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Northern Range Expansion of California Coastal Bottlenose Dolphins (*Tursiops truncatus*)

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Abstract

The California coastal stock of bottlenose dolphins (*Tursiops truncatus*) expanded its range north from the Southern California Bight, its historical range, into Central California coincident with the 1982-1983 El Niño event. Since the late 1980s, bottlenose dolphin sightings north of Central California have been increasingly reported. To determine the present-day northern range limit for these dolphins, photo-identification efforts were carried out from 2007 to 2018 in San Francisco Bay and nearby coastal waters during which 84 individuals were identified. The results demonstrate a significant range expansion along the Northern California coast at least as far as Sonoma County (38.7º N). Comparisons with photo-identification catalogs compiled south of San Francisco from 1981 to 2015 revealed that 92% of the 84 dolphins were matched to Monterey Bay (n = 77), Santa Barbara (n = 27), Santa Monica Bay (n = 29), Orange County (n = 9), Corona Del Mar (n = 2), San Diego (n = 31), and Ensenada, Mexico (n = 1). Many of the 84 dolphins (54%) showed long-range movements across the stock's range between the Southern California Bight and the San Francisco Bay Area. The greatest movement distance recorded was by two individuals first observed in San Diego, California, in the 1980s and subsequently in Puget Sound, Washington (47º N), in 2017, setting a coastal bottlenose dolphin long-distance movement record of at least 2,500 km.

Key Words: coastal stock, San Francisco Bay, California, range expansion, photo-identification, bottlenose dolphin, *Tursiops truncatus*

Introduction

Marine predator distribution is often driven by environmental parameters and shifting prey availability (Block et al., 2011). Bottlenose dolphins (*Tursiops truncatus*) are apex predators that exhibit flexibility in terms of diet and habitat use (Wells et al., 1999). Longitudinal studies of this species, which live 50 to 60 y (Wells & Scott, 2018), have provided valuable information regarding their social lives, population structure, habitat use, distribution, and movements (Wells, 1991). In this article, we report on the continued northward range expansion of California coastal

bottlenose dolphins over the last four decades. We use new photo-identification records from Northern California and coastal waters farther north to update our understanding on the range of dolphins previously identified in the Southern California Bight and Monterey Bay. Herein, the San Francisco Bay Area (SF Bay Area) refers to our study area encompassing bay and ocean coastlines of multiple counties, and San Francisco Bay (SF Bay) refers only to the semi-enclosed estuarine waterbody of the bay.

California Coastal Bottlenose Dolphins

Bottlenose dolphins inhabit the nearshore waters of Southern and Central California where two distinct ecotypes occur: (1) a coastal form found < 1 km from shore, typically within 500 m (Carretta et al., 1998; Defran & Weller, 1999; Defran et al., 1999; Perrin et al., 2011) and (2) an offshore form found in deeper waters, usually more than a few km from shore (Defran & Weller, 1999; Bearzi et al., 2009; Lowther-Thieleking et al., 2014). These ecotypes are managed as separate stocks by the National Marine Fisheries Service (Carretta et al., 2017) and are differentiated by morphology (Walker, 1981; Perrin et al., 2011) and genetics (Lowther-Thieleking et al., 2014). The California coastal stock, the subject of this study, has an estimated abundance of 453 marked animals, not including a proportion of unmarked dolphins, and may have experienced a recent population increase (Weller et al., 2016). This stock displays little site fidelity and is thought to be panmictic throughout its range (Weller, 1991; Dudzik et al., 2006; Weller et al., 2016; Carretta et al., 2017). Currently, dolphins in the California coastal stock are not listed as threatened or endangered under the U.S. Endangered Species Act or depleted under the U.S. Marine Mammal Protection Act (Carretta et al., 2017). The southern range limit for this stock is considered to be near Ensenada in northern Baja California, Mexico (Defran et al., 2015). Previously, photo-identification catalogs have been compiled and compared for six coastal study areas: (1) Ensenada, (2) San Diego, (3) Orange County, (4) Santa Monica Bay, (5) Santa Barbara, and (6) Monterey Bay (Defran et al., 1999; Hwang et al., 2014; Weller et al., 2016). Range and movement data derived from those comparisons showed that these coastal dolphins are highly mobile, regularly moving back and forth within as well as between locations in their Ensenada to Monterey Bay range (Defran et al., 1999; Hwang et al., 2014). These sighting comparisons also support the concept of coastal dolphins progressively expanding their use of the more northern portions of their range to at least as far north as Monterey Bay (Hwang et al., 2014).

Until 1983, the northern range limit of California coastal bottlenose dolphins was thought to be restricted to the Southern California Bight (Norris & Prescott, 1961; Dohl et al., 1981; Leatherwood & Reeves, 1982). However, 19th century records indicate the stock may have once occurred farther north as the type specimen for *T. gilli* (a synonym of *T. truncatus*) was collected in Monterey Bay (Dall, 1873; Scammon, 1874; True, 1889; Walker, 1981). During a strong El Niño event that brought a temporary incursion of warm water to California in 1982-1983, the coastal stock of bottlenose dolphins extended their range north to at least Monterey Bay where they persist to this day (Wells et al., 1990; Maldini et al., 2010; Riggin & Maldini, 2010; Defran et al., 2015). Bottlenose dolphins have not been considered to be part of the marine fauna of SF Bay, yet skeletal remains found on the bay's eastern shore confirm the occurrence of this species (stock unknown) in small numbers during the active period of a native midden, *ca* 2,600 to 700 y before present (Broughton, 1999); similar zooarchaeological material was reported from a midden in Oregon (Colten, 2015). In 1958, the cranium of a bottlenose dolphin was dredged from the bottom of SF Bay, estimated to have been in the water for 50 to 100 y (Orr, 1963). A second skull was dredged from the bay in 1980, preliminarily identified as belonging to the offshore ecotype (Walker, 1981).

