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Breeding Phenology and Reproductive Success of the Brandt's Cormorant at Three Nearshore Colonies in Central California, 1997-2001

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Abstract.—Brandt's Cormorant (*Phalacrocorax penicillatus*) breeding effort, phenology and success were studied in 1997-2001 at three colonies spanning approximately 200 km of the central California coast: Point Reyes (PR); Devil's Slide Rock and Mainland (DS); and Castle-Hurricane Colony Complex (CH). Breeding effort was reduced at all three colonies in the 1998 El Niño event. Mean clutch initiation dates differed significantly among colonies, with cormorants at the southernmost colony (CH) laying earliest, and those at the northernmost colony (PR) laying latest. Productivity at individual colonies varied greatly among years (range 0.7-2.5 fledglings per pair). Overall colony means were lowest (1.6 fledglings/pair) during the 1998 El Niño event and highest (2.5 fledglings/pair) in the 1999 La Niña event. Productivity at CH (1.7 fledglings/pair) was significantly lower than at PR (2.2 fledglings/pair), and interannual variation was greatest at CH. Late-nesting birds laid fewer eggs, hatched fewer chicks, and fledged fewer chicks per pair than early-nesters. The rapid rate of growth at some nearshore colonies in central California suggests immigration from elsewhere, most likely the large offshore colony at the South Farallon Islands. Variation in timing of breeding and reproductive success among colonies demonstrates a value in maintaining multiple study locations when assessing Brandt's Cormorant population parameters in the California Current System. *Received 27 June 2007, accepted 26 November 2007.*

Key words.—Brandt's Cormorant, breeding phenology, California Current, El Niño, Gulf of the Farallones, La Niña, reproductive success, *Phalacrocorax penicillatus*.

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The Brandt's Cormorant (*Phalacrocorax penicillatus*) is endemic to the west coast of North America, breeds colonially on cliffs, rocks and islands, and feeds mainly on fish in nearshore and continental shelf waters (Boekelheide *et al.* 1990). Its range is largely associated with the California Current Upwelling System; nearly 80% of the known world population breeds along the coast of California, and the largest colony is located

on the South Farallon Islands (Sowls *et al.* 1980; Boekelheide *et al.* 1990; Carter *et al.* 1992; Wallace and Wallace 1998; Capitolo *et al.* 2004). In general, breeding begins earlier in southern latitudes, but initiation dates at individual colonies can vary widely from year to year (Sowls *et al.* 1980; Boekelheide *et al.* 1990; Wallace and Wallace 1998). Although some of the largest colonies occur on offshore islands, this species is one of the most

common and widespread breeding seabirds in the nearshore waters of California.

Most studies of Brandt's Cormorant breeding ecology have been limited temporally (< four y) or geographically (only one colony site), and nearly all have been limited to offshore islands more than 20 km from the mainland (Hunt *et al.* 1981; Boekelheide *et al.* 1990; McChesney 1997). The most intensive studies have occurred at Southeast Farallon Island (hereafter, Farallones), located 35 km west of San Francisco, California. At this offshore colony two study plots, each consisting of 25-40 active nest sites, were monitored from 1971-83, and work has continued on at least one plot in each year since 1983 (Boekelheide and Ainley 1989; Boekelheide *et al.* 1990; Nur and Sydeman 1999; Sydeman *et al.* 2001; Saenz *et al.* 2006). At the Farallones, Brandt's Cormorant breeding performance has been closely linked to fluctuations in marine conditions, correlating strongly with sea surface temperatures and abundance of juvenile rockfish (*Sebastes* spp.; Boekelheide and Ainley 1989; Nur and Sydeman 1999). In cool-water years (e.g., La Niña events), cormorants nested earlier, and with higher success, than in warm-water years (e.g., El Niño events). In 1971-83 (a period containing both strong El Niño and La Niña events), clutch initiation dates at the Farallones fluctuated from 12 April to 22 May and breeding success varied from 0-70%, often differing substantially between plots (Boekelheide *et al.* 1990). Following the strong 1982-83 El Niño, the Farallones population declined dramatically and only partially recovered by 2003 (Boekelheide *et al.* 1990; Carter *et al.* 1992; Nur and Sydeman 1999; Capitolo *et al.* 2004; PRBO, unpubl. data; USFWS, unpubl. data). However, during the mid-1990s numbers at nearby mainland colonies began to increase and new nearshore colonies formed (Carter *et al.* 1996, 2000; McChesney *et al.* 1998, 1999; Capitolo *et al.* 2004; Saenz *et al.* 2006). Although the Brandt's Cormorant is an important component of the nearshore central California ecosystem during the breeding season, little information is available on their breeding ecology in these areas.

In this study we monitored three Brandt's Cormorant colonies between 1997 and 2001 to better understand their breeding performance in the central California nearshore environment. Observations were conducted as a component of a restoration project focused on coastal Common Murre (*Uria aalge*) populations (Parker *et al.* 2007). Here we present the results of our studies of Brandt's Cormorant breeding phenology and reproductive performance, make general comparisons to cormorants studied on the Farallones and elsewhere, and discuss the influence of climate on timing and success.

STUDY AREAS AND METHODS

Study Areas

Brandt's Cormorant breeding population size, breeding phenology and reproductive success were studied at: Point Reyes (PR; 37°59'N, 122°59'W); Devil's Slide Rock and Mainland (DS; 37°34'N, 122°31'W); and the Castle-Hurricane Colony Complex (CH; 36°22'N, 121°54'W; Fig. 1). These three colonies are distributed over 200 km of the central California coast. CH combines colonies known as Bench Mark-227X, Castle Rocks and Mainland, and Hurricane Point Rocks (Sowls *et al.* 1980; Carter *et al.* 1992, 2001). The PR and DS colonies are within the Gulf of the Farallones region, an area of high marine productivity and large concentrations of breeding and migratory seabirds (Briggs *et al.* 1987; Ainley *et al.* 1990). PR is within the Point Reyes National Seashore (managed by the National Park Service), and the nearshore rocks of DS and CH are within the California Coastal National Monument (managed by the U.S. Bureau of Land Management) with some mainland portions of the latter two colonies on private lands.

