CHANGES IN ABUNDANCE AND DISTRIBUTION OF NESTING DOUBLE-CRESTED CORMORANTS *PHALACROCORAX AURITUS* IN THE SAN FRANCISCO BAY AREA, 1975–2017

MARK J. RAUZON[1*], MEREDITH L. ELLIOTT[2], PHILLIP J. CAPITOLO[3], L. MAX TARJAN[4], GERARD J. McCHESNEY[5], JOHN P. KELLY[6] & HARRY R. CARTER[7†]

[1]*Laney College, Geography Department, 900 Fallon Street, Oakland, CA 94607, USA *(mrauzon@peralta.edu)*
[2]*Point Blue Conservation Science, 3820 Cypress Drive, #11, Petaluma, CA 94954, USA*
[3]*Institute of Marine Sciences, University of California Santa Cruz, 115 McAllister Way, Santa Cruz, CA 95060, USA*
[4]*San Francisco Bay Bird Observatory, 524 Valley Way, Milpitas, CA 95035, USA*
[5]*US Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex, 1 Marshlands Road, Fremont, CA 94555, USA*
[6]*Audubon Canyon Ranch, Cypress Grove Research Center, P.O. Box 808, Marshall, CA 94940, USA*
[7]*Humboldt State University, Department of Wildlife, 1 Harpst Street, Arcata, CA 95521, USA*
[†]*Deceased*

Received 19 October 2018, accepted 13 February 2019

ABSTRACT

RAUZON, M.J., ELLIOTT, M.L., CAPITOLO, P.J., TARJAN, L.M., McCHESNEY, G.J., KELLY, J.P. & CARTER, H.R. 2019. Changes in abundance and distribution of nesting Double-crested Cormorants *Phalacrocorax auritus* in the San Francisco Bay area, 1975–2017. *Marine Ornithology* 47: 127–138.

In the San Francisco Bay area, California, the Double-crested Cormorant *Phalacrocorax auritus* population has recovered from significant declines to reach breeding population sizes comparable to those from the late 19th century, when only one colony offshore at the South Farallon Islands (SFI) was known. The recent replacement of the bridge hosting one of the current largest colonies prompted a comprehensive assessment of Bay Area breeding population trends through 2017. Since the early 1970s, the Bay Area population has expanded from < 50 pairs at one site, SFI, to nearly 3 500 pairs at > 20 colonies, with breeding documented at 31 different locations. However, missing counts at many colonies before 2003 prevented calculation of precise, long-term growth rates. Expansion has been facilitated by cormorant adaptations to the urbanized estuary, including nesting on bridges, electrical towers, non-native trees, and managed pond levees. Breeding colonies that formed by 1984 on the San Francisco-Oakland Bay Bridge (SFOBB) and Richmond-San Rafael Bridge (RSRB) grew quickly, and in several different years totaled more than 1 000 nests. From 2003 to 2017, when construction of a new east span of the SFOBB (and demolition of the old span) was underway and when substantial maintenance of the RSRB occurred, the colonies on the bridges declined by 71 % and the overall Bay Area population declined by 39 %. The decline was likely due to reduced prey availability, although construction disturbance may have driven some birds from the bridges to colonies outside the region. On the Outer Coast, the colony at Hog Island was formed in 2001 and has become the largest in the study area since 2011. Nesting on artificial platforms installed on the new SFOBB east span in 2017 occurred only after demolition of the old span was complete, despite social attractions being in place since 2011.

Key words: San Francisco-Oakland Bay Bridge, Double-crested Cormorant, *Phalacrocorax auritus,* San Francisco Bay, regional expansion, urbanized estuary

INTRODUCTION

The Double-crested Cormorant *Phalacrocorax auritus* (DCCO) is widely distributed across North America (Wires & Cuthbert 2006, Dorr *et al*. 2014). About 21 000 breeding pairs were estimated in 2008–2009 within the Western population (west of the continental divide excluding Alaska and Mexico; USFWS 2017a), along the Pacific coast from British Columbia through California. The largest colony—at East Sand Island (ESI) in the Columbia River Estuary, Oregon—accounted for 57 % of nests. The population in the San Francisco Bay area (Bay Area), including the offshore colony at the South Farallon Islands (SFI), was a distant second, accounting for 10 % of Pacific coast breeders (Adkins *et al*. 2014). The estimated nest total along the Pacific coast in 2008–2009 was about 68 % higher than the total in 1987–1992 (Adkins *et al*. 2014), which itself represented a substantial increase in nests since the 1970s (Carter *et al*. 1995).

Declines in Double-crested Cormorant nests throughout North America in the 19th century, and again in the 1950s–1970s, were due, in part, to anthropogenic activities, including disturbance to nesting colonies, fisheries depletion, and eggshell thinning from DDT pollution (Dorr *et al*. 2014). The elimination of organochlorine pesticides in the early 1970s reduced their deleterious effects on cormorant reproduction. Several additional factors have contributed to substantial population recovery, especially among Interior, Atlantic, and Southeast populations. Human disturbance has been reduced and food availability has increased through aquaculture, stocking of water bodies with hatchery-reared fish, introductions of invasive fish species, and overfishing of large predatory fish that compete with cormorants (Hatch 1995, Wires *et al*. 2001). This recovery has led to conflict with commercial and recreational fishing interests, resulting in the permitted take of DCCO in 37 central and eastern states (USFWS 2017b). In the Western

cormorant population, management of the large ESI colony began in 2015 with the goal of reducing DCCO consumption of threatened and endangered salmonids *Oncorhynchus* spp. (USACE 2015).

In San Francisco Bay, archaeological evidence (including bones of DCCO juveniles) from the Emeryville Shellmound indicates there were likely breeding colonies in the central bay and that hunting by Native Americans may have caused their extirpation (Broughton 2004). In the late 19th century, only the large breeding colony at SFI was known to be active, estimated to be approximately 2 500 breeding pairs (Ainley & Lewis 1974). The central coast-breeding white-plumed subspecies was once called the Farallon Cormorant *P. a. albociliatus* (Grinnell 1915, Grinnell & Wythe 1927). The Farallon colony declined dramatically to fewer than 50 pairs due to disturbance from egg harvesting, lighthouse maintenance, and other human activities (Boekelheide *et al*. 1990, White 1995, Capitolo *et al*. 2009). Other small colonies were noted on the outer coast during the first half of the 20th century in the Drakes Bay area at Point Resistance in 1929 (Bolander & Bryant 1930; Carter *et al*. 1992, 1995), at Pillar Point in 1940 (Carter *et al*. 1992), and at Seal Rocks at the mouth of the Golden Gate in 1912 and 1917 (Hansen & Squires 1917, Squires 1917, Grinnell & Wythe 1927). Nesting inside San Francisco Bay proper was not noted until 1975, despite observations of foraging throughout the Bay earlier in the 20th century (Grinnell & Wythe 1927, Carter *et al*. 1992). Numbers may have been augmented in winter by birds from other populations, such as a 1940 count of 2 300 birds roosting on power lines near the site of the present-day Richmond-San Rafael Bridge (RSRB; Bartholomew 1943).

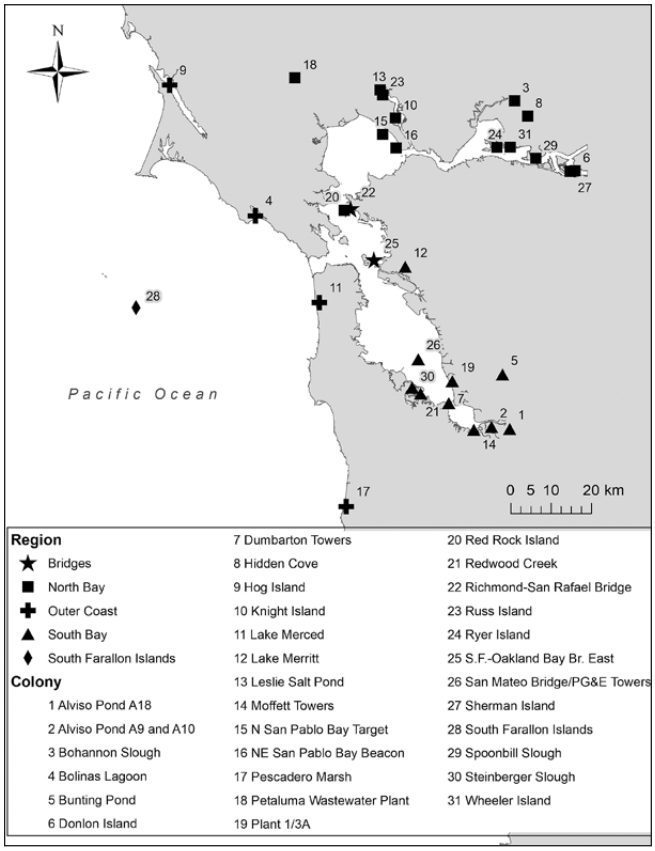

Fig. 1. Double-crested Cormorant nesting colonies from 1984 to 2017 in the San Francisco Bay area. Colonies are symbol-coded by the sub-regions used for cataloging.

