CHANGES IN BREEDING POPULATION SIZES OF DOUBLE-CRESTED CORMORANTS *PHALACROCORAX AURITUS* IN THE HUMBOLDT BAY AREA, CALIFORNIA, 1924–2017

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ABSTRACT

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To better understand recent population growth of the Double-crested Cormorant *Phalacrocorax auritus* along the Pacific coast of North America, we assessed long-term breeding population trends in the Humboldt Bay area, California, using aerial photographic survey data collected since 1989 as well as available prior data. The earliest documentations of breeding (but without nest counts) are from 1924, 1943, and 1947 on the outer coast near Trinidad, and from 1959 in Humboldt Bay at Old Arcata Wharf. The breeding population increased from 188 nests (376 breeding birds) at one colony in 1961 to ~ 350 nests (700 breeding birds) at four colonies by 1980, and then to peaks of nearly 1 700 nests (3 400 breeding birds) in 1997 and 2004 at eight colonies. Breeding was documented at 13 coastal colonies through 2017. The population increased 100 % (9 % per annum) from 1989 to 1997, decreased during the strong 1998 El Niño, and rebounded by 2004. After the 2004 peak, three years of available data indicated slight population decline. For the entire 1989–2017 period, the population increased by 91 % (2 % per annum). Artificial habitats in Humboldt Bay allowed most of the population growth, especially Teal Island, which was colonized in 1993 and became the largest colony in all but one year thereafter. Nest totals on the outer coast decreased, likely because of movements to the Humboldt Bay colonies, which are closer to main foraging areas, and because of competition for nesting space with Common Murres *Uria aalge* at one colony (False Cape Rocks). Future growth of the population in the Humboldt Bay area appears limited by the availability of disturbance-free breeding habitat. Declines may occur if artificial habitats are lost.

Key words: aerial surveys, California, Double-crested Cormorant, Humboldt Bay, *Phalacrocorax auritus*, population trends

INTRODUCTION

Along the Pacific coast of North America, the Double-crested Cormorant *Phalacrocorax auritus* (DCCO) breeds from southern British Columbia, Canada, to Sinaloa, Mexico (Carter *et al.* 1995). The largest colony in this region is currently located at East Sand Island in the Columbia River Estuary, Oregon, where more than 12 000 pairs were estimated in 2009 (Adkins *et al.* 2014) and nearly 15 000 pairs were estimated in 2013 (USACE 2015). Across the range of the species, which includes four described subspecies over much of North America (Mercer *et al.* 2013, Dorr *et al.* 2014), two colonies in Manitoba and Ontario, Canada, have rivaled East Sand Island as the largest (King 2013, TRCA 2017, McDonald *et al.* 2018; M. McDowell pers. comm.). Since 2015, however, due to concerns regarding cormorant predation on smolts of threatened and endangered salmonids *Onchorhyncus* spp., the East Sand Island colony has been reduced in size by management actions that include culling and hazing cormorants, oiling nests, and limiting breeding habitat (USACE 2015, USACE unpubl. data). To help assess these management actions, annual monitoring of sample colonies throughout the population west of the Continental Divide (excluding Alaska and Mexico) has been coordinated since 2014 (USFWS 2017).

Historically, the Pacific coast population was likely much larger, as evidenced by the 1913 estimate of more than 200 000 pairs breeding at Isla San Martín, Baja California, Mexico (Wright 1913, Hatch 1995, Wires & Cuthbert 2006). Extensive declines at Pacific coast colonies occurred between the late 19th and mid-20th centuries due to human disturbance during a period of rapid settlement by European Americans. These declines were followed by a partial recovery over the last few decades of the 20th century, during which increased protections allowed DCCO to colonize new breeding habitats that are associated with extensive human modification of estuaries (Carter *et al.* 1995, Rauzon *et al.* 2019). For example, in the San Francisco Bay area, the offshore colony at the South Farallon Islands numbered at least in the low thousands of pairs as late as 1887 (Ainley & Lewis 1974) before declining to fewer than

50 pairs during most of the 20th century; nesting in San Francisco Bay was historically unknown. Since the 1970s, the South Farallon Islands colony has grown (though not nearly to historic levels), and nesting in San Francisco Bay is now widespread on electrical power towers, salt pond levees, and the superstructure beneath the roadways of bridges (Boekelheide *et al.* 1990; Carter *et al.* 1992, 1995; Rauzon *et al.* 2019).

In California, most colonies are currently distributed along the mainland coast near the major bays and river mouths (Carter *et al.* 1995), adjacent to estuarine waters where most foraging occurs; even at the South Farallon Islands, DCCO commute to the mainland to forage (Ainley *et al.* 1981, 1990). Breeding habitat includes islands, sea stacks, mainland cliffs, trees, and various man-made structures. In northern California, the DCCO population centered around Humboldt Bay (Fig. 1) is separated from other populations to the north by about 50 km (Klamath River area) and to the south by about 250 km (Russian River area). Hundreds of birds use Humboldt Bay year-round (Monroe *et al.* 1973, Nelson 1989), and some foraging also occurs in coastal lagoons and inland, though no inland colonies in the Humboldt Bay area have been documented (Harris 2005, Hunter *et al.* 2005). All colonies within this population were surveyed during decadal, broad-scale seabird surveys from 1969 to 1990 (Osborne 1972, Sowls *et al.* 1980, Carter *et al.* 1992) and have been surveyed annually with aerial photographs since 1993 during statewide coastal surveys (Carter *et al.* 1996, 2001; Capitolo *et al.* 2004, 2014). In this paper, we examine changes in sizes of the DCCO breeding population in the Humboldt Bay area using available data from 1924 to 2017, describe statistical trends since 1989, and discuss anthropogenic and natural factors affecting nesting within this population. The long-term time series presented here will improve understanding of the recent population growth along the Pacific coast and help address potential resource conflicts with humans and other species.

