 cm in diameter and were 1.3 to 1.9 cm thick, based on our measurements of net remnants. The torpedo net was shackled to the top support boom and hung next to the submarine net down to approximately 12 m below the surface (Shortridge, 2010). Harbor porpoises would have been unable to pass through the small torpedo net rings (Figure 2). The net system was reported to have entangled whales and marine debris ("Golden Gate Sub Net," 1945). Although the location of the net would have allowed porpoises to enter the west-central bay as far as approximately 2 km east of the study area, they would have been cut off from most of the bay habitat.

Harbor porpoises are sensitive to noise (Forney et al., 2017), whether from vessels (Dyndo et al., 2015), marine construction zones (Carstensen et al., 2006), underwater explosions (Sundermeyer et al., 2011), or pile-driving activities at distances of over 20 km (Tougaard et al., 2009; Brandt et al., 2011). Because harbor porpoises feed almost continuously to support their high metabolic rates, they are especially vulnerable to anthropogenic disturbances (Wiśniewska et al., 2016). The anti-submarine net system may have posed a significant acoustic deterrent due to sounds generated by the metal mesh, anchoring cables, and surface floats straining in energetic tidal currents, as well as by return signals from the porpoises' echolocation clicks. Prior to the net installation, porpoises were seen regularly in SF Bay, but after its installation, a few were seen up to 7 mo later, presumably trapped inside the bay (Benson, 1939-1942).

Once the submarine net was removed, the harbor porpoises did not immediately return to SF Bay. Once displaced, this species can be slow to return to noisy areas. For example, an offshore wind farm in the Baltic showed long-term (10 y) negative effects on porpoise activity (Teilmann & Carstensen, 2012). Moreover, harbor porpoises are short-lived cetaceans (Read & Hohn, 1995), and the 4 y of the net's deployment represented a large fraction of an individual's lifespan. A study of stranded California

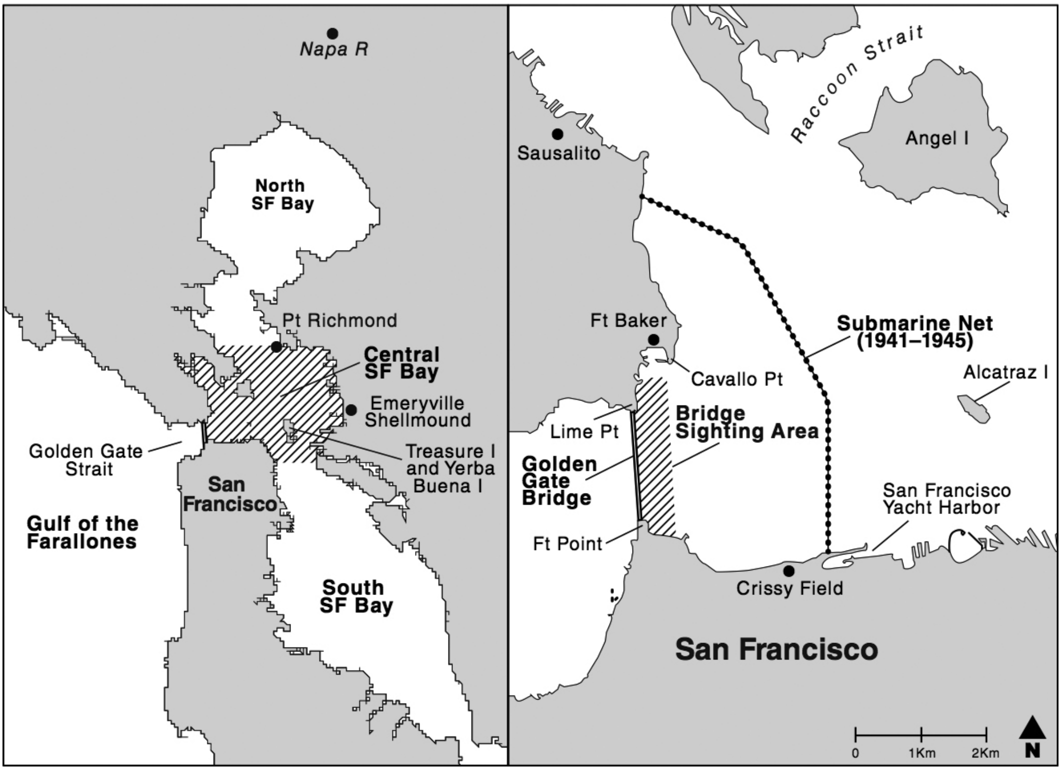

Figure 1. Study area maps: San Francisco Bay, California, and harbor porpoise (*Phocoena phocoena*) sighting area in the bay

