

# CHANGES IN BREEDING POPULATION SIZES OF BRANDT'S CORMORANTS *PHALACROCORAX PENICILLATUS* IN THE GULF OF THE FARALLONES, CALIFORNIA, 1979–2006

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## SUMMARY

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Using aerial photography, we examined Brandt's Cormorant *Phalacrocorax penicillatus* breeding population trends during the 1979–2006 period in the Gulf of the Farallones (GF), California, at the center of the species' breeding range and where its largest single breeding assemblage has occurred (South Farallon Islands [SFI]). In 1979, about 22 000 Brandt's Cormorants bred in the GF, mostly at SFI and mainland colonies north of San Francisco Bay. By 1985, breeding populations were greatly reduced at all active GF colonies following impacts from the strong 1982–1983 El Niño event. During the 1985–1995 period, no trend was detected for SFI, whereas mainland colonies combined increased by 19% per annum. Alcatraz Island inside San Francisco Bay and Año Nuevo Island at the southern end of the GF were colonized, and the new colonies grew rapidly. In 1998, the GF breeding population was again reduced during a strong El Niño. Subsequent growth during the 1998–2006 period was dramatic for all colonies (range 13–29% per annum; 18% combined), associated with strong La Niña conditions during 1999–2000 and high reproductive success during 1999–2006 (except 2003). By 2006, the GF total breeding population was the largest ever recorded (34 876 birds), and the SFI colony had reached a size (~23 500 breeding birds) similar to the previous peak estimate in 1974. Population increase at mainland colonies since the late 1980s likely reflected: 1) immigration of SFI birds; as a result of 2) reduced availability of juvenile rockfishes *Sebastes* spp. offshore and increased use of Northern Anchovies *Engraulis mordax* nearshore as prey; and 3) protection of potential breeding habitat.

Key words: aerial photographic surveys, California, Brandt's Cormorant, El Niño, Gulf of the Farallones, immigration, *Phalacrocorax penicillatus*, population trends

## INTRODUCTION

The Brandt's Cormorant *Phalacrocorax penicillatus* breeds along the North American west coast, mainly from Washington to the Gulf of California, Mexico, with small numbers as far north as southeast Alaska (Wallace & Wallace 1998, Heintz & Piston 2007). This cormorant forages in continental shelf waters on both schooling and non-schooling fish (Ainley *et al.* 1981, 1990; Sydeman *et al.* 1997). It is one of the most abundant breeding seabird species in the California Current System (CCS; Tyler *et al.* 1993), often forming intermixed colonies with Common Murres *Uria aalge*. The global population was estimated at about 150 000 breeding birds in 1979, with roughly 75% in California (see Boekelheide *et al.* 1990). However, numbers of breeding birds can vary substantially among years due to annual differences in the proportion of adults that breed, strength of year-classes of potential recruits, degree of recruitment of first-time breeders, and survivorship (Boekelheide & Ainley 1989, Boekelheide *et al.* 1990, Nur & Sydeman 1999). Strong El Niño and La Niña events associated with the El Niño–Southern Oscillation (ENSO) also have pronounced effects on annual

breeding population sizes due to changes in marine productivity and prey availability (Ainley *et al.* 1988, Ainley & Boekelheide 1990). The largest known colony has been at the South Farallon Islands (SFI) in the Gulf of the Farallones (GF), central California, with up to 12 000 pairs (Boekelheide *et al.* 1990, this study).

An annual index of the size of a Brandt's Cormorant colony can be readily determined through single or multiple aerial photographic surveys during the late egg-laying to early chick-hatching periods, by counting of nests from photographs. Brandt's Cormorants build conspicuous nests and breed in relatively dense colonies, facilitating photographic coverage. In California, aerial photographic surveys of all major Brandt's Cormorant breeding colonies (as well as those of the Double-crested Cormorant *P. auritus* and the Common Murre) have been conducted since 1979 for 1) periodic statewide assessments of seabird population sizes and distributions (Sowls *et al.* 1980; Carter *et al.* 1992, 1995a, 2001; Capitolo *et al.* 2004; Adkins & Roby 2010); 2) identification of anthropogenic impacts to seabirds, including gill net fishing, oil spills and human disturbance at colonies (Takekawa *et al.*

1990; Carter *et al.* 1998, 2003a,b); 3) determination of breeding population trends (Takekawa *et al.* 1990; Carter *et al.* 1995b, 2001; USFWS, unpubl. data); and 4) identification and monitoring of the effectiveness of seabird restoration projects (McChesney *et al.* 2007, Capitolo *et al.* 2008, Jones *et al.* 2008). In the GF, Brandt's Cormorant colony counts were determined annually from 1996 to 2006 as part of monitoring efforts associated with Common Murre colony restoration (McChesney *et al.* 2007, Parker *et al.* 2007, Jones *et al.* 2008).

In this paper, we examine Brandt's Cormorant breeding population trends throughout the GF during the 1979–2006 period. To provide historical context, we also summarize available information on colony sizes before 1979. Other published descriptions of Brandt's Cormorant breeding population trends (in the GF or elsewhere) are limited to two earlier studies at individual colonies, SFI (Boekelheide *et al.* 1990, Nur & Sydeman 1999) and Alcatraz Island (in San Francisco Bay; Saenz *et al.* 2006). The broad spatial and temporal scales of Brandt's Cormorant population trends presented here are valuable for helping to interpret how CCS seabirds are affected by 1) long- and short-term environmental variability; and 2) fisheries, oil spills, colony disturbances, climate change and other anthropogenic impacts.

## STUDY AREA AND METHODS

### Colonies and colony complexes

The GF comprises California coastal waters roughly from Point Reyes to Point Año Nuevo and offshore to the continental slope (Steger *et al.* 2000; Fig. 1). During 1979–2006, Brandt's Cormorants were documented to breed at 15 colonies, two on offshore islands and 13 on islands, sea stacks, and cliffs along the mainland coast, including two within San Francisco Bay. Three colonies (Yerba Buena Island, Seal Rock Cliffs, and Martins Beach) could not be surveyed well with aerial photography and were not included in analyses, but contained only small numbers (<50 pairs). All colonies were previously identified with a colony name and a US Fish and Wildlife Service (USFWS) Colony Number (Sowls *et al.* 1980, Carter *et al.* 1992). Based on proximity of colonies and possible colony shifting among years, certain colonies were lumped into colony complexes, described below.

SFI (37°42'N, 123°00'W) and the North Farallon Islands (NFI; 37°46'N, 123°06'W) are at the outer edge of the continental shelf. The Farallon National Wildlife Refuge has included all of these islands since 1969. Colony trends were analyzed only for SFI, as