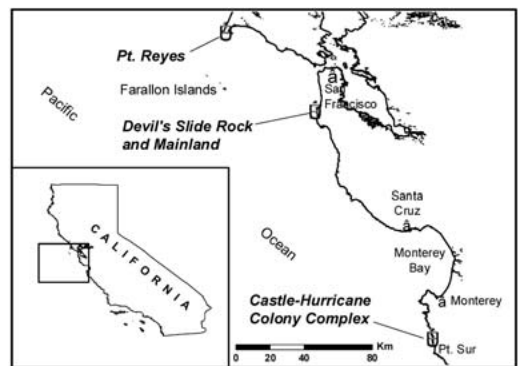


Figure 1. Locations of three Brandt's Cormorant colonies studied in central California in 1997-2001: Point Reyes; Devil's Slide Rock and Mainland; and Castle-Hurricane Colony Complex.

Cormorants nested mostly on bare rock surfaces, including: ledges, slopes and flatter portions of steep, relatively inaccessible sections of mainland cliffs and bluffs, and slopes and tops of nearshore rocks within 400 m of the mainland. The density of breeding groups varied with available substrate; flatter areas tended to hold higher densities of birds, while steeper sections generally supported lower densities. Overall, nesting habitats were similar to those reported elsewhere (Sowls *et al.* 1980; Hunt *et al.* 1981; Boekelheide *et al.* 1990; Carter *et al.* 1992).

Data Collection

To estimate breeding population sizes, aerial photographic surveys were conducted each year in late May or early June, during the middle of the incubation and early chick-rearing periods (see Carter *et al.* 2001 for survey methods). From photographs, numbers of cormorant nests, territorial sites, and birds were counted at each subcolony. When more than one survey per year was conducted, highest counts at each subcolony were summed to determine colony totals.

To examine breeding phenology and success, annual monitoring was conducted from mainland vantage points, and proceeded from pre-laying through fledging or nest abandonment. One to two distinct breeding groups, or subcolonies, were monitored each year at each colony. Subcolonies and individual nests monitored were chosen based on their visibility, at distances of 50-400 m from viewing locations. To avoid some biases associated with differing phenology and reproductive success within certain portions of cormorant colonies (Siegel-Causey and Hunt 1986; Boekelheide *et al.* 1990), entire subcolonies or contiguous portions (including center and edge nests) were followed, and a second subcolony was added when possible to reflect overall colony performance. The samples were assumed to be generally representative for each colony because they often comprised a relatively large proportion of the nests counted each year during aerial surveys (35-95%). Researcher disturbance was not noted during monitoring. At PR and CH, the numbers and locations of active subcolonies varied between years as breeding birds shifted among numerous nearshore rocks and mainland cliffs. At PR, monitored subcolonies occurred on the following rocks and cliffs in the associated years: Northwest Rock (subcolony 10A; 1999); Wishbone and Spine points (subcolony 11E; 1997, 2000, 2001); Cone Rock (subcolony 13; 1998); and Miwok Rock (subcolony 14D; 1998, 2000). At CH, cormorants were monitored at Castle Rocks and Mainland subcolony 03-East in all years except 1998, when cormorants on Hurricane Point Rocks subcolony 04 were followed instead. At DS, cormorants were monitored in all years on both Devil's Slide Rock (subcolony 01) and a nearby mainland promontory known as "Turtlehead Rock" (subcolony 05). For more specific subcolony locations, see Carter *et al.* (1992) and McChesney *et al.* (2005).

Nests were monitored using either 60-120× or 20-60× spotting scopes. During nest building, nests were qualified as being one of the following: 1) sparse, loose collection of nesting material ("nest material"); 2) small, loose pile of nesting material with rudimentary flat structure ("poorly built nest"); 3) nest structure with consolidated material and beginnings of a nest bowl ("fairly built nest"); and 4) nest with a large, well-defined nest bowl and a densely-packed, often guano-en-

crusted structure ("well-built nest"). Each nest site was mapped, numbered, and checked a minimum of every three to eight days, depending on breeding status. The most frequent monitoring (often daily) occurred during the egg-laying, hatching, and fledging periods. For each nest on each observation day the number of attending adults, adult breeding posture, and nest contents were recorded. Breeding postures were defined as incubating, brooding, or standing. In most cases it was possible to see directly into nest bowls to record exact numbers of eggs and chicks when adults stood or shifted positions. In some nests the contents could not be completely seen until chicks were large enough to reach their heads above the rim of the nest bowl (approximately five to ten d of age or older). Only sites yielding exact numbers of eggs and chicks were used for analyses.

Clutch initiation dates were defined as the day the first egg was laid, which was easily determined as eggs are incompletely incubated until the clutch is completed (Boekelheide *et al.* 1990) and attending adults stood up frequently during the egg-laying period. All nest sites were followed until failure and subsequent abandonment or until chicks reached a minimum of 25 d of age from first sighting (assuring that most were at least 27 d old, given a typical three-d nest check interval). At this age chicks were largely feathered on the wings and tail, at least partially independent of the nest site, and were assumed to have later fledged. Since most chick mortality occurs prior to 20 d of age, survival to 25 d was considered to be a relatively accurate and standardized measure of fledging success. In any case, further tracking of these unbanded chicks was not possible because they were quite mobile and often left their nest of origin to join crèches (Carter and Hobson 1988; Boekelheide *et al.* 1990; McChesney 1997).

Data Analyses

All monitored subcolonies within a single colony complex were grouped together by year for analyses. Because no birds were marked, it was not possible to distinguish relay attempts with absolute certainty. Fewer than ten probable relays were treated as separate nesting attempts, and had a minimal effect on analyses.