San Francisco Bay Area Sightings

Aerial surveys conducted from March 1980 through February 1983 found no bottlenose dolphins in Central or Northern California (Dohl et al., 1983). By November 1983, the first sighting of bottlenose dolphins nearshore in the SF Bay Area occurred in San Mateo County (Wells et al., 1990). From 1988 to 1993, the species was observed multiple times from beaches as far north as Pacifica, San Mateo County (Maldini-Feinholz, 1996). However, during boat-based censuses targeting harbor porpoises (*Phocoena phocoena*) in the Gulf of the Farallones from 1987 to 1989, observers (including co-authors WK and MAW) on survey vessels originating from within SF Bay counted no bottlenose dolphins (Calambokidis et al., 1990). Two sightings of presumably the same lone bottlenose dolphin in SF Bay east of the Golden Gate Bridge occurred on 31 May and 1 June 2001 (M. J. Schramm, pers. comm., 29 July 2014; P. Pyle, pers. comm., 18 August 2014), but no further live sightings were made in the SF Bay Area for 6 y. Beach surveys conducted bimonthly since 1993 by the Greater Farallones National Marine Sanctuary reported the first sighting of a group of bottlenose dolphins in San Francisco at Ocean Beach in November 2006 (Beach Watch, 2022). The presence of the coastal stock of bottlenose dolphins in SF Bay was not

confirmed until June 2007 based on photographs taken from the bay shore. Increasing encounters following 2007 prompted the efforts reported herein to examine the occurrence of coastal bottlenose dolphins off Northern California.

Research Objectives

Our research aimed to monitor photo-identified individual bottlenose dolphins and document changes in confirmed sighting locations from the 1980s to 2010s. The goals were as follows:

1. To develop a database of photo-identified coastal bottlenose dolphins found in the nearshore and bay waters of the SF Bay Area.

2. To compare dolphins identified in the SF Bay Area with those found in previously established photo-identification catalogs from study areas to the south of the SF Bay Area.

3. To confirm occurrence and movement patterns of photo-identified individuals.

4. To document changes in the range of these individual dolphins over time.

Methods

Study Areas

San Francisco Bay Area—The SF Bay Area includes 265 km of Pacific coast shore in four California counties (San Mateo, San Francisco, Marin, and Sonoma) plus the open waters of SF Bay (Figure 1A). SF Bay, the largest estuary on the West Coast of the United States (Feyrer et al., 2007) is a turbid ecosystem, generally shallow except where tidal currents scour the bottom to >100 m at the Golden Gate strait (Barnard et al., 2006). Shore-based coastal observations occurred at multiple locations between Sea Ranch (Sonoma County) in the north (38.7° N) to Pigeon Point (San Mateo County) in the south (37.2° N). Boat-based observations were made within the central portion of SF Bay, which covers 435 km^2 with 333 km of shoreline (Baylands Goals Project, 1999; San Francisco Estuary Institute, 2016; Figure 1A).

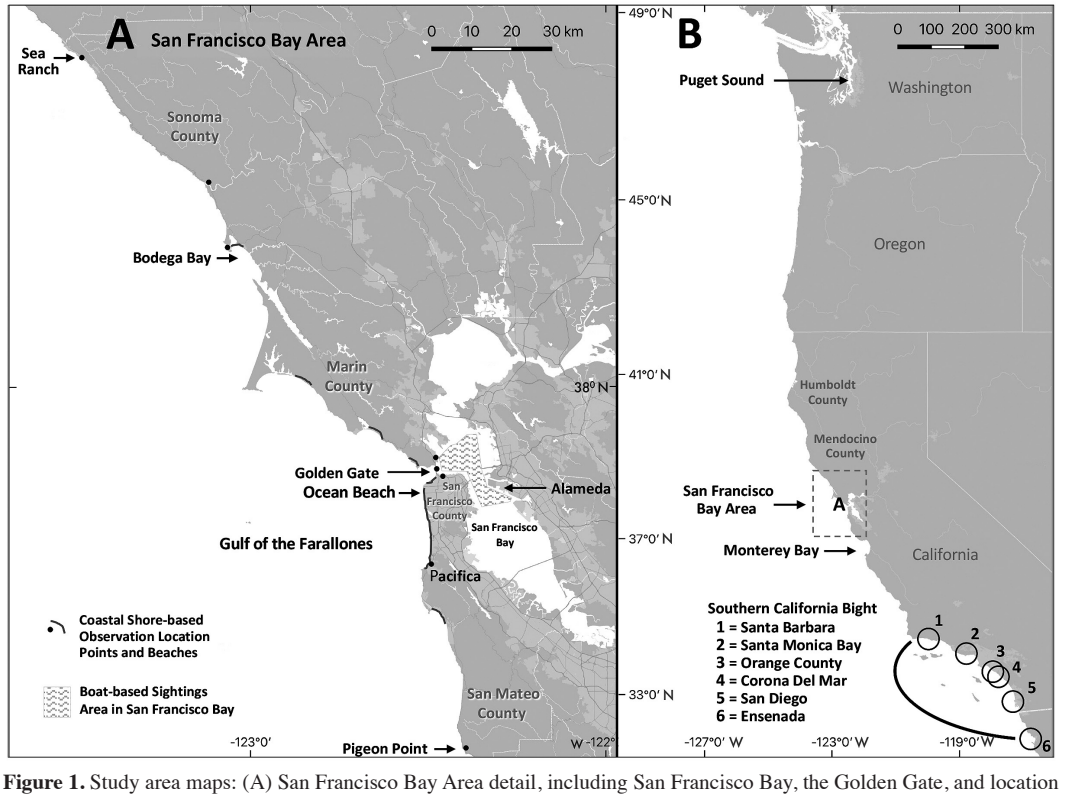

Figure 1. Study area maps: (A) San Francisco Bay Area detail, including San Francisco Bay, the Golden Gate, and location of the four counties with Pacific Ocean coastlines comprising that study area; and (B) U.S. West Coast and northern Mexico, showing geographical relationship of the California/Baja California study areas and Puget Sound.

