AN URBAN SUCCESS STORY: BREEDING SEABIRDS ON ALCATRAZ ISLAND, CALIFORNIA, 1990–2002

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SUMMARY

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Located in the San Francisco Bay estuary, Alcatraz Island has in recent years become an important breeding site for seabirds, including Brandt's Cormorant *Phalacrocorax penicillatus,* Pelagic Cormorant *P. pelagicus,* Pigeon Guillemot *Cepphus columba* and Western Gull *Larus occidentalis.* We synthesized available data on breeding populations from 1990–2002 for those four species and calculated annual productivity in 1997–2002 for Brandt's Cormorants and 1999–2002 for Pelagic Cormorants and Western Gulls. Population trends and productivity were compared to those on larger, offshore Southeast Farallon Island (SEFI). Brandt's Cormorants established a colony that grew to more than 460 breeding pairs during the study period. Small populations of Pelagic Cormorants and Pigeon Guillemots on Alcatraz remained relatively stable during 1995–2002. Breeding Western Gulls increased at a 6.0% annual rate from 1990–2002. Productivity of Brandt's Cormorants and Western Gulls on Alcatraz was higher than on SEFI in the years monitored. We propose that high availability of forage fishes in the San Francisco Bay estuary, combined with seasonal protection of nesting habitat, contributed to the recent growth and success of Alcatraz seabird populations. Because seabirds on Alcatraz breed in close proximity to myriad human activities, they present a unique opportunity to investigate the ecology of urban seabird populations.

Key words: Brandt's Cormorant *Phalacrocorax penicillatus*, Pelagic Cormorant *Phalacrocorax pelagicus*, Pigeon Guillemot *Cepphus columba*, Western Gull *Larus occidentalis*, population trends, seabird productivity, central California, disturbance

INTRODUCTION

In recent years, Alcatraz Island has become an important breeding site for seabirds, including Brandt's Cormorant *Phalacrocorax penicillatus,* Pelagic Cormorant *P. pelagicus,* Pigeon Guillemot *Cepphus columba* and Western Gull *Larus occidentalis.* Colonization and growth of Alcatraz as a seabird colony is of interest because of its close proximity to a busy urban center, and because the island itself is subject to heavy tourism year-round. In addition, Alcatraz Island is located in the central San Francisco Bay estuary, where productive waters and a shallow benthos provide foraging opportunities that are different from those in the oceanic waters where these seabirds are most often found. The environment on and near Alcatraz contrasts with that of the nearby Farallon Islands, where a similar assemblage of nesting seabirds is protected within the Farallon Islands National Wildlife Refuge and is surrounded by neritic and pelagic marine habitats.

The historical record of breeding seabirds on Alcatraz Island is sparse. Seabirds were likely almost entirely extirpated from the island during its period of human occupation (*c.* 1853–1972). Seabird recolonization of Alcatraz began soon after human habitation of the island ceased in 1972 (Golden Gate National Recreation Area [GGNRA] unpubl. data). Western Gulls, apparently always present on the island in small numbers, began to increase after 1972 and have since been the subject of several investigations (Annett & Pierotti 1989, Brown 1997). A pair of Heermann's Gulls *Larus heermanni* attempted to breed in 1979–1981 (Howell *et al.* 1983). Boarman (1989) noted 2–20 Pigeon Guillemots on and around the island during casual surveys in 1981–1983, and confirmed at least one active nest in 1982. Six Pelagic Cormorant nests were first located in 1986 (GGNRA unpubl. data). To date, a summary of Alcatraz seabird populations and breeding biology has not been attempted.

Here, we report trends in breeding populations for Brandt's Cormorants, Pelagic Cormorants, Pigeon Guillemots and Western Gulls from 1990–2002, and estimate productivity for Brandt's Cormorants (1997–2002), Pelagic Cormorants (1999–2002) and Western Gulls (1999–2002). We compare productivity and population trends of Alcatraz seabirds with conspecifics on nearby Southeast Farallon Island (SEFI) and discuss the ecology of these seabirds within the context of the San Francisco Bay estuary.