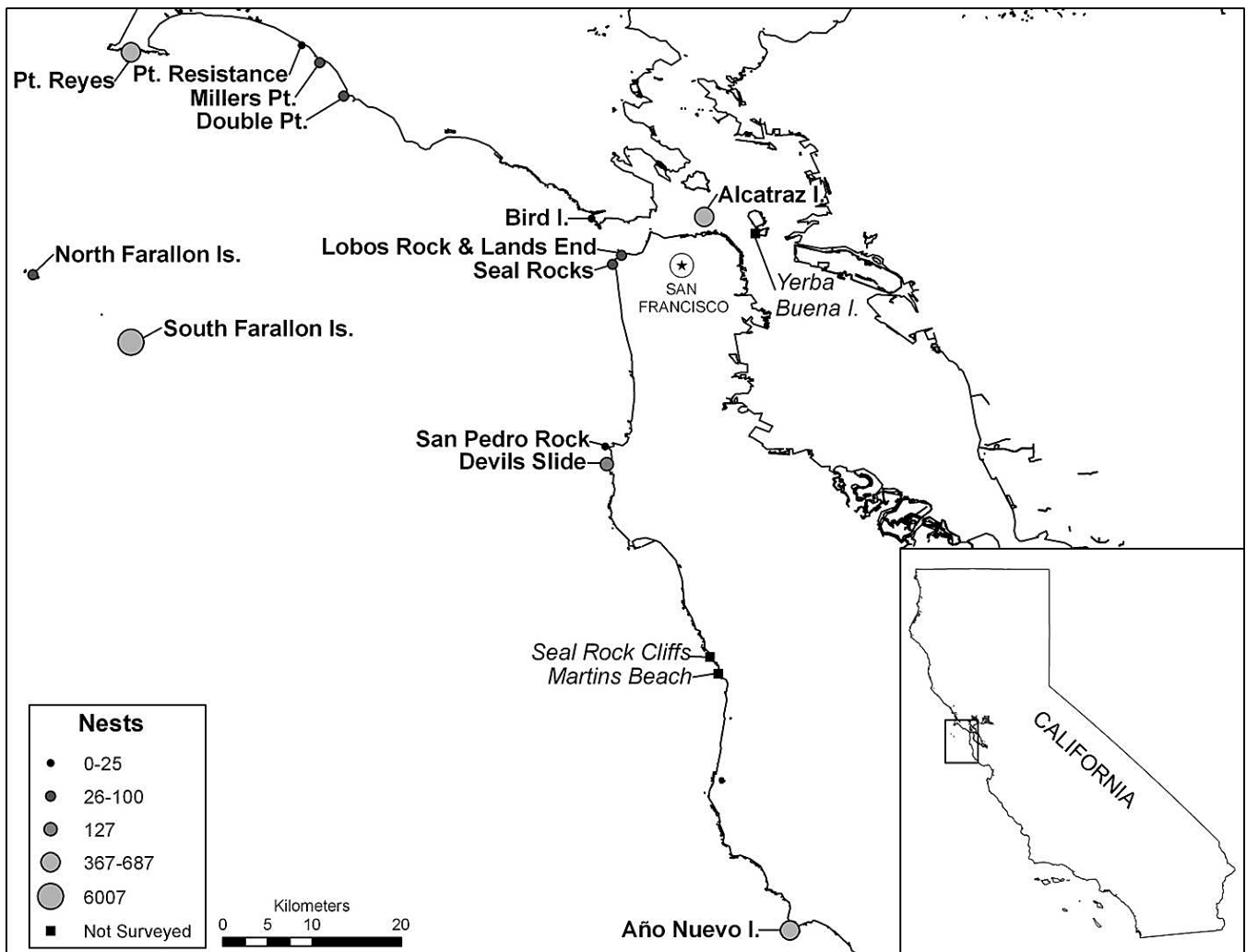


Fig. 1. Locations and average annual sizes of Brandt's Cormorant breeding colonies in the Gulf of the Farallones, California, 1979–2006.

few nests occurred at NFI. However, NFI nests were included in trend analyses of the combined GF population. At NFI, cormorants nested near the top of steep islets amid large, dense murre colonies. At SFI, cormorants nested mainly on broad, gradual slopes, often intermixed with murre, in many subcolonies spread out over the approximately 57 ha archipelago.

Along the mainland coast, cormorant breeding colonies were widely distributed. At Point Reyes (37°59'30"N, 123°00'W), nests were placed on mainland cliffs at the bases of steep slopes and on adjacent sea stacks along a 5 km stretch of south-facing headlands. The Drakes Bay Colony Complex (37°58'N, 122°48'30"W) included colonies on sea stacks along 7 km of shoreline at Point Resistance, Millers Point Rocks and Double Point Rocks (also known as Stormy Stack). Point Reyes and Drakes Bay have been managed by the National Park Service (NPS; Point Reyes National Seashore) since 1962. At Alcatraz Island (37°49'30"N, 122°25'30"W), in central San Francisco Bay about 5 km east of the Golden Gate Bridge, cormorants nested along the 0.5 km-long southwest perimeter. At the entrance to San Francisco Bay, the Lobos/Seal Colony Complex (37°47'N, 122°31'W) included colonies on sea stacks at Lobos Rock and Lands End, Seal Rocks and Bird Island. Alcatraz and Lobos/Seal have been managed by NPS (Golden Gate National Recreation Area) since 1972. At Devils Slide Rock and Mainland (37°34'30"N, 122°31'W), about 25 km south of Lobos/Seal, cormorants bred on one sea stack (Devils Slide Rock) and adjacent mainland cliffs. Historically, nesting also occurred nearby at San Pedro Rock (Ray 1909), about 2 km north of Devils Slide Rock. Devils Slide Rock has been managed by the US Bureau of Land Management (California Coastal National Monument) since 2000, while the adjacent mainland was privately owned. At Año Nuevo Island (37°06'30"N, 122°20'W), cormorants nested on the flat, sandy surface of the low-lying 10 ha island. The island has been managed by California State Parks (Año Nuevo State Reserve) since 1970. Waters around all colonies except Alcatraz and Lobos/Seal are part of the National Oceanic and Atmospheric Administration's Gulf of the Farallones (since 1981) or Monterey Bay (since 1992) national marine sanctuaries. Sanctuary regulations affect levels of pollution and human disturbance, but not fishing.

## Data sources

### *Before 1979*

Before the aerial photographic survey period examined here, there is much information for the Brandt's Cormorant colony at SFI, but little about mainland colonies. For SFI, Ainley & Lewis (1974) summarized large-scale changes in colony size since the mid 1800s. From 1971 to the present, annual estimates of population size have been made from ground- and boat-based observations by Point Blue Conservation Science (hereafter, Point Blue; Boekelheide *et al.* 1990). For mainland colonies, surveys were conducted during 1969–1972 (e.g. Osborne & Reynolds 1971, Ainley & Whitt 1973), but historical information is incomplete (e.g. Bolander & Bryant 1930) and references to cormorant breeding in earlier literature often included only relative colony-size information.

### *1979–1982*

Aerial photographic surveys were first conducted in 1979 and 1980 by Sowls *et al.* (1980) and during 1980–1982 by Briggs *et al.* (1983). Data from surveys from boat and the adjacent mainland also were

used in 1979 and 1980 (Sowls *et al.* 1980). Sowls *et al.* (1980) did not photograph SFI, and Briggs *et al.* (1983) counted only birds and not nests, and did not count all colonies. We re-counted 1979–1982 slides of Point Reyes, Drakes Bay Colony Complex, and Devils Slide Rock and Mainland using standardized methods developed since 1985 (McChesney *et al.* 1998, this study). For 1982, however, we could only determine a nest count for Devils Slide Rock and Mainland because of poor photograph quality at other colonies. For SFI in 1979 and 1980, we used estimates determined from ground- and boat-based surveys (Boekelheide *et al.* 1990; Point Blue, unpubl. data) in non-linear regression analyses (see below). We did not include SFI ground/boat data from 1981 and 1982 because aerial survey coverage of mainland colonies was incomplete in these years and a GF total would not have been possible.