The Bay Area has become highly urbanized over the past 200 years, creating significant impacts on fisheries and wildlife (Conomos 1979, Scott 1985, Nichols *et al*. 1986). The built environment, however, has provided new breeding sites not just for DCCO, but also for other waterbirds (e.g., Strong *et al*. 2004), including Osprey *Pandion haliaetus* (Brake *et al*. 2014). What are now among the largest DCCO colonies in this region originally formed in the early 1980s on the east spans of bridges in central San Francisco Bay. Construction to replace the earthquake-damaged east span of the San Francisco-Oakland Bay Bridge (SFOBB) began in 2003 and ended in 2017, when demolition of the old span was complete. During the same period, seismic retrofitting of the east span of the RSRB took place. To help assess the impacts of bridge construction and maintenance, as well as other factors affecting DCCO in the Bay Area, we collated nest count data for 31 colonies during the 1984–2017 period. We then analyzed regional trends for the entire timespan, including periods before and during bridge construction activities. In our summary of these trends, we discuss the importance of the bridge colonies and how DCCO have exploited novel nesting sites in this urbanized estuary. Going forward, the Bay Area trends will help interpret monitoring of the Western population, which is scheduled through 2023 to help assess the effects of management of the ESI colony on the population as a whole (USFWS 2017a).

METHODS

Study Area

Our study area included colonies 1) offshore at SFI, because DCCO breeding there are known to forage in mainland estuaries (Ainley & Boekelheide 1990); 2) in San Franciso Bay and adjacent water bodies (fresh and estuarine); and 3) on the Outer Coast, which we defined as the mainland coast of the Gulf of the Farallones (including adjacent areas) from roughly Tomales Point to Point Año Nuevo. We further divided San Francisco Bay into three sub-

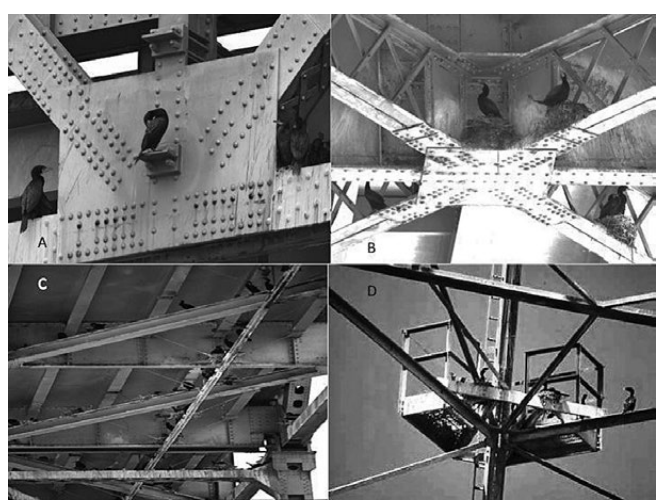

Fig. 2. Nesting substrates used by Double-crested Cormorants in the San Francisco Bay area: (A) Richmond-San Rafael Bridge (Colony 25); (B) San Francisco-Oakland Bay Bridge girders (Colony 22); (C) Richmond-San Rafael Bridge girders (Colony 22); (D) San Mateo Bridge Power Towers (26). Colony numbers in parenthesis correspond to colonies in Figure 1. Photographs in Figs. 2–5 by Mark Rauzon unless otherwise noted.

regions: 1) North Bay, including San Pablo Bay, former salt ponds to the north, and Suisun Bay to the east; 2) Bridges, which included RSRB and SFOBB; and 3) South Bay, including all shoreline areas south of the SFOBB. A total of 31 colonies were documented within these five sub-regions, including SFI, 14 North Bay colonies (10 in trees, one on a power tower, one on a levee, and two on other artificial structures in San Pablo Bay), two Bridge colonies, 10 South Bay colonies (six on power towers, two in trees, and two on levees), and four Outer Coast colonies in trees (Figs. 1–5). The study area represents the Central Coast-Outer Coast North and Central Coast-San Francisco Bay sub-regions of previous DCCO status assessments in the Western region (Carter *et al*. 1995, Adkins *et al*. 2014).

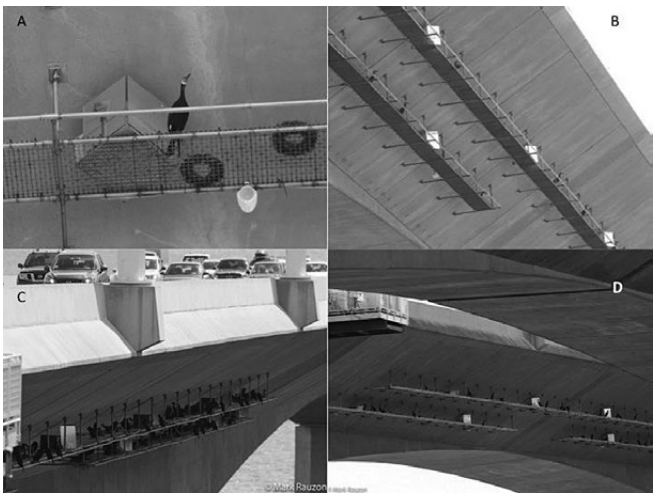

Fig. 3. New San Francisco-Oakland Bay Bridge "Corm Condos" specifically designed in 2001: (A) decoy, mirror box, sound system, and artificial nests made of Christmas wreaths added in 2012; (B) platforms went unused for six years; (C) platform positioning on New Bridge relative to traffic; (D) adoption of platforms after old bridge was demolished in 2017.

Fig. 4. Variation in DCCO nesting habitat: (A) eucalyptus trees, Lake Merritt, Oakland (Colony 12); (B) Russ Island colony (Colony 23); (C) A9/A10 pond levee (Colony 2), photo courtesy of Cheryl Strong; (D) A9/A10 pond levee (Colony 2), photo courtesy of Amanda Alsumidaie-Reynolds.

Surveys of breeding colonies

A combination of ground, boat, and aerial photographic surveys were conducted by several sources during peak nesting between mid-May and early July since 1987, and we collated other available nest counts (Appendix 1, available on the website). However, not all colonies were surveyed in all years and not all archived aerial photographs were analyzed, especially before 2003. In cases where counts of a colony were available from two different sources, both counts were used in models but only the high count was shown in charts. We report only raw nest counts and did not apply correction factors (see Capitolo *et al*. 2019).

Bridges Roadway and Boat Surveys (Point Blue Conservation Science [Point Blue])

Cormorant nesting habitat underneath bridge roadways included various structures (e.g., cords, I-beams, and painting platforms), as well as structural support girders that spanned the north and south sides of each bridge (positioned about 3 m below the outer edge of the lower roadway; Rauzon *et al*. 2001). The RSRB is a two-deck steel bridge, spanning about 7 km from Richmond, Contra Costa County (on the east side) to San Quentin, Marin County (Historic Bridges 2018). The SFOBB stretches about 7.2 km from Oakland, Alameda County (on the east side) to San Francisco, San Francisco County, with Yerba Buena Island in the middle (San Francisco-Oakland Bay Bridge 2018). The former eastern span where DCCO nested was a two-deck steel bridge built in 1936. In 2013, a new cement eastern span with two parallel decks was completed (Skyway 2018). Removal of the old eastern span was completed in March 2017. The RSRB and SFOBB host cormorant colonies only on their eastern portions, where the height over the water is lower and where roosting structures are available for post-fledging parental care (e.g., Castro Rocks near the RSRB, and a cable crossing structure near the SFOBB).

In most years of the study, a boat survey was conducted on a single day in May or June by Point Blue to count nests underneath the roadways and in the support girders along the roadway of both the RSRB (years 1994, 1999, 2004–2005, 2007–2016) and SFOBB (years 1988, 1990, 1994, 1999, 2000, 2004–2005, 2007–2016).

Fig. 5. An aerial photograph (north at top) showing the extent of the Double-crested Cormorant colony (nests among guano-covered areas at center, top, and right) on Maintop, South Farallon Islands, 04 June 2017. A large Common Murre colony is at the far right; photo by Mike Parker, University of California Santa Cruz.

Experienced observers using binoculars counted nests that were visible on the sides and underneath the roadways of each bridge (Fig. 2). The boat transited the length of a bridge section to view all angles while three observers conducted independent counts; observer count totals were averaged for the official tally. Surveys in 2003 were conducted by Humboldt State University (HSU; Capitolo *et al*. 2004).

Both road and boat surveys of RSRB were conducted from 1988 to 1990, and in 2000, as part of a DCCO breeding study (Stenzel *et al*. 1995, Rauzon *et al*. 2001). Road surveys were conducted every two weeks from the lower roadway to count nests in the support girders (on the north and south sides of the bridge). Road surveys required lane closures and escorts by California Department of Transportation (CalTrans) maintenance crews. Boat surveys were also conducted biweekly to count nests on structures underneath the lower roadway. Each biweekly road and boat survey was summed, and the peak total count was used. Only the seasonal total count was available in 1988 and it was not used in our analyses. These comprehensive surveys allowed reproductive success rates to be determined in addition to complete colony counts.