harbor porpoises revealed that 97 to 98% did not survive beyond 9 y (Hohn & Brownell, 1990). Approximately one third of the porpoises examined by Hohn & Brownell were killed in gillnets, which skewed the results toward younger animals; nevertheless, out of a total 210 porpoises, only two reached the age of 14 or more. Assuming a stable age-structure, by the time the net was removed, about 50% of the population that had previously used the bay would have died, leaving younger members with no experience using bay habitat. Conceivably, this loss of "institutional memory" (*sensu* El Sawy et al., 1986; Wade et al., 2012; Whitehead & Rendell, 2015) would have made their rapid reoccupation of SF Bay more challenging.

In addition to loss of bay habitat through development and military activities, water quality deteriorated over the course of the 20th century, negatively affecting the bay's biological communities. Kofoid (1915) reported the decline of invertebrates in SF Bay "by reason of its . . . sewage, and industrial wastes" (p. 127). Brownell (1964) transited SF Bay and the Golden Gate strait in 1963 without spotting harbor porpoises, and he suggested water pollution and boat traffic as probable causes for their being uncommon in the bay.

The decline of fish species in the bay may have been another reason for the porpoises' decreased presence by the mid-20th century, but information about prey resources is complex and incomplete. Historical commercial fish landing data lump the in-bay catches with catches made outside the bay along the coast (Eldridge & Kaill, 1973; San Francisco Bay and Development Commission [SFBDC], 1986). Yet, SF Bay area landing data collected from 1916 to 1958 for northern anchovy, Pacific herring, and Pacific sardine (*Sardinops sagax*) indicate these species supported productive fisheries (Skinner, 1962). Fisheries effort varied over time, with the peak sardine catch in the 1940s motivated by World War II protein shortages. Sardines then declined in the late 1940s in association with an oceanographic regime change, followed by an anchovy peak in the 1950s (Chavez et al., 2003). Both anchovy and herring abundances reached 30-y (1980 to 2010) maxima in the bay during the period when few porpoises were reported (Fish et al., 2012).

During their prolonged absence from SF Bay, harbor porpoises continued to occur outside the Golden Gate in nearby coastal waters (Brownell, 1964; Orr, 1972; Leatherwood et al., 1982; Szczepaniak, 1990). A dedicated boat-based census