For each nest the study determined clutch initiation date, clutch size, hatch date of first chick, number of eggs hatched, and number of chicks "fledged" (i.e., reaching 25 d of age). When exact clutch initiation dates were not obtained, the midpoint of a five-d range was calculated based on nest status, adult breeding posture, and back-dating from exact chick hatch dates (assuming an average 30-d incubation period; Boekelheide *et al.* 1990; McChesney 1997). Hatch dates were handled similarly in a few cases, by adding 30 d from exact clutch initiation dates. Hatching success (number of eggs hatched per eggs laid), fledging success (number of chicks fledged per chicks hatched), and breeding success (number of chicks fledged per eggs laid) were determined for each colony complex. Additionally, in a method comparable to Farallon analyses, clutch initiation dates were grouped at each colony in each year at ± 0.5 standard deviations (SD) from annual means to examine the success of early-, middle-, and late-nesting cormorants. By this definition, middle-nesting birds laid eggs within 0.5 SD of the mean at a given colony in a given year (see also Boekelheide *et al.* 1990).

A total of 950 nests were monitored among all colonies between 1997 and 2001; 858 had at least one recorded egg (i.e., breeding attempts). From 858 breeding attempts, 714 nests yielded sufficient data for calculating clutch initiation dates and numbers of chicks fledged per pair, and 457 of these nests yielded sufficient data for calculating clutch sizes, brood sizes, and success parameters. Hatching and breeding success were analyzed from 1,487 eggs laid, and fledging success from 1,130 chicks hatched. On average, 63 nests were monitored at each colony per year, ranging from 30 nests at CH in 1998 to 118 nests at DS in 2000.

Phenology, clutch size, numbers of chicks hatched, and numbers of chicks fledged per pair were tested using F-tests in ANOVA models, followed by Tukey-Kramer multiple comparisons to identify differences between pairs of colonies or years if F-tests found significant differences. Similarly, hatching success, fledging success, and breeding success were tested using F-tests in log-linear models followed by multiple comparisons. The association between phenology and other breeding parameters was further examined by using ANOVA and log-linear models to test for differences between phenology groups while controlling for year and colony effects. Model-based estimates of means and standard errors (SE) were calculated using the least-squares method for each colony, year, and phenology group. Since log-linear models only produce least squares estimates of log odds for success, the logistic function $y = \exp(x)/(1 + \exp(x))$ and the delta method were then applied to obtain estimated probabilities of success and standard errors (Agresti 2002).

RESULTS

Breeding Population Sizes

All three study areas hosted moderately-sized cormorant colonies. During the 1997-2001 period, numbers of breeding pairs averaged 307 (range 247-338) at PR, 131 (range 32-185) at DS, and 180 (range 33-271) at CH (Table 1). No discernible trends in nest counts were detected during the study period. However, nest totals were lower at all colonies during the 1998 El Niño event, when many birds apparently skipped breed-

ing. This decrease in 1998 was less dramatic at PR than at DS and CH. In 1999, numbers of nesting pairs returned to higher levels at all colonies, suggesting that adult mortality during the 1998 El Niño was not greatly elevated.

Breeding Phenology

Overall clutch initiation (all colonies and all years combined) occurred on 2 May, but varied widely within and among colonies (range 30 March-15 June; Fig. 2a). Mean initiation dates at CH, DS, and PR differed significantly among colonies and initiation occurred earliest at the most southerly colony (CH) and latest at the most northerly colony (PR; Table 2). Cormorants at CH demonstrated the most variation in lay dates (30 March-10 June, SE 0.64), whereas birds at DS (11 April-15 June, SE 0.58) and PR (16 April-5 June, SE 0.6) were less variable. Mean initiation dates at CH differed from PR in all years but 1999 and were earlier than the more northerly colonies in all years but 1998 ($F_{8,699} = 21.01$, $P < 0.01$). Mean initiation dates at PR and DS were within two to three d of each other in 1998, 1999, and 2001, and in 1997 and 2000, PR cormorants bred later than at DS (n.s.; Fig. 2a). During the severe 1998 El Niño event (Hayward *et al.* 1999), breeding was delayed at all three colonies (combined mean 18 May) and 1998 differed significantly from all other years for all colonies combined (Table 3). In 1998, the mean initiation date of 23 May at CH was 24 d later than the five-year colony mean, while mean initiation dates for DS and PR were twelve d and eight d later than their averages, respectively (Fig. 2a).

Table 1. Numbers of Brandt's Cormorant nests counted from aerial photographic surveys at Point Reyes, Devil's Slide Rock and Mainland, and Castle-Hurricane Colony Complex, 1997-2001.

	Point Reyes	Devil's Slide Rock and Mainland	Castle-Hurricane Colony Complex
1997	327	119	271
1998	247	32	33
1999	338	182	173
2000	296	185	180
2001	328	136	241