STUDY AREA

From 1959 to 2017, breeding DCCO were documented at 13 coastal locations in the Humboldt Bay area, from Big Lagoon (41°10′00″N, 124°07′30″W) south to Sugarloaf Island at Cape Mendocino (40°26′20″N, 124°24′50″W), including colonies in Humboldt Bay (Fig. 1). This region is a subset of the Northern Coast–North Section of western North America DCCO status assessments (Carter *et al.* 1995, Adkins *et al.* 2014). All locations except Big Lagoon had been previously named and mapped (Sowls *et al.* 1980; Carter *et al.* 1992, 1996). At eight breeding colonies (Sea Gull Rock, Sea Lion Rock, White Rock, Pilot Rock, Trinidad Bay Rocks, Little River Rock, False Cape Rocks, and Sugarloaf Island), nests were built on the ground on sea stacks within 1 km of shore (Fig. 2). At Big Lagoon, cormorants nested in Sitka spruce *Picea sitchensis*. Four breeding colonies (Old Arcata Wharf, Arcata Bay Sand Islands [hereafter, Sand Island], Humboldt Bay Duck Blinds, and Teal Island) were on artificial habitats in Humboldt Bay (Figs. 3, 4). The northern and southern arms of Humboldt Bay are known as Arcata Bay and South Bay,

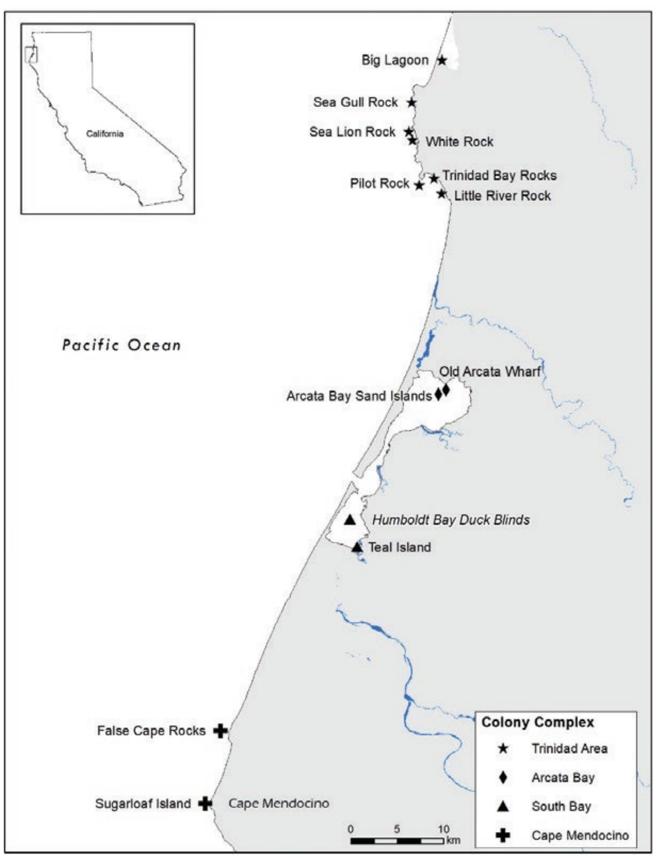

Fig. 1. Double-crested Cormorant colonies and colony complexes in the Humboldt Bay area, California. Italics indicate colony habitat that no longer exists.

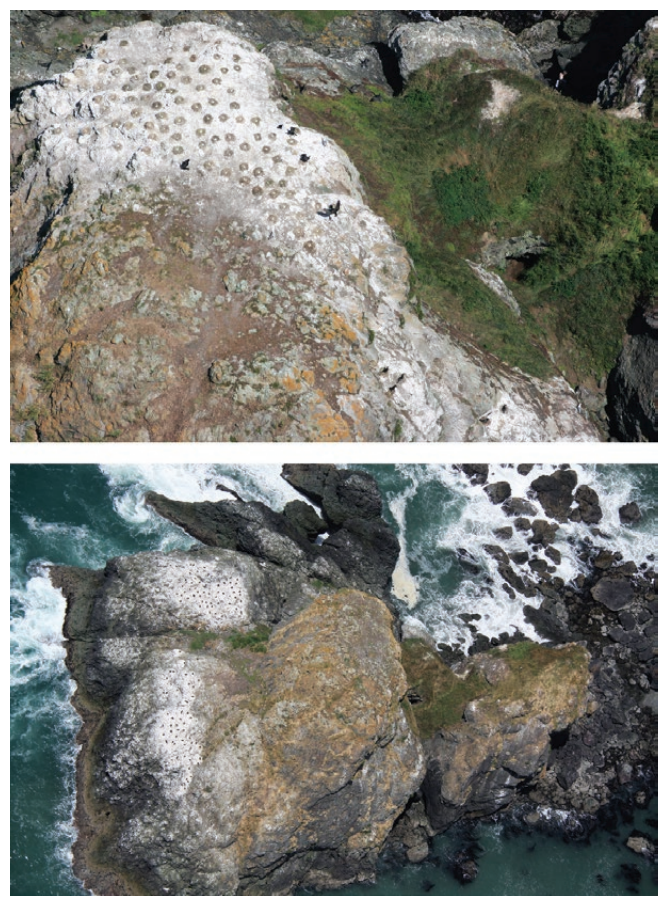

Fig. 2. Little River Rock on 28 May 2009 (top; showing deserted nests and human disturbance) and 05 June 2017 (bottom; after the colony moved to the lower west side of the rock).

respectively (Barnhart *et al.* 1992). Due to possible inter-annual movement between nearby colonies, we grouped colonies into four colony complexes (Fig. 1): Trinidad Area (Big Lagoon south to Little River Rock), Arcata Bay (Old Arcata Wharf and Sand Island), South Bay (Humboldt Bay Duck Blinds and Teal Island), and Cape Mendocino (False Cape Rocks and Sugarloaf Island). Complexes were separated by gaps of 19–25 km. Colonies within each complex were 2.5–10.5 km apart. Movement between complexes may also have occurred during this study.

METHODS

Surveys

Data from limited local observations were gleaned from published literature, from egg records and field notes archived in museum collections, and through conversations with local biologists. Periodic broad-scale surveys of seabird colonies throughout the region were first conducted in 1969 and 1970. These included boat surveys, on-island surveys, and surveys from the adjacent mainland (Osborne 1972). Similar methods were used in 1979 and 1980 for the Catalog of California Seabird Colonies (Sowls *et al.* 1980), but aerial photographic surveys were also employed, though mainly for Common Murres *Uria aalge* and Brandt's Cormorants *P. penicillatus*. By the 1989–1991 update to the colony catalog (Carter *et al.* 1992), aerial photographic surveys of murre and cormorant colonies in California were more standardized, but a mixture of methods were still used for cormorant colonies in northern California. In 1990, Sea Gull Rock and Sea Lion Rock were not surveyed; therefore, we substituted 1989 data. A similar approach was used for certain colonies in 1969, 1970, 1979, and 1980 (see Table 1A).