METHODS

Study areas

Alcatraz Island

Alcatraz is an island of 8.6 ha located in the central San Francisco Bay estuary (37°49′N, 122°25′W). It is managed primarily as a cultural historic site as part of the GGNRA by the U.S. National Park Service (NPS). Breeding and roosting birds on Alcatraz are afforded legal protection by the *Migratory Bird Treaty Act* of 1918. In 1993, the NPS implemented a revised General Management Plan for Alcatraz that called for closure of parts of the island during the seabird breeding season and for monitoring to assess the effects of management decisions on Alcatraz wildlife populations.

Historically, Alcatraz was used as a roost, and possibly as a breeding site, by seabirds. The island was originally christened Isla de los Alcatraces, or "island of the pelicans" (or cormorants, depending on Spanish dialect), by Spanish Lieutenant Juan Manuel de Ayala in 1755. The original Alcatraz Island was a sloping sandstone rock with little vegetation except for sparse grass, and was and largely covered with seabird guano. Human habitation of Alcatraz began in 1853, when the island became the site of the first lighthouse on the west coast of the United States. Alcatraz was then variably used as a Civil War fortress, a military prison, and a federal penitentiary. Ultimately, after the Indian Occupation of 1969–1971, it became a part of the National Park system in 1972. There are no records of breeding seabirds on the island following human occupation, with the exception of small numbers of Western Gulls, until the transfer of the island to the NPS (NPS historical files).

Today, Alcatraz is covered by cement roads, deteriorating structures, and rubble piles from razed buildings. Introduced vegetation, including Nasturtium *Tropaeolum majus,* Monterey Cypress *Cupressus macrocarpa, Eucalyptus* spp., Mirror Bush *Coprosma baueri, Agave* spp., various ornamental trees and exotic annual grasses grow wild in soil brought to the island during the tenure of the U.S. military. The south and southwestern shoreline consists of relatively inaccessible 20-m cliffs, where most seabirds nest. The north- and east-facing shores have a more gradual slope and are terraced with various structures, roads, and patches of vegetation (Fig. 1). In addition to seabirds, Alcatraz has hosted a substantial population of Black-crowned Night Herons *Nycticorax nycticorax* since the mid-1980s (Hothem & Hatch 2004).

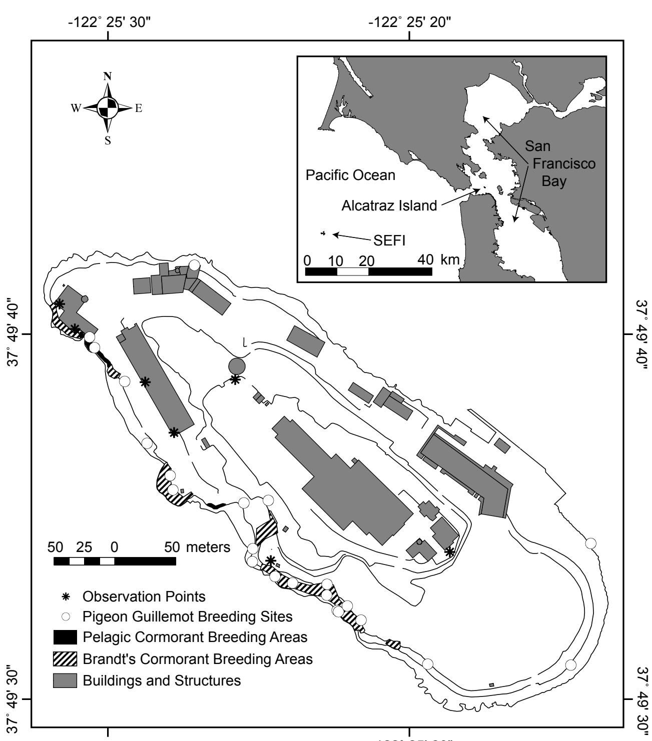

Fig. 1. Alcatraz Island: significant structures, observation points, and seabird breeding areas in 2002. The inset map shows the regional positions of Alcatraz Island and Southeast Farallon Island (SEFI), which host several species of breeding seabirds in common.

Located 1.6 km from San Francisco, Alcatraz is immediately adjacent to one of the largest urban centers in the United States, and as a result, wildlife on the island is subjected to many potentially disrupting human activities. As a popular tourist destination, Alcatraz receives more than one million visitors annually (NPS historical files). Alcatraz is subject to almost constant nearshore boat traffic and aircraft overflights. Fishing and pleasure boats often cruise within 15 m of seabird colonies, and news helicopters, tourist float-planes and military aircraft routinely fly at altitudes below 300 m over Alcatraz. Sand-dredging operations occur daily in the estuary surrounding the island, and a dredge spoil disposal area is located approximately 500 m south of the island.