In 2017, when the SFOBB colony relocated to the new east span, CalTrans arranged for a lane closure on the eastbound side (southern structure) on 09 June so biologists could count nests on the specially-designed and manufactured stainless steel nesting platforms underneath the interior edges of the roadways (Fig. 3). Beginning in 2011, in an attempt to attract cormorants to the new habitat, nesting platforms were enhanced with commercially available decoys of Great Cormorants *P. carbo*, artificial nests made from wreaths, mirrors, and a sound system playing DCCO vocalizations.

North Bay and Outer Coast Ground and Boat Surveys (Audubon Canyon Ranch [ACR])

Annual counts at most North Bay colonies were based on peak nesting abundance among repeated surveys conducted at monthly intervals in early April, May, and June. Surveys were conducted using binoculars and telescopes from vantage points on the ground near each colony. Surveys of Bohannon Slough, Hidden Cove, Leslie Salt Pond, Petaluma Wastewater Treatment Plant, Russ Island, and Spoonbill Slough were conducted once per year, in the third week in May. This coincided with the time when most DCCO pairs were well into the nestling period, and when many or most were in the later post-guardian phase of nest attendance (when chicks were no longer attended continuously by adults). Nests at Ryer Island, Sherman Island, and Wheeler Island were counted from a boat in a stable position along the shore close to the colony. Surveys at two of the Outer Coast colonies (Hog Island and Bolinas Lagoon) were also conducted once per year, between June and early July, when most nests were still in the nestling phase. At sites visited once per year, empty, well-built nests with substantial amounts of guano or other clear evidence of nesting activity in the current year were included in the counts.

South Bay and Outer Coast Ground Surveys (San Francisco Bay Bird Observatory [SFBBO])

South Bay colonies (Alviso Pond A9/A10, Alviso Pond A18, Bunting Pond, Dumbarton Bridge Power Towers, Lake Merritt, Moffett Towers, Pond 1/3A, Redwood Creek, Steinberger Slough, and San Mateo Bridge Power Towers) and two Outer Coast colonies (Pescadero Marsh and Lake Merced) were visited at least once a month from early March to early August, and twice a month in May and June, for a total of eight survey dates per year. Trained volunteers used binoculars and spotting scopes to count active nests from vantage points on the ground near each colony. For sites with multiple survey dates, peak nest counts in each year were used in the analysis. DCCOs that nested within California Gull *Larus californicus* colonies (Alviso Pond A9/A10 and Pond 1/3A) were surveyed by SFBBO staff and volunteers once per year in the second week of May, during annual California Gull walk-through surveys. To avoid disturbing nesting cormorants and to decrease the risk of depredation of eggs and chicks by California Gulls, staff used scopes and binoculars from levees or kayaks to estimate the number of cormorant adults and nests from a minimum distance of 20 m (Fig. 4). Counts for the first years of nesting at Moffett Towers and Alviso Pond A9/A10 were taken from Bousman (2007).

Aerial Photographic and Boat Surveys (US Fish & Wildlife Service, Humboldt State University & University of California, Santa Cruz)

For all sub-regions except Bridges, standardized aerial photographic surveys of coastal DCCO colonies were conducted during 1985–2017 (except 1991 and 1992) as part of surveys that also targeted Common Murre *Uria aalge* and Brandt's Cormorant *P. penicillatus* colonies throughout central and northern California (Takekawa *et al*. 1990; Carter *et al.* 1992, 1995, 1996, 2000, 2001; Capitolo *et al*. 2004, 2014, 2019). Single aerial surveys of DCCO colonies occurred from 23 May to 19 June. Data on numbers of DCCO nests derived from aerial photography were first available for SFI in 1987. Ground counts of SFI conducted throughout the breeding season by Point Blue were not used in determining trends because they were known to include only a portion of the colony (Fig. 5; Carter *et al*. 1992). However, the highest annual ground counts (Point Blue, unpubl. data) were compared with counts from aerial photography of SFI (see Statistical Analyses below). Colonies inside San Francisco Bay were not regularly surveyed by air until 1993, and certain colonies surveyed by ACR and SFBBO, as well as Lake Merced on the Outer Coast, were not regularly surveyed using aerial photography. San Mateo Bridge Power Towers were not surveyed by aircraft after 2003 due to the difficulty associated with accessing airspace near San Francisco International Airport.

Aerial surveys were conducted mostly from a twin-engine Partenavia fixed-wing aircraft. Survey altitudes ranged from 150 m to 365 m above sea level. Prior to 1997, photographs were taken obliquely through side windows and window ports. From 1997 to 2017, photographs were taken vertically through a port in the belly of the aircraft. Before 2007, photographs were taken with handheld 35 mm cameras and color slide film (ASA 200) with 300 mm lenses for close-up photographs; 50 mm or zoom lenses were used for overview photographs. Thereafter, digital APS-C cameras were used, with 200 mm telephoto lenses for close-ups.

Whole-colony counts were determined by 1) selecting the best images; 2) marking each nest, territorial site, and bird; and 3) summing counts. Image analysis was initially done from slides projected on paper, and later using manual methods of software; automated methods of categorizing and counting species and nests have thus far proved inadequate for analyzing aerial photographs of seabird colonies in California (PJC, unpubl. data). Nests included poorly-built to well-built nests attended by adults or chicks and

empty or abandoned nests that were clearly active in the survey year. Territorial sites (i.e., locations attended by adults with little or no nesting material) and birds were not used in our analyses. Effort was made to complete counting of archived aerial photographs since 2003 (the onset of SFOBB construction), but some aerial photographs remain uncounted, especially those of SFI from 2009, 2010, and 2012. Some earlier photographs also remain uncounted, especially those of Knight Island taken between 1995–2002. Since 2015, five colonies in the study area have been counted annually from aerial photographs as part of an effort to monitor the size of the Western population of DCCO (USFWS 2017a).

In 1990, boat surveys of all DCCO colonies that could be viewed from the Bay were conducted by HSU as part of a survey of all seabird colonies within the estuary (Carter *et al*. 1992). Also, the San Mateo Bridge Power Towers colony was surveyed opportunistically by boat in 2005, 2014, and 2015 by the US Fish and Wildlife Service (USFWS) and HSU (Fig. 2D). The 2014 survey did not include towers at the east end of the bridge that had been colonized in the previous one to three years (based on anecdotal observations by GJM), but these represented a relatively low proportion (15 %) of the colony in 2015.

Statistical Analyses

In addition to entire time periods, two sub-periods of interest were identified and analyzed for each region: the first year of data available through 2002, and 2003–2017. For the Bay Area total, analyses began with 1990, as it was the first year in which all regions were nearly completely surveyed (Carter *et al*. 1992). The first sub-period represents the years before construction of the new SFOBB span began, while the second encompasses the construction of the new bridge and demolition of the old one. These two periods were chosen under the assumption that DCCO would be dispersing away from the disturbance created by construction and demolition activities. In addition to estimating regional population trends, we performed a linear regression to define a correction factor between aerial and ground counts of SFI.

To account for potential biases arising in raw counts due to differences in the survey date and method, we tested competing models that included measured covariates—comprising the day of the season and survey type (aerial, boat, ground)—in our estimates of regional trends for each time-period. Long-term population dynamics are frequently non-linear, so we used Generalized Additive Mixed Models (GAMM), which allow each colony to grow non-linearly over time. We estimated the regional counts by summing across error-weighted colony counts to correct for years when certain colonies were not visited. GAMMs were developed using the mgcv package (Wood 2011) in R version 3.3.2 (R Core Team 2016), following the approach of Shadish *et al*. (2014). We considered the following models for Poisson-distributed count data:

Model 0: count ~ s(year × colony) + colony
Model 1: count ~ s(year × colony) + colony + s(day)
Model 2: count ~ s(year × colony) + colony + survey type
Model 3: count ~ s(year × colony) + colony + s(day) + survey type

The s() function allows the estimate to vary non-linearly, and the year-by-colony interaction allows the colony trend to change non-linearly across years. We assessed the model fit using the unbiased risk estimator (UBRE), which is the minimized, generalized cross-validation score of the fitted GAMM. Lower UBRE scores indicate a better model fit to the data (Wood 2006). We also compared the models using Akaike's information criterion for small sample sizes (AICc), implemented using the AICc function in the MuMIn package (Barton 2018).