From 1993 to 2017, aerial photographic surveys throughout northern and central California were conducted annually (Carter *et al.* 1996, 2001; Capitolo *et al.* 2014). Colonies were surveyed once, typically in early June (range: 30 May–16 June for this paper), which generally coincides with the late incubation to early chick-rearing period for DCCO in this area. Surveys were conducted from a single-engine Cessna from 1989 to 1994 and from a twin-engine Partenavia aircraft beginning in 1995. Altitude ranged from 150 to 300 m above sea level. Photographs were taken obliquely through side windows and window ports until 1997, when we switched to vertical photography at the suggestion of pilots. The Partenavia features a hatch in the belly of the aircraft with an opening that is 63 cm long by 47 cm wide. All photographs were taken with handheld cameras, initially 35-mm cameras with color slide film (200 ASA) coupled to 50-mm or zoom lenses for overview photographs and to 300-mm lenses for the highest-resolution photographs; these latter images were typically used for counting (ground sample distance < 1 cm). Beginning in 2007, we switched to digital APS-C cameras and a 200-mm telephoto lens for the highest-resolution images.

For each colony, we summed counts from multiple aerial photographs to determine whole-colony counts of nests. For the 1989–2004 period, slide images were projected onto large sheets of white paper and each cormorant nest, territorial site, and bird was marked; manual methods of image analysis software (Image-Pro®; Media Cybernetics, Rockville, MD, USA) were used for 2008, 2014, and 2017. Photographs of most colonies in other years since 2004 were not analyzed and remain archived. Big Lagoon and Sand Island counts for 2015 and 2016 are presented here because these are sample colonies for Western-population monitoring (USFWS 2017), but these counts were not used in analyses because data by colony complex in these years were incomplete. Nests were categorized by their stage of development, including poorly built (no eggs laid yet), well-built nests (with an incubating adult), nests with chicks evident, empty nests (well-built with standing adult attending, no eggs or chicks present), and abandoned nests. Territorial sites included locations with little or no nesting material

Fig. 3. Portions of Sand Island on 12 June 2013 (top) and Old Arcata Wharf on 05 June 2017 (bottom).

Fig. 4. Looking southeast at a portion of Teal Island, 05 June 2014. Cormorants nest on the narrow perimeter dike.

TABLE 1A
Total numbers of Double-crested Cormorant nests counted at colonies and colony complexes (bold italics) in the Humboldt Bay area, California, 1969–1997

Colony Name	1969[a]	1970[a]	1979[b]	1980[b]	1989[c]	1990	1993	1994	1995	1996	1997
Sea Gull Rock	0	0	48	68	54	[54][d]	51	50	76	91	115
Sea Lion Rock	[8]	8	[0]	0	37	[37]	0	0	18	16	12
White Rock	[12]	12	[0]	0	0	0	0	0	0	0	0
Pilot Rock	0	[0]	[0]	0	4	0	0	0	0	0	27
Trinidad Bay Rocks	0	0	0	0	0	0	0	0	0	0	0
Little River Rock	0	0	60	50	226	208	243	280	309	190	143
Trinidad Area Complex	***20***	***20***	***108***	***118***	***321***	***299***	***294***	***330***	***403***	***297***	***297***
Arcata Bay Sand Islands	0	0	0	0	0	0	0	0	0	0	0
Old Arcata Wharf	[133]	133	[170]	170	119	200	292	253	154	60[e]	19
Arcata Bay Complex	***133***	***133***	***170***	***170***	***119***	***200***	***292***	***253***	***154***	***60***	***19***
Humboldt Bay Duck Blinds	0	0	0	0	39	44[c]	38	22	19	14	0
Teal Island	0	0	0	0	0	0	118	294	464	750	1 189
South Bay Complex	***0***	***0***	***0***	***0***	***39***	***44***	***156***	***316***	***483***	***764***	***1 189***
False Cape Rocks	0	[0]	[0]	0	37	42	39	50	77	62	77
Sugarloaf Island	3	16	{69}	{69}	114	143	143	123	110	66	104
Cape Mendocino Complex	***3***	***16***	***69***	***69***	***151***	***185***	***182***	***173***	***187***	***128***	***181***
TOTAL	**156**	**169**	**347**	**357**	**630**	**728**	**924**	**1 072**	**1 227**	**1 249**	**1 686**

[a] Source: Osborne (1972)
[b] Source: Sowls *et al.* (1980)
[c] Source: Carter *et al.* (1992)
[d] When no data were available, brackets [] indicate totals from the previous or following year, and braces { } indicate an average of the surrounding four years.
[e] See text; 58 nests abandoned.

TABLE 1B
Total numbers of Double-crested Cormorant nests counted at colonies and colony complexes (bold italics) in the Humboldt Bay area, California, 1998–2017

Colony Name	1998	1999	2000	2001	2002	2003	2004	2008	2014	2017
Big Lagoon								42	20	16
Sea Gull Rock	57	36	24	37	61	21	40	13	10	7
Sea Lion Rock	0	0	0	19	19	20	11	0	0	0
White Rock	0	0	0	0	0	0	0	0	0	0
Pilot Rock	0	0	0	0	0	0	0	0	0	0
Trinidad Bay Rocks	0	0	0	0	0	0	12	5	0	0
Little River Rock	87	99	147	143	192	141	201	100	102	98
Trinidad Area Complex	***144***	***135***	***171***	***199***	***272***	***182***	***264***	***160***	***132***	***121***
Arcata Bay Sand Islands	0	0	0	0	0	809	0	103	417	175
Old Arcata Wharf	109	94	111	148	204	70	219	51	31	106
Arcata Bay Complex	***109***	***94***	***111***	***148***	***204***	***879***	***219***	***154***	***448***	***281***
Humboldt Bay Duck Blinds	0	0	0	0	0	0	0	0	0	0
Teal Island	613	719	660	706	746	365	1 046	485	700	720
South Bay Complex	***613***	***719***	***660***	***706***	***746***	***365***	***1 046***	***485***	***700***	***720***
False Cape Rocks	47	64	55	77	63	52	38	1	0	0
Sugarloaf Island	50	54	61	81	93	53	121	69	91	70
Cape Mendocino Complex	***97***	***118***	***116***	***158***	***156***	***105***	***159***	***70***	***91***	***70***
TOTAL	**963**	**1 066**	**1 058**	**1 211**	**1 378**	**1 531**	**1 688**	**869**	**1 371**	**1 192**