Southeast Farallon Island

SEFI is located 48 km west of Alcatraz, near the edge of the continental shelf (37°42′N, 122°60′W). It is home to the largest seabird colonies in the continental United States and hosts the largest breeding populations worldwide of Brandt's Cormorants and Western Gulls. SEFI is included in the Farallon Islands National Wildlife Refuge as well as the Farallon Islands Ecological Reserve, and the surrounding waters are protected as a part of the Gulf of the Farallones National Marine Sanctuary. Seabirds breeding on SEFI are the subjects of a 32-year study by PRBO Conservation Science in cooperation with the U.S. Fish and Wildlife Service. For a detailed account of the seabird ecology of the Farallon Islands see Ainley & Boekelheide (1990).

Data collection and analysis

During 1990–1995, seabird species, excepting Western Gulls, were counted opportunistically by the NPS, and reported populations during this period should be considered minimum estimates. Western Gulls were systematically censused during 1990–2002. From 1996 onward, we conducted regular island- and boat-based surveys around Alcatraz Island during the breeding season of March through mid-September. Island-based surveys occurred biweekly between 09h00 and 12h00, using 8×42 binoculars and 40–60×spotting scopes. We made observations remotely or under the cover of blinds or existing structures (Fig. 1) to minimize disturbance to nesting birds. We conducted boat surveys between 07h00 and 11h00, remaining at least 100 m offshore, and making observations using 8×42 binoculars. To reduce human error, population surveys were double-counted using two observers, counted from photographs taken during the survey, or determined from nests mapped and followed individually. During all surveys, we recorded events that produced a disturbance (caused birds to assume an alert posture or flush) among nesting and roosting cormorants.

All population data are reported as numbers of breeding pairs. For all species, we calculated breeding population trends using log-transformed annual breeding pairs as the dependant variable, and year as explanatory variable in a linear regression. We back-transformed regression coefficients to obtain estimates of annual rates of population growth (Caughley 1977). Productivity was calculated for Brandt's and Pelagic Cormorants and Western Gulls as the number of chicks surviving to fledging age in a sub-sample of nests. We compared clutch size and productivity between Alcatraz and SEFI using analysis of variance (ANOVA) on individual nest success.

Productivity of seabirds on SEFI was calculated as for those on Alcatraz, using a sub-sample of individual nests. For a detailed description of the methods used to determine breeding population size on SEFI see Sydeman *et al.* (2001).

Brandt's Cormorant

For cormorant species, a pair was considered to be breeding if eggs or chicks were observed, or if a bird was observed for at least one week (two consecutive surveys) in incubation or brooding position on a well-built nest. Seasonal high counts from island- or boat-based surveys for each subcolony were summed to arrive at the annual number of breeding pairs, a method that contains potential for overestimation of breeding numbers. Any overestimation is likely to be very small, however, because we mapped and individually followed many nests (21%–100%), and observed little movement between subcolonies or few changes in population counts following egg-laying. We obtained annual productivity estimates in 1997–2002 from biweekly monitoring of individual nests in several study plots. Study plots were chosen based on accessibility, because only two subcolonies afforded views of nest contents during incubation and early brooding. Chicks often form crèches and become indistinguishable from one another, unless they return to the nest to be fed (Carter & Hobson 1988). At 28 days of age, cormorant chicks are developed enough to form crèches and survive away from parents for the night, and they are large enough to repel attacks from Western Gulls. We therefore considered chicks fledged when they were first noted missing from the nest site and were at least 28 days old.

Pelagic Cormorant

Pelagic Cormorants nests were censused opportunistically in 1993 and 1995. In 1996–2002, all nests visible from the island were monitored twice weekly. Fledging criteria were the same as those for Brandt's Cormorants.

Pigeon Guillemot

Most Pigeon Guillemot nest crevices on Alcatraz were inaccessible because of their proximity to sensitive breeding cormorants, precluding estimates of guillemot productivity. Nest numbers were determined by observation of the delivery of fish to a crevice by adult birds, indicating the presence of a chick. This method may underestimate the guillemot breeding population, because we could not document nests that failed before hatching.