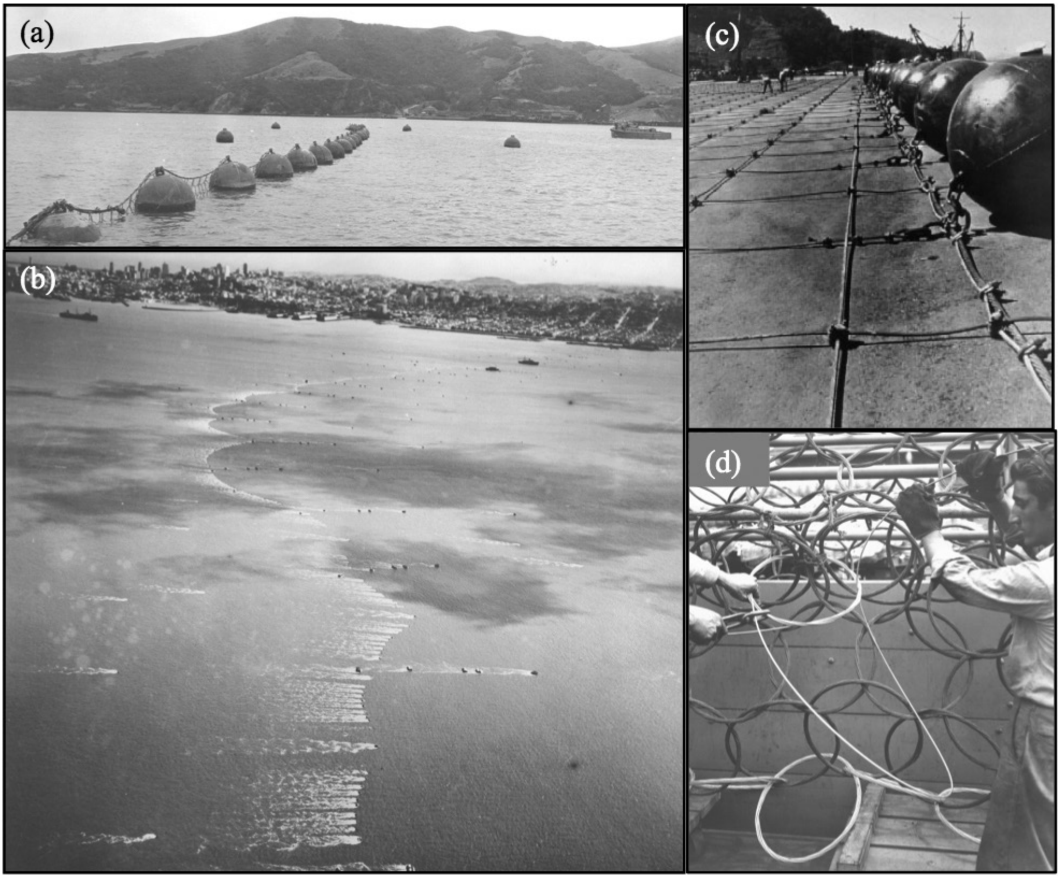

Figure 2. Anti-submarine net system deployed in San Francisco Bay (SF Bay) during World War II: (a) section of net off Sausalito, Marin County, with torpedo rings at the surface; (b) aerial view of net at flood tide, looking south toward San Francisco, May 1942; and construction of submarine netting (c) and torpedo netting (d) at U.S. Navy Net Depot, Tiburon, California. (Photographs are courtesy of the Belvedere-Tiburon Landmarks Society's Nagy Collection)

in the waters of the Gulf of the Farallones was conducted from 1987 to 1989 (Calambokidis et al., 1990), resulting in an estimate of 2,109 (CV = 0.63) harbor porpoises. Observers (including WK, IDS, and MAW) on 20 surveys on vessels originating within SF Bay counted no harbor porpoises inside the bay, although sightings were recorded 2 to 3 km west of the Golden Gate Bridge. This census occurred just after the northern California population of harbor porpoises sustained peak bycatch mortalities of more than 200/y due to the set gillnet fishery that was active along the outer coast, not in SF Bay (Barlow & Forney, 1994). Annual aerial surveys furnished porpoise counts along the central California coast from 1986 to 2007 (Barlow & Forney, 1994; Forney, 1999; Carretta et al., 2009). For example, during the 1990s, a decade when no live sightings of porpoises were reported in SF Bay, their abundance between Half Moon Bay and Bodega Head, covering the central portion of the San Francisco–Russian River stock's range, was estimated to be 2,519 (CV = 0.27), based on 1993-1997 surveys (Forney, 1999). The latest abundance estimate, based on 2007-2011 surveys, indicates a stable population (Forney et al., 2014), despite an unusual mortality event (UME) in 2008-2009 that impacted California harbor porpoises (Wilkin et al., 2012). Factors that contributed to the UME, such as lethal attacks by coastal bottlenose dolphins, persist (Cotter et al., 2012; Chantra et al., 2016).

Sightings of harbor porpoises in the bay began to increase in the 21st century with the first photo-documented records from July 2007 in the Napa River in the north bay (Todorov, 2007), and from November 2007 during an oil spill in the central bay (KCRA TV, 2007). See Appendix in Supplementary Material on the *Aquatic Mammals* website (www.aquaticmammalsjournal.org/index.php?option=com_ content&view=article&id=10&Itemid=147) for a chronology of harbor porpoise occurrences in SF Bay prior to October 2008 when SJS observed a group of porpoises, including mother–calf pairs, within the bay off Cavallo Point, approximately 1 km northeast of the Golden Gate Bridge. Over the next 2 y, preliminary searches from shore, bridge, and boat resulted in porpoise sightings throughout central SF Bay (see Figure 1, map of SF Bay, with the shaded area indicating where harbor porpoises occur), prompting our 2011-2014 effort to document the porpoises' occurrence and our review of local stranding records. Our objective was to visually confirm their reoccupation and regular use of the central bay, and to record their behaviors photographically. Observations made post-study confirmed their continued presence in the central bay (Golden Gate Cetacean Research, unpub. data, 2015-2017).