present that were attended by adults; they were not included in nest totals used for analysis, though some may have become egg-laying sites following surveys. We did not apply correction factors to nest totals to account for nests that were not active during surveys. Carter *et al.* (1992) calculated a mean "J correction factor" (i.e., a seasonal nest total divided by the number of active nests on a single census day) of 1.2 for April–July 1989 at the South Farallon Islands. A similar value (1.24; using just one aerial photographic census date) was calculated from a sample of nests at three colonies on the northern California coast in 2003 (Capitolo *et al.* 2004). Carter *et al.* (1992) applied the J correction factor to estimate breeding population sizes from 1989 to 1991 for the seabird colony catalog; we chose not to do so for trend analyses without annual local values, although use of a single value would not have affected our trend estimates. Also, the inclusion of poorly built, empty, and abandoned nests (i.e., portions of the population that have not yet laid eggs or that failed in breeding) partially offsets the need for correction factors.

We often zoomed images to 200 % during counting to best assign nest categories and identify species. DCCO and Brandt's Cormorants rarely co-occur at colonies in the Humboldt Bay area but regularly co-occur at several other northern California colonies (Capitolo *et al.* 2004). DCCO are usually readily distinguished by a combination of features, including nest structure (sticks can be seen), adult plumage (browner and less iridescent), phenology (chicks more likely than in Brandt's nests in northern California), habitat characteristics (steeper slopes, e.g.), and occasionally throat color. Pelagic Cormorants *P. pelagicus* are easily distinguished by habitat.

Statistical analyses

Using aerial photographic survey data from the 1989–2017 period, we statistically modeled changes in total numbers of nests in the Humboldt Bay area and for each of the four colony complexes. We used generalized additive models (GAMs) to model nest counts by colony complex according to an over-dispersed Poisson distribution as a nonlinear function of year. Specifically, we utilized the quasipoisson distribution with the gam function from the "mgcv" package in R statistical software to estimate over-dispersion (i.e., data dispersion beyond that expected from a Poisson model) and to fit GAMs to the nest count data; we used the "s" function to represent trends as a smooth spline function based on year (Hastie & Pregibon 1992, R Core Team 2017, Wood 2017). Data from 1969–1970 and 1979–1980 were excluded from regressions because of large time gaps and less standardized data. We examined regressions for 1989–2017, 1989–1997, and 1998–2017; the latter two periods were included because severe El Niño conditions resulted in greatly reduced breeding effort in 1998. Over-dispersion was estimated to be 31.1; values greater than 1.0 indicate over-dispersion. Therefore, all standard errors and confidence bands were corrected for over-dispersion via the gam function in R software (McCullagh & Nelder 1989, R Core Team 2017).

We calculated period percent changes by taking the difference in GAM-based estimates of mean nest sums from the first year to the last year of each period and expressing it as a percentage of the first year. For example, $(N_{2017} - N_{1989}) / N_{1989} \times 100$ %, which can also be expressed as $(\lambda - 1) \times 100$ %, where λ is population growth N_{2017}/N_{1989}. We similarly calculated percent per annum changes from annualized rates of growth. For example, for the 28 years spanning 1989–2017, the annualized rate is $\lambda^{1/28}$ and percent per annum change is $(\lambda^{1/28} - 1) \times 100$ %. The standard errors of mean nest sums and of growth rates reflect the statistical uncertainty caused by sampling variation in nest counts because the model separates out the process variation. Because standard errors for mean nest sums (N_t) were estimated by GAM on the log scale (i.e., $se(\log(N_t))$), we calculated standard errors for $\log(\lambda)$, e.g., $\log\left(\frac{N_{2017}}{N_{1989}}\right) = \log(N_{2017}) - \log(N_{1989})$, based on variance properties that define the standard error as the square root of the combination of variance and covariance components, e.g., $(se(\log(N_{2017}))^2 + se(\log(N_{1989}))^2 - 2\mathrm{cov}(\log(N_{2017}), \log(N_{1989})))^{0.5}$. We assumed that period endpoints were sufficiently spaced so that GAM-based estimates of mean nest sums have 0 or negligible covariances. We calculated 95 % confidence intervals for $\log(\lambda)$ by adding and subtracting two standard errors and then transformed the interval end points to obtain 95 % confidence intervals for percent changes. We used R statistical software for all analyses (R Core Team 2017).

RESULTS

Trinidad Area colony complex

Colony histories

The first records of DCCO nesting in the Humboldt Bay area are from May–June 1924–1925. These exist as ten sets of eggs collected from the outer coast near Trinidad by G.A. Howatt and J.M. Davis (Harris 2005; Eureka High School, Eureka, California). The collection location for three of these sets was recorded as "Trinidad Rocks", but the specific colony is unknown; no location was recorded for the other seven sets. The unpublished field notes of W. Anderson (Humboldt State University [HSU] library) included two additional references to historical nesting: a) in 1943, nests were noted on "Bishop Point, Trinidad Region"; and b) in 1947, "about 100 pairs" were noted on "Bishop's Head," including "one nest situated atop of low bush." Bishop's Head is not a place name that is currently used near Trinidad, but it may refer to the mainland point just south of White Rock (Fig. 1), which has been known as "Whale's Head" since the 1960s (N. Simmons pers. comm.). Nesting in the colony complex was not reported again until 1970, when 20 nests were counted at Sea Lion Rock and White Rock combined (Table 1). In 1972, two nests were noted at Little River Rock (Harris 2005) and a lack of nesting between 1965 and 1970 was confirmed (Osborne 1972, Harris 1974, S.W. Harris pers. comm.). By 1979–1980, the colony complex exceeded 100 nests in total.