### *1985–2006*

During 1985–2006, standardized aerial photographic surveys of Brandt's Cormorant, Double-crested Cormorant and Common Murre breeding colonies throughout coastal northern and central California were scheduled for late May or early June, generally coinciding with the late incubation or early chick period for these species (Ainley & Boekelheide 1990; Takekawa *et al.* 1990; Carter *et al.* 1992, 1995a,b, 1996, 2000, 2001, 2003a; Capitolo *et al.* 2004; Jones *et al.* 2008; USFWS, unpubl. data). No surveys were conducted in 1991 and 1992. Survey dates for individual colonies in the GF ranged from 23 May to 20 June, depending on aircraft availability and weather conditions. All colonies were surveyed once, except during 1996–2001, when a variable number of replicate surveys were conducted at Point Reyes, Drakes Bay Colony Complex, and Devils Slide Rock and Mainland (USFWS, unpubl. data). For Brandt's Cormorants, we summed highest subcolony totals from among replicate surveys for a colony complex total. In most cases, highest subcolony totals within a complex occurred on the same survey date, and nest counts on consecutive dates were nearly identical. During 1996–1998, replicate surveys also were conducted before 23 May and as early as 7 May, but cormorant nest counts from these surveys were lower. In addition, the Drakes Bay Colony Complex was surveyed throughout the breeding season in 1998 (Carter *et al.* 2003a). Replicate survey data supported continued scheduling of single annual surveys of all colonies in late May to early June.

Surveys were conducted from either a single-engine Cessna or a twin-engine Partenavia fixed-wing aircraft. Survey altitudes ranged from 150 to 365 m above sea level. Before 1997, photographs were taken obliquely through side windows and window ports. During 1997–2006, photographs were taken vertically through a port in the belly of the aircraft. Switch to vertical photography increased efficiency of surveys by reducing the need for aircraft-banking. Image quality also improved in some cases (more readily enabling detection of chicks in nests, for example), but nest total estimates were comparable with either oblique or vertical photography. Photographs were taken with handheld 35 mm cameras and color slide film (ASA 200) with 300 mm lenses for close-up photographs and 50 mm or zoom lenses for overview photographs. Switch to digital single-lens reflex cameras for surveys in this region occurred in 2007.

Whole-colony counts were determined by projecting slide images onto large sheets of white paper and marking each nest, territorial site and bird with a felt pen. Nests and territorial sites were categorized by their stage of development. Nests included poorly

built to well-built nests attended by adults or chicks, and empty or abandoned nests that had clearly been active in the survey year. Territorial sites included locations in suitable breeding habitat with little or no nesting material present that were attended by adults in breeding densities. We judged that most territorial sites likely did not become egg-laying sites, and we used only nests in analyses (see below). Some colony counts during 1989–1995 were determined before these categories were developed, when any location with nesting material was considered to be a nest (Carter *et al.* 1992, 1996). However, because relatively few territorial sites typically were counted in the GF during the late May and early June survey period, we felt that nest totals derived with earlier methods were comparable for analyses. Detection probabilities for Brandt's Cormorant birds and nests were near 100% (Steinkamp *et al.* 2005).

When aerial photographic data were not available, ground- or boat-survey data were used when possible. For 1989, the Point Reyes total includes partial boat-survey data, and Año Nuevo Island data were from boat and on-island surveys (Carter *et al.* 1992). On-island survey data also were used for Alcatraz Island during 1991–1994 (Saenz *et al.* 2006; NPS, unpubl. data) and Año Nuevo Island in 1993 (Hester & Sydeman 1995). Ground and boat survey data for SFI were used only in one instance, when aerial photographic data were available but incomplete. For 1986, aerial photographic data were available for West End Island and combined with ground and boat survey data for Southeast Farallon Island and surrounding islets to determine a total SFI estimate. In 1985, aerial data also were available only for West End Island, but ground- and boat-based subcolony data were not found, so no total SFI estimate was possible. Similarly, no total SFI estimate was available for 1996, when aerial data were compromised by camera malfunctions. Finally, no data were available for 1) NFI in 1996, 2) Millers Point Rocks in 1986, 3) Lobos/Seal Colony Complex during 1985–1987 and 4) Devils Slide Rock and Mainland in 1985.

### Analyses

We performed linear Poisson regression analyses to determine annual percentage changes in total numbers of nests during five time periods: 1) 1985–2006, 2) 1985–1995, 3) 1993–2006, 4) 1993–1997 and 5) 1998–2006. The first time period provided overall trends. The 1985–1995 time period was selected to allow future comparison to Common Murre trend analyses; the period was chosen for murre analyses because direct inspection of data indicated a distinct trend (Carter *et al.* 2001; USFWS, unpubl. data). The 1993–2006 period was the only period in which surveys were conducted in all years. The latter two periods were selected to compare trends before and after the strong El Niño in 1998. Data from strong El Niño years were included in regression analyses, despite reduced breeding effort. For newly formed colonies, the zero count in the year before colonization was included in regressions, but earlier zero counts were not. All standard errors were corrected for overdispersion. For the 1993–2006 period, we also conducted linear regressions using data from every other year or every third year, to assess our ability to detect trends with less-than-annual data; we describe where significant trends were lost compared with analyses of annual data.

Regression analyses were performed for 1) seven colony complexes, 2) all mainland colonies combined and 3) all GF colonies combined. Additionally, for SFI, we performed analyses for Corm Blind Hill, an individual subcolony. Total SFI estimates for 1973–1979 and

1983 were calculated based on Corm Blind Hill's percentage of the SFI total during 1980–1982 (Boekelheide *et al.* 1990).

The 1979–1982 period was excluded from linear regression analyses because data during this period were incomplete and less standardized than later data. However, we also produced locally weighted scatterplot smoothing (LOESS) plots to show general population trends for the entire 1979–2006 period. Plots were fitted with a LOESS smooth curve ( $\alpha = 0.75$ ) and pointwise 95% confidence intervals. All analyses were performed using the software R (version 2.10.0, R Development Core Team, Vienna, Austria).

### Ground monitoring

To assess the completeness of breeding population estimates determined from single aerial photographic surveys, we used productivity monitoring data to calculate the proportions of seasonal nest totals that were active on aerial survey dates for Point Reyes and Devils Slide Rock and Mainland. Productivity monitoring data were available for certain subcolonies at Point Reyes during 1997–2001 and in 2006 and at Devils Slide Rock and Mainland during 1997–2006 (Jones *et al.* 2008; USFWS, unpubl. data).

## RESULTS

### Farallon Islands

*Colony Histories:* Ainley & Lewis (1974) summarized large-scale changes in SFI population size since the mid 1800s. The peak estimate before this study was 11 900 nests (or 23 800 breeding birds) in 1974 (Boekelheide *et al.* 1990). Human activities heavily impacted the population throughout the 19th century and first half of the 20th century (Ainley & Lewis 1974, White 1995, Carter *et al.* 2001, Capitolo 2009). Before the 1800s, the population was likely limited by competition for nesting space with murre, which may have numbered more than 1 000 000 breeding birds (Carter *et al.* 2001), and Northern Fur Seals *Callorhinus ursinus*, which may have numbered close to 100 000 animals (Pyle *et al.* 2001). For NFI, no information before the 1979–2006 period was available.

*Recent Trends:* At SFI, the total number of nests was relatively high during 1979–1980, had declined substantially by 1986 and increased through 1989. Thereafter, numbers fluctuated at lower levels through 2001, with noticeably reduced numbers during 1998. Numbers increased substantially after 2001, with colony size reaching a level similar to the previous peak estimate (in 1974; see above) by 2006 (11 739 nests; Table 1; Fig. 2). SFI increased by 3.2% per annum during 1985–2006 ( $P = 0.02$ ), 6.9% during 1993–2006 ( $P = 0.006$ ) and 17.0% during 1998–2006 ( $P < 0.001$ ). During 1993–2006, results were no longer significant when data from just every other year were used (3.7% per annum;  $P = 0.081$ ; USFWS, unpubl. data). The Corm Blind Hill subcolony, for which separate aerial counts were first available in 1993, increased by 15.6% per annum during 1993–2006 ( $P < 0.001$ ) and 22.5% during 1998–2006 ( $P < 0.001$ ), rates that were 126% and 32% greater than for the SFI total (Table 2). SFI accounted for roughly 90% of all nests in the GF from 1979 to 1989; the proportion declined thereafter to 67% in 2006 (Table 1).