Methods

Study Area

SF Bay is the largest estuary on the west coast of the U.S., draining more than 40% of California's surface water through the Golden Gate to the Pacific Ocean (Feyrer et al., 2007). The bay is a turbid ecosystem with a mixed semi-diurnal tidal regime (Conomos et al., 1985), and currents exceed 2.5 m/s during peak exchange, scouring the bottom to 113 m, one of the deepest estuarine outlet channels in the world (Barnard et al., 2006). SF Bay is composed of several subembayments, including the central bay, situated due east of the Golden Gate (Conomos et al., 1985; Chin et al., 2004). The Golden Gate is a strait, 4.5 km long, 3.2 km wide at the western (ocean) end and 1.6 km wide at the eastern (SF Bay) end (*United States Coast Pilot*, 2016). It connects the coastal waters of the Gulf of the Farallones with the bay (Figure 1). The Golden Gate Bridge spans the strait at its narrowest and deepest point.

Observation Platform

Observations were made from the Golden Gate Bridge (37° 48' 59" N, 122° 28' 39" W). The east sidewalk, approximately 70 m above sea level (*United States Coast Pilot*, 2016), is open to the public during daylight hours and provided unobstructed views into central SF Bay, as well as a stable overhead view of the porpoises.

Data Collection

To ensure robust data covering seasonality, we planned a study from January 2011 through December 2014, with data to be collected on multiple days in all 48 mo. During observation periods that ranged from 0.2 to 4.7 h, we maintained continuous naked eye searches for harbor porpoises while crossing the bridge's east sidewalk on foot between the San Francisco anchorage and the Marin anchorage at opposite ends of the bridge. The sighting area was a 2.41 km strip extending from 0 m (directly below) to 500 m east of the bridge. This 1.2 km^2 polygon is shown in Figure 1. Other data collected included time, weather, group size, heading, and age class (adult or dependent calf, based on smaller size and consistent escort by an adult). Basic behaviors, such as traveling, foraging, or mating, were also recorded.

Observations were conducted only in sea state conditions of Beaufort 0 to 2 and when fog (most prevalent during summer months) did not hamper visibility. Ocean swells are greatly reduced in height by the time they reach this location and have no effect on visibility from the elevated vantage point of the bridge. Other than low-lying fog and rain, weather conditions had little impact on data collection since the animals were readily visible and no optical equipment was used.

Preferred times to conduct counts, tested in 2010 during the pre-study phase, were at high tides and the beginning of ebb tides, when harbor porpoises typically left the bay in response to ebb currents, reducing the chance of double counting. This maximized our opportunities to sight porpoises approaching the bridge, allowing us to more efficiently predict their heading and to photograph individuals and their behavior (see Keener et al., 2011). Day-to-day sightings were assumed to be independent since porpoises left the bay in response to ebb currents.

Data Analysis

R open-source programming language (www.r-project.org) was used for data analysis and graphs. In addition to arithmetic means, harmonic means were calculated for actual (non-effort corrected) counts to reduce the skewing effect of a few very large counts. Only arithmetic means were calculated for calves as their numbers did not exhibit extreme values. Sightings per unit effort (SPUE) accounted for sighting effort in assessing relative abundances summarized for each observation period (see Stern, 1990). One unit of effort was defined as 1 h of dedicated search, thus

$$\text{SPUE} = \frac{\text{Number sighted}}{\text{Hours searched}}$$

All results are given as mean ± SD.

Stranding Records

Dead marine mammals in the SF Bay area have been collected by the California Academy of Sciences and the University of

California–Berkeley's Museum of Vertebrate Zoology since the early 1900s. Since 1975, the NOAA's California Marine Mammal Stranding Network, including The Marine Mammal Center in Sausalito, has collected and archived records of cetacean strandings. These records were searched for all harbor porpoise strandings in SF Bay from 1900 to 2010.