We assumed that the regional trend estimate in a given year was equal to the sum of the estimated colony trends, where the colony trends were weighted by their relative size and error. We limited the colonies that we included in the regional trend estimate to those with sufficient data to identify a trend over the periods of interest, which we defined as colonies with a minimum of 10 nests and 10 years of count data, namely: RSRB, SFOBB, Bohannon Slough, Knight Island, N. SP Bay Target, Petaluma Plant, Russ Island, Spoonbill Slough, Wheeler Island, Hog Island, Lake Merced, Alviso Pond A18, Alviso Pond A9/A10, Dumbarton Towers, Lake Merritt, Moffett Towers, Redwood Creek, San Mateo Towers, Steinberger Slough, and SFI. We used a simulation approach of 10 000 replicate estimates of each colony-by-year parameter to generate confidence intervals around the regional estimates. For our time periods of interest, we calculated a mean and confidence interval for percent change. Percent change was calculated as (final count–initial count)/initial count × 100. Due to missing counts in early years and the compounding effect of summing estimate errors across many colonies—particularly in the North Bay region, the South Bay region, and for the Bay Area total—estimates for the 2003–2017 sub-period are more precise than estimates for the time periods encompassing earlier years.

RESULTS

Model Selection

The full model, i.e., Model 3 (nest count as a function of year, colony, survey date, and survey type), had the lowest AICc score and UBRE (6.12), and the highest explained deviance (96 %; Table 1), of the four models tested. This model indicated that the effects of survey type and the day of the season were significant, so

TABLE 1
Model fit and deviance explained for the four models tested

Model		d*f*	ΔAICc	UBRE[a]	Deviance explained
M0	Count ~ s(Year, by = Colony) + Colony	209	749	6.753	0.955
M1	Count ~ s(Year, by = Colony) + Colony + s(Day)	216	310	6.309	0.958
M2	Count ~ s(Year, by = Colony) + Colony + Survey.type	208	438	6.570	0.956
M3	Count ~ s(Year, by = Colony) + Colony + s(Day) + Survey.type	218	0	6.116	0.959

[a] unbiased risk estimator

we selected Model 3 to estimate regional trends while accounting for these effects. Survey date showed a non-linear trend, where surveys early in the season and at the very end of the season resulted in lower trend estimates (Fig. 6). The parameter estimates for aerial surveys differed significantly from those for boat/ground, boat, and ground surveys ($P < 0.0001$).

Regional Trends

South Farallon Islands

SFI represents the only location in the Bay Area at which a DCCO colony was continuously active over the last century (Ainley & Lewis 1974, Carter *et al*. 1995). Since at least 1903, DCCO have nested atop Maintop on West End Island. As late as 1887, DCCO also nested in two locations on Lighthouse Hill on Southeast Farallon Island (Emerson 1904, Ainley & Lewis 1974). Recovery from earlier declines was first noted in the mid-1970s, when the colony increased from fewer than 50 nests to 229 nests in 1982. The nest total decreased to < 100 in 1983 during strong El Niño conditions. Despite incomplete viewing of the colony during ground surveys, an increase in the size of the colony from the 1970s to the early 2000s was conspicuous (Boekelheide *et al*. 1990; Carter *et al*. 1992, 1995; Point Blue, unpubl. data). Colony size peaked in the early 2000s, with aerial photographic counts of > 500 nests in 2002 and 2004, and > 600 nests in 2006, before declining through the end of the study period (Fig. 7; low count of 142 nests in 2015). The size of the SFI colony increased from 1987 to 2002 by 122 % (95 % CI = 64 %–205 %) but then declined by 61 % (95 % CI = 72 %–49 %) from 2003 to 2017 (Table 2, Fig. 8).

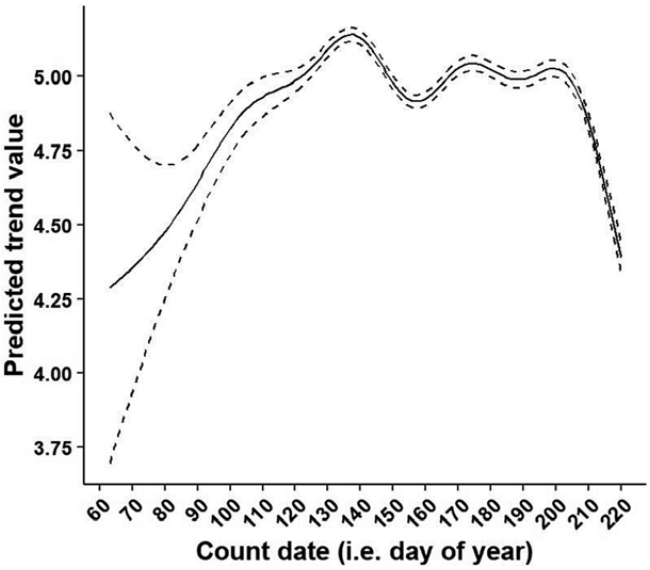

Fig. 6. Effect of count date (i.e., day of the year) on Double-crested Cormorant colony counts illustrated using predicted trend values for a standardized site, year, and survey type.

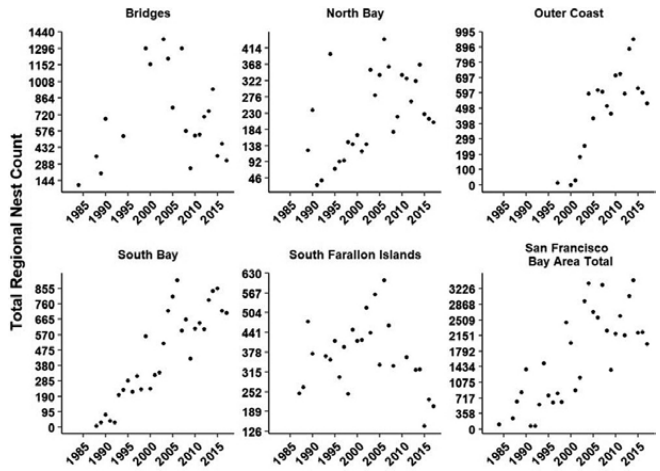

Fig. 7. Counts of Double-crested Cormorant nests summed by year for each Bay Area region, 1984–2017.

TABLE 2
Model-estimated percent change in the number of Double-crested Cormorant nests for sub-regions of the San Francisco Bay area from 1990–2017[a]

Sub-region	1990–2002[b]	2003–2017	1990–2017[b]
Bridges	2 828 % (1 409, 6 191)[c]	-71 % (-79, -61)[c]	721 % (319, 1 681)[c]
North Bay	225 % (60, 445)[c]	-60 % (-70, -48)[c]	18 % (-21, 78)
Outer Coast	5 955 % (3 686, 8 261)[c]	165 % (102, 245)[c]	28 581 % (23 745, 33 241)[c]
South Bay	3 720 % (-100, 8 896)	8 % (-25, 44)	4 371 % (-100, 11 266)
South Farallon Islands	122 % (64, 205)[c]	-61 % (-72, -49)[c]	-11 % (-41, 31)
San Francisco Bay Area Total	16 989 % (-100, 38 708)	-39 % (-50, -26)[c]	9 047 % (-100, 20 529)

[a] Values are followed by 95 % confidence intervals in parentheses.
[b] The study period begins in 1984, 1987, and 1997 for Bridges, South Farallon Islands, and Outer Coast, respectively.
[c] Indicates estimates whose confidence intervals exclude 0 % change.

Aerial counts were always higher than ground counts, but colony size data from the two survey methods were not strongly correlated (Fig. 9). In years of greater colony size, a larger proportion of nests was likely in areas not visible from ground vantage points, resulting in comparatively lower ground counts.

North Bay

The first known nesting by DCCO within San Francisco Bay was in September 1975, when 33 active nests were observed on power towers along a highway at the north end of San Pablo Bay (Stallcup & Winter 1976). At nearby Russ Island, 25 nests were counted on 24 June 1978 (Varoujean 1979, Carter *et al*. 1995). Also in 1978, one nest occurred within a colony of Great Blue Herons *Ardea herodias* in the city of Novato (Shuford 1993). By 1990, the total number of North Bay nests had increased to 270 at five colonies (Carter *et al*. 1992). Russ Island and Knight Island were the two largest colonies, with high counts of 155 nests in 1994 and 200 nests in 2003, respectively. Both colonies, as well as the colony at North San Pablo Radar Target, declined to zero over time due to loss of breeding habitat. In Suisun Bay, nesting was first noted at Wheeler Island in 1991. Since then, the colony has been active in all but one year, with a high count of 203 nests in 2006. Several additional colonies formed in Suisun Bay during the last decade of our study period, most notably Bohannon Slough, which was the largest colony and was active annually after it formed in 2007. For all colonies combined, total nest counts peaked at just over 400 in 1994 and 2014 (Fig. 7). Model outputs for the North Bay showed an increase from 1990 to 2002 of 225 % (95 % CI = 60 %–445 %) and a decline of 60 % (95 % CI = 70 %–48 %) from 2003 to 2017 (Table 2, Fig. 8).

Bridges

Nesting was first reported at RSRB and SFOBB in July 1984 (Campbell & LeValley 1984), although CalTrans maintenance workers suggested that DCCO had nested at RSRB for up to 15 years prior to the first reports by biologists (Stenzel *et al*. 1995). The 1979–1980 California seabird survey (Sowls *et al*. 1980) did not survey San Francisco Bay, so the bridge colonies may have gone undetected (Carter *et al*. 1992). The RSRB colony grew from five nests reported in 1984 to > 200 nests by the beginning of the 1990s, reaching a peak of 632 nests in 2003. Thereafter, the colony declined to 276 nests in 2016. The SFOBB colony grew to 465 nests in 1990, then up to 796 nests in 1999. The highest nest count of 814 nests was recorded in 2007, followed by a dramatic decline to just 83 nests in 2009. Numbers then slowly increased through 2014, before declining again to 187 nests in 2016. In 2017, the first year of nesting on the new span, 353 nests were counted.