Trends since 1989

Additional growth had occurred by 1989, especially at Little River Rock, which grew gradually to a high count of 309 nests in 1995; about 100–200 nests have been present since then (Table 1). By 1989, the central peak of Little River Rock had been denuded of vegetation and soil by cormorant nesting, and nesting had begun on the northeast peak. The denuding caused a dramatic decline in numbers of nesting Leach's Storm Petrels *Oceanodroma leucorhoa*, with redistribution of some storm petrels to nearby rocks in Trinidad Bay (Harris 1974, Sowls *et al.* 1980, Carter *et al.* 1992). During surveys in 2009, a disturbance by two people present on lower portions of the mainland side of the rock left most cormorant nests unattended with eggs exposed. Since then, cormorant nesting has mostly occurred on lower slopes on the west side of the rock (Fig. 2). The Trinidad Seabird

Protection Network has documented additional disturbance events at this colony, including human visits to the island during nesting season (D. Barton pers. comm). Sea Gull Rock is the only other colony with annual nesting in all years since 1989, though numbers have been small in recent years. Some birds may have moved north to Big Lagoon, where nesting in spruce trees was first confirmed in 2008, although it may have occurred as early as two or three years prior, as deemed from local observations of birds in the trees (G. Wengert pers. comm.). Detecting nests in the conifers is difficult and colony size was likely larger than our surveys indicated (Table 1; plus counts of 32 and 31 nests in 2015 and 2016, respectively). The total number of nests in the complex decreased only slightly from 1989 to 1997, was

TABLE 2
Period (top) and per annum (bottom) percent changes in mean sums of Double-crested Cormorant nests for the Humboldt Bay area, California, and four colony complexes therein, 1989–2017

Colony Complex	1989–1997	1998–2017	1989–2017
Trinidad Area	−26 % (−48, 5) −4 % (−8, 1)	−51 % (−72, −15) *[a] −4 % (−6, −1) *	−65 % (−81, −36) * −4 % (−6, −2) *
Arcata Bay	−45 % (−79, 49) −7 % (−18, 5)	320 % (72, 920) * 8 % (3, 13) *	120 % (−21, 500) 3 % (−1, 7)
South Bay	2600 % (620, 10000) * 51 % (28, 78) *	−13 % (−45, 37) −1 % (−3, 2)	2200 % (490, 8900) * 12 % (7, 17) *
Cape Mendocino	−22 % (−51, 23) −3 % (−8, 3)	−45 % (−73, 13) −3 % (−7, 1)	−58 % (−81, −9) * −3 % (−6, 0) *
Humboldt Total	100 % (36, 210) * 9 % (4, 15) *	1 % (−29, 45) 0 % (−2, 2)	91 % (18, 210) * 2 % (1, 4) *

[a] Asterisks indicate 95 % confidence intervals that do not overlap zero.

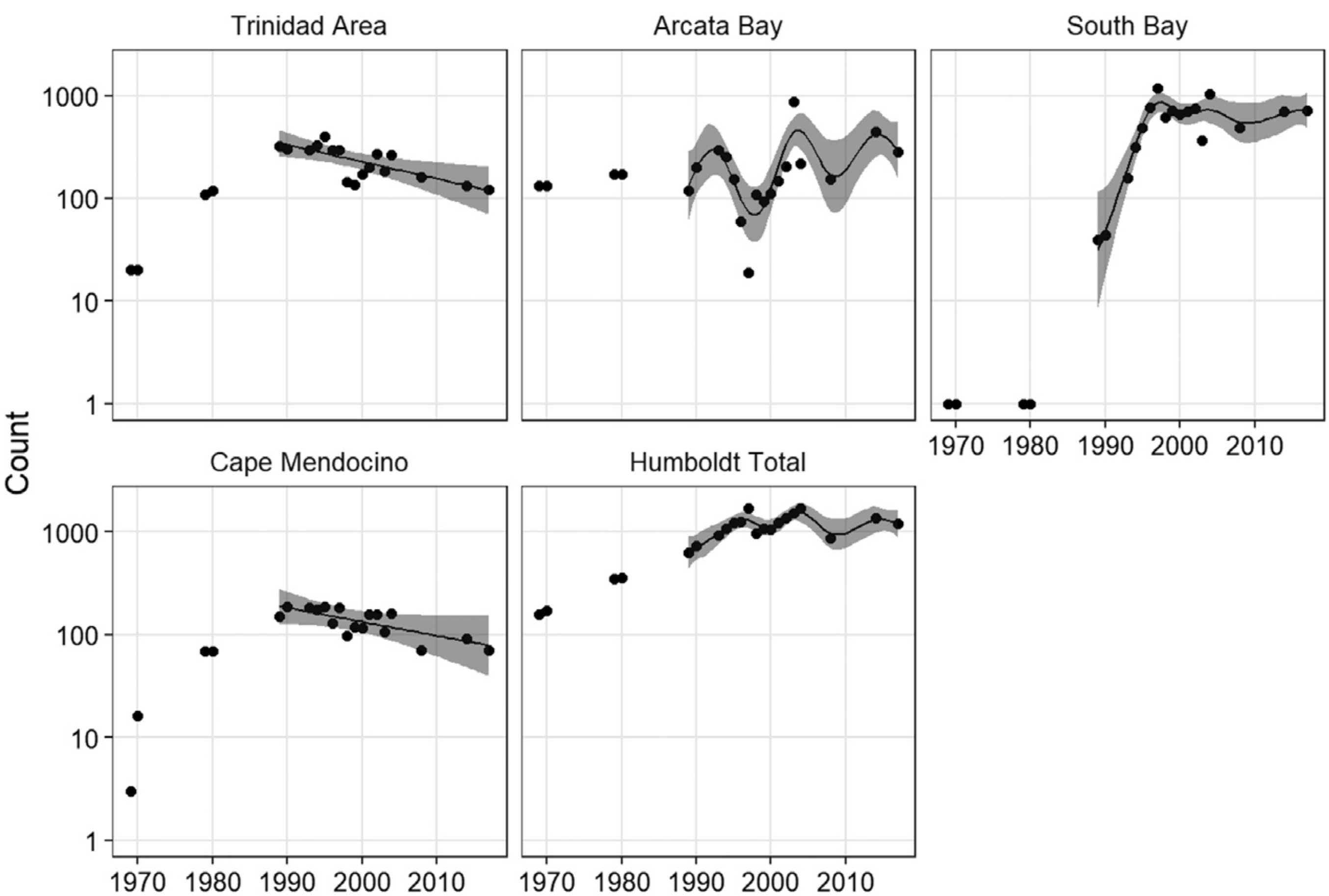

Fig. 5. Sums of Double-crested Cormorant nests for the Humboldt Bay area, California, and four colony complexes therein, 1969–2017 (dots). Zero values are displayed as 1 to allow plotting on the log-scaled axis. Mean sums were estimated by generalized additive models as functions of the years 1989–2017 (solid line) enclosed by 95 % confidence bands (shaded area).

reduced by more than 50 % during the strong 1998 El Niño, and was variable thereafter. Overall, nest totals decreased by 65 % (95 % CI = 81 %–36 %; −4 % per year) from 1989 to 2017 (Tables 1, 2; Fig. 5).