At NFI during 1985–2006, small numbers of nests occurred on each of the four islets, but most nesting was on the West and East islets. Total numbers of nests were low in all years (range 2–98 nests), with highest counts in 2002 and 2003 (Table 1).



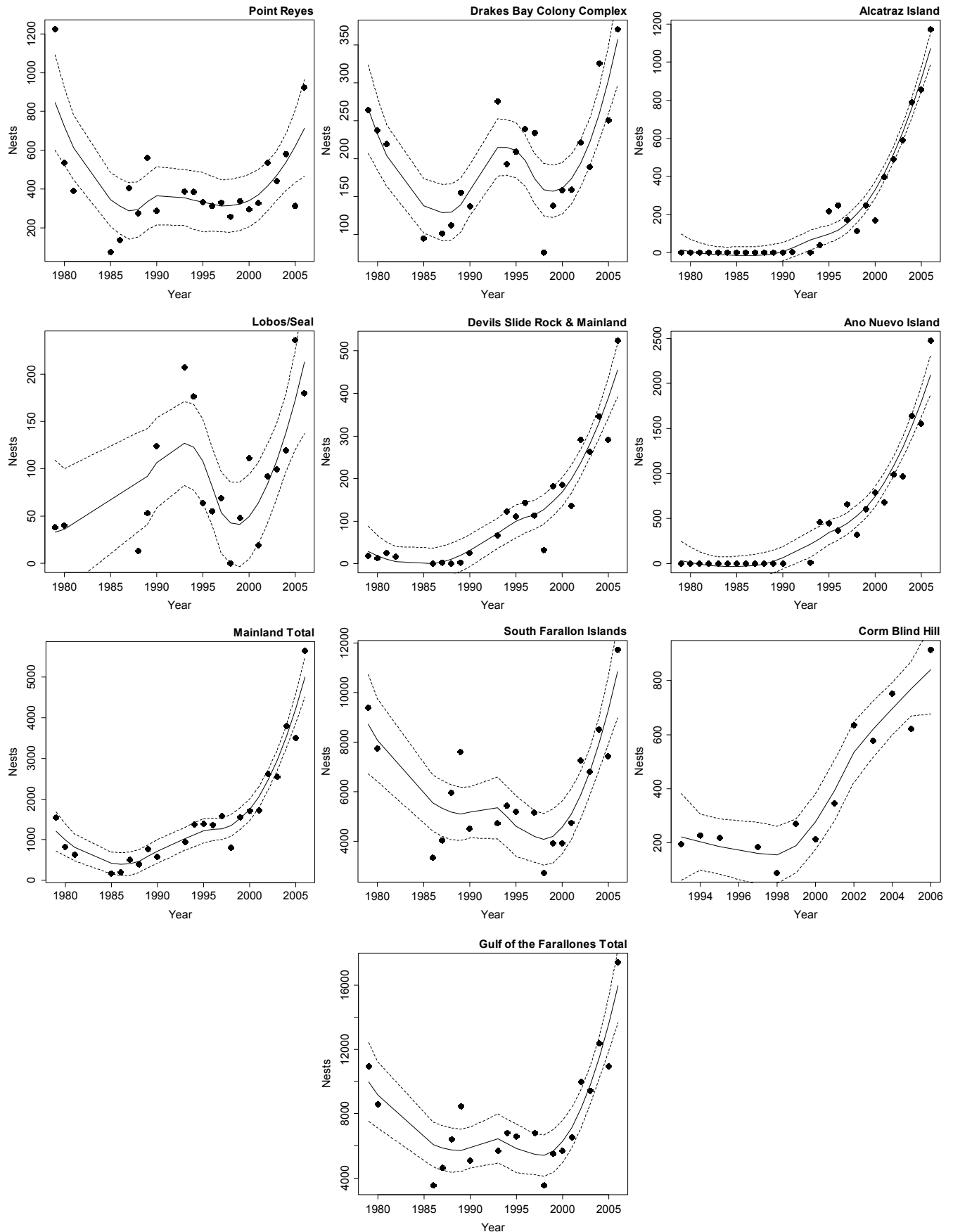
**TABLE 1A**  
**Total numbers of Brandt's Cormorant nests at breeding colonies in the Gulf of the Farallones (GF), California, 1979–1992**

Colony or colony complex Colony within complex	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992
Point Reyes	1 226	535	390	ND <sup>a</sup>			73	136	404	275	559	287		
Drakes Bay	264	237	219				95	59	101	112	155	137		
Point Resistance	75	40	45				7	13	14	16	21	17		
Millers Point Rocks	60	97	68				33		25	46	52	71		
Double Point Rocks	129	100	106				55	46	62	50	82	49		
Alcatraz Island											0	0	3	
Lobos/Seal	38	40								13	53	138		
Bird Island											0	14		
Lobos Rock and Lands End	0	40									53	19		
Seal Rocks	38	0								13	0	105		
Devils Slide Rock and Mainland	19	13	25	16				0	2	0	3	25		
Año Nuevo Island										0	2	0		
<b>Mainland total</b>	<b>1 547</b>	<b>825</b>	<b>634</b>				<b>168</b>	<b>195</b>	<b>507</b>	<b>400</b>	<b>772</b>	<b>587</b>		
North Farallon Islands							15	11	74	45	73	12		
South Farallon Islands	9 400	7 750						3 331	4 037	5 962	7 610	4 498		
<b>GF total</b>	<b>10 947</b>	<b>8 575</b>						<b>3 537</b>	<b>4 618</b>	<b>6 407</b>	<b>8 455</b>	<b>5 097</b>		

**TABLE 1B**  
**Total numbers of Brandt's Cormorant nests at breeding colonies in the Gulf of the Farallones (GF), California, 1993–2006**

Colony or colony complex Colony within complex	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006
Point Reyes	386	384	333	312	329	256	338	294	328	534	439	580	311	923
Drakes Bay	276	193	209	239	234	76	138	158	159	221	189	326	251	371
Point Resistance	18	17	7	8	17	3	0	0	1	0	26	14	1	0
Millers Point Rocks	66	95	148	152	114	18	79	108	94	118	29	148	103	185
Double Point Rocks	192	81	54	79	103	55	59	50	64	103	134	164	147	186
Alcatraz Island	1	40	218	248	171	114	247	170	396	490	589	789	856	1173
Lobos/Seal	207	176	64	55	69	0	48	111	19	92	99	119	236	180
Bird Island	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lobos Rock and Lands End	0	0	64	0	69	0	48		16	0	99	119	0	160
Seal Rocks	207	176	0	55	0	0	0	111	3	92	0	0	236	20
Devils Slide Rock and Mainland	66	123	111	143	113	32	182	185	136	292	263	346	292	525
Año Nuevo Island	11	459	451	366	661	320	605	788	680	990	969	1 639	1 556	2 479
<b>Mainland total</b>	<b>947</b>	<b>1 375</b>	<b>1 386</b>	<b>1 363</b>	<b>1 577</b>	<b>798</b>	<b>1 558</b>	<b>1 706</b>	<b>1 718</b>	<b>2 619</b>	<b>2 548</b>	<b>3 799</b>	<b>3 502</b>	<b>5 651</b>
North Farallon Islands	22	16	2		50	12	27	58	58	98	98	51	20	48
South Farallon Islands	4 719	5 425	5 201		5 162	2 716	3 924	3 918	4 746	7 259	6 801	8 507	7 437	11 739
Corm Blind Hill	196	227	219		185	89	270	213	346	635	577	752	620	914
<b>GF total</b>	<b>5 688</b>	<b>6 816</b>	<b>6 589</b>		<b>6 789</b>	<b>3 526</b>	<b>5 509</b>	<b>5 682</b>	<b>6 522</b>	<b>9 976</b>	<b>9 447</b>	<b>12 357</b>	<b>10 959</b>	<b>17 438</b>

<sup>a</sup> Empty cells indicate no data.