DCCO nesting on the two bridges combined totaled > 1 200 nests in at least five years from 1999 to 2007, before plummeting in 2008–2009 (Fig. 7). Nest totals increased dramatically, by 2 828 % (95 % CI = 1 409 %–6 191 %), from small initial numbers from 1984 to 2002; nest totals then decreased by 71 % (95 % CI = 79 %–61 %) from 2003 to 2017 (Table 2, Fig. 8).

South Bay

In 1977, there were no reports of DCCO breeding in the South Bay from Bair Island to Alviso (Gill 1977). South Bay nesting was first reported in 1988 at the San Mateo Bridge Power Towers (16 nests; Carter *et al*. 1992). By 1994, three additional colonies had been observed on power towers farther south, and the nest total had increased to 229 (Bousman 2007, this study). In 1991, all nests on the San Mateo Bridge Power Towers were reportedly removed by maintenance workers (Carter *et al*. 1992). Nesting was first noted at Lake Merritt and Alviso Pond A9/A10 in 1998. The highest nest total for the South Bay sub-region was in 2006 (905 nests, though the San Mateo Bridge was not surveyed), with similar totals in complete survey years of 2014 and 2015. The largest individual colonies were at Alviso Pond A9/A10 (343 nests in 2015) and Steinberger Slough (325 nests in 1999).

The total number of DCCO nests in the South Bay grew dramatically from 1990 to 2002, by 3 720 % (95 % CI = 100 %–8 896%), and

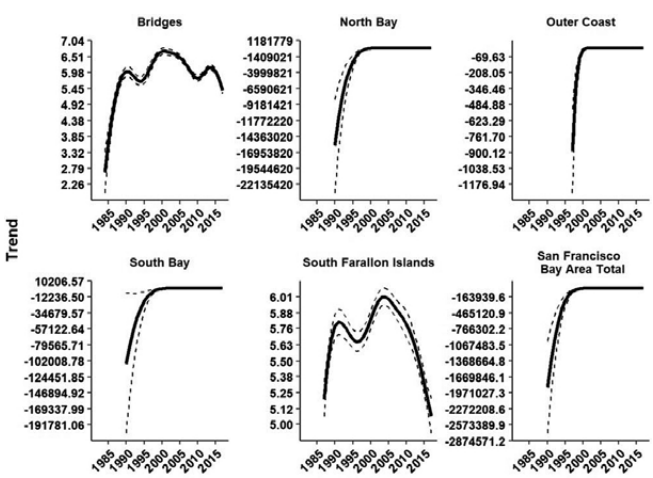

Fig. 8. Linear predictor Generalized Additive Mixed Model (GAMM) trends of Double-crested Cormorant nest counts for each Bay Area sub-region. Solid lines denote the mean estimate, and dashed lines show the 95 % confidence intervals. The last panel shows the trend estimate for all sub-regions combined.

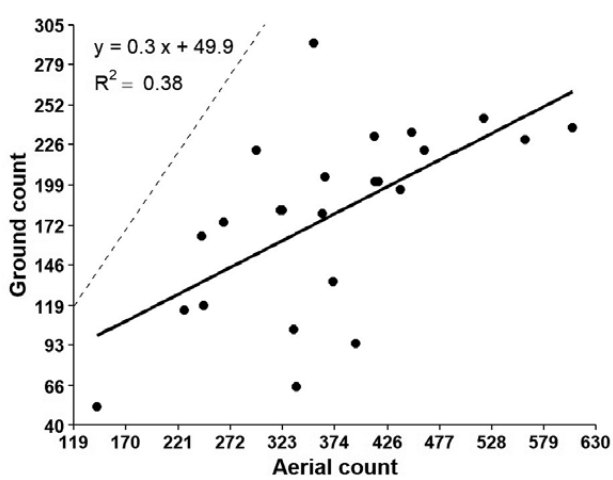

Fig. 9. Comparison of aerial and ground counts of Double-crested Cormorant nests at the South Farallon Islands. The solid line shows a linear model with the equation and R^2 values displayed in the upper left corner of the plot. The dashed line shows the expected 1:1 relationship under the null assumption that counts are similar for every survey type.

then remained stable from 2003 to 2017 (Table 2, Fig. 8). Lower model certainty in the 1990–2002 estimate compared with other sub-regions (i.e., CIs overlapping 0 % change) reflects the larger number of colonies included in the sub-region, as well as missing count data during incomplete survey years.

Outer Coast

The Outer Coast was the last sub-region to be colonized (or re-colonized) during the study period, with first nesting noted at Lake Merced (11 nests) and Hog Island (12 nests) in 1997 and 2001, respectively. The only other locations with known nesting since 2013 were Pescadero Marsh (high count of five nests) and Bolinas Lagoon (only two nests counted in 2016; P. Pyle, unpubl. data). The Lake Merced colony peaked in 2007 at 319 nests and declined thereafter, but remained at over 100 nests. The Hog Island colony grew steadily and has been the largest individual colony in the study area since 2011, peaking in 2014 at 771 nests. Together, the Outer Coast experienced large initial growth from 1997 to 2002 (5955 %; 95 % CI = 3686 %–8261 %) and at least doubled from 2003 to 2017 (165 %; 95 % CI = 102 %–245 %; Table 2, Fig. 8). The three historical nesting sites at Point Resistance, Seal Rocks, and Pillar Point (see Introduction) were not re-colonized.

San Francisco Bay Area Total

Although many missing colony counts before 2003 prevented determination of precise trends since 1990, in years when data were available for all large colonies and most small ones, the total number of nests in the Bay Area increased from about 1400 in 1990 to more than 2900 in 2003. Numbers increased slightly to > 3100 nests in 2004 and > 3200 nests in 2007, although we did not have data for the San Mateo Bridge Power Towers in those years. Nest numbers declined dramatically in 2008–2009, but rebounded to > 3300 nests in 2014 before declining again from 2015 to 2017. Model estimates indicated a moderate-to-large increase of 16989 % (95 % CI = 100 %–38708 %) from 1990 to 2002, followed by a slight decline of 39 % (95 % CI = 50 %–26 %) during the bridge construction period of 2003–2017. Despite the decline late in the study period, the regional numbers of nesting DCCOs increased by about 9047 % (95 % CI = 100 %–20529 %) during the entire 1990–2017 study period. The uncertainty of the 1990–2017 growth estimate can be attributed to cumulative error across estimates from all colonies, as well as an incomplete dataset in the early period as colonies were discovered and not surveyed annually. Nonetheless, there is substantial evidence that the Bay Area population has increased significantly.

DISCUSSION

In the Bay Area, the DCCO population expanded from < 50 breeding pairs at the core colony offshore at SFI in the early 1970s to nearly 3500 breeding pairs in peak years since 2000. A significant factor in DCCO recolonization of San Francisco Bay has been their adaptive use of human-made structures, especially the bridges spanning the bay. Substantial population decline at bridge colonies occurred in 2008–2009, apparently due to food shortage. The major bridge construction from 2003 to 2017 appeared to adversely affect numbers of nests only after 2014, but other colonies in the study area also declined during this time.

The adoption of bridges and power towers for nesting is a natural extension of DCCO behavior as an arboreal-nesting Pelecaniformes. However, the extent to which DCCO have utilized anthropogenic structures as nesting habitat is a relatively recent behavioral adaptation on the Pacific Coast—one that may have begun on bridges in the Bay Area. More recent nesting on bridges is also known in the Columbia River Estuary, Oregon, and in the Strait of Georgia, British Columbia (USACE 2015, Carter *et al*. 2018). The proximity of the bridges to historical roosting sites, and the type of protected truss-work under the bridges, have afforded cormorants a shaded, predator-free place to nest, allowing the recovering DCCO population to expand throughout the estuary. The bridges were the first large colonies formed, growing rapidly in the early years (1984–2002) and providing recruits for other colony formations (e.g., Outer Coast and South Bay colonies), just as the bridges received colonists from SFI and possibly other colonies outside the region. DCCO are known to fly from SFI to coastal estuaries in the region for foraging trips (Ainley & Boekelheide 1990), and DCCO banded as chicks on SFI were observed breeding on the RSRB in 1988 and 2000 (Stenzel *et al*. 1995, Rauzon *et al*. 2001).