Results

We spent a total of 288.1 h counting harbor porpoises during 176 observation periods on 169 d across all months of the year from January 2011 through December 2014 (see Table 1), resulting in 2,698 porpoise groups sighted. Group size averaged 2.15, with a maximum group size of 16. Of the groups, 48.3% (n = 1,302) were single animals and 23.7% (n = 639) were groups of two porpoises. Mean effort per observation period was 1.7 ± 0.6 h (range: 0.2 to 4.7 h). Survey effort varied by year, with approximately 64% of all effort occurring in 2011-2012, the first half of the 4-y study. An average of 34.4 ± 29.2 (harmonic mean = 14.3) porpoises were seen per day, ranging up to a maximum of 175 porpoises (165 adults, 10 calves) in a single survey (2-h period). Calves were sighted in 518 groups and overall comprised 10% of porpoises counted per group (aggregated count = 582/5,809). Calves

Table 1. Combined number of observation days by month (2011–2014)

Jan	Feb	March	April	May	June	July	Aug	Sept	Oct	Nov	Dec	Total
17	18	15	19	9	13	10	16	12	17	9	14	169

Table 2. Summary statistics for harbor porpoise counts from the Golden Gate Bridge (2011-2014); SPUE = sightings per unit of effort

Year	Effort (d)	Effort (h)	Survey interval (d)	All porpoises	Calves	SPUE
		Total	-	Sightings/total	Sightings/total	Total/h effort
		Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD
		-	-	Harmonic mean	-	Harmonic mean
		Range	Range	Range	Range	Range
2011	61	105.7	-	685/1,792	120/145	16.9
		1.7 ± 0.6	5.8 ± 5.2	29.4 ± 25.1	2.4 ± 2.4	16.6 ± 11.6
		-	-	10.81	-	6.93
		(0.5-4.3)	(1-28)	(1-128)	(0-10)	(0.6-60)
2012	48	80.1	-	1,118/2,249	211/237	28.1
		1.7 ± 0.7	7.7 ± 5.7	46.9 ± 36.5	4.9 ± 4.1	27.2 ± 15.2
		-	-	19.2	-	14.8
		(0.2-3.6)	(1-23)	(3-175)	(0-15)	(1.9-68.6)
2013	32	52.33	-	418/802	108/113	15.3
		1.6 ± 0.5	11.3 ± 9	25 ± 13.7	3.5 ± 3.7	14.4 ± 9.1
		-	-	13.7	-	9.7
		(0.8-2.7)	(1-35)	(3-97)	(0-14)	(3.1-37.7)
2014	28	49.9	-	477/966	79/87	19.4
		1.8 ± 0.9	12.9 ± 12.2	34.5 ± 26.7	3.1 ± 4.4	20.0 ± 13.9
		-	-	20.4	-	13.6
		(0.7-4.7)	(1-48)	(5-102)	(0-22)	(6.3-54.5)
Total	169	288.1	-	2,698/5,809	518/582	20.2
		1.7 ± 0.6	8.6 ± 8.1	34.4 ± 29.2	3.4 ± 3.7	19.9 ± 13.5
		-	-	14.3	-	20.2
		(0.2-4.7)	(1-48)	(1-175)	(0-22)	(0.6-68.6)

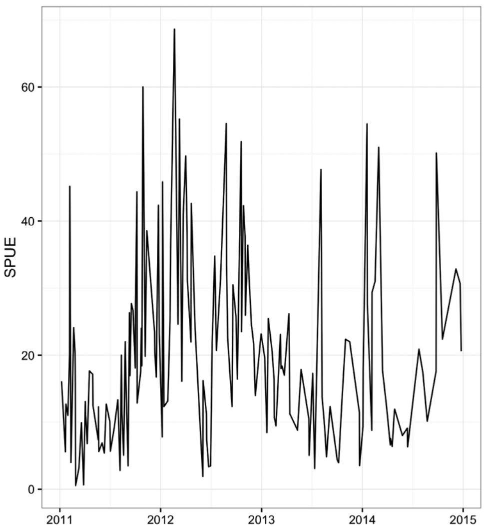

Figure 3. Daily porpoise SPUE (sightings per unit of effort, = h) from January 2011 to December 2014