Arcata Bay colony complex

Colony histories

Nesting in Arcata Bay was first noted in 1959 at Old Arcata Wharf, but the first nest count was from 1961 (188 nests; S.W. Harris pers. comm.). On 07 May 1960, C.I. Clay collected two clutches of four eggs from "North Bay" (HSU Wildlife Museum specimens #621, 622), which is likely Old Arcata Wharf. Osborne (1972) counted 133 nests on 06 May 1970 (Table 1), and Ayers (1975) counted 161, 176, and 212 nests over consecutive breeding seasons from 1971 to 1973. In an unknown year during the 1960s, all nests were reportedly destroyed by vandalism (Osborne 1971). This wharf had been used for shipping lumber and other goods since the 1850s and was extended into deeper bay waters in 1875 (Coy 1982). It was abandoned by the 1930s, as many lumber mills closed during the Great Depression and transport by road became more common. Cormorants likely roosted on the old wharf while foraging in the waters of Arcata Bay, but it is unknown when the wharf began to break up and provide nesting habitat that was free from mammalian predators. Sand Island is a dredge spoil island created in the early 20th century (A. Laird pers. comm.). It is a popular winter location for persons hunting Brant *Branta bernicla* (B. Leigh pers. comm.).

Trends since 1989

Little change had occurred by 1989, but the Old Arcata Wharf colony then increased to its peak size of 292 nests in 1993, when nearly all available habitat was occupied (Table 1). Human disturbance may have impacted nesting in 1996, when 58 of 60 nests were abandoned. Available nesting space was reduced between 1999 and 2000 when a large wooden platform and associated beams disappeared; this area held more than 60 nests in 1993. By 2008, the remaining platforms had disappeared, with only pilings and the surrounding rocky ground available for nesting (Fig. 3). Human footprints in mudflats immediately adjacent to this area were evident in 2016 aerial photographs, with no nests present.

At Sand Island, cormorant nesting was first noted in 2003, although small numbers of nests may have been present in 2002, when "velvety black" birds too small to have fledged from Old Arcata Wharf were noted during late summer (M. Colwell pers. comm.). Many nests were built on non-native cordgrass *Spartina densiflora* growing on the island (Fig. 3). In 2003, the large number of nests (809) and late breeding phenology appeared to reflect mid-season movements following a possible disturbance at the large Teal Island colony in South Bay (see below). Numbers were reduced at Teal Island that year, but 20 % of nests had visible chicks, compared with none at Sand Island. No nests were seen at Sand Island in 2004, also possibly due to human disturbance, as two scarecrows on the island were seen in aerial photographs. A hunting blind also was on the island during the 2018 breeding season. Nesting at Sand Island has occurred annually since 2005, but nest numbers have fluctuated widely (e.g., 365 nests in 2015 and just 25 nests in 2016; see Table 1). Caspian Terns *Hydroprogne caspia* also nested at Sand Island in 2003 and in more recent years, alongside but not intermixed with cormorants (Fig. 3). Caspian Terns nested at Sand Island in the 1960s but were not known to breed there from 1970 to 1990; they recolonized the island by 2001 (Gill & Mewaldt 1983, Carter *et al.* 1992, Capitolo *et al.* 2004, Harris 2005). From 1998 to 2017, total numbers of cormorant nests in the complex increased by 320 % (95 % CI = 72 %–920 %; 8 % per year), driven by fluctuating peaks at Sand Island (Tables 1, 2; Fig. 5).

South Bay colony complex

Colony histories

The first recorded nesting in South Bay was in 1987 at Humboldt Bay Duck Blinds (Nelson 1989). Cormorants nested on six of seven waterfowl-hunting blinds that were suspended on small pilings in the mudflats on the edge of slough channels and were accessible to hunters by boat. The total number of nests was not reported but was likely similar to the 1989 count (39 nests on six blinds; Carter *et al.* 1992; Table 1). The blinds were constructed by waterfowl hunters as early as the 1940s (E.T. Nelson pers. comm.) but were probably not colonized by cormorants before the 1970s or 1980s. Activities of and possible persecution by hunters likely prevented cormorants from using the blinds until increased protection was provided in 1971, with the formation of the adjacent Humboldt Bay National Wildlife Refuge (NWR; USFWS 2009), and in 1972, under the Migratory Bird Treaty Act (Wires *et al.* 2001). The blinds gradually deteriorated and fell into the bay between the late 1980s and the late 1990s (E.T. Nelson pers. comm.).

Teal Island (Fig. 4) was acquired by the Humboldt Bay NWR in 1988. It was historically a salt marsh but was diked by the early 20th century to convert the central portion of the island to pasture and farmland. Cattle were barged to and from the island during late spring and summer for grazing. The central portion is now largely mudflat; the perimeter dike was first breached during the late 1960s. The dike has been covered with coyote bush *Baccharis pilularis* and other brush, grass, and weeds since at least the 1970s (E.T. Nelson pers. comm.).

Trends since 1989

Nesting on the duck blinds continued through 1996. As the blinds disappeared, cormorants likely shifted to Teal Island, where nesting was first noted in 1993 (Carter *et al.* 1996; Table 1). The colony initially formed north of the main breach in the dike on the east side of the island, adjacent to Hookton Slough, into which Salmon Creek drains. Most nests were constructed on the dike, though some were in and under vegetation, and nesting areas became denuded of vegetation. Colony size increased quickly from 118 nests in 1993 to 1189 nests in 1997. Nest totals were lower during and after the strong 1998 El Niño, but colony size was again similar to the 1997 peak by 2004. The lower nest count in 2008 was accompanied by nearly 200 territorial sites and 1800 birds, indicating many non-breeding birds and possibly late breeding birds. In 2014 and 2017, Teal Island remained the largest colony in the study area, with about 700 nests. Total numbers of cormorant nests in the complex increased from 1989 to 1997 by 2600 % (95 % CI = 620 %–10000 %; 51 % per year); the increase for the entire 1989–2017 period was 2200 % (95 % CI = 490 %–8900 %; 12 % per year) (Tables 1, 2; Fig. 5).