Despite the known movement of birds from SFI to RSRB, nest numbers for both the SFI and Bridges sub-regions peaked in the mid-2000s. This was also a time of dramatic population increase for other seabird species, such as Brandt's Cormorants and Common Murres, which was associated with the protection of breeding locations, more informed fishery management, and the resurgence of suitable prey in the Gulf of the Farallones (Capitolo *et al*. 2014, Elliott *et al*. 2016, Ainley *et al*. 2018, Warzybok *et al*. 2018). However, the DCCO colony at SFI declined after peaking in 2006 and remained at low levels through 2017, whereas the Hog Island colony increased later in the study period and became the largest colony in the Bay Area beginning in 2011. Studies in the mid-1970s (Ainley *et al*. 1981) showed that SFI DCCO preyed almost entirely on shiner perch *Cymatogaster aggregata* (a species common to estuaries and shallow inshore waters of the region) and showed little overlap in diet with any other SFI seabirds (Ainley *et al*. 1990). These patterns may indicate further emigration of SFI birds as alternative breeding sites closer to prey sources (such as the trees on Hog Island) became colonized.

Construction of the new east span of the SFOBB (which began in 2002, with the louder, potentially more disturbing work beginning in 2003) did not appear to have major effects on DCCO nesting patterns. Increases in nest numbers at Hog Island and Alviso Pond A9/A10 after construction began may indicate some movement of birds to other established colonies. However, in 2007, during the most active construction phase—with pile driving adjacent to the colony and boat traffic under it—the colony had its highest recorded number of nests, while the dramatic decline in 2009 was attributed to food shortages (see below). Only as the birds were driven from the old bridge by hazing to allow for demolition during 2015–2017 was SFOBB nesting obviously impacted by construction. Similarly, the sections of the RSRB typically used by DCCO were all blocked off for maintenance activities during 2015–2017; DCCO began using sections west of this area for nesting, which are presumed to be less suitable habitat (i.e., higher above the water and farther from a local roosting location).

The low numbers of DCCO observed at the bridges in 2009 can likely be attributed to declines in prey availability. As central place foragers (Orians & Pearson 1979), DCCO forage in nearby waters and return to breeding colonies with food for dependent offspring. Size and success of colonies are therefore affected by the abundance

of prey near breeding sites. During the 2009 breeding season, based on bay trawls, northern anchovy *Engraulis mordax* appeared to be significantly reduced, with larger anchovy (≥ 100 mm) being conspicuously absent (Elliott *et al*. 2010). Northern anchovy is the most abundant forage fish species in San Francisco Bay, and it has an extended spawning period compared to many other species that spawn in the bay (Baxter *et al*. 1999). It is thus a widely available, abundant prey source throughout the DCCO breeding season. Northern anchovy was a known diet item of RSRB DCCO in the late 1980s (Point Blue unpubl. data, Stenzel *et al*. 1995), and is also the most prevalent prey type in the diet of ESI DCCO (USACE 2015). The decline in availability of this high-energy fish could negatively affect DCCO breeding efforts and breeding success, as has been shown for SFI Brandt's Cormorants (Elliott *et al*. 2016, Ainley *et al*. 2018); unfortunately, recent diet information for DCCO in the Bay Area is lacking. However, for Brandt's Cormorants in 2009, numbers of nests also declined dramatically throughout central California, including at Alcatraz Island in central San Francisco Bay, and a die-off occurred in the Gulf of the Farallones and Monterey Bay areas (Capitolo *et al*. 2014, Ainley *et al*. 2018).

In addition to the decline of anchovy, cormorant diets may have been affected by stocked and invasive fish species, which can supplement wild fish stocks. The seasonal stocking of local lakes and reservoirs with hatchery-raised rainbow trout *Oncorhynchus mykiss* is a periodic boon to DCCO food sources (Fig. 10). In 1998, 20 of the 44 lakes in the Bay Area were stocked during times coinciding with DCCO peak metabolic needs (Stienstra 1998). Also, the invasive yellowfin goby *Acanthogobius flavimanus* underwent a population explosion in the Bay Area in the late 1960s and early 1970s, with the first report in 1967 from Suisun Marsh in the northern portion of the estuary (Brittan *et al*. 1970). By the early 1980s, it was reported as the third most abundant fish in trawl catches (Meng *et al*. 1994). Recent drought in California has reduced freshwater outflows and may have allowed this goby to gain an advantage over native freshwater and estuarine fishes that are less able to tolerate high salinity (Herbold *et al*. 1992, Meng *et al*. 1994, USFWS 2014). The goby's expansion may have increased its importance as a prey item for DCCO (Fig. 11).

Other DCCO prey types that were opportunistically collected from the RSRB colony include plainfin midshipman *Porichthys notatus*, Pacific staghorn sculpin *Leptocottus armatus*, shiner perch, jacksmelt *Atherinopsis californiensis*, and white croaker *Genyonemus lineatus* (Point Blue unpubl. data, Stenzel *et al*. 1995). These prey species are mostly bottom-dwelling fish common to shallow bays and intertidal zones of California coastal marine areas (Miller & Lea 1972).

While some connectivity of ESI and Bay Area colonies has previously been shown (Courtot *et al*. 2012), immigration of DCCO from outside of the region was not considered an important factor in Bay Area population increases. Linkage to the ESI population was further observed in February 2015 when 11 color-banded DCCO from ESI, including one with a transmitter, were seen on the old SFOBB. These observations in 2015 were made possible by completion of the new SFOBB that included a bike path/walkway with views of the old span, enabling detection of bands that normally cannot be seen from below during boat surveys. However, available data have indicated that some banded DCCO return to the Columbia River estuary in spring (Courtot *et al*. 2012). Furthermore, Bay Area nest totals declined after 2014, as ESI management was beginning.

DCCO continued to nest on the old SFOBB during the 2015–2016 demolition phase by moving onto portions of the bridge not previously used for nesting. Avoidance of the new span until 2017 was despite the availability of stainless steel platforms, referred to as "Corm Condos," that were designed in 2001 by the lead author, and erected and made accessible to the birds beginning in 2011. Although four social attraction techniques were implemented on the platforms for six years, no cormorants were detected using the platforms. Only when the final section of the old span was completely removed in March 2017 did birds relocate to the new bridge. On 02 April 2017, two cormorants were first observed using the roosting rails of the new platforms, but by 09 June at least 318 nests had been built on the platforms. The delayed occupation and eventual colonization of these "Corm Condos" provides insight for future endeavors to restore breeding habitat for DCCO and other waterbirds (Jones & Kress 2012).

Fig. 10. A Double-crested Cormorant eating a hatchery-reared rainbow trout, Heather Farm, Walnut Creek, CA.

Fig. 11. A Double-crested Cormorant eating a yellowfin goby, Lake Merritt, Oakland, CA.

Although most DCCO colonies in the Bay Area are located near food sources and protected from predators by the built environment, colonies are also vulnerable over time to other threats. For example, at Lake Merritt, a historical foraging site where DCCO have utilized alien trees (e.g., *Eucalyptus* spp. and Monterey pines *Pinus radiata*) as nesting habitat, numbers peaked in 2006 (201 nests) but have declined in recent years in part because nest trees died due to guano burn. Colonies on the ground on pond levees are vulnerable to changes in land use (including tidal marsh restoration), eroding levees, and sea level rise. For example, nest numbers at Knight Island in the North Bay declined over a period of several years and the colony was abandoned by 2015 as the pond was flooded, possibly leading to the formation of new colonies in Suisun Bay. In 2018, the Alviso Pond A9/A10 colony in the South Bay was empty, at least in part due to levee erosion, despite having hosted low 100s of nests in each of the previous seven years. Colonies on bridges and power towers are threatened by hazing during periodic maintenance.

Despite all the changes, numbers of breeding DCCO in the Bay Area remain comparable to the large SFI estimate from the late 1880s. That DCCO can survive, and even flourish, within San Francisco Bay is a testament to their ability to adapt—not only to the modern, built environment in an ecosystem that itself is impacted by a growing human population's need for freshwater and open space, but also to climate change and rises in sea level which threaten cormorant habitat. We hope that this review of Bay Area colonies will add a historical perspective to the remarkable population dynamics of this avian indicator of ecosystem health.

ACKNOWLEDGMENTS

We thank the many staff and numerous highly qualified volunteers at Point Blue Conservation Science, the San Francisco Bay Bird Observatory, the US Fish and Wildlife Service, Audubon Canyon Ranch, and Humboldt State University for their help in conducting field surveys and for important contributions to project coordination and data management. We thank Point Blue (formerly known as the Point Reyes Bird Observatory) staff (Lynne Stenzel, Phil Henderson, Gary Page, Craig Strong, and Jennifer Roth) who conducted road surveys on the bridges, and Pete Warzybok for providing SFI ground counts for comparison to aerial counts. In later years, Eric Lichtwardt (LSA & Associates) assisted in bridge surveys, with Ganda & Associates and Lauren Bingham (Johnson Marigot Consulting, LLC) providing boats and access to the bridges. Appreciation extends to CalTrans managers Stefan Galvez-Abadia and others who have been critical to carrying out the colony transfer work. We thank Natalie Washburn for SFBBO project management; SFBBO members and donors, the Oiled Wildlife Care Network, and Patagonia for financial support; and the San Francisco Public Utilities Commission, East Bay Regional Park District, California Department of Fish & Wildlife (CDFW), and Don Edwards San Francisco Bay National Wildlife Refuge for access and monitoring permission. We thank the Dennis and Carol Ann Rockey Fund of the Marin Community Foundation, The Robert J. and Helen H. Glaser Family Foundation, and the contributions of numerous individuals for their financial support of work conducted by Audubon Canyon Ranch. This is Point Blue Conservation Science contribution number 2218.