Western Gull

To census Western Gulls, we divided the island into 28 areas and counted the number of nests with eggs and chicks in each using walk-through counts. Two complete island surveys were conducted one week apart around peak hatching (usually the last week of May and first week of June), and the two totals were averaged to estimate the final number of breeding pairs for each year. Parts of Alcatraz have dense cover, and although we exhaustively searched all accessible areas, a small number of nests may have been overlooked if they were under vegetation on inaccessible cliffs. For 1999–2002, we derived productivity estimates from individual nests in two study plots monitored with either weekly or biweekly frequency. The two study plots were chosen because they captured a cross-section of vegetative cover, exposure to weather and wind and exposure to humans, and because their location offered vantage points from which nests could be monitored remotely to avoid disturbance to nesting birds. We defined a fledged chick as being fully-feathered (capable of flight) when it disappeared from the nesting territory.

RESULTS

Brandt's Cormorant

Brandt's Cormorants were first observed nesting on Alcatraz in 1991, when three nests were located. No observations were made

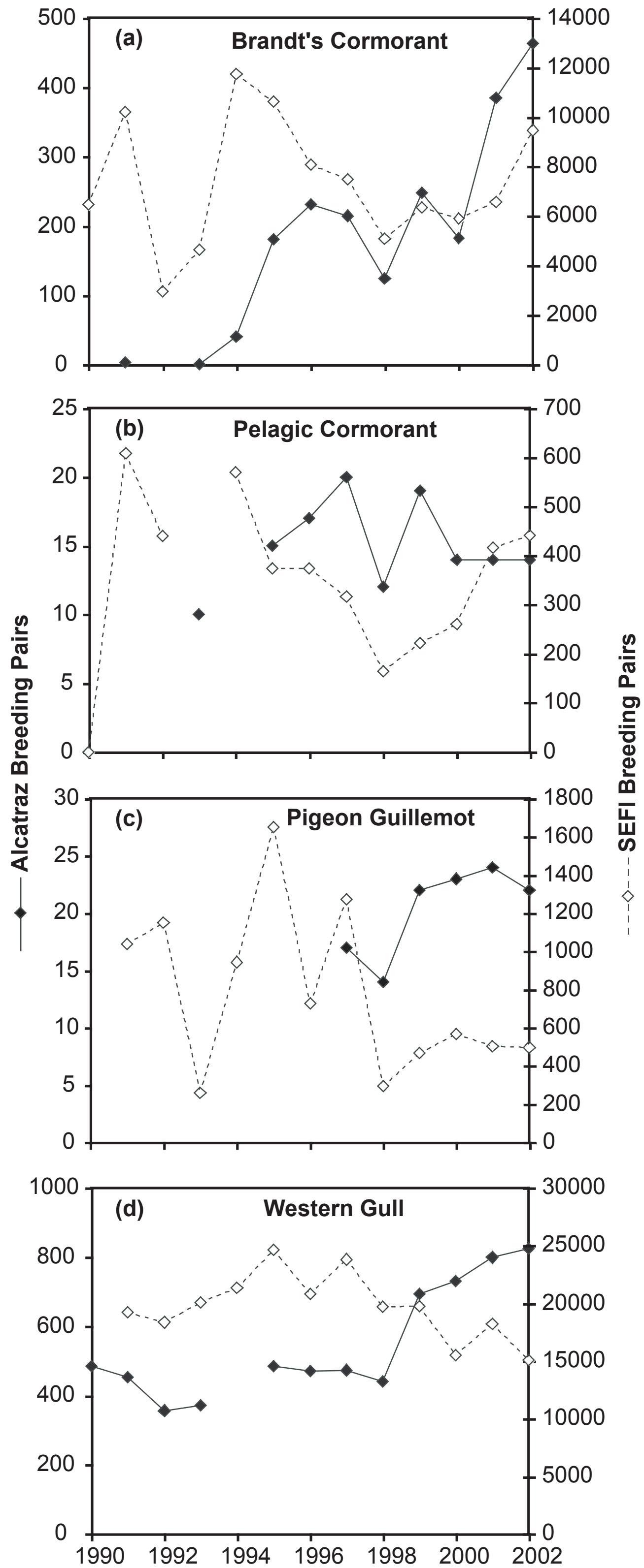

Fig. 2. Breeding population sizes of seabirds on Alcatraz Island and Southeast Farallon Island (SEFI), 1990–2002: (a) Brandt's Cormorants, (b) Pelagic Cormorants, (c) Pigeon Guillemots and (d) Western Gulls. Years with missing data points indicate no data was taken. Lines between data points indicate consecutive years of population data.