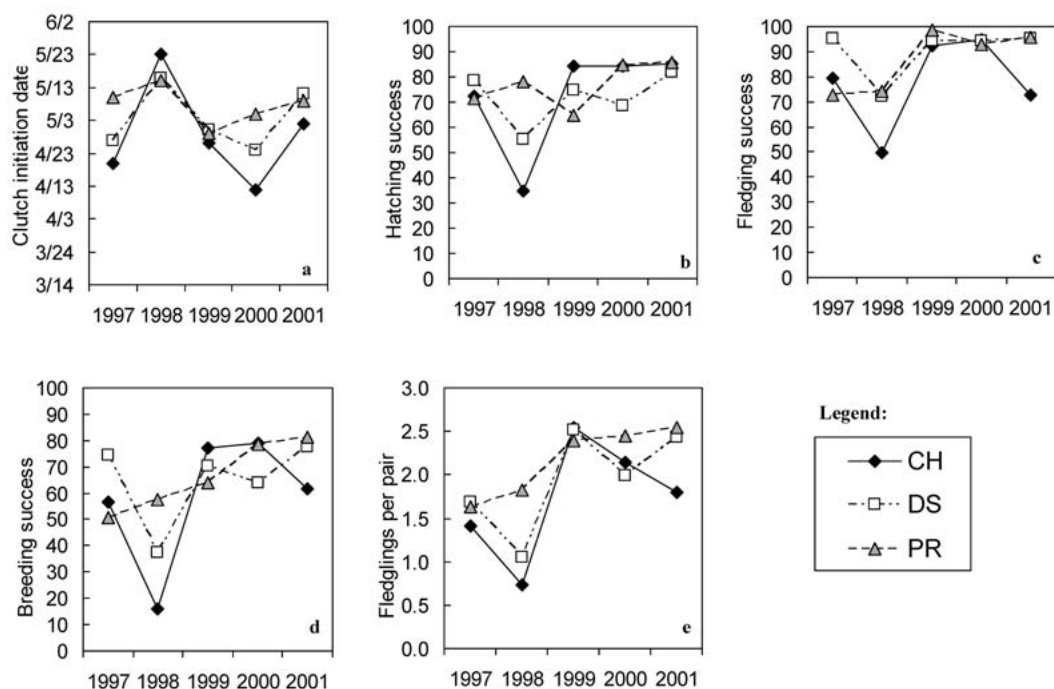


Figure 2. Comparisons of average breeding parameters in 1997-2001 for Brandt's Cormorants at Point Reyes (PR), Devil's Slide Rock and Mainland (DS), and Castle-Hurricane Colony Complex (CH): a) clutch initiation dates; b) hatching success (%); c) fledging success (%); d) breeding success (%); and e) fledglings per pair.

Clutch Size

Overall, cormorants laid an average of 3.2 eggs per clutch (range one to five eggs). Of all clutches, 89% contained three or four eggs, and 97% contained two to four eggs. Although there were no significant within-year differences among colonies, clutch sizes were marginally smaller at CH ($3.1 \pm \text{SE } 0.06$) than at PR ($3.3 \pm \text{SE } 0.05$; Table 2). Among years, mean clutch size was lowest ($2.9 \pm \text{SE } 0.09$) in the 1998 El Niño, and differed significantly from all other years except 1997. Clutch size was greatest ($3.6 \pm \text{SE } .07$) in the 1999 La Niña and differed significantly from all other years except 2000 (Table 3). Late-nesters differed significantly from both early- and mid-nesters, and produced smaller clutches than early-nesting birds within a colony in a given year, contributing to a 10% decline in clutch sizes as seasons progressed (Table 4).

Hatching Success and Brood Sizes

Overall hatching success (all colonies and all years combined) averaged 75% (range 35-86%) and did not differ significantly among colonies in any consistent pattern (Fig. 2b; Table 2). CH exhibited the widest range in hatching success (35-85%) and PR the narrowest (65-86%). Among years, hatching success varied widely (range 57-84%). Low hatching success in 1998 (57%) differed from all other years, while high success in 2001 (84%) differed from all other years but 2000 (Table 3). At CH, hatching success in 1998 differed from all other years (54% below its average) while PR remained relatively stable (Fig. 2b). DS also experienced reduced hatching success in 1998 and, as at CH, this was largely a result of high nest abandonment during incubation. Only 50% of CH nests and 55% of DS nests hatched at least one egg in 1998, while 100% of nests at PR

Table 2. Mean \pm SE (sample size) and F-tests comparing reproductive parameters of Brandt's Cormorants for the period 1997-2001 at Castle-Hurricane Colony Complex, Devil's Slide Rock and Mainland, and Point Reyes. For F-tests indicating a significant difference among colonies ($P < 0.05$), means were compared in pairs and superscripted with similar capital letters if not statistically different ($P > 0.05$). Single asterisks indicate pairs of colonies that differed at the 0.06 level but not the 0.05 level.

	Statistic	P	N	Castle- Hurricane	Devil's Slide	Point Reyes
Clutch Initiation Date	$F_{2,699} = 55.5$	0.0001	714	29 Apr ^A	4 May ^B	8 May ^C
Clutch Size	$F_{2,428} = 6.3$	0.0019	457	± 0.64 (203)	± 0.58 (296)	± 0.60 (215)
				3.1 ^{A*}	3.3 ^{B*}	3.3 ^B
Brood Size	$F_{2,428} = 4.3$	0.0139	457	± 0.06 (122)	± 0.06 (138)	± 0.05 (197)
				2.2 ^A	2.3 ^{AB}	2.5 ^B
Hatching Success (%)	$F_{2,428} = 1.2$	0.2930	1487	± 0.08 (122)	± 0.08 (138)	± 0.06 (197)
				75.0	72.6	77.8
Fledging Success (%)	$F_{2,404} = 5.3$	0.0055	1133	± 3.1 (380)	± 2.8 (460)	± 2.0 (647)
				82.3 ^{A*}	92.4 ^{B*}	91.5 ^{B*}
Breeding Success (%)	$F_{2,428} = 2.1$	0.1296	1487	± 3.1 (294)	± 1.7 (340)	± 1.9 (499)
				58.0	65.6	67.5
Fledglings per Pair	$F_{2,685} = 6.8$	0.0011	714	± 4.1 (380)	± 3.3 (460)	± 2.5 (647)
				1.7 ^A	1.9 ^{AB}	2.2 ^B
				± 0.10 (193)	± 0.08 (301)	± 0.07 (220)

did so (Fig. 3). Nest abandonment following egg-laying was infrequent in most other years, with the exception of CH during the chick-rearing period in 2001 (see fledging section, below). Early-, middle-, and late-nesting birds were not significantly different, although hatching success tended to decline slightly as seasons progressed (Table 4).