Aerial photographic surveys were conducted by USFWS and Humboldt State University (HSU) from 1985–2006, and by USFWS, University of California, Santa Cruz, and HSU since 2007. We thank Rick Golightly (HSU) for his long-term support and assistance. Funding for surveys and counting has been provided mainly by CDFW's Office of Spill Prevention and Response, USFWS, and the Apex Houston Trustee Council. Since 2015, funding for survey staff and image analysis for sample Bay Area colonies has been provided by the USFWS Office of Migratory Birds, Regions 1 and 8 with assistance from Michelle McDowell and Amadee Brickee. Permits for low-level aerial surveys within the Greater Farallones and Monterey Bay National Marine Sanctuaries were provided by the National Oceanic and Atmospheric Administration; permit numbers were GFNMS/MBNMS-04-93, GFNMS/MBNMS-02-94, GFNMS/MBNMS-04-95, GFNMS/MBNMS-03-96, GFNMS/MBNMS-03-97, GFNMS/MBNMS-2000-003-G, MULTI-2003-003, MULTI-2008-002, MULTI-2012-001, and MULTI-2017-009. Point Blue interns (B. Cummings, S. Gee, K. Taylor, and others) helped count nests from certain 2004–2014 aerial photographs. We thank Julie Yee and Pete Raimondi for valuable discussions regarding statistical analyses, and Cheryl Strong, Dan Roby, and an anonymous reviewer for their helpful comments on an earlier draft of the manuscript.

REFERENCES

AINLEY, D.G. & BOEKELHEIDE, R.J. 1990. *Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community*. Stanford, CA: Stanford University Press.

AINLEY, D.G., ANDERSON, D.W. & KELLY, P.R. 1981. Feeding ecology of marine cormorants in southwestern North America. *The Condor* 83: 120–131.

AINLEY, D.G., STRONG, C.S., PENNIMAN, T.M., & BOEKELHEIDE, R.J. 1990. The feeding ecology of Farallon seabirds. In: AINLEY, D.G. & BOEKELHEIDE, R.J. (Eds.). *Seabirds of the Farallon Islands: ecology, structure, and dynamics of an upwelling system community*. Stanford, CA: Stanford University Press, pp. 51–127.

AINLEY, D.G. & LEWIS, T.J. 1974. The history of Farallon Island marine bird populations, 1854–1972. *The Condor* 76: 432–446.

AINLEY, D.G., SANTORA, J.A., CAPITOLO, P.J. ET AL. 2018. Ecosystem-based management affecting Brandt's cormorant resources and populations in the Gulf of the Farallones, California. *Biological Conservation* 217: 407–418.

ADKINS, J.Y., ROBY, D.D., LYONS, D.E., ET AL. 2014. Review: recent population size, trends, and limiting factors for the Double-crested Cormorant in western North America. *Journal of Wildlife Management* 78: 1131–1142.

ANDERSON, C.D., ROBY, D.D. & COLLIS, K. 2004. Conservation implications of the large colony of Double-crested Cormorants on East Sand Island, Columbia River Estuary, Oregon, U.S.A. *Waterbirds* 27: 155–160.

BARTHOLOMEW, G.A. JR. 1943. The daily movements of cormorants on San Francisco Bay. *The Condor* 45: 3–18.

BARTON, K. 2018. MuMIn: Multi-Model Inference. R package version 1.42.1. https://CRAN.R-project.org/package=MuMIn

BOEKELHEIDE , R.J., AINLEY, D.G., HUBER, H.R. & LEWIS, T.J. 1990. Pelagic Cormorant and Double-crested Cormorant. In: AINLEY, D.G. & BOEKELHEIDE, R.J. (Eds.). *Seabirds of the Farallon Islands: ecology, structure, and dynamics of an upwelling system community*. Stanford, CA: Stanford University Press, pp. 195–217.

BOLANDER, L.P. & BRYANT, C.A. 1930. Some notes on Point Reyes birds. *The Condor* 32: 70–72.

BOUSMAN, W.G. 2007. B*reeding Bird Atlas of Santa Clara County, CA*. Cupertino, CA: Santa Clara Valley Audubon Society.

BRAKE, A.J., WILSON, H.A., LEONG, R. & FISH, A.M. 2014. Status of Ospreys Nesting on San Francisco Bay. *Western Birds* 45: 190–198.

BRITTAN, M.R., HOPKIRK, J.D. CONNERS, J.D. & MARTIN, M. 1970. Explosive spread of the oriental goby *Acanthogobius flavimanus* in the San Francisco Bay-Delta region of California. *Proceedings of the California Academy of Sciences* 38: 207–214.

BROUGHTON, J. 2004. Prehistoric human impacts on California birds: evidence from the Emeryville Shellmound avifauna. *Ornithological Monographs* 56: 1–90.

CAMPBELL, K.F. & LEVALLEY, R. 1984. The nesting season: Middle Pacific Coast region. *American Birds* 38: 1056–1060.

CAPITOLO, P.J. 2009. Farallon Islands. In: GILLESPIE, R. (Ed.) *Encyclopedia of Islands.* Berkeley, CA: University of California Press. pp. 287–291. [Available online at: http://colibri-ecology.com/wp-content/uploads/2015/01/Capitolo-2009_Farallon-Islands_UC-Press.pdf. Accessed 18 October 2018].

CAPITOLO, P.J., CARTER, H.R., YOUNG, R.J., ET AL. 2004. Changes in breeding population size of Brandt's and Double-crested Cormorants in California, 1975–2003, *unpublished report*. Department of Wildlife, Humboldt State University, Arcata, California. [Available online at: http://humboldt-dspace.calstate.edu/handle/2148/930. Accessed 1 Aug 2018].

CAPITOLO, P.J., McCHESNEY, G.J., CARTER, H.R., PARKER, M.W., EIGNER L.E. & GOLIGHTLY, R.T. 2014. Changes in breeding population sizes of Brandt's Cormorants *Phalacrocorax penicillatus* in the Gulf of the Farallones, California, 1979–2006. *Marine Ornithology* 42: 35–48.

CAPITOLO, P.J., CARTER, H.R., YEE, J.L. ET AL. 2019. Changes in breeding population sizes of Double-crested Cormorants (*Phalacrocorax auritus*) in the Humboldt Bay area, California, 1924–2017. *Marine Ornithology* 47: 115–126.

CARTER, H.R., McCHESNEY, G.J., JAQUES, D.L., ET AL. 1992. *Breeding populations of seabirds in California, 1989–1991: unpublished draft final report*. Volumes 1 and 2. Dixon, CA: US Fish and Wildlife Service, Northern Prairie Wildlife Research Center [Available online at: http://farallones.noaa.gov/eco/seabird/pdf/news/journal/monitoringandstatus.pdf. Accessed 01 August 2018].

CARTER, H.R., SOWLS, A.L., RODWAY, M.S., ET AL. 1995. Population size, trends, and conservation problems of the Double-crested Cormorant on the Pacific coast of North America. *Colonial Waterbirds* 18: 189–215.

CARTER, H.R., McCHESNEY, G.J., TAKEKAWA, J.E., ET AL. 1996. *Population monitoring of seabirds in California: 1993–1995 aerial photographic surveys of breeding colonies of Common Murres, Brandt's Cormorants and Double-crested Cormorants: unpublished final report*. Dixon, CA: US Geological Survey, California Science Center.

CARTER, H.R., CAPITOLO, P.J., McCHESNEY, G.J., McIVER, W.R. & TAKEKAWA, J.E. 2000. *Population monitoring of seabirds in California: colony and subcolony databases for 1985–1995 surveys of breeding colonies of Common Murres, Brandt's Cormorants, and Double-crested Cormorants between Point Arena and Point Conception: unpublished final report*. Dixon, CA: US Geological Survey, Western Ecological Research Center; Arcata, CA: Humboldt State University, Department of Wildlife; and Newark, CA: US Fish and Wildlife Service, San Francisco Bay National Wildlife Refuge Complex.

CARTER, H.R., WILSON, U.W., LOWE, R.W., ET AL. 2001. Population trends of the Common Murre (*Uria aalge californica*). In: MANUWAL, D.A., CARTER, H.R., ZIMMERMAN, T.S. & ORTHMEYER, D.L. (Eds). *Biology and conservation of the Common Murre in California, Oregon, Washington, and British Columbia, Volume 1: Natural history and population trends*. Washington, DC: US Geological Survey, Information and Technology Report USGS/BRD/ITR-2000-0012.