Ground counts of nests at Teal Island by researchers from the Humboldt Bay NWR and HSU were also available for certain years, and they generally agreed with aerial photographic counts when survey dates were similar (Table 3). In 1995 and 1996, ground counts were 2 % to 9 % higher than aerial counts, but whether definitions of nests were the same is not known. For example, ground counts would only be 1 % to 4 % higher if we included territorial sites in our aerial nest counts. In 2002, nest contents were recorded for 430 of 656 nests counted during a walk-through of the colony on 08 May. Of 347 nests without chicks, full or partial clutches contained 1–6 eggs (240 nests had three or four eggs). Eggs had not yet been laid in 33 freshly built nests, and one or more chicks had hatched in 50 nests (J. Black & K. Griggs unpubl. data). The aerial survey nest count on 04 June was 14 % higher (746 nests). Caspian Terns bred at Teal Island each year from 2015 to 2017; the species had not previously been documented breeding there.

Cape Mendocino colony complex

Colony histories

Nesting was first noted within the Cape Mendocino colony complex in 1969, when three nests were counted at Sugarloaf Island (Table 1). Cape Mendocino is remote and not easily observed, but the lack of prior recorded nesting may reflect extensive early human disturbance; for example, Thornbury (1923) described a system of ropes and ladders over the top of Sugarloaf Island that was used by sea lion hunters.

Trends since 1989

By 1989, population growth at the complex was evident, with increased nest numbers at Sugarloaf Island and colonization of False Cape Rocks (Table 1). Brandt's Cormorants also nested at Sugarloaf Island in 1989 and 2003 (Carter *et al.* 1992, Capitolo *et al.* 2004). In other years, some nests were counted (27 in 1994, 2 in 2001, and 17 in 2002) that could not be identified to species, and they were not included in analyses. False Cape Rocks had high counts of 77 DCCO nests in three years, but by 2008 the colony had been mostly abandoned, reflecting competition for nesting space with a recovering breeding population of Common Murres (Carter *et al.* 2001, USFWS & HSU unpubl. data). Only one nest was counted in 2008, and none in 2014 and 2017. Cormorants had mostly nested on the ridgeline of the largest sea stack (Subcolony 03), which became occupied entirely by Common Murres. The count of murres from aerial photographs of this colony in 2014 (> 25 000 birds) was 170 % greater than the 1989 count (Carter *et al.* 1992, 2001; Barton *et al.* 2017). Total numbers of nests in the complex decreased by 58 % (95 % CI = 81 %–9 %; −3 % per year) from 1989 to 2017 (Tables 1, 2; Fig. 5).

Humboldt Bay area total

Colony histories

Although Grinnell & Miller (1944) did not report DCCO nesting along the California coast north of Marin County prior to 1944, we discovered unpublished records of nesting as early as 1924. Colony size estimates in the Trinidad Area complex in 1947 and at Old Arcata Wharf in 1961 indicated the Humboldt population likely never exceeded low hundreds of pairs during at least the first half of the 20th century. New colonies were documented in 1969 and 1970, and population growth was evident by 1979 (Table 1).

Trends since 1989

Additional growth had occurred by 1989 and continued with colonization of Teal Island in 1993 (Table 1). The population peaked in 1997 (1 686 nests), decreased by more than 40 % during the strong 1998 El Niño, and grew again to a nearly identical peak in 2004 (1 688 nests). Total numbers of nests increased by 100 % (95 % CI = 36 %–210 %; 9 % per year) from 1989 to 1997. No trend was detected from 1998 to 2017, but available data after the 2004 peak indicated a slight decline. The overall increase during the 1989–2017 period was 91 % (95 % CI = 18 %–210 %; 2 % per year; Tables 1, 2; Fig. 5).

DISCUSSION

The breeding population of DCCO in the Humboldt Bay area increased substantially from the 1970s to the 1990s, peaking around 1 700 nests in 1997 and again in 2004. Since 2004, three years of available data indicate the population declined slightly and was notably reduced in 2008. Changes at individual colonies since 2004 included abandonment of False Cape Rocks, habitat loss at Old Arcata Wharf, and colonization of Big Lagoon. Population increases starting in the 1970s also occurred statewide along the California coast. Total numbers of nests increased from fewer than 1 000 per year (1975–1980) to about 4 400 (1989–1991) and 6 600 (2001–2003), before they decreased to about 5 000 in 2008 (Hunt *et al.* 1979; Sowls *et al.* 1980; Carter *et al.* 1992, 1995; Capitolo *et al.* 2004; Adkins *et al.* 2014). The lower statewide coastal estimate in 2008 likely reflected reduced breeding effort due to changes in prey availability that were not associated with El Niño. Substantially reduced nesting in 2008 and 2009 that occurred for both Double-crested and Brandt's Cormorants in central California was associated with decreases in the numbers and sizes of northern anchovy *Engraulis mordax* (Capitolo *et al.* 2014, Elliott *et al.* 2016, Ainley *et al.* 2018, Rauzon *et al.* 2019). Northern anchovy is an important prey species for DCCO at Pacific coast colonies (Ainley *et al.* 1981, USACE 2015), and it is abundant in Humboldt Bay during summer (Barnhart *et al.* 1992, Cole 2004). By 2014, nest numbers had increased not just in the Humboldt Bay area, but also to the north from the Klamath River area to the Oregon border (28 % higher in 2014 compared with 2008; Adkins & Roby 2010, Barton *et al.* 2017). The large numbers of territorial sites and non-breeding birds at Teal Island in 2008 may further indicate poor foraging conditions in that year.