Monterey Bay and Southern California Bight—A series of boat-based surveys conducted across all seasons in seven study areas along the Pacific coast of California and Mexico, including Monterey Bay, Santa Barbara, Santa Monica Bay, Orange County, Corona Del Mar (within Orange County), San Diego, and Ensenada, Baja California, Mexico, collected photo-identification images independently from the SF Bay Area effort (Figure 1B). In addition to coastal surveys, the Corona Del Mar study area also included waters in Newport Bay reaching as far as the Corona Del Mar Bend in the channel entrance.

These study areas are generally similar to each other and consist of beaches with gently sloping sand, steeply inclined cobblestone, estuary mouths, and rocky outcrops. Nearshore underwater topography ranges from submerged reefs, seagrass flats, and dense kelp canopies to relatively barren, sandy expanses differing primarily in the amount of coastline surveyed and some topographic and bathymetric aspects (Dailey et al., 1993; Defran & Weller, 1999; Defran et al., 1999; Bearzi, 2005; Hwang et al., 2014). Several study areas, including Monterey Bay, Santa Monica Bay, and San Diego, are interrupted by deep water canyons. All eight areas studied were noncontiguous and extended from 31.7º to 38.8ºN (Table 1).

Data Collection

San Francisco Bay Area—The SF Bay Area photo-identification effort was conducted from 2010 to 2018 and also incorporated images taken during 3 d in 2007. Data were collected primarily through dedicated shore-based efforts by researchers using high-resolution Canon digital cameras equipped with 300 mm and 100-400 mm lenses. Shore-based photography was often feasible because most California coastal bottlenose dolphins occur close to land, typically within 500 m (Hanson & Defran, 1993; Carretta et al., 2017), allowing the successful capture of dolphin dorsal fin images for dolphins < 250 m distant (see Defran et al., 2017) and species confirmation out to approximately 1 km offshore. The only other inshore cetacean species in the SF Bay Area is the smaller harbor porpoise. In addition to photography, dolphin sightings could also be confirmed from shore through use of binoculars and the naked eye. Rather than using fixed shore-based stations, researchers visually surveyed beaches and points on coastal bluffs to maximize opportunities to encounter dolphins. Surveys were conducted approximately biweekly year-round, depending on weather. Data were also obtained from citizen scientists, local whale-watching vessels, and incidentally from the general public (recreational observers). To help cover the large extent of the bay and coastline, a network of citizen scientists trained or vetted by research team members was developed to conduct regular coastal surveys (Embling et al., 2015). We set up a formal collaboration with whale-watch naturalists practiced in photographing and recording sighting data. Typically, a minimum of one whale-watching vessel operated out of SF Bay an average of 5 d/wk throughout the spring to fall seasons.

Members of the research team photographed 78 (93%) of the 84 uniquely identified dolphins in the SF Bay Area catalog. Contributions to the entire SF Bay Area dataset of 555 sightings were made by the research team (46%, $n = 256$), citizen scientists (41%, $n = 229$), and members of the public (13%, $n = 70$). Observers trained in cetacean

Table 1. Study area boundaries, coastline lengths, and inter-study area distances

	S Boundary		N Boundary			
Study area	Lat. N	Long. W	Lat. N	Long. W	Coastline length	Distance to area to the N
Ensenada	31.70	116.67	31.83	116.62	15 km	161 km
San Diego	32.87	117.25	33.10	116.33	32 km	28 km
Orange County	33.38	117.59	33.73	118.12	67 km	38 km
Corona Del Mar	33.42	117.65	33.64	118.00	45 km	54 km
Santa Monica Bay	33.75	118.42	34.00	118.80	66 km	56 km
Santa Barbara	34.25	119.27	34.40	119.70	48 km	453 km
Oil Spill Surveys	34.16	119.23	34.47	120.20	110 km	400 km
Monterey Bay	36.70	121.82	36.97	121.92	34 km	42 km
San Francisco Bay Area	37.11	122.30	38.77	123.54	265 km*	--

*Does not include 333 km of bay shoreline length. **Notes:** The Corona Del Mar study area lies within the initial Orange County study area; the Santa Barbara oil spill surveys covered more coastline than the initial Santa Barbara study area.

photo-identification techniques were responsible for documenting 87% of all photo-identifiable sightings. While data reliability can be a concern when using citizen scientists, photographs are verifiable, and fin matching was conducted only by the research team (Cheney et al., 2013; Alessi et al., 2019). Data associated with the photographs included date and location, metadata (e.g., date and time stamps) from digital images, and, in some cases, GPS coordinates. Locations were checked by personal communication with each contributor. Dolphins with identifiable dorsal fins were assigned TMMC (The Marine Mammal Center) catalog numbers. (Individual dolphins are referred to by their numbers or nicknames.)

Puget Sound—Data on coastal bottlenose dolphins from Puget Sound came from dedicated boat-based surveys for cetaceans and an established observer network that included local whale-watching vessels, as well as incidental observations from the general public collected in collaboration with Orca Network. Small boat photo-identification surveys, using techniques essentially similar to those described in Hwang et al. (2014), were initiated by Cascadia Research Collective in August 2016, with monthly transects covering the southern Puget Sound between the Tacoma Narrows and Olympia, Washington. The primary target species were harbor porpoises and common dolphins (*Delphinus delphis*).