in 1992, and at least one nest was present in 1993. Starting in 1993, the population increased rapidly, and by 2002, it reached more than 460 breeding pairs. From 1991 to 2002 the population grew at an average rate of 60% annually [standard error (SE) = 0.114, $r^2 = 0.654$, $P = 0.003$]. We observed up to three breeding adults each year on Alcatraz that were banded as chicks on SEFI, indicating that immigration played a role in population growth. During the same time period on SEFI, the Brandt's Cormorant population varied from year to year, and we found no linear trend (SE = 0.035, $r^2 = 0.007$, $P = 0.799$). Since 1996, interannual changes in the Brandt's Cormorant population on Alcatraz appear similar in direction to SEFI, yet the rate of growth on Alcatraz was much higher (Fig. 2).

Brandt's Cormorants nested in six distinct subcolonies on the southwest and west shores of Alcatraz (Fig. 1), along the tops of cliffs or walls, on sloping ledges, about scaffolding, and at the base of abandoned buildings. Nests were located almost exclusively in areas closed to all human and vehicular traffic and were predominately hidden from view of visitors on the island. However, in 2002, Brandt's Cormorants nested successfully in clear view of human visitors after forming a new subcolony near a popular overlook.

During each season, we observed cormorants flush from nests as a result of being approached by persons who violated the breeding closure boundaries or when boats and aircraft passed close (within *c.* 100 m and *c.* 500 m, respectively) to the colony, but these disturbances only occasionally resulted in abandonment of affected nests. However, several major disturbances to Brandt's Cormorants in 1998 and 1999 had measurable negative effects on breeding numbers. During 1998, repeated human-caused disturbance at one particular subcolony before egg-laying likely caused its abandonment; poor environmental conditions associated with the El Niño event that year may have also played a role. In early April 1999, before egg-laying began, jet-ski watercraft landed on the west side of the island, triggering the abandonment of all nests within view of the incident (55 nests, 40% of the 1999 breeding population). Birds returned and laid eggs starting on 20 May, approximately one month later than the mean egg-laying date from other years in our study.

During 1997–2002, clutch size for Brandt's Cormorants varied annually from 3.1 to 3.8 eggs ($df = 5$, $F = 9.61$, $P < 0.001$), which was higher than on SEFI during all years measured (SEFI: 2.6–3.3 eggs; $df = 1$, $F = 70.65$, $P < 0.001$; Table 1). Productivity varied annually between 1.6 and 2.5 chicks per pair ($df = 5$, $F = 9.06$, $P < 0.001$). As with clutch size, productivity was higher on Alcatraz than on SEFI during all years measured (SEFI: 0.4–2.4 chicks per pair; $df = 1$, $F = 29.92$, $P < 0.001$; Table 1). The interaction between colony and year was also significant in the productivity ANOVA model ($df = 5$, $F = 5.18$, $P = 0.001$), because of a more pronounced influence of the 1998 El Niño event at SEFI than at Alcatraz. In 1998, productivity on Alcatraz was lowest among recorded years (1.6 chicks per pair); however, it was still much higher than on SEFI (0.4 chicks per pair). Excluding 1998 from analysis, Brandt's Cormorants produced more chicks on Alcatraz than on SEFI independent of year ($df = 1$, $F = 10.23$, $P = 0.001$).

Pelagic Cormorant

Pelagic Cormorants nest on small ledges among the most vertical cliffs on the west shore of Alcatraz. Nests were also located in *c.* 50-cm–diameter anchor holes drilled into the rock of western-facing cliffs, which are the remains of support anchors for a walkway that formerly ringed the island. During 2000–2002, Brandt's Cormorants occupied approximately four nest sites that had been used by Pelagic Cormorants in 1997–1999, and another nest site was lost between 2000 and 2001 because of cliff erosion. We observed between 10 and 20 Pelagic Cormorant nests annually on Alcatraz between 1993 and 2002, and we found no significant population trend (SE = 0.027, $r^2 = 0.045$, $P = 0.584$; Fig. 2). Similarly, no trend in the Pelagic Cormorant breeding population on SEFI was observed during the same period (SE = 0.052, $r^2 = 0.045$, $P = 0.584$).