**Fig. 2.** Non-linear trends in numbers of Brandt's Cormorant nests in the Gulf of the Farallones, California, 1979–2006. Shown are locally weighted scatterplot smoothing (LOESS) curves and 95% confidence intervals.

**TABLE 2**  
**Trends in sums of whole-colony counts of Brandt's Cormorant nests for colony complexes**  
**and regional totals in the Gulf of the Farallones (GF), California**

Time period	Colony complex	Slope of $\ln(N)$				$H_0 = 0$ <i>P</i> value	Percent per annum = $e^{\beta} - 100\%$		
		Estimate	SE	95% CI			Estimate, %	95% CI	
				Lower	Upper			Lower, %	Upper, %
1985–2006	Point Reyes	0.041	0.014	0.013	0.069	0.011	4.1	1.3	7.2
	Drakes Bay	0.042	0.012	0.018	0.066	0.003	4.3	1.8	6.9
	South Farallon Is.	0.031	0.012	0.007	0.056	0.023	3.2	0.7	5.7
	Alcatraz Island <sup>a</sup>	0.232	0.025	0.185	0.282	<0.001	26.1	20.4	32.6
	Lobos/Seal <sup>a</sup>	0.039	0.033	-0.023	0.106	0.247	4.0	-2.3	11.1
	Devils Slide	0.171	0.019	0.134	0.211	<0.001	18.7	14.4	23.5
	Año Nuevo Island <sup>a</sup>	0.207	0.021	0.168	0.249	<0.001	23.0	18.3	28.3
	Mainland total	0.129	0.011	0.108	0.150	<0.001	13.8	11.4	16.2
	GF total	0.050	0.012	0.027	0.075	0.001	5.2	2.7	7.8
1985–1995	Point Reyes	0.062	0.046	-0.028	0.153	0.217	6.4	-2.8	16.5
	Drakes Bay	0.095	0.023	0.050	0.140	0.006	9.9	5.1	15.0
	South Farallon Is.	0.016	0.031	-0.044	0.076	0.611	1.7	-4.3	7.9
	Corm Blind Hill <sup>b</sup>	0.054	0.054	-0.051	0.159	0.499	5.5	-5.0	17.2
	Alcatraz Island <sup>a</sup>	1.714	0.464	0.958	2.821	0.035	455.2	160.6	1 580.0
	Lobos/Seal <sup>a</sup>	0.144	0.110	-0.065	0.378	0.262	15.5	-6.3	45.9
	Devils Slide	0.470	0.078	0.331	0.641	0.001	60.0	39.2	89.8
	Año Nuevo Island <sup>a</sup>	0.886	0.338	0.379	1.719	0.059	142.6	46.1	457.7
	Mainland total	0.174	0.025	0.127	0.224	<0.001	19.0	13.5	25.0
GF total	0.034	0.029	-0.022	0.090	0.277	3.5	-2.2	9.5	
1993–2006	Point Reyes	0.057	0.022	0.015	0.099	0.022	5.8	1.5	10.5
	Drakes Bay	0.028	0.023	-0.016	0.073	0.235	2.9	-1.6	7.5
	South Farallon Is.	0.067	0.020	0.029	0.106	0.006	6.9	2.9	11.2
	Corm Blind Hill	0.145	0.023	0.101	0.192	<0.001	15.6	10.6	21.1
	Alcatraz Island	0.219	0.025	0.171	0.269	<0.001	24.5	18.7	30.9
	Lobos/Seal	0.028	0.047	-0.063	0.121	0.557	2.9	-6.1	12.9
	Devils Slide	0.140	0.021	0.099	0.182	<0.001	15.0	10.4	20.0
	Año Nuevo Island	0.175	0.022	0.133	0.218	<0.001	19.1	14.2	24.4
	Mainland total	0.130	0.017	0.097	0.164	<0.001	13.9	10.2	17.8
GF total	0.084	0.019	0.047	0.123	0.001	8.8	4.8	13.0	
1993–1997	Point Reyes	-0.053	0.018	-0.088	-0.019	0.057	-5.2	-8.4	-1.9
	Drakes Bay	-0.017	0.049	-0.113	0.079	0.758	-1.6	-10.6	8.3
	South Farallon Is.	0.013	0.022	-0.030	0.056	0.615	1.3	-3.0	5.8
	Corm Blind Hill	-0.024	0.036	-0.094	0.046	0.579	-2.3	-9.0	4.7
	Alcatraz Island	0.437	0.264	-0.050	1.014	0.197	54.7	-4.9	175.6
	Lobos/Seal	-0.368	0.105	-0.581	-0.167	0.040	-30.8	-44.0	-15.4
	Devils Slide	0.103	0.076	-0.046	0.254	0.270	10.8	-4.5	28.9
	Año Nuevo Island	0.324	0.194	-0.043	0.728	0.194	38.2	-4.2	107.2
	Mainland total	0.094	0.037	0.022	0.167	0.083	9.9	2.2	18.1
GF total	0.032	0.025	-0.018	0.082	0.329	3.3	-1.7	8.5	
1998–2006	Point Reyes	0.125	0.040	0.048	0.204	0.016	13.3	4.9	22.6
	Drakes Bay	0.155	0.024	0.107	0.203	<0.001	16.7	11.3	22.5
	South Farallon Is.	0.157	0.020	0.119	0.196	<0.001	17.0	12.6	21.7
	Corm Blind Hill	0.203	0.037	0.132	0.277	0.001	22.5	14.1	31.9
	Alcatraz Island	0.253	0.022	0.210	0.296	<0.001	28.7	23.4	34.5
	Lobos/Seal	0.248	0.072	0.112	0.395	0.011	28.1	11.8	48.4
	Devils Slide	0.192	0.041	0.114	0.273	0.002	21.2	12.1	31.4
	Año Nuevo Island	0.214	0.023	0.169	0.260	<0.001	23.9	18.4	29.7
	Mainland total	0.200	0.021	0.159	0.242	<0.001	22.2	17.3	27.3
GF total	0.169	0.019	0.131	0.207	<0.001	18.4	14.0	23.0	

<sup>a</sup> See Table 1 for limited breeding or missing data at these colonies during these time periods.

<sup>b</sup> Dataset for Corm Blind Hill begins in 1993.

### Point Reyes

*Colony History:* This colony was first noted in the late 19th century (Grinnell and Miller 1944). Detailed behavioral observations from the 1930s were summarized by Williams (1942). In 1972, 480 nests were counted during a boat survey conducted 3 July (Ainley & Whitt 1973).