The annual growth rate of 9 % from 1989 to 1997 probably reflected local production and recruitment primarily, without

TABLE 3
Comparison of ground survey (G) and aerial photographic survey (A) counts of Double-crested Cormorant nests at Teal Island, Humboldt Bay, California, 1995–2002

1995		1996		2002	
Date	Nests	Date	Nests	Date	Nests
31 May (G)[a]	507	30 May (G)[b]	768	08 May (G)[c]	656
07 June (A)	464	04 June (A)	750	04 June (A)	746

Ground surveys by: [a] P. Schmidt; [b] P. Schmidt and C. Goss; [c] J. Black and K. Griggs substantial immigration from the Columbia River Estuary or other populations, whereas the larger increase of 51 % per year for South Bay reflected a redistribution of birds from the other colony complexes to Teal Island. High rates of annual percent change have similarly indicated colony-switching by Brandt's Cormorants in central California, from the offshore South Farallon Islands to mainland colonies, with support from sightings of banded birds (Capitolo *et al.* 2014, Ainley *et al.* 2018). Nur & Ainley (1992) also discuss annual growth rates that would reflect substantial immigration. In contrast to the local redistribution of DCCO in the Humboldt Bay area (within less than 50 km), initial rapid growth of the large East Sand Island colony involved immigration of birds from more distant colonies in coastal British Columbia and Washington and interior Oregon (Carter *et al.* 1995, Anderson *et al.* 2004). Recoveries of birds banded as nestlings and satellite-tracking of tagged adults indicate that colony connectivity of the Columbia River Estuary population is greatest with coastal regions to the north (Clark *et al.* 2006, Courtot *et al.* 2012). And although two of these satellite-tagged adults occurred at Sand Island in Arcata Bay in October during post-breeding dispersal, of 11 adults tracked through spring migration, all returned to the Columbia River Estuary.

Despite the recent population increase to about 1700 pairs, DCCO may have been still more numerous historically near Humboldt Bay before rapid settlement of the area by European Americans in the mid-19th century (Coy 1982). Habitats that cormorants used in the past for breeding may no longer exist due to natural or anthropogenic factors. Healthier fish populations also could have sustained larger numbers of birds (Wires & Cuthbert 2006); three species of salmonids along the northern California coast are currently federally listed as Threatened by the National Marine Fisheries Service (Williams *et al.* 2016). Indeed, throughout much of their North American range, DCCO appear to have been more abundant at the time of settlement than today (Wires & Cuthbert 2006). After settlement, the Humboldt population likely totaled in the low hundreds of pairs at most and may have been extirpated for periods. However, Townsend (1887) observed roosting cormorants along the Mad River in early winter 1885 "occupying every tree along the bank for several hundred yards", indicating a potential for past nesting in trees. During the first half of the 20th century, before Old Arcata Wharf also became available, nesting was apparently restricted to an isolated coastal location near Trinidad, perhaps because of limited exposure to human disturbance, mammalian predator access, and avian predator impacts.

Increased protections since then have allowed population growth and the colonization of other coastal rocks and artificial habitats in Humboldt Bay. In 1972, DDT (dichloro-diphenyl-trichloroethane; see below) was banned and the DCCO was among the species added to the Migratory Bird Treaty Act protected bird list (Wires *et al.* 2001). However, human disturbance continues to affect nesting cormorants. We observed disturbances directly at Little River Rock and indirectly at Old Arcata Wharf and Sand Island. Changes in colony sizes also indicated possible disturbance at Teal Island. Current potential sources of human disturbance include activities at nearby oyster farming facilities in Humboldt Bay and recreation such as windsurfing, boating, and kayaking, both in Humboldt Bay and near Trinidad. During our survey of the Humboldt Bay Duck Blinds in 1990, cormorants were noted as easily disturbed by the inflatable boat; roosting and nesting birds, respectively, began to flush when the boat was 200 m and 40 m distant.

Contaminants and strong El Niño events also may have affected breeding population sizes in recent decades. In the early 1970s, contamination by dichlorodiphenyl-dichloro-ethylene (DDE, a metabolic breakdown product of DDT) was deemed a principal cause of egg loss at Old Arcata Wharf (Ayers 1975). Eggshell thickness and DDE concentration were significantly negatively correlated, and shells of destroyed eggs were 8 %–57 % thinner than shells of eggs collected before 1947, when the widespread, general use of DDT began. DDE concentrations, however, were much lower than those observed in 1969 at colonies in southern California and northwestern Baja California, close to the area where liquid wastes of DDT manufacturing in Los Angles had entered the ocean directly through sewage outfall (Gress *et al.* 1973). In addition to the 1998 El Niño (Lynn *et al.* 1998), when the Humboldt population declined 40 % from 1997 numbers, additional El Niño events with well-documented impacts on murres and Brandt's Cormorants (focal species of aerial surveys) in California occurred in 1982/83 and from 1992 to 1993 (Ainley *et al.* 1988; Carter *et al.* 1996, 2001; Capitolo *et al.* 2004, 2014; USFWS & HSU unpubl. data). In 1993, murre attendance was greatly reduced at Flatiron Rock (in the Trinidad Area colony complex) and at False Cape Rocks (Carter *et al.* 1996, 2001), although without data in 1991 or 1992 we cannot assess whether DCCO nesting was also reduced. Colonization of Teal Island in 1993, however, may further reflect the redistribution of birds to areas closer to more reliable prey resources during El Niño events. Movements from outer coast areas to inner waters were also suspected during the 1982/83 El Niño, both in Washington and in the San Francisco Bay region (Carter *et al.* 1995, Stenzel *et al.* 1995).

Despite increased breeding population sizes of DCCO in the Humboldt Bay area since the 1970s, future population decline is likely if the artificial habitats used by cormorants for nesting do not persist. At Teal Island, dikes are eroding, and restoration of the former salt marsh could be considered in the future (USFWS 2009). At Old Arcata Wharf, a restoration project to construct permanent artificial habitat was proposed following legal settlements for oil spills in the Humboldt Bay area, but other measures to protect roosting Brown Pelicans *Pelecanus occidentalis* and cormorants from human disturbance were selected instead. Response to public comments indicated that natural resource trustees were concerned about construction disturbance to shoreline habitat associated with wharf restoration. About 50 DCCO were estimated to have died due to oil spills in November 1997 and September 1999 (Kure/Stuyvesant Trustee Council 2007, 2008). And ultimately, each Humboldt Bay colony is vulnerable to rising sea levels and land subsidence over time (Laird 2015; Figs. 3, 4).

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