Pelagic Cormorant clutch size ranged from 3.8 to 4.2 eggs, with sample sizes between five and six nests annually. Because of small samples sizes at both Alcatraz and SEFI, clutch size was not compared between colonies. Annual productivity for Pelagic Cormorants on Alcatraz averaged 1.9–2.9 chicks per nest during 1999–2002, although again, our sample of nests was often small (Table 2). Over the four years monitored, Pelagic Cormorant

TABLE 1
Average clutch size and productivity (± standard deviation, n = sample size) of Brandt's Cormorants on Alcatraz and Southeast Farallon Island (SEFI), 1997–2002

Year	Clutch size (eggs laid per pair)		Productivity (chicks per pair)	
	Alcatraz	SEFI	Alcatraz	SEFI
1997	3.5±0.7	3.2±0.7	2.2±1.2	1.9±0.9
	n=43	n=92	n=87	n=85
1998	3.1±0.4	2.6±0.6	1.6±1.0	0.4±0.6
	n=39	n=62	n=88	n=73
1999	3.6±0.6	3.1±0.7	2.4±1.1	2.2±1.1
	n=48	n=74	n=161	n=86
2000	3.8±0.5	3.3±0.5	2.4±1.2	2.4±0.8
	n=52	n=65	n=123	n=71
2001	3.7±0.7	3.2±0.7	2.0±1.3	1.9±1.1
	n=59	n=98	n=188	n=98
2002	3.5±0.6	3.3±0.7	2.5±1.0	2.0±1.3
	n=73	n=96	n=98	n=103

TABLE 2
Average productivity (± standard deviation, n = sample size) of Pelagic Cormorants on Alcatraz and Southeast Farallon Island (SEFI), 1999–2002

Year	Productivity (chicks per pair)	
	Alcatraz	SEFI
1999	1.9±1.1	1.2±1.1
	n=16	n=52
2000	2.2±1.5	1.2±1.2
	n=10	n=45
2001	2.2±1.7	2.3±1.2
	n=6	n=57
2002	2.9±1.3	2.6±1.2
	n=7	n=51

productivity did not vary significantly ($df = 3$, $F = 0.77$, $P = 0.52$), but it was higher than productivity on SEFI (SEFI: 1.2–2.6 chicks per pair; $df = 1$, $F = 4.75$, $P = 0.030$; Table 2).

Pigeon Guillemot

Pigeon Guillemots nest in deep holes and crevices on the shores of Alcatraz. Guillemots make use of many of the 50-cm–diameter anchor holes (those not used by Pelagic Cormorants), as well as other human-made structures including piles of cement rubble, eroding masonry, drainpipes and holes in the walls of buildings. Most nests were located on the southwest and south sides of the island in areas closed to the public, although between 2000 and 2002, we found nests on the more heavily-trafficked northeast facing shore (Fig. 1) in areas frequented by Alcatraz staff and construction workers.

We confirmed between 17 and 24 Pigeon Guillemot breeding pairs during 1997–2002, except in 1998, when numbers dropped to 14. At least eight breeding pairs were observed in 1993, and at least three pairs were confirmed in 1996, but the island was not completely surveyed before 1997. We found no significant trend in the Pigeon Guillemot population on Alcatraz from 1997 to 2002 (SE = 0.038, $r^2 = 0.554$, $P = 0.090$), nor in the SEFI population during the same period (SE = 0.121, $r^2 = 0.104$, $P = 0.530$).

Western Gull

Western Gulls use all areas of the island for nesting, including human-made structures. The population varied from 372 to 486 breeding pairs during 1990–1998. From 1998 to 2002, the population increased to 825 pairs (Fig. 2). The average annual population growth for all monitored years was 6.0% (SE = 0.01, $r^2 = 0.658$, $P = 0.001$). We found no trend in the Western Gull breeding population on SEFI during the same period (SE = 0.01, $r^2 = 0.223$, $P = 0.121$; Fig. 2). Clutch size ranged from 2.6 to 2.9 eggs between years and colonies (Table 2); however, on SEFI, clutch size varied among years ($df = 3$, $F = 8.89$, $P < 0.001$) and was slightly higher than on Alcatraz ($df = 1$, $F = 18.14$, $P < 0.001$). Western Gulls produced between 1.1 and 1.9 chicks per pair during 1999–2002, much higher than productivity on SEFI (SEFI: 0.3–1.0 chicks per pair; $df = 1$, $F = 296.43$, $P < 0.001$; Table 3), although the ANOVA model showed an interaction between year and colony ($df = 3$, $F = 22.62$, $P < 0.001$). Western Gull productivity on Alcatraz also varied significantly among years ($df = 3$, $F = 10.40$, $P < 0.001$).