CARTER, H.R., CHATWIN, T.A. & DREVER, M.C. 2018. Breeding population sizes, distributions, and trends of Pelagic, Double-Crested, and Brandt's Cormorants in the Strait of Georgia, British Columbia, 1955–2015. *Northwestern Naturalist* 99: 31–48.

CONOMOS, T.J. 1979. San Francisco Bay—the urbanized estuary. San Francisco, CA: American Association for the Advancement of Science-Pacific Division, pp 483.

COURTOT, K.N., ROBY, D.D., ADKINS, J.Y., LYONS, D.E., KING, D.T. & LARSEN, R.S. 2012. Colony connectivity of Pacific Coast Double-crested Cormorants based on post-breeding dispersal from the region's largest colony. *Journal of Wildlife Management* 76: 1462–1471.

DORR, S., HATCH, J.J., & WESELOH, D.V. 2014. Double-crested Cormorant (Phalacrocorax auritus), version 2.0. In: A.F. POOLE (Ed.) *The Birds of North America*. Ithaca, NY: Cornell Lab of Ornithology.

ELLIOTT, M.L., SCHMIDT, A., ACOSTA, S. ET AL. 2016. Brandt's cormorant diet (1994–2012) indicates the importance of fall ocean conditions for northern anchovy in central California. *Fisheries Oceanography* 25: 515–528.

ELLIOTT, M.L., RAUZON, M.J., ROTH, J.E. & HIEB, K. 2010. Double-crested Cormorant declines in San Francisco Bay: poster presentation. Long Beach, CA: Pacific Seabird Group Annual Meeting.

EMERSON, W. 0. 1904. The Farallone Islands re-visited, 1887–1903. *The Condor* 6: 61–68.

GILL, R. Jr. 1977. Breeding Avifauna of the South San Francisco Bay Estuary. *Western Birds* 8: 1–12.

GRINNELL, J. 1915. *A distributional list of the birds of California*. Hollywood, CA: Cooper Ornithological Club.

GRINNELL, J. & WYTHE, M.W. 1927. *Directory to the bird-life of the San Francisco Bay region*. Berkeley, CA: Cooper Ornithological Club.

HANSEN, H.E. & SQUIRES, W.A. 1917. A list of the birds breeding in San Francisco County, California. *The Condor* 19: 54–62.

HATCH, J.J. 1995. Changing populations of Double-crested Cormorants. *Colonial Waterbirds* 18(Special Publication 1): 8–24.

HERBOLD, B.A., A.D. JASSBY & MOYLE, P.B. 1992. *Status and trends report on aquatic resources in the San Francisco estuary*. EPA Public Report. San Francisco, CA: San Francisco Estuary Project.

Historic Bridges: Richmond-San Rafael Bridge [Online]. [Available online at: http://historicbridges.org/bridges/browser/?bridgebrowser=california/sanrafael/. Accessed 07 August 2018].

JONES, H.P. & KRESS, S.W. 2012. A review of the world's active seabird restoration projects. *Journal of Wildlife Management* 76: 2–9.

MENG, L., MOYLE, P. B. & HERBOLD, B. 1994. Changes in abundance and distribution of native and introduced fishes of Suisun Marsh. *Transactions of the American Fisheries Society* 123: 498–507.

MILLER, D. J. & LEA, R.N. 1972. *Guide to the Coastal Marine Fishes of California. Fish Bulletin No. 157.* Sacramento, CA: California Department of Fish and Game and the University of California.

ORIANS, G.H. and PEARSON, N.E. 1979. On the theory of central place foraging. In: HORN, D.J., STAIRS, G.R. & MITCHELL, R.D. (Eds.) *Analysis of Ecological Systems*. Columbus, OH: Ohio State University Press, pp. 154–177.

RAUZON, M.J., SYDEMAN, W.J., ELLIOTT, M.L. & ROTH, J. 2001. *Population size and breeding success of Double-crested Cormorants (Phalacrocorax auritus) on the Richmond-San Rafael Bridge, California, in 2000: unpublished report*. San Francisco and Stinson Beach, CA: San Francisco State University and Point Reyes Bird Observatory. [Available online at: http://www.prbo.org/refs/files/11434_Rauzon_etal2000.pdf. Accessed 18 October 2018].

R CORETEAM. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. [Available online at: https://www.R-project.org/].

SCOTT, M. 1985. *The San Francisco Bay Area: A Metropolis in Perspective*. Berkeley, CA: University of California Press.

SHADISH, W.R., ZUUR, A.F., & SULLIVAN, K. J. 2014. Using generalized additive (mixed) models to analyze single case designs. *Journal of School Psychology* 52: 149–178.

San Francisco-Oakland Bay Bridge [Online]. Sacramento, CA: California Department of Transportation. [Available online at http://www.dot.ca.gov/hq/esc/tollbridge/SFOBB/Sfobbfacts.html. Accessed 03 April 2018].

Skyway [Online]. Oakland, CA: Caltrans District 4. [Available online at http://www.baybridgeinfo.org/skyway. Accessed 03 April 2018].

SHUFORD, W.D. 1993. *The Marin County Breeding Bird Atlas*. Bolinas, CA: Bushtit Books.

STALLCUP, R. & WINTER, J. 1976. Middle Pacific Coast Region. *American Birds* 30: 118.

SOWLS, A.L., DEGANGE, A.R., NELSON, J.W. & LESTER, G.S. 1980. *Catalog of California seabird colonies.* FWS/OBS 37/80. Sacramento, CA: US Department of the Interior, Bureau of Land Management, Fish and Wildlife Service, Biological Services Program.

SQUIRES, W.A. 1917. Some field notes for 1917. *The Condor* 19: 185–186.

STENZEL, L.E., CARTER, H.R., HENDERSON, R.P., ET AL. 1995. Breeding success of Double-crested Cormorants in the San Francisco Bay Area, California. Colonial Waterbirds 18(Special Publication 1): 216–224.

STIENSTRA, T. 1998. *20 Bay area lakes for trout fishing*. San Francisco Chronicle, 6 November 1998. [Available online at: https://www.sfgate.com/news/article/20-Bay-Area-lakes-for-trout-fishing-3060983.php. Accessed 07 August 2018].

STRONG, C.M., SPEAR, L.B., RYAN, T.P. & DAKIN, R.E. 2004. Forster's Tern, Caspian Tern, and California Gull colonies in San Francisco Bay: habitat use, numbers and trends, 1982–2003. *Waterbirds* 27: 411–423.

TAKEKAWA, J.E., CARTER, H.R. & HARVEY, T.E. 1990. Decline of the Common Murre in central California, 1980–1986. *Studies in Avian Biology* 14: 149–163.

US ARMY CORPS OF ENGINEERS (USACE). 2015. *Double-crested cormorant management plan to reduce predation of juvenile salmonids in the Columbia River Estuary: Final environmental impact statement*. Portland, OR: US Army Corps of Engineers, Portland District. [Available online at: http://www.nwp.usace.army.mil/Portals/24/docs/environment/EIS/Cormorants/DCCO-DEIS_Exec_Sum.pdf; Accessed 2019 February 20].

US FISH & WILDLIFE SERVICE (USFWS). 2014. *Ecological Risk Screening Summary: Yellowfin Goby Acanthaogobius flavimanus*. Washington, DC: US Fish and Wildlife Service [Available online at: https://www.fws.gov/fisheries/ans/erss/highrisk/Acanthogobius-flavimanus-WEB-8-19-2014.pdf. Accessed 08 August 2018].

USFWS. 2017a. *Double-crested Cormorant western population status evaluation: final annual 2016 report.* Portland, OR: US Fish and Wildlife Service, Migratory Birds and Habitat Programs.

USFWS. 2017b. *Environmental Assessment for Issuing Depredation Permits for Double-crested Cormorant Management.* Portland, OR: US Fish and Wildlife Service, Division of Migratory Bird Management.

VAROUJEAN, D.H. 1979. *Seabird colony catalog, Washington, Oregon, and California: unpublished report*. Sacramento, CA: US Department of the Interior, Fish and Wildlife Service.

WARZYBOK, P.M., SANTORA, J.A., AINLEY, D.G. ET AL. 2018. Prey switching and consumption by seabirds in the central California Current upwelling ecosystem: Implications for forage fish management. *Journal of Marine Systems* 185: 25–39.

WHITE, P. 1995. *The Farallon Islands: sentinels of the Golden Gate*. San Francisco, CA: Scottwall Associates.

WIRES, L.R. & CUTHBERT, F.J. 2006. Historic populations of the Double-crested Cormorant (*Phalacrocorax auritus*): implications for conservation and management in the 21st century. *Waterbirds* 29: 9–37.

WIRES, L.R., CUTHBERT, F.J., TREXEL, D.R. & JOSHI, A.R. 2001. *Status of Double-crested Cormorant in North America (Phalacrocorax auritus): Final report to U.S. Fish and Wildlife Service.* St. Paul, MI: University of Minnesota.

WOOD, S.N. 2006. *Generalized Additive Models: An Introduction with R*. New York, NY: Chapman and Hall/CRC Press.

WOOD, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)* 73: 3–36.