Monterey Bay and Southern California Bight—High-resolution photographs of naturally marked coastal bottlenose dolphin dorsal fins were collected with digital or film single-lens reflex (SLR) cameras equipped with telephoto lenses. Boat-based data collection methods in the Ensenada, San Diego, Orange County, Corona Del Mar, Santa Monica Bay, Santa Barbara, and Monterey Bay study areas from 1981 to 2014 were similar and have been previously described (Defran & Weller, 1999; Defran et al., 1999, 2015, 2017; Bearzi, 2005; Hwang et al., 2014). In addition to boat-based survey data, some of the Santa Barbara study area surveys conducted during the 2015 Refugio Beach oil spill were from fixed shore-based observation stations (Defran et al., 2017).

Photo-Identification and Data Analysis

In all study areas, only high-quality images of dorsal fins with two or more distinctive notches on the trailing edge were used for analysis. Similarly, only unambiguous matches were accepted as a re-sighting (i.e., a re-identification of a previously identified individual) within or between study areas. Each date an individual dolphin was identified was defined as a "sighting day." Survey effort and catalog information are summarized in Table 2. Maps used to construct Figures 1A, 1B, and 4 were created with *QGIS*, Version 3.18 (https://qgis.org); Microsoft *Excel* was used to produce data figures and tables.

Table 2. Information on effort conducted across all seasons for study areas, including number of photo-identified bottlenose dolphins (*Tursiops truncatus*; catalog size) compared in this study

Study area	# surveys	# dolphins	Years	References
Ensenada	23	137	1985-1986	Defran et al., 1999
			1999-2000	Guzón-Zatarain, 2002
San Diego	369	997	1981-1989	Defran & Weller, 1999
			1996-1997	Dudzik, 1999
			1998-1999	Lang, 2002
			2004-2005	Dudzik et al., 2006
			2009-2011	Weller et al., 2016
			2011-2014	NMFS, unpub. data
Orange County	44	129	1982-1989	Defran et al., 1999
Corona Del Mar	24	109	2013	This study
Santa Monica Bay	241	408	1997-2014	Bearzi et al., 2009
Santa Barbara	73	182	1987-1989	Defran et al., 1999
			1998-1999	Lang, 2002
Oil Spill Surveys	16	66	2015	Defran et al., 2017
Monterey Bay	409	314	1990-1995	Hwang et al., 2014
			2006-2011	Hwang et al., 2014
			2014-2015	Okeanis, unpub. data
SF Bay Area	186*	84	2007-2018	This study

*Number of days dolphins were photo-identified in the SF Bay Area where effort was primarily shore-based, in contrast to the other study areas where effort was boat-based

Results

San Francisco Bay Study Area

Photo-identification research effort within the SF Bay Area began in June 2007 when photographs of eight distinctly marked bottlenose dolphins were taken from shore. Following this initial image analysis, systematic research effort was initiated in July 2010 and continued through November 2018, resulting in a total of 555 photo-identification records. Research platforms included shore sites, which accounted for 91% (n = 504) of photo-identification records, boats (8%, n = 47), and the Golden Gate Bridge (< 1%, n = 4). During the 2007-2018 study period, a total of 84 distinctly marked dolphins were photographed. The yearly rate at which new dolphins were added to the photo-identification catalog varied from 0 to 25. The number of dolphins resighted from previous years ranged annually from 4 to 37, equivalent to 12 to 51% of the catalog size. The total number of identified dolphins sighted per year in the SF Bay Area ranged from 8 to 43 (Figure 2).

At least one distinct dolphin was photographed on 186 sighting days. Most individuals photo-identified in the SF Bay Area (74%, n = 66) were recorded there in more than 1 y, with 24% (n = 22) sighted in only a single year (mean = 3.26 y ± 0.22 SEM; harmonic mean = 2.1 y; range = 1 to 10 y). The number of resightings for individual dolphins ranged from 0 to 29 (mean = 7 resightings ± 0.67 SEM; median = 5 resightings), with 16 individuals (19% of all marked animals) never resighted (Figure 3). The most frequently sighted dolphin, No. 25 "Bliss," was photographed on 30 d from 2012 to 2018. (See "Supplemental Material" section of the *Aquatic Mammals* website for a table of sightings for the 84 dolphins photo-identified in the SF Bay Area.)