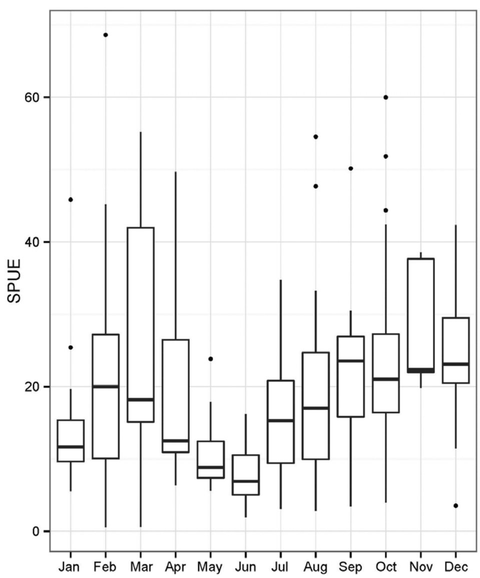

Figure 4. Combined monthly porpoise SPUE (h) from 2011 to 2014; horizontal bars = mean, vertical lines = 95% CI, dots = outliers, and boxes = 25th to 75th percentile of the total combined monthly SPUE.

were present in all months of the year, and the mean number of calves per observation period was 3.44 ± 3.69. No porpoises were seen during seven (4%) observation periods. Summary statistics are provided in Table 2.

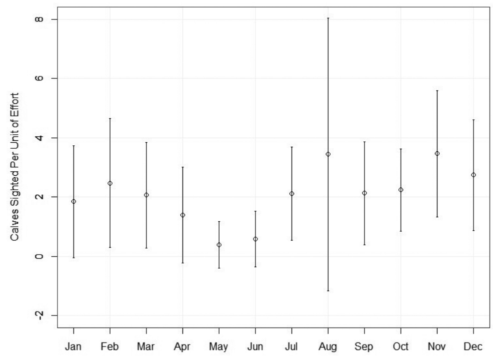

Figure 5. Combined monthly calf SPUE (h); circles = mean and vertical lines = SD.

Total porpoise SPUE (the total number of porpoises/total h of effort) of 20.2 was close to the mean daily SPUE of 19.9 ± 13.5. SPUE varied between sampling periods over the 4 y of observations (Figure 3), indicating variable use patterns. SPUE plotted by month indicated that porpoises were present in all months of the year (Figure 4), with reduced SPUE in May and June. However, no sampling occurred in November 2014 due to inclement weather. There was a significant difference in SPUE between years ($F_{(3,165)} = 8.52$; $p < 0.0001$; Table 2). Tukey's HSD test showed significant differences between 2011 and 2012 (diff = 10.61; $p < 0.001$) and 2012 and 2013 (diff = -12.78; $p < 0.001$), with the highest SPUE occurring in 2011. Calf SPUE was plotted separately (Figure 5).

Marine mammal stranding records for SF Bay show a total of 23 harbor porpoises stranded from 1938 to 2010. See Table 3 for a breakdown by year.

Discussion

Our study demonstrated that harbor porpoises now use SF Bay habitat on a daily basis across all months of the year. Although seven observation periods resulted in zero porpoise sightings, those efforts were conducted in off-peak portions of the tidal cycle such as low tide. Porpoises were sighted on 100% ($n = 169$) of counts during the preferred high tide/beginning ebb tide periods. Our findings should interest resource managers charged with the conservation of cetaceans. Mitigation plans and alternatives required by the U.S. Marine Mammal Protection Act for project permits will now need to take into account the harbor porpoise's common year-round occurrence in the central bay.

During an average 90- to 100-min observation period, approximately 20 porpoises were sighted per hour. The average group size of 2.15 porpoises per sighting generally agrees with a 2.3 average

Table 3. Stranding history of harbor porpoises in San Francisco Bay (1900-2010)[a]

Year:	1938	1939	1940	1941	1963	1971	1973	1974	1976	1977	1997	2002	2008	2009	2010	Total
No.:	1[b]	1[b]	1[b]	2[b]	1[c]	1[c]	1[c]	1[c]	1[b]	1[c]	1[d]	3[d]	2[d]	4[d]	2[d]	23

[a]San Francisco Bay is defined as waters east of the strait at the Golden Gate Bridge; no harbor porpoise carcasses are recorded prior to 1938. Footnotes for stranding numbers refer to institutions where records are archived.
[b]Museum of Vertebrate Zoology, University of California–Berkeley
[c]California Academy of Sciences, San Francisco
[d]The Marine Mammal Center, Sausalito

group size resulting from boat-based surveys in the Gulf of the Farallones (Calambokidis et al., 1990), and it is higher than the average group size of 1.75 found by aerial surveys along the northern California coast (Forney et al., 2014). The maximum group size of 16, observed 27 October 2012, is less than the groups of 50 to 100 harbor porpoises recorded for other populations (Jefferson et al., 2015), perhaps because this stock does not aggregate for seasonal migrations (Forney et al., 2014).