Overall, cormorants hatched an average of 2.3 eggs per pair (range 1.0-2.8). Brood sizes ranged from one to four, with 85% of broods consisting of two or three chicks. Overall brood sizes at CH ($2.2 \pm$ SE 0.08) were smaller than at PR ($2.5 \pm$ SE 0.06), largely because of the small brood sizes at CH in 1998 (Table 2). In that year, both CH ($1.0 \pm$ SE 0.23) and DS ($1.5 \pm$ SE 0.20) differed from PR ($2.4 \pm$ SE 0.14; $F_{8,428} = 2.10$, $P < 0.05$). As in hatching success, CH exhibited the widest range in brood sizes (range 1.0-2.8) and PR the narrowest (range 2.4-2.8). Among-year comparisons of brood sizes revealed patterns similar to hatching success, with lowest brood sizes occurring in 1998 (1.6 chicks) and differing from all other years (Table 3). Brood sizes in late-nesters differed from both early- and middle-nesters, and were approximately 10-20% smaller (Table 4).

Fledging Success, Breeding Success, and Numbers of Chicks Fledged Per Pair

Fledging success averaged 89% (range 50-95%) overall (all colonies and all years combined) and differed among colonies. At CH (82%), fledging success differed significantly from DS (92%) and PR (92%) and exhibited the widest range and greatest variation (Fig. 2c; Table 2). In comparisons among years, 1998 (66%) was significantly different from all others, and 1999-2001 were similar to one another (92-96%; Table 3). Greater rates of nest abandonment during the chick-rearing period occurred at all three colonies in 1998; at CH only 56% of nests with hatchlings fledged at least one chick, while 82% of nests at both DS and PR did so. Abandonment during the chick-rearing period also occurred at CH and PR in 1997 and at CH in 2001 (Fig. 3). Fledging success among early-, middle-, and late-nesters was not significantly different (Table 4).

Overall breeding success averaged 63% (range 16-81%). Among-colony differences were not significant, although breeding success at CH (58%) was considerably lower than DS (66%) and PR (68%). In addition, CH exhibited the widest range and PR the narrowest (Fig. 2d; Table 2). Within colonies,

Table 3. Mean \pm SE (sample size) and statistical F-test for comparing Brandt's Cormorant reproductive parameters at three central California colonies among five years, 1997-2001. All F-tests indicated significant differences among years ($p < 0.05$), and means were compared in pairs and superscripted with similar capital letters if not statistically different ($P > 0.05$).

	Statistic	P	N	1997	1998	1999	2000	2001
Clutch Initiation Date	$F_{4,699} = 118.9$	0.0001	714	29 Apr ^B ± 0.78 (118)	18 May ^D ± 1.00 (83)	28 Apr ^B ± 0.77 (133)	25 Apr ^A ± 0.66 (191)	7 May ^C ± 0.64 (189)
Clutch Size	$F_{4,428} = 9.9$	0.0001	457	3.1 ^{AB} ± 0.08 (80)	2.9 ^A ± 0.09 (72)	3.6 ^C ± 0.07 (83)	3.3 ^B ± 0.07 (101)	3.2 ^B ± 0.06 (121)
Brood Size	$F_{4,428} = 16.9$	0.0001	457	2.3 ^B ± 0.10 (80)	1.6 ^A ± 0.11 (72)	2.6 ^{BC} ± 0.09 (83)	2.6 ^{BC} ± 0.09 (101)	2.7 ^C ± 0.08 (121)
Hatching Success (%)	$F_{4,428} = 6.9$	0.0001	1487	74.3 ^B ± 3.3 (252)	56.9 ^A ± 5.2 (212)	75.6 ^B ± 3.0 (294)	80.1 ^{BC} ± 2.9 (334)	84.3 ^C ± 2.3 (395)
Fledging Success (%)	$F_{4,404} = 10.2$	0.0001	1133	85.3 ^B ± 3.4 (188)	66.2 ^A ± 6.0 (133)	95.9 ^C ± 1.7 (223)	93.8 ^C ± 1.7 (262)	91.6 ^{BC} ± 1.8 (327)
Breeding Success (%)	$F_{4,428} = 12.3$	0.0001	1487	61.0 ^B ± 4.2 (252)	34.7 ^A ± 5.5 (212)	70.8 ^{BC} ± 3.4 (294)	74.4 ^C ± 3.3 (334)	74.2 ^C ± 2.9 (395)
Fledglings per Pair	$F_{4,685} = 21.1$	0.0001	714	1.6 ^A ± 0.15 (118)	1.2 ^A ± 0.13 (83)	2.5 ^B ± 0.09 (133)	2.2 ^B ± 0.12 (191)	2.3 ^B ± 0.08 (189)

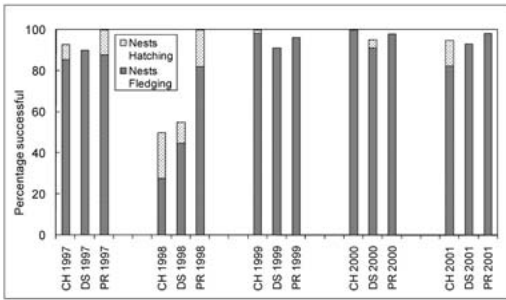


Figure 3. Percentage of Brandt's Cormorant nests hatching or fledging at least one chick in 1997-2001 at Point Reyes (PR), Devil's Slide Rock and Mainland (DS), and Castle-Hurricane Colony Complex (CH).

breeding success was lowest in 1998 at DS (37%) and CH (16%; $F_{8,428} = 4.06$, $P < 0.01$) while at PR there were no differences among years. In 1997, DS (74%) differed significantly from PR (51%; $F_{8,428} = 4.06$, $P < 0.01$) but not CH (56%), and in 2001 CH (62%) differed from both DS (78%) and PR (81%; $F_{8,428} = 4.06$, $P < 0.01$; Fig. 2d). Among years, low breeding success in 1998 (35%) differed from all others, while breeding success was highest (74%) in 2000-2001 (Table 3). When early, middle, and late-nesting birds were compared, there were no significant differences, although breeding success declined slightly as seasons progressed (Table 4).