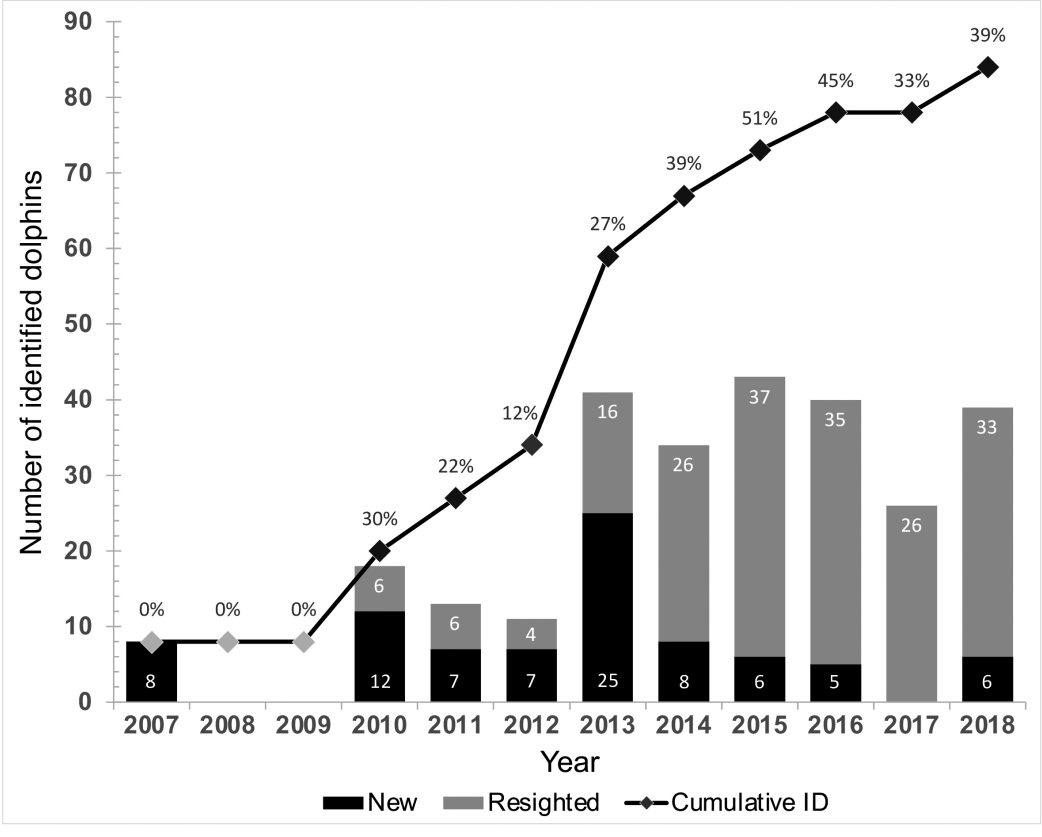

Figure 2. Discovery curve (catalog size) for coastal bottlenose dolphins (*Tursiops truncatus*) in the SF Bay Area and stacked columns with number of individuals (new and resighted) photo-identified (2007 to 2018). Data labels above the cumulative ID markers show dolphins resighted as a percentage of the total number of photo-identified dolphins in the catalog (n = 84). Photo-identification of eight dolphins in 2007 (first gray marker) occurred prior to the 2010-2018 research effort.

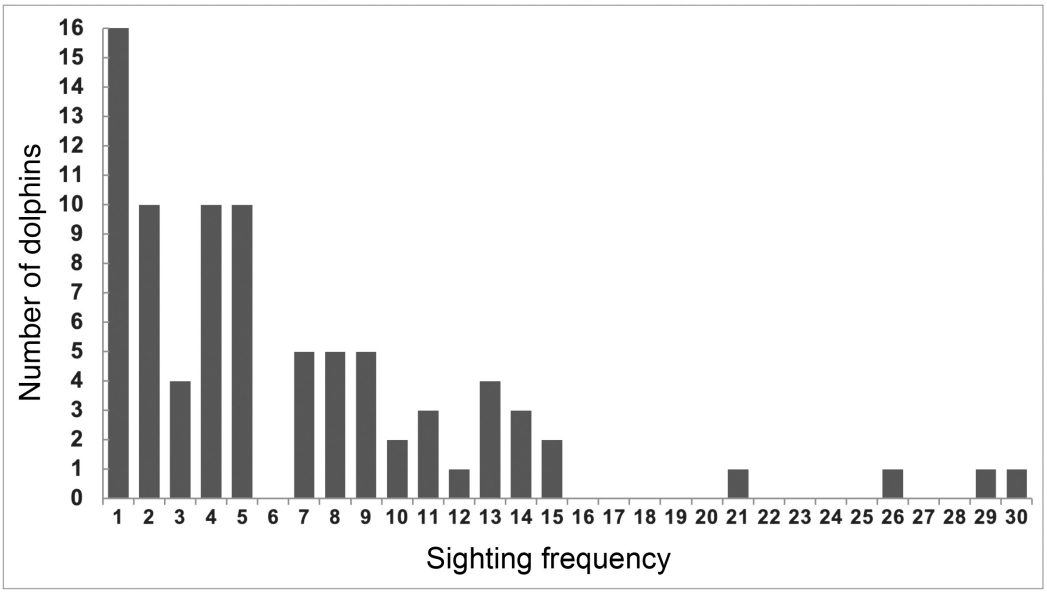

Figure 3. Frequency of sightings (n = 555) for 84 bottlenose dolphins photo-identified in the SF Bay Area from 2007 to 2018

Analysis of the 555 photo-identification records compiled in the study area showed 53% of dolphin sightings (n = 294) were distributed along the Pacific coast while 24% (n = 135) occurred in the Golden Gate strait west of and adjacent to SF Bay. Twenty-three percent (n = 126) of sightings were located in the bay, with records as far as Alameda, 18 km east of the Golden Gate Bridge. The southernmost coastal record came from Pigeon Point, San Mateo County. Thirty-one percent (n = 173) of the photo-identification records came from coastal locations north of San Francisco, including 13% (n = 70) from the Sonoma County coast between Bodega Bay and Sea Ranch. Ten dolphins (2%, 11 sightings) were photo-identified north of the SF Bay Area along the California coast in Mendocino and Humboldt Counties (to 41° N). Nine of these ten dolphins were later resighted back in the SF Bay Area.

Inter-Study Area Movements

The 84 dolphins photographed in the SF Bay Area from 2007 to 2018 were examined for overlap with the photo-identified dolphins catalogued in each of the seven other study areas to the south between 1981 to 2015 (Table 2). Seventy-eight (93%) of the 84 SF Bay Area dolphins were matched to one or more of these catalogs. The highest degree of overlap for the 84 dolphins was with Monterey Bay (92%; n = 77 matches; 1,909 sightings), with lower match rates in study areas located farther south. A total of 33 SF Bay Area dolphins (39%) were in catalogs from the Southern California Bight: San Diego (37%; n = 31; 169 sightings), Santa Monica Bay (35%; n = 29; 87 sightings), Santa Barbara (32%; n = 27; 78 sightings), Orange County (11%; n = 9; 16 sightings), Corona Del Mar (2%; n = 2; 2 sightings), and Ensenada, Baja California, Mexico (1%; n = 1; 1 sighting).