*Recent Trends:* The total number of nests was highest in 1979 (1 226 nests) and lowest in 1985 (73 nests). Numbers increased in 1986 and 1987, and thereafter fluctuated through 2005 (range 256–580 nests), before increasing sharply in 2006 (923 nests; Table 1; Fig. 2). The colony increased by 4.1% per annum during 1985–2006 ( $P = 0.01$ ), 5.8% during 1993–2006 ( $P = 0.02$ ) and 13.3% during 1998–2006 ( $P = 0.02$ ; Table 2). During 1993–2006, results were no longer significant when data from just every other year were used (-0.1% per annum;  $P = 0.959$ ; USFWS, unpubl. data). In 2006, a cormorant banded as a chick at SFI in 1999 was observed breeding at Point Reyes (USFWS and Point Blue, unpubl. data).

### Drakes Bay

*Colony Histories:* In 1929 and 1935, nesting was documented on mainland cliffs in the area (Bolander & Bryant 1930, Carter *et al.* 2001). In 1969, Osborne & Reynolds (1971) estimated 15 nests at Millers Point Rocks and 170 nests at Double Point Rocks.

*Recent Trends:* The total number of nests was relatively stable during 1979–1981 (<300 nests), had declined by 1985, had begun to increase by 1989, was reduced during the 1998 El Niño and increased after 1998 to a peak in 2006 (371 nests; Table 1; Fig. 2). The complex increased by 9.9% per annum during 1985–1995 ( $P = 0.006$ ), 4.3% during 1985–2006 ( $P = 0.003$ ) and 16.7% during 1998–2006 ( $P < 0.001$ ; Table 2). Among individual colonies, Double Point Rocks was the largest and most consistently attended, typically accounting for 40%–70% of the complex total. In certain years, when a lower percentage nested at Double Point Rocks, colony shifting to Millers Point Rocks was likely. Point Resistance declined from 75 nests in 1979 to seven nests in 1985 and remained at a low level thereafter, with no nests in some years.

### Alcatraz Island

*Colony History:* No nesting was recorded at Alcatraz Island before the 1979–2006 period. The island was inhabited by humans beginning in 1853, served as a federal prison from 1934 to 1963 and has been managed since 1972 primarily as a historic cultural site (see Saenz *et al.* 2006). Nesting of cormorants (Brandt's or Double-crested) was reported on Arch Rock, about 1.5 km northwest of Alcatraz Island (Grinnell 1927). Arch Rock and two other nearby rocks (including "Shag Rock") were considered navigation hazards and destroyed around 1900. Bryant (1848) noted that in 1847 large numbers of "waterbird" eggs were taken from islands in the harbor, near San Francisco. Broughton (2004) suggested prehistoric nesting was likely at Alcatraz Island or nearby Yerba Buena Island or both, based on archaeological evidence from the Emeryville Shellmound, along the east shore of San Francisco Bay, of harvesting of Brandt's Cormorant chicks.

*Recent Trends:* With access to parts of the island restricted since 1972, nesting was first noted in 1991 (three nests) and 1993 (one nest) from ground-based observations; no observations were made in 1992. Numbers of nests increased substantially by 1995, remained relatively stable through 2000 (<300 nests), then increased exponentially through 2006, when >1100 nests were counted. During the 1998 El Niño, the nest total was reduced compared to 1997 (-33%), but less so than at most other colonies (Table 1; Fig. 2). The colony increased by 24.5% per annum during 1993–2006 ( $P < 0.001$ ) and 28.7% during 1998–2006 ( $P < 0.001$ ; Table 2). Birds banded as chicks at SFI were observed breeding at Alcatraz Island in most years during 1991–2002 (high count: three; Saenz *et al.* 2006). Saenz & Thayer (2007) noted seven cases of double-clutching during 2000–2003. At nearby Yerba Buena Island, nesting was documented in 1990 (four nests; Carter *et al.* 1992), but the colony was inactive during 1991–1994 (J.E. Takekawa, USFWS, pers. comm.) and was not surveyed during 1995–2006. Little breeding habitat occurs there, and human disturbance potential is high.

### Lobos/Seal

*Colony Histories:* Squires (1919) reported nesting at Seal Rocks from 15 July 1917 observations. Osborne & Reynolds (1971) reported 75 breeding birds at Bird Island in August 1969.

*Recent Trends:* In most years during 1979–2006, nesting occurred primarily at either Lobos Rock and Lands End or Seal Rocks but not both, indicating colony shifting. Nesting at Bird Island occurred only in 1990. The complex was not surveyed during 1985–1987, but increase from low numbers in 1979–1980 was evident by 1990 (Table 1; Fig. 2). Numbers of nests decreased by 30.8% per annum during 1993–1997 ( $P = 0.04$ ), likely due to movement of birds to the nascent colony at nearby Alcatraz Island. No nesting occurred during the 1998 El Niño, but numbers then increased by 28.1% per annum during 1998–2006 ( $P = 0.01$ ; Table 2).

### Devils Slide Rock and Mainland

*Colony Histories:* Before the 1979–2006 period, the only available nesting record was from 12 July 1908 at San Pedro Rock, based on "many deserted cormorant nests" present on a "long level ledge" near the summit (Ray 1909). Human disturbance from murre egg collecting activities and from construction of the Ocean Shore Railroad may have contributed to the extirpation of murre and cormorants from San Pedro Rock (Ray 1909, Carter *et al.* 2001).

*Recent Trends:* At Devils Slide Rock, numbers of nests were low from 1979 to 1990 (range 0–25 nests), but had increased by 1993. In 1994, nesting on the adjacent mainland was first noted (46 nests), indicating colony expansion. Gradual increase continued through the 1990s, with some annual fluctuation, despite reduced numbers during the 1998 El Niño. Rapid increase occurred after 2001, with peak nest numbers on both Devils Slide Rock (118 nests) and the adjacent mainland (407 nests) in 2006 (Table 1; Fig. 2). The colony increased by 18.7% per annum during 1985–2006 ( $P < 0.001$ ), 60.0% during 1985–1995 ( $P < 0.001$ ), 15.0% during 1993–2006 ( $P < 0.001$ ) and 21.2% during 1998–2006 ( $P = 0.002$ ; Table 2). In 2005 and 2006, respectively, one bird and four birds banded as chicks at SFI bred at Devils Slide Rock and Mainland; cohort years ranged from 1994 to 2003. A 1985 cohort bird was observed several times during 2006–2007, but not at a breeding site (USFWS and Point Blue, unpubl. data). Observations of banded birds were facilitated by remotely controlled video cameras installed in 2005.



### Año Nuevo Island

**Colony History:** No nesting before the 1979–2006 period is known. The island likely formed by the late 1700s, as erosion processes created a channel separating it from Point Año Nuevo (Weber 1981). The island served as a light station from 1872 to 1948, and decades of pinniped research began there in the early 1960s (LeBoeuf 1981).

**Recent Trends:** Nesting was first noted in 1989 (two nests) from boat- and ground-based surveys. No nests were noted during aerial surveys in 1990, and no observations were made in 1991 and 1992. On 2 June 1993, researchers studying the Rhinoceros Auklet *Cerorhinca monocerata* colony counted 29 fairly built Brandt's Cormorant nests, 11 with eggs (Hester & Sydeman 1995). Based on aerial photographs of marine mammals taken by National Marine Fisheries Service on 8 July in both 1992 and 1993, a small cormorant nesting effort may have occurred in 1992, and additional nests may have been built later in the season in 1993. However, whether image quality and methods for counting birds were comparable to ours was unknown (M. Hester and M. Elliott, pers. comm.). In 1994, after initiation of cormorant nesting was detected by 11 April, Año Nuevo State Reserve protected the colony by closing the southern part of the island (i.e., around the abandoned lightkeeper's buildings, where most nests occurred) to all human activities (Hester & Sydeman 1995). After a large influx of cormorants bred on the island in 1994 (459 nests), numbers fluctuated and gradually increased through 2001, and then substantially increased through 2006 to nearly 2 500 nests (Table 1, Fig. 2). The colony increased by 19.1% per annum during 1993–2006 ( $P < 0.001$ ) and 23.9% during 1998–2006 ( $P < 0.001$ ; Table 2).