Overall Brandt's Cormorant productivity averaged 1.9 chicks fledged per pair (range 0.7-2.5). Productivity at CH ($1.7 \pm SE 0.1$) differed from PR ($2.2 \pm SE 0.07$), while DS ($1.9 \pm SE 0.08$) was not significantly different from the other colonies (Table 2). In 1998 and 2001, CH differed from PR ($F_{8,685} = 13.3$, $P < 0.01$) but not DS (Fig. 2e). CH had the widest range (0.7-2.5) and greatest variation, while PR had the narrowest range (1.6-2.5) and was less variable than CH. In 1997 and 1998 all three colonies experienced reduced productivity, and these two years differed significantly from all subsequent years (Table 3). Lowest productivity occurred during the 1998 El Niño ($1.2 \pm SE 0.13$). Greater productivity in early-nesters was significantly different from middle- and late-nesting birds. Productivity declined as seasons progressed; middle and late-nesting birds fledged 17%

and 30% fewer chicks than early-nesting birds, respectively (Table 4).

DISCUSSION

Comparisons to Other Studies

Average clutch sizes at study colonies (range 3.1-3.3 per colony) were similar to the Farallones in: a) 1971-83 ($3.1 \pm SD 0.4$; range 2.4-3.8; Boekelheide and Ainley 1990); b) 1986 (3.2; Feldman 1992); and c) 1997-2001, during the same time-period as our study ($3.1 \pm SD 0.3$, range 2.6-3.3; calculated from Saenz *et al.* 2006). In comparisons to southern California colonies, clutch sizes were similar to those on San Nicolas Island in 1992-94 (2.4, 3.1, and 3.4, respectively; McChesney 1997), and appeared larger than those on Santa Barbara Island in 1976 ($2.4 \pm SD 0.9$) and 1977 (2.3; Hunt *et al.* 1981). Smaller clutch sizes also were reported at newly-formed colonies (which may have included incomplete clutches) in southern British Columbia ($2.6 \pm 1.0 SD$; Campbell *et al.* 1990). However, during the 1997-2001 period, clutch sizes at our study colonies were somewhat lower than at the recently-formed estuarine Alcatraz Island colony in nearby San Francisco Bay ($3.5 \pm SD 0.24$; range 3.1-3.8; Saenz *et al.* 2006).

Mean hatching success (73-78%), fledging success (82-92%), and fledglings per pair (1.7-2.2) appeared higher in this study than at the two Farallon study plots during the period 1971-83 (41-51% hatching success, 74-76% fledging success, and 1.0-1.5 fledglings per pair; Boekelheide *et al.* 1990). Hatching and fledging success per nest also were higher in this study, demonstrating lower rates of nest abandonment. At our study colonies, 93% of all nests hatched at least one chick and 89% of nests fledged young in 1997-2001, compared to 60-70% hatching and 55-69% fledging success per nest at the Farallones in 1971-83 (Boekelheide *et al.* 1990). During the 1997-2001 period, cormorant productivity at the Farallones ($1.8 \pm SD 0.84$, range 0.4-2.4; calculated from Saenz *et al.* 2006) appeared most similar to the CH colony ($1.7 \pm SE 0.10$) in overall average and an-

Table 4. Mean \pm SE (sample size) and statistical F-test for comparing reproductive parameters between early, middle, and late-nesting Brandt's Cormorants at three central California colonies, 1997-2001. Early is defined as $-1/2$ SD, late as $+1/2$ SD, and middle as within $1/2$ SD of the mean. For F-tests indicating significant differences among colonies ($P < 0.05$), means were compared in pairs and superscripted with similar capital letters if not statistically significant ($P > 0.05$).

	Statistic	P	N	Early	Middle	Late
Clutch Size	$F_{2,428} = 6.8$	0.0012	457	3.3 ^A ± 0.06 (136)	3.3 ^A ± 0.05 (205)	3.0 ^B ± 0.06 (116)
Brood Size	$F_{2,428} = 11.2$	0.0001	457	2.6 ^A ± 0.08 (136)	2.4 ^A ± 0.06 (205)	2.1 ^B ± 0.08 (116)
Hatching Success (%)	$F_{2,428} = 2.4$	0.0943	1,487	79.4 ± 2.4 (458)	74.7 ± 2.2 (672)	71.0 ± 3.2 (357)
Fledging Success (%)	$F_{2,404} = 1.0$	0.3764	1,133	89.8 ± 1.9 (356)	87.1 ± 2.6 (517)	91.1 ± 1.7 (260)
Breeding Success (%)	$F_{2,428} = 2.4$	0.0905	1,487	67.9 ± 3.0 (458)	65.3 ± 2.7 (672)	57.7 ± 3.8 (357)
Fledglings per Pair	$F_{2,685} = 13.3$	0.0001	714	2.3 ^A ± 0.07 (383)	1.9 ^B ± 0.09 (182)	1.6 ^B ± 0.1 (149)

nual trends, and somewhat lower overall than at DS ($1.9 \pm$ SE 0.08) and PR ($2.2 \pm$ SE 0.07).

For the 1971-97 period, Sydeman *et al.* (2001) reported a significant increasing trend in Brandt's Cormorant hatching success at the Farallones (excluding El Niño years in 1983 and 1992), but not for clutch size or fledging success. The greatest increase occurred towards the end of the period, with higher productivity at the Farallones in 1995-2000 than in 1971-1983. To explain high productivity in the mid-1990s, they suggested that Farallon-breeding cormorants might have switched to foraging on alternate prey in nearshore waters. At the Farallones during the 1970s and 1980s, many seabirds, including Brandt's Cormorants, depended primarily on juvenile rockfish to feed chicks. When rockfish were not available, reproductive success suffered (Boekelheide *et al.* 1990; Nur and Sydeman 1999). During the 1990s, juvenile rockfish abundance in the Gulf of the Farallones and in Farallon seabird diets declined, but then reappeared in abundance in 2001 (Miller and Sydeman 2004; Mills *et al.* 2007).