More than half of the 84 SF Bay Area dolphins (54%, n = 45) traveled widely across the stock's range from 1981 to 2018, occurring in one or more of the Southern California Bight study areas. Of these 45 dolphins, 23 exhibited back-and-forth movements (longshore reversals) between the Southern California Bight and the SF Bay Area, while 22 first occurred in the Southern California Bight, followed by sightings in Monterey Bay and then the SF Bay Area. Thirty-nine dolphins (46% of 84) were recorded moving back and forth between Monterey Bay and the SF Bay Area. Of the 84 dolphins photo-identified in the SF Bay Area, 40 (48%) were first identified in the Southern California Bight, 37 (44%) in Monterey Bay, and 7 (8%) in the SF Bay Area. Some dolphins were sighted in the Southern California Bight in the 1980s, then in the Southern California Bight and Monterey Bay in the 1990s, followed by sightings in the Southern California Bight, Monterey Bay, and SF Bay Area in the 2000s and 2010s (Figure 4).

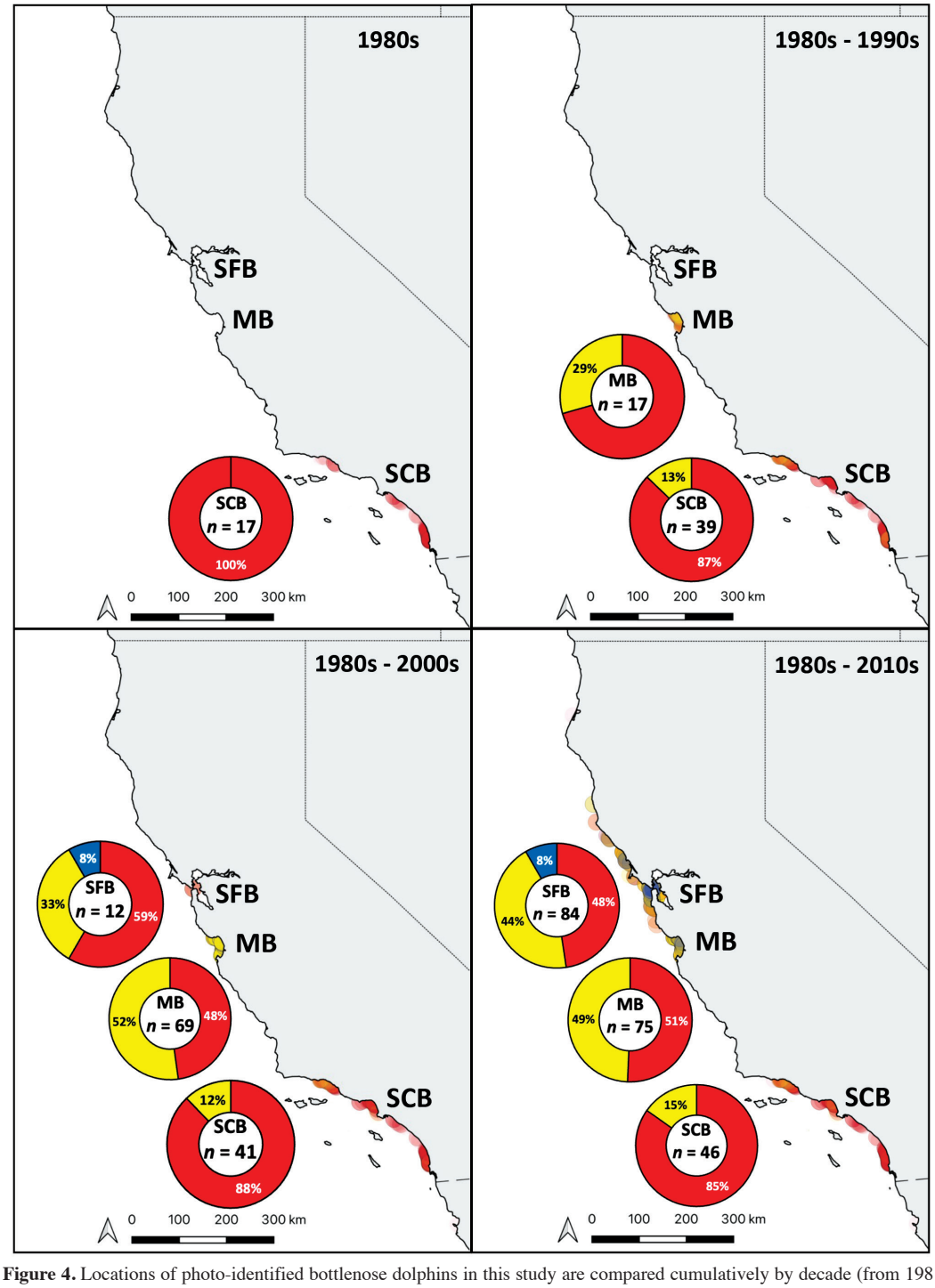

Figure 4. Locations of photo-identified bottlenose dolphins in this study are compared cumulatively by decade (from 1981 to 2018). Doughnut charts show number and percentage of individuals sighted in each region by decade and location of first sighting: red = Southern California Bight (SCB), yellow = Monterey Bay (MB), and blue = San Francisco Bay Area (SFB). Color intensity along the coastline reflects dolphin density (based on sighting counts) and is set to 10% opacity that generates tint blends where dolphins overlapped (e.g., a mix of yellow and blue appears as green).

Extreme Cases of Distance Traveled and Movements Between Areas

No. 3 "Stump" and No. 23 "Miss"—The most northerly latitude reached by coastal bottlenose dolphins during the study was 47° N in southern Puget Sound, Washington, by Stump and Miss in November 2017; Stump was resighted there in 2018. Both dolphins had earlier photo-identification capture histories in the Southern California Bight beginning in 1983. After being first identified in the SF Bay Area in June 2007, Stump was later sighted off Sonoma County (38.7° N) in September 2014; and Miss, first identified in the SF Bay Area in September 2012, was sighted in Mendocino County (39° N) in August 2015, and was last seen in the SF Bay Area in March 2017.