### Mainland total

**Recent Trends:** For all mainland colonies combined (i.e., excluding SFI and NFI), the total number of nests was relatively high in 1979 (1 547 nests), but was greatly reduced by 1985 (168 nests).

Numbers were somewhat higher during 1987–1990 and had increased further by 1993. Increase continued thereafter, despite about 50% lower numbers during the 1998 El Niño, and was rapid after 2001, leading to a maximum count in 2006 (5 651 nests; Table 1, Fig. 2). The mainland total increased by 19.0% per annum during 1985–1995, 13.8% during 1985–2006, 13.9% during 1993–2006 and 22.2% during 1998–2006 ( $P < 0.001$ ; Table 2).

### Gulf of the Farallones total

**Recent Trends:** For all GF colonies combined, the total number of nests was relatively high in 1979 (>10 000 nests) but had declined greatly by 1986. Numbers increased from 1986 to 1989 (<8 500 nests) and then were relatively stable at somewhat lower numbers through 2001 (~5 000–7 000 nests). However, during the 1998 El Niño, numbers were 48% lower than in 1997. Numbers increased rapidly during 2001–2006, with especially large levels of recruitment apparently occurring in 2002, 2004 and 2006. The peak breeding population size occurred in 2006 (17 438 nests; Table 1, Fig. 2). The total number of nests in the GF increased by 5.2% per annum during 1985–2006 ( $P < 0.001$ ), 8.8% during 1993–2006 ( $P = 0.001$ ) and 18.4% during 1998–2006 ( $P < 0.001$ ; Table 2). During 1993–2006, trends remained significant when data from just every other year were used (5.5% per annum;  $P = 0.019$ ; USFWS, unpubl. data), but were no longer significant when data from just every third year were used (9.5% per annum;  $P = 0.07$ ; USFWS, unpubl. data).

### Ground monitoring

Ground monitoring during 1997–2006 at Point Reyes and Devils Slide Rock and Mainland indicated that aerial survey dates in late May and early July were appropriate for capturing near-peak nest counts. In nearly all cases, more than 90% of clutches had been initiated by the date of the aerial survey (Table 3). The samples of nests from productivity plots were representative of the colonies, as no late-season nesting groups formed elsewhere in the colonies in those years (USFWS, unpubl. data). Furthermore, nests abandoned before aerial surveys can often be detected in aerial photographs. For example, in 2006, a subcolony of 42 nests at Devils Slide Rock and Mainland failed completely (likely due to predation) before the aerial survey date, yet 40 empty nests and 2 sites still were counted in aerial photographs.

### DISCUSSION

During the 1979–2006 period, the Brandt's Cormorant breeding population in the GF underwent major fluctuations in size: it began relatively large, declined by the mid 1980s, remained at relatively low and variable levels through the 1990s, and finally increased substantially after 2001 to its largest size by 2006. The large SFI colony followed this pattern, but mainland colonies began increasing substantially by 1995, in part as a result of apparent immigration of SFI birds. In addition to major fluctuations, breeding population sizes also varied annually for the GF as a whole and at individual colonies, resulting from the cormorant's "boom or bust" reproductive strategy, reflected in annual differences in clutch/brood size, the proportion of adults that breed, strength of year-classes of potential recruits, degree of recruitment of first-time breeders, and survivorship (Boekelheide & Ainley 1989, Boekelheide *et al.* 1990, Nur & Sydeman 1999). Given marked annual variability and relative ease of monitoring with aerial photographs, Brandt's Cormorant breeding population sizes are

TABLE 3

Seasonal Brandt's Cormorant nest totals in ground-monitored areas that were active on dates of aerial surveys at Point Reyes and Devils Slide Rock and Mainland, 1997–2006

Year	% (number) of nests active	
	Point Reyes	Devils Slide
1997	100 (35)	94.5 (73)
1998	96.4 (55)	87.5 (32)
1999	96.3 (27)	98.9 (95)
2000	100 (51)	98.1 (105)
2001	100 (64)	93.1 (101)
2002	ND <sup>a</sup>	98.3 (115)
2003	ND	98.9 (92)
2004	ND	92.0 (176)
2005	ND	98.5 (137)
2006	97.8 (134)	93.1 (145)

<sup>a</sup> ND = no data.

excellent indicators of annual marine conditions in coastal waters of the CCS. Breeding population sizes of other CCS seabirds, most of which have smaller clutch sizes, are either more stable from year to year, difficult to monitor, or monitored only with small samples that may not be representative of the study colony or broader region (Carter *et al.* 1992).

Variability in Brandt's Cormorant breeding population sizes was especially influenced by El Niño and La Niña events and subsequent impacts on year-class strength of prey (Ainley 1990). Population decline by 1985 was related to food web impacts of the strong 1982–1983 El Niño. At SFI in 1983, the estimated breeding population (~2 150 nests) was among the lowest on record, and no chicks fledged from monitored areas (Ainley *et al.* 1988, Boekelheide *et al.* 1990), also leading to reduced recruitment in subsequent years. High levels of cormorant mortality (especially older females) likely resulted from the El Niño (Boekelheide & Ainley 1989), and mortality from gill net fisheries and oil spills also may have contributed to population decline by 1985 (e.g., Wild 1990, Page *et al.* 1990). In contrast, strong La Niña conditions during 1999–2000 led to increased prey availability and dramatic population increases at all GF colonies after 2001. Breeding success was above long-term averages during 1999–2007 (except 2003) at SFI (Point Blue, unpubl. data) and at mainland colonies (Jones *et al.* 2008, USFWS unpubl. data). This period of high breeding success, apparently associated with high survival to breeding age, led to high recruitment beginning in 2002. During the middle of the study period, other El Niño and La Niña events occurred, resulting in a GF total breeding population that oscillated at low levels. For example, La Niña in 1985 led to breeding success at SFI that was the highest on record (Point Blue, unpubl. data), whereas El Niño in 1992 led to near zero success (Sydeman *et al.* 2001).

In addition to food web impacts of ENSO, commercial and recreational fisheries, and possibly competition from other marine organisms affected prey availability for cormorants. Juveniles of several species of rockfishes *Sebastes* spp., but especially the Shortbelly Rockfish *S. jordani*, were the primary prey provisioned to young by Brandt's Cormorants and other seabird species at SFI during the 1970s and 1980s (Ainley *et al.* 1990). Commercial landings of rockfishes in California increased sharply in the mid 1970s, peaked in 1982, and declined thereafter through the 1990s, by which time several species of rockfishes were declared overfished (Moser *et al.* 2000, Leet *et al.* 2001). However, the Shortbelly Rockfish was not a target of fisheries, yet it too had declined since the early 1990s, apparently with only modest impacts from bycatch. Declines were thought to be related to variable environmental conditions but may have involved other factors such as increased predation by growing populations of California Sea Lions *Zalophus californianus* (Field *et al.* 2007a). Predation by the Humboldt Squid *Dosidicus gigas*, which increased in abundance and distribution in the CCS since the 1997–1998 El Niño and is a known predator of the Shortbelly Rockfish (Field *et al.* 2007b), may also have contributed substantially to declines (D. Ainley, pers. comm.).