Interannual Variability

Brandt's Cormorants at the three study colonies demonstrated considerable vari-

ability in their reproductive success between years. Substantial variation in cormorant breeding population size, phenology, and reproductive success has been correlated with annual fluctuations in the California Current. Highest reproductive success and largest breeding population sizes tend to occur when upwelling is high, sea surface temperatures (SST) are cold, and prey species are most abundant (conditions typically associated with La Niña events), while lowest values coincide with warm-water, El Niño periods (Boekelheide *et al.* 1990; Ainley *et al.* 1995; McChesney 1997; Nur and Sydeman 1999; Sydeman *et al.* 2001; USFWS, unpubl. data).

The 1997-2001 period was dominated by two major oceanographic events: the 1997-98 El Niño that peaked in early 1998, and the 1999-2001 La Niña event that peaked in early 1999 (e.g., Hayward *et al.* 1999; Bograd *et al.* 2000; Schwing *et al.* 2000, 2002). El Niño conditions in 1998 (low upwelling, elevated SST, and low marine productivity) had clear negative effects on Brandt's Cormorant reproductive performance. In 1998, breeding population sizes were reduced, breeding was delayed and was less successful, resulting in the lowest productivity of the study period. The effects of the subsequent La Niña event were also evident, with a rebound in breeding effort and high reproductive success in 1999-2001.

Intra-annual Variability

Early nesters produced larger clutches, hatched more chicks, and fledged more chicks per pair than late nesters. Similar patterns were noted on the Farallones in 1986 (Feldman 1992). At San Nicolas Island in 1992-1994, late breeders also tended to exhibit lower reproductive success (McChesney 1997). In Double-crested Cormorants (*Phalacrocorax auritus*), productivity decreased as the season progressed in the Gulf of Saint Lawrence in 1980, as well as at colonies within the San Francisco Bay and the Farallones in 1988 (McNeil and Leger 1987; Stenzel *et al.* 1995). Boekelheide *et al.* (1990) reported that middle-nesters produced larger clutches than late-nesters, but found no overall differences in hatching or fledging success. Similarly, we recorded no significant differences in hatching or fledging success between early-, middle-, and late-nesting birds, although both hatching and breeding success declined slightly as seasons progressed.

Intra-annual differences in reproductive success likely reflected influences of age and experience in breeding birds. Older male cormorants arrive to breed earliest, on average, and often claim the most desirable nesting habitat (Boekelheide and Ainley 1989; Boekelheide *et al.* 1990; Feldman 1992). Older breeders (both male and female) on the Farallones produced larger clutches and fledged more chicks per pair than younger breeders (Boekelheide and Ainley 1989; Feldman 1992). However, none of the birds in our study were marked, and we could not quantify age-related factors.

Intercolony Variability

The onset of upwelling conditions in spring is earlier in the more southerly portions of the California Current System (Bakun 1973), and the breeding phenology of Brandt's Cormorants tends to reflect this pattern (Ainley and Boekelheide 1990). For example, most Brandt's Cormorants in southern California (33-34°N) breed considerably earlier than at the Farallones, with

egg-laying beginning as early as January or February at some colonies (Michael 1935; SOWLS *et al.* 1980; HUNT *et al.* 1981; McChesney 1997). In this study, clutch initiation dates were almost consistently (four of five years) earliest at the southernmost CH colony. Although study colonies were within a 200 km section of coast at similar latitudes (36-38°N), this pattern suggests that the timing of upwelling and related prey availability can vary over relatively short distances, although other local factors might be involved as well.

As found elsewhere in the California Current, each colony exhibited considerable interannual variation in reproductive parameters. In 1997-2001, PR was least variable in breeding population size, timing of breeding, hatching success, brood sizes, and productivity. PR birds did not experience the pronounced delay in egg-laying and reduced reproductive effort and success that occurred at DS and CH during the 1998 El Niño. Annual "stability" in reproductive effort and success at PR also contrasted with the offshore Farallones colony (Saenz *et al.* 2006), where alternating "boom and bust" cycles have been associated with availability of upwelling-dependent prey such as juvenile rockfish (e.g., Ainley and Boekelheide 1990; Boekelheide *et al.* 1990; Ainley *et al.* 1995; Nur and Sydeman 1999). Poor hatching and fledging success in 1998 at DS and CH demonstrated the magnitude of the impact that poor years can have on the life history of Brandt's Cormorants (see also Boekelheide and Ainley 1989).

Ecological factors, such as local marine productivity, likely played a substantial role in explaining differences between colonies. Point Reyes is within a large upwelling center where local marine productivity is exceptionally high (Parrish *et al.* 1983). Local eddies that are sometimes present in the waters near Point Reyes retain nutrients, plankton, and probably cormorant prey (Wing *et al.* 2003; Largier *et al.* 2006; Vander Woude *et al.* 2006). In addition, coastal habitats near PR are more varied than those at DS or CH, and include large amounts of rock and soft-bottom substrates, scattered kelp forests, and estuaries, each of which support diverse prey

species identified in the Brandt's Cormorant diet (Hubbs *et al.* 1970; Ainley *et al.* 1981; Talent 1984). It is possible, then, that prey resources associated with the highly productive and diverse habitats near PR may buffer this colony from fluctuations in food availability during most warm-water years, providing PR cormorants the opportunity to switch their diet when upwelling-dependent prey become less available. Similarly, Saenz *et al.* (2006) reported that Brandt's Cormorants breeding on Alcatraz Island, located nearby in the San Francisco Bay and feeding primarily on estuarine prey, exhibited less variability and greater success than the offshore Farallones colony. However, cormorants at the Drake's Bay Colony Complex, located on nearshore rocks just south of Point Reyes, exhibited reduced population size and reproductive success in 1998, a pattern more similar to the Farallones (Carter *et al.* 2003).