No. 25 "Bliss"—Within California, Bliss was photo-identified off Humboldt County (41° N), 460 km north of San Francisco, on 10 August 2018, before returning to northern Sonoma County (Sea Ranch) 9 d later. Bliss was first photo-identified in the Southern California Bight from 1982 to 1999 and then in Monterey Bay from 2006 to 2011 before being sighted in the SF Bay Area every year from 2011 to 2018.

No. 24 "Smootch"—Smootch was sighted the farthest south (Ensenada, Mexico; 31.7° N) of all dolphins recorded in the SF Bay Area. Exhibiting a high degree of inter-area movement, Smootch was first photo-identified in San Diego in 1984 prior to sightings in Monterey Bay from 1992 to 1994. Smootch was again sighted in the Southern California Bight in 1998 and 1999, in Ensenada in 2000, and in Santa Monica Bay in 2001. After an 11-y sightings gap, Smootch was identified for the first time in the SF Bay Area at Bodega Bay, Sonoma County, in 2012.

Discussion

Range Expansion over a 40-Year Period

We report multiple lines of evidence for the range expansion of California coastal bottlenose dolphins to the SF Bay Area. The 84 photo-identified dolphins cataloged in the SF Bay Area represent approximately 18% of the estimated 453 marked bottlenose dolphins in the California coastal stock (Weller et al., 2016). The annual number of resighted dolphins (Figure 2) and the resighting frequency (Figure 3), plus the finding that most of the dolphins were sighted in multiple years, indicate that after their arrival in the SF Bay Area, coastal bottlenose dolphins became regular occupants of the area to some degree. Overall, presuming its southern limit remained in Ensenada (Carretta et al., 1998; Hwang et al., 2014; Defran et al., 2015), in a 35-y period, members of this stock expanded the total length of their coastal habitat from the Southern California Bight (where they occupied a range of approximately 500 km) to Sonoma County (occupying a range of 1,300 km), a 260% increase. Thus, these data represent *prima facie* evidence of a northerly range expansion for some individuals and support an increased presence of the stock well north of Monterey Bay, the northern range limit previously noted by Hwang et al. (2014). The high proportion of sightings (31%, n = 173) north of San Francisco suggests the range for some or many members of this stock now extends to at least Sonoma County (38.7° N).

The coastal bottlenose dolphin dataset from the SF Bay Area provides a more complete, contemporary, and regional perspective of the range for this stock than previously available. While coastal bottlenose dolphins were sporadically sighted north of Monterey Bay in the 1980s and 1990s, regular sightings and photo-identification records showed an increase in their occurrence in the SF Bay Area and waters to the north in the 2000s and 2010s, indicating a continued northward range expansion during this time. Hwang et al. (2014) observed regular back and forth movements of coastal bottlenose dolphins between study areas in the Southern California Bight and Monterey Bay. Analysis of photo-identification records from SF Bay confirmed that this pattern of regular back and forth movement continued with the recent range expansion as dolphins moved between SF Bay and other study areas across their range.

Extralimital Sightings

The northernmost coastal bottlenose dolphin sightings in Washington State, where occurrences of this species are rare (Ferrero & Tsunoda, 1989), establish a new distance record for coastal bottlenose dolphins, based on a coastal range of 2,500 km from San Diego to Puget Sound. This exceeds the distance records of photo-identified coastal bottlenose dolphins reported in European waters of 1,076 km (Wood, 1998), 1,277 km (Robinson et al., 2012), and 2,053 km (Genov et al., 2022). By comparison, the offshore ecotype of bottlenose dolphin has exhibited movements of up to 4,200 km in the Gulf of Mexico (Wells et al., 1999).

During the time when Stump and Miss were traveling north to Puget Sound, likely between March to November 2017, no bottlenose dolphins were reported on the coasts of Oregon or Washington, although marine mammal research and local whale-watch trips were active in selected areas along that coast. The only known sighting of live bottlenose dolphins in coastal Oregon during the study period occurred in Port Orford on 9 August 2018 when Oregon State University researchers took video footage of a group of three (including a calf), but there were

no usable photo-identification images (L. Torres, pers. comm., 15 August 2022). The day after this Oregon sighting, on 10 August 2018, Bliss was photo-identified incidentally off Humboldt County (41° N), approximately 200 km south of Port Orford. Given the distance between the two locations, and the fastest travel speed of 95 km/d reported for the stock (Hwang et al., 2014), it seems plausible that multiple bottlenose dolphin groups were near the Northern California–Southern Oregon area during that time frame.

Study Limitations

The analysis we present draws upon data collected from multiple sources and researchers over a period of four decades. Field research effort, platforms, methods, and photographic equipment were often variable throughout this time. For example, almost all of the data collected in Southern California and Monterey Bay were through dedicated research vessel surveys (Hwang et al., 2014), while more recent data from the SF Bay Area were primarily shore-based. Coastal bottlenose dolphins are typically found within 500 m of shore, and shore-based photography had an effective range of about 250 m for dolphin identification. Thus, sampling of identifiable coastal bottlenose dolphins in the SF Bay Area was likely subject to imperfect detection, and the lack of a plateau in the discovery curve (Figure 2) suggests more as-yet unidentified dolphins may be present, and still arriving, in that study area. The SF Bay Area data were collected from a variety of sources, including records obtained from research and tour vessels, and from shore-based researchers, citizen scientists, and the general public. Due to differences in observational effort and methods, caution should be exercised when interpreting the frequency of occurrence of bottlenose dolphins in various study areas. What remained consistent throughout this time period and across study areas was the use of high-quality images showing individually identifiable dolphins with unambiguous dorsal fin markings for photo-identification records, including confirmed dates, times, and locations (Weller & Defran, 2016). We have a high degree of confidence in what photo-identification records confirm about the range and movement patterns of distinctively marked dolphins.