#### Nearshore movement

Loss of rockfishes as nearby prey apparently led SFI cormorants to rely more on Northern Anchovies *Engraulis mordax* in nearshore waters as prey. In contrast to rockfish predominance in 1970s diet samples (Ainley *et al.* 1990), recent Brandt's Cormorant diet samples from SFI in the mid 1990s and mid 2000s contained

mostly anchovies (M. Elliott, pers. comm.; Point Blue, unpubl. data). Similarly, as rockfishes declined, proportions of anchovies increased in diets of SFI Common Murres after 1989 and through 2008 (Miller & Sydeman 2004, Mills *et al.* 2007, Warzybok *et al.* 2012), with a simultaneous nearshore shift in murre at-sea distribution (Oedekoven *et al.* 2001). At Alcatraz Island in San Francisco Bay during 2000–2002, anchovies were present in 69% of Brandt's Cormorant pellets and rockfishes in just 7% (Yakich 2005). Similar observations were made at a recently formed colony in the northern CCS at the Columbia River Estuary, Oregon, in 2000, with anchovies in 43% of pellets and rockfishes in none (Couch & Lance 2004). Higher breeding success at Alcatraz Island compared with SFI during the 1998 El Niño (1.6 vs. 0.4 chicks/pair; Saenz *et al.* 2006) also indicated greater prey availability closer to shore and inside San Francisco Bay. Increased use of the Northern Anchovy as prey, and its more coastal distribution compared with the Shortbelly Rockfish (Ainley 1990), likely led to the observed population increases at mainland colonies because of their close proximity to abundant prey resources.

Increased numbers of birds at mainland colonies included immigrants from SFI. Direct evidence of immigration was obtained during 1991–2006 with observations of SFI-banded Brandt's Cormorants breeding at Point Reyes, Alcatraz Island and Devils Slide Rock and Mainland. In 1988, SFI-banded Double-crested Cormorants also were noted breeding in San Francisco Bay (Stenzel *et al.* 1995). Brandt's Cormorant immigration could also be deduced from trend analyses for the 1985–1995 period, when all mainland colonies combined increased by 19% per annum while SFI showed no trend. The several hundred pairs suddenly breeding at Alcatraz and Año Nuevo islands by 1995 likely cannot be accounted for by possible movements of birds from other mainland colonies alone. Drakes Bay Colony Complex and Devils Slide Rock and Mainland were also growing at this time, and mainland colonies north and south of the GF appeared stable (Carter *et al.* 2000, Bechaver *et al.* 2013). And yet a declining trend for SFI due to emigration was not detected because of its much larger population size. Additionally, before the 1985–1995 regression period, SFI had already declined substantially following the 1982–1983 El Niño (Fig. 2; Ainley & Boekelheide 1990). Previous assessments of Brandt's Cormorant survival and breeding probability based on re-sightings of banded birds at SFI (Boekelheide & Ainley 1989, Nur & Sydeman 1999) were made before emigration had been documented.

Availability of protected breeding habitat was also important in allowing mainland population increase. Establishment of the Gulf of the Farallones and Monterey Bay national marine sanctuaries led to regulations requiring permits for aircraft overflights of <1 000 feet (304.8 m) above sea level, in order to prevent disturbance to wildlife. At Alcatraz Island, the western cliffs and the bluffs overlooking them had been closed to the public because of safety concerns since 1972, when the island became managed by NPS. Tourist visitation of the island increased during the period of cormorant colony growth (D. Hatch, pers. comm.), indicating NPS management policies have been efficient in protecting cormorant nesting areas. Año Nuevo Island had been protected since at least 1970, although Brandt's Cormorant nesting before 1989 may have been inhibited by intensive year-round studies of Elephant Seals *Mirounga angustirostris*. Point Reyes stands out as the sole mainland colony that was already large at the beginning of the study period, likely reflecting more reliable prey resources compared with other colonies (Jones *et al.* 2008), as well as protected habitats.

### Aerial photographic versus boat- and ground-based surveys

Because of standardized counting methods, complete colony viewing and ease of wide geographic coverage, aerial photographic surveys are the most appropriate survey method for determining trends in Brandt's Cormorant breeding population sizes, both regionally and for individual colonies that cannot be censused readily with boat- and ground-based surveys without causing disturbance. During 1989–1991, when all California seabird colonies were surveyed, many Brandt's Cormorant colonies were surveyed with aerial, boat-based, or mainland surveys, or a combination thereof. In nearly all cases, aerial surveys provided higher nest counts due to more complete colony viewing (Carter *et al.* 1992). For SFI during 1997–2006, breeding bird estimates from aerial photographs (this study) averaged 29% higher (range 2%–53%) than estimates from boat- and ground-survey data (Point Blue, unpubl. data; USFWS 2009).

Ground-based productivity surveys were important to this study in determining that single aerial surveys likely captured more than 90% of seasonal nest totals in most years. Possible changes in breeding phenology over time should be carefully considered in future monitoring and trends analyses. In southern California, for example, aerial photographic surveys of Brandt's Cormorant breeding colonies since the late 1990s have included an April survey in addition to a May survey to capture possible early nesting at certain islands. In some cases, summing monthly subcolony counts has been necessary to determine population estimates (HRC, GJM, & PJC, unpubl. data). Continuing annual surveys will also be important in detecting trends, as shown by loss of significant trends for SFI, Point Reyes and the GF total during 1993–2006 when using data from every other year or every third year. Significant trends at other colonies were maintained with less-than-annual data, but those colonies all were experiencing at least 14% per annum growth (Table 2). Finally, aerial photographic surveys of breeding colonies also can add insight into species distribution information from at-sea surveys. For example, at-sea survey data in the GF during May–June 1985–2006 did not detect trends in abundance for the Brandt's Cormorant (Ainley & Hyrenbach 2010), whereas our surveys indicated population increase and a mainland shift of breeding. Coverage of at-sea transects would not have detected increased foraging inside San Francisco Bay (D. Ainley, pers. comm.).

### Addendum: observations since 2006

Major changes in the breeding populations of Brandt's Cormorants in the GF have continued since the end of our study period. In 2007, population sizes in the GF continued to increase beyond the 2006 peaks. However, dramatic population declines began in 2008, and continued in 2009 with nearly complete colony abandonments (USFWS and Point Blue, unpubl. data). Beginning in mid April 2009, a large-scale die-off of Brandt's Cormorants and other seabirds occurred; necropsy results indicated mortality was due to starvation (Gibble *et al.* 2010). The scale of the die-off was unprecedented for the Brandt's Cormorant, as were an unusually large number of birds foraging at inland reservoirs (Rogers *et al.* 2010). The die-off and colony abandonments were largely restricted to the GF, based on aerial photographic surveys along the remainder of the California coastline. Nest numbers at colonies south of the GF along the California coast and at the Channel Islands in southern California also were reduced in 2008, but rebounded to earlier higher levels at variable times during the 2009–2011

period, whereas colonies in the GF remained at reduced levels with poor breeding success (Capitolo *et al.* 2012, Bechaver *et al.* 2013; USFWS, UC Santa Cruz, and Point Blue, unpubl. data). The 2009 die-off began during a period of prolonged, strong northwest winds that may have negatively impacted foraging conditions or availability of small, schooling fish, especially Northern Anchovies, which became largely absent from seabird chick diets at SFI in 2009–2012 (Warzybok *et al.* 2012). The localized impacts since 2009 underscore the importance of annual data over broad spatial and temporal scales in analyzing trends and understanding impacts of ecosystem change.

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