Porpoise count numbers fluctuated per period (Figure 3). The peak SPUE of 28.1 in 2012 (Table 2) might be due to factors such as local variations in the availability of prey fish. The maximum count of 175 on 20 February 2012 coincided with a winter herring run in SF Bay (California Department of Fish and Game, 2012). SPUE also varied across the months, with generally higher sightings per hour in fall and winter (Figure 4). Note that the timing of our observation periods inflated SPUE because counts tended to avoid tidal phases when porpoise numbers were low, a preference supporting our goal of confirming the species' presence and abundance. The reduced porpoise SPUE in May and June seen in Figure 4 may be an artifact resulting from less data collected during those months due to fog.

Calves comprised approximately 10% ($n = 582$) of all harbor porpoises sighted ($n = 5{,}809$). They were present in every month, but lower sightings per hour in May and June (Figure 5) are attributed to the fact that older calves separate from their mothers in spring and are no longer readily distinguished from adults. Other studies found that harbor porpoise calves are born in May and June (Hohn & Brownell, 1990; Read & Hohn, 1995), and lactation lasts for 8 to 12 mo (Mohl-Hansen, 1954; Read, 1990).

Local aerial coastal surveys (Forney et al., 2014) did not collect data on calves. Elsewhere, a preferred harbor porpoise calving ground off the German islands of Sylt and Amrum was identified based on aerial survey data showing a proportion of 14% calves in contrast to an overall proportion of 5.4% calves for the North Sea (Sonntag et al., 1999). Similarly, a ship survey off southwestern Ireland revealed a proportion of 15% calves, leading investigators to conclude that it may be a major breeding/nursery area after comparing their results to a 4% calf proportion observed for the entire British Isles (Leopold et al., 1992). Both European surveys were conducted during summer months when young calves are more easily counted because of proximity to their mothers and relatively small size. The SF Bay porpoise counts were partly derived from seasons when calves may be undercounted from winter through spring as calves grow larger and gain independence. Summer (June-August) observations for the 4 y of this study show a total of 96 calves out of 798 porpoises, a proportion of 12% calves, which approached the European high counts, suggesting the bay may be an important foraging habitat for females facing the energetic demands of lactation (Lockyer, 2007).

The results of our records search for harbor porpoise strandings within SF Bay reflect the general pattern of the porpoises' decades-long absence and the date of their approximate return (Table 3). Of 23 strandings from 1938 to 2010, two occurred in July 1941, a month before the submarine net was installed, followed by a 22-y gap, supporting our contention that the net played a role in the porpoises' abandonment of the bay. After their return to the bay, four carcasses were reported in 2009: two from the central bay's eastern shoreline, one in the south bay, and one in the north bay's Carquinez Strait, which was asphyxiated by a fish lodged in its throat, indicating recent feeding. By comparison, from 1970 to 2010, 389 harbor porpoises stranded on the outer coastal beaches near SF Bay (San Francisco, San Mateo, Marin, and Sonoma Counties; Szczepaniak, 1990).

After displacement, reestablishment depends on the resilience of the species and its former ecosystem and, at times, human action to restore the environment (Palumbi et al., 2008; Thrush et al., 2008). Harbor porpoises can be flexible in diet, shifting to coincide with changes in prey availability (Santos Vazquez et al., 2004). Their occurrences correlate with resource distributions and seasons (Sveegaard et al., 2012) or may change for unknown reasons (Dahlheim et al., 2015). The decline and recent recovery of harbor porpoises in Puget Sound may have some causes in common with the SF Bay porpoises, such as habitat degradation through development, pollution, and noise, but there are differences. The SF Bay porpoises contended with a World War II anti-submarine net and abandoned the bay prior to any bycatch losses due to coastal gillnetting. They also did not suffer competition with, and replacement by, other cetaceans (i.e., Dall's porpoise [*Phocoenoides dalli*]) as in the case of the Puget Sound porpoises (see Evenson et al., 2016; Jefferson et al., 2016).