Greater variability at CH, located more than 200 km south of PR, more closely tracked broad-scale upwelling conditions in 1997-2001, suggesting greater reliance on upwelling-dependent prey and perhaps fewer opportunities for prey switching in poor food years. In addition, human (boats and aircraft) and avian disturbances (e.g., Brown Pelican, *Pelecanus occidentalis*) have impacted Common Murre breeding success at CH more frequently than at DS or PR (Rojek *et al.* 2007; USFWS, unpubl. data). Although impacts to cormorant breeding success were not documented, human or avian disturbance events might have influenced the reproductive success of cormorants at CH.

Implications for Population Dynamics and Environmental Monitoring

High interannual variability in reproductive success is common in cormorants and many other seabird species, and trends in breeding population sizes, reproductive performance, and diet are often correlated with fluctuations in marine conditions. This suggests the use of seabirds as effective indicators of both local and broad-scale marine ecological parameters (e.g., Cairns 1987, 1992; Ainley *et al.* 1994, 1995; Montevecchi and My-

ers 1995; Furness and Camphuysen 1997; Sydeman *et al.* 2001; Piatt *et al.* 2007a). Considering its near endemism, regional prominence in biomass, and measurable response to marine conditions, the Brandt's Cormorant is an important component of California Current seabird monitoring programs. After the Common Murre, the Brandt's Cormorant is currently one of the most abundant breeding seabird species in central California and, like the Common Murre, it nests in dense groups above ground, making it a relatively easy species to monitor. As a piscivore it can serve as a valuable comparison species to the more well-studied Common Murre, which has been the subject of long-term monitoring on the Farallones (e.g., Ainley and Boekelheide 1990; Ainley *et al.* 1993; Sydeman *et al.* 2001; Miller and Sydeman 2004; Mills *et al.* 2007) and intensive restoration efforts in central California (Parker *et al.* 2007). Although there has been considerable dietary overlap between central California cormorants and murre, especially in the case of juvenile rockfish, stable isotope analyses have indicated that Common Murres forage farther offshore and occupy a significantly different trophic level than do Brandt's Cormorants (Ainley *et al.* 1981, 1995, 1996; Sydeman *et al.* 1997). This suggests Brandt's Cormorants are perhaps better indicators of nearshore prey availability. Additionally, a conservative breeding strategy in murre (laying only a single egg per clutch) allows them more flexibility to allocate otherwise discretionary 'loafing' time to increase foraging effort when conditions are poor (Burger and Piatt 1990; Ainley *et al.* 1995; Parker 2005; Harding *et al.* 2007; Piatt *et al.* 2007b). In comparison, the breeding success of cormorants (which lay multi-egg clutches) more often reflects even relatively small changes in marine productivity (Ainley *et al.* 1995). Finally, murre in central California historically have been more adversely affected than cormorants by mortality from anthropogenic factors; for example, egg harvesting, oiling from spills and as incidental take in gill-net fisheries (Ainley and Lewis 1974; Page *et al.* 1990; Takekawa *et al.* 1990; Carter *et al.* 2001, 2003). Such influences can complicate the

assessment of seabird population trends in relation to oceanographic conditions. Long-term comparisons of Brandt's Cormorant and Common Murre populations and reproductive success can therefore provide complementary measures of seabird response to environmental variability, and can help differentiate between natural and anthropogenic impacts on seabird populations.

Prior to the mid-1990s, a relatively small proportion of the Gulf of the Farallones Brandt's Cormorant population nested along the mainland coast (Sowls *et al.* 1980; Carter *et al.* 1992). Since then, numbers at nearshore colonies in the Gulf of the Farallones have increased dramatically, mainly at a few sites (including DS) where breeding was rare or unknown previously (Carter *et al.* 1996; Capitolo *et al.* 2004; Saenz *et al.* 2006; USFWS, unpubl. data). This change might reflect a population shift, driven most likely by the emigration of young birds from the very large offshore Farallones colony to mainland coastal colonies. Farallon-banded cormorants have been observed roosting and breeding at all three of our study colonies (McChesney *et al.* 2006), and Saenz *et al.* (2006) reported similar activity on Alcatraz Island. This shift from offshore to nearshore habitats could be associated with a reduction in juvenile rockfish availability along the outer continental shelf. Although we did not sample cormorant diet, evidence of a decline in juvenile rockfish in the Common Murre diet is available for this period. During the 1990s, Farallon Common Murres switched from feeding chicks mainly rockfish to Northern Anchovy (*Engraulis mordax*) and possibly Pacific Sardine (*Sardinops sargax*) (Miller and Sydeman 2004; Mills *et al.* 2007). In most recent years, murre foraging distribution during the chick-rearing period has also shifted towards the mainland (Ainley *et al.* 1996; Oedekoven *et al.* 2001). High reproductive success at nearshore colonies is suggestive of good foraging conditions, and it is likely that as Farallon cormorants experienced similar changes in prey availability, some were prompted to begin breeding closer to alternate prey resources in nearshore waters.

This study occurred at what was initially perceived to be an interdecadal transition in the North Pacific Ocean from an extended warm-water phase that began in 1976 to a new, cold-water phase that began with the 1999-2001 La Niña (e.g., Bograd *et al.* 2002; Schwing *et al.* 2002). However, more recent assessments have questioned that theory (Goericke *et al.* 2004). Brandt's Cormorants at nearshore central California colonies responded to the short-term cold-water period with high breeding success that should lead to high future recruitment and increased population sizes. Continued monitoring will contribute to a longer-term dataset that can be integrated into broader, ecosystem-wide monitoring programs for central California and the California Current Upwelling System. Additional study of cormorant foraging ecology in nearshore central California waters would facilitate a better understanding of Brandt's Cormorant population dynamics in the region.

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