Potential Environmental Drivers of Range Expansion

The extensive coastal movements exhibited by California coastal bottlenose dolphins may be the result of the interplay between environmental variables, food resources, and foraging strategies (Defran et al., 1999). Wells et al. (1990) suggested increased water temperature is a mechanism for range expansion, and Defran et al. (1999) pointed to California's spatially fluctuating marine food resources as a factor promoting the dolphins' wide-ranging movements. The California Current Ecosystem (CCE), which stretches along the West Coast of the U.S. to Baja California, features wind-driven upwelling that leads to high biological productivity (Chavez & Messié, 2009; Checkley & Barth, 2009), with a reputation for variability (Ralston et al., 2015). Recently, more severe and prolonged marine heatwaves have been superimposed on regular El Niño Southern Oscillation/Pacific Decadal Oscillation fluctuations in the CCE upwelling (Hobday et al., 2016).

Coincident with increasing records of bottlenose dolphins in the SF Bay Area and on the coast farther north, the West Coast of North America experienced the most powerful marine heatwave ever recorded (Di Lorenzo & Mantua, 2016). From 2014 to 2016, high sea surface temperatures led to unprecedented impacts on multiple trophic levels in the CCE, including harmful algal blooms (Trainer et al., 2020), and mass seabird and marine mammal mortality due to changes in the distribution of their prey (Cavole et al., 2016; National Marine Fisheries Service [NMFS], 2016; Jacox et al., 2018; Piatt et al., 2020). Increased sea surface temperatures were detected by 2013, the year that a pulse of 25 previously unidentified dolphins were photographed in the SF Bay Area (Piatt et al., 2020; Figure 2). The August 2015 occurrence of the dolphin Miss as far north as Mendocino County (39° N) coincided with the unusually elevated sea surface temperatures. At the height of this marine heatwave, numerous invertebrate and vertebrate marine species set new northern range records on the West Coast (Sanford et al., 2019). These records included a large group of likely offshore ecotype bottlenose dolphins sighted in 2017 at 50° N off British Columbia (Halpin et al., 2018), approximately 1,000 km north of this stock's typical range, suggesting at least a temporary shift in response to ocean warming in the eastern North Pacific.

Complex atmospheric and oceanic variables driving coastal upwelling productivity make it difficult to predict the timing or extent of a distribution change for any species (Hazen et al., 2013; Bakun et al., 2015; Nykänen et al., 2019). Nevertheless, projected climate change on the West Coast is anticipated to have a strong poleward trajectory along the shore (Morley et al., 2018). The CCE has been identified as one of the global marine "hotspots" where ocean warming is proceeding at the fastest rate (Hobday & Pecl, 2014), increasing the probability of extreme environmental conditions such as marine heatwaves attributable to anthropogenic warming (Laufkötter et al., 2020). California coastal bottlenose dolphins, like other marine taxa,

can reasonably be expected to continue moving to higher latitudes (MacLeod, 2009; Pinsky et al., 2013).

Ecological Consequences of Range Expansion

As top marine predators expanding their range north, California coastal bottlenose dolphins may encounter new prey and interact with other species. For example, as the dolphins move into cooler waters, they share habitat with populations of harbor porpoises (Jacobsen et al., 2015; Forney et al., 2020). Interspecies encounters have been known to trigger aggressive behavior by the coastal dolphins toward the smaller porpoises (Cotter et al., 2012). Lethal aggression, termed "porpicide," was a primary factor contributing to a harbor porpoise unusual mortality event declared off Central California (NMFS, 2008). Spikes in porpoise deaths due to the type of blunt force trauma associated with porpicide, such as fractures and hemorrhages, often accompanied by tooth rake marks, were documented in 2008 and 2009 from as far north as Sonoma County (Wilkin et al., 2012) shortly after coastal bottlenose dolphins reached the SF Bay Area.

The California coastal bottlenose dolphin dataset from the SF Bay Area provides a more complete, contemporary, and regional perspective of the range for this stock than previously available. These dolphins demonstrated a surprising capacity for long distance movements, and their range may continue to expand even farther north. Investigators should be alert for sightings of bottlenose dolphins in Oregon and Washington; and marine mammal stranding networks in those areas should be attentive to harbor porpoise necropsy findings consistent with trauma inflicted by bottlenose dolphins.

Management Implications

The results of this study should interest resource managers charged with dolphin conservation. Currently, the California coastal bottlenose dolphin population is not considered threatened or depleted. Nevertheless, it remains a small, genetically distinct stock that may be vulnerable to human threats and ecosystem changes. The minimum population size estimate for all California coastal bottlenose dolphins, including marked and unmarked animals, is about 600 (Weller et al., 2016). Although range expansion may have a positive effect on the coastal bottlenose dolphins by reducing the chances of a population-wide impact from a local catastrophic event (e.g., an oil spill) by extending their range into the SF Bay Area, this stock is exposed to a new suite of human-related threats. Despite recent habitat restoration that led to dramatically improved water quality (San Francisco Estuary Project, 1992), the bay remains one of the most human-altered major estuaries in the U.S. Intensely developed, it is subject to toxic pollution, anthropogenic underwater noise, and congested vessel traffic (Nichols et al., 1986; Cope et al., 2020, 2021). Effective management depends on accurate information about stock boundaries, structure, abundance, and habitat requirements. Therefore, ongoing monitoring is warranted as increased efforts would produce a more informed foundation for decision-making with regard to this dynamic population of coastal bottlenose dolphins. Coordinated mark-recapture surveys and collaborative photo-identification efforts, supported by genetic studies, in the Southern California Bight, Monterey Bay, and the SF Bay Area could resolve the degree to which distribution patterns are changing and what the population trend is in light of the range expansion described herein.

Note: A supplemental table for this article is available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147.

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