While a study of the factors that may have contributed to the harbor porpoises' return to SF Bay is beyond the scope of this paper, we note that beginning in the 1960s, the grassroots efforts of citizen groups led to enforceable legislation and government agencies that curbed bay fill and municipal and industrial pollution (Holmes, 2012). The result was dramatically improved water quality in the bay by the 1990s (SFEP, 1992) when watershed-wide planning and habitat restoration projects were underway. The central bay is currently considered relatively healthy with stable fish populations, which may be due in part to this environmental success story (SFEP, 2015) and to increased productivity resulting from large-scale oceanographic processes, including a regime shift to a cold phase in 1999-2000 (Cloern et al., 2007, 2010). Thus, the confluence of natural cycles in the estuarine and marine environment and human intervention in SF Bay set the stage for the return of harbor porpoises.

Acknowledgments

We are grateful for support provided by the National Wildlife Federation, the Baraka Charitable Fund, Mr. & Mrs. Clinton Kelly, Michael Day, and Anise Feldman. Thanks go to our colleagues Mary Jane Schramm, Jan Roletto, Flip Nicklin, and Laura Duffy, and the Greater Farallones National Marine Sanctuary, The Marine Mammal Center, San Francisco State University's Romberg Tiburon Center, Oceanic Society, California Academy of Sciences, and the San Francisco Bay Chapter of the American Cetacean Society for their assistance. Cara Gallagher contributed key assistance with maps and charts, and Nina Lisowski provided graphic design. Archival submarine net photographs are courtesy of the Belvedere-Tiburon Landmarks Society (Nagy Collection). Activities were permitted under NOAA General Authorization LOC No. 15477. Our appreciation goes to Karin Forney who helped shape an early manuscript draft, and to three anonymous reviewers for their helpful comments and suggestions. This paper is dedicated to Hal Markowitz (1934-2012), who encouraged us in the study of marine mammals.

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Return of Harbor Porpoises (*Phocoena phocoena*) to San Francisco Bay

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Supplemental Appendix

Chronology of San Francisco Bay (SF Bay) harbor porpoise (*Phocoena phocoena*) observations prior to October 2008*

Date	Location	Observation	Reference
2600-700 BP	Emeryville	Skeletal remains in midden	Broughton, 1999
1874	SF Bay	Seine fishing bycatch	Scammon, 1874
1906	SF Bay	"Formerly abundant"	"Save the Seal," 1906
1915	SF Bay	"Still enter . . . occasionally"	Kofoid, 1915
1924	SF Bay	Bycaught individual	Hohn & Brownell, 1990
Late 1920s	Raccoon Strait	Multiple sightings	M. McDonough, pers. comm., 15 November 2008
1939, 1941 & 1942	Point Richmond	Multiple sightings	Benson, 1939-1942
1958	Point Richmond	Few sightings	K. Clausen, pers. comm., 29 November 2015
1972	SF Bay	"Occasionally sighted"	Orr, 1972
1975	Fort Baker	Sighting of one	Huber, 1982
1978	Sausalito	Sighting of one	Szczepaniak, 1990
1985	SF Yacht Harbor	Sighting of one	Szczepaniak, 1990
2000	Yerba Buena Island	Sighting of one	Green et al., 2006
2004	Crissy Field	Sighting of one	J. Yakich, pers. comm., 4 September 2012
2005-2006	Central Bay	Sailboat log entry, four sighted	S. G. Allen, pers. comm., 20 March 2012
2007 July	Napa River	Photographed two	Todorov, 2007
2007 September	Central Bay	Sailboat log entry, one sighted	S. G. Allen, pers. comm., 20 March 2012
2007 November	Central Bay	Videotaped two in oil spill	KCRA TV, 2007
2008 July	SF Yacht Harbor	Sailboat log entry, few sighted	K. Clausen, pers. comm., 29 November 2015

*San Francisco Bay is defined as waters east of the strait at the Golden Gate Bridge; locations are noted on map (Figure 1 in text). Authors' initial observations of porpoises began in October 2008.

Appendix References

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