TABLE 3
Average clutch size and productivity (± standard deviation, n = sample size) of Western Gulls on Alcatraz and Southeast Fallaron Island (SEFI), 1999–2002

Year	Clutch size (eggs laid per pair)		Productivity (chicks per pair)	
	Alcatraz	SEFI	Alcatraz	SEFI
1999	2.6±0.7	2.6±0.6	1.9±1.1	0.3±0.6
	n=65	n=192	n=117	n=193
2000	2.6±0.7	2.9±0.4	1.1±1.1	0.7±0.9
	n=108	n=203	n=113	n=203
2001	2.7±0.6	2.8±0.5	1.6±1.2	0.3±0.7
	n=101	n=185	n=97	n=191
2002	2.6±0.6	2.8±0.5	1.6±1.2	1.0±1.0
	n=138	n=185	n=107	n=181

DISCUSSION

Previous studies that compared inshore and offshore seabird colonies found similar patterns of higher inshore clutch size in Arctic Terns (Lemmetyinen 1973) and higher inshore productivity in Herring Gulls (Hunt 1972) and Common Terns (Hall & Kress 2004). Breeding population and productivity of seabirds is often related to prey availability (Cairns 1987), and in these cases, greater inshore breeding success was theorized to result from greater foraging success or opportunity near to the inshore colony. On SEFI, population and reproductive performance of seabirds have been linked to availability of juvenile rockfish *Sebastes* spp. (Ainely *et al.* 1990, Nur & Sydeman 1999, Sydeman *et al.* 2001), but these species are not regularly found in San Francisco Bay (Baxter *et al.* 1999). Despite the absence of this key prey group, we frequently observed all Alcatraz-breeding seabird species foraging in central San Francisco Bay. As in previous studies, we postulate that consistent and high levels of alternate prey in the surrounding San Francisco Bay may be supporting the expansion of seabird breeding populations on Alcatraz and the relatively high productivity calculated for Brandt's Cormorants and Western Gulls relative to SEFI.

Brandt's Cormorants are known to vary breeding effort between years based on resource availability (Boekelheide & Ainley 1989, Nur & Sydeman 1999). Similar fluctuations in breeding populations of Brandt's Cormorants on Alcatraz and SEFI during the study period indicate analogous ecologies in the two populations, and yet Alcatraz cormorants produced more chicks, especially during the strong El Niño event in 1998.

Brandt's Cormorants take benthic and pelagic prey in varying amounts (Ainley *et al.* 1981). Furthermore, diet analysis of Alcatraz Brandt's Cormorants has shown evidence of several species of benthic fishes as well as Northern Anchovy *Engraulis mordax* as food items (PRBO unpubl. data), all of which are common in San Francisco Bay (Baxter 1999a,b; Fleming 1999). We speculate that the large quantity of shallow, benthic habitat available to foraging Brandt's Cormorants in San Francisco Bay likely played a role in the growth of the Alcatraz breeding population, and may have contributed to the higher clutch size and breeding productivity observed in 1998 relative to SEFI.

No significant Pelagic Cormorant population trend was found during the study, however the population may have been constrained to 14 pairs during 2000–2002. During this period, available nesting habitat was reduced by cliff erosion and through interspecies competition for nest sites with Brandt's Cormorants. The small ledges on sheer cliffs utilized by Pelagic Cormorants on Alcatraz are few in number and most are already occupied. Productivity of Pelagic Cormorants on Alcatraz was similar to that at SEFI.

The population of Pigeon Guillemots on Alcatraz increased in 1999 following the 1998 El Niño, but was fairly stable in 1999–2002. This population may be constrained by a lack of suitable nest sites; crevices with dimensions and locations acceptable to Pigeon Guillemots are likely already filled. Guillemots appear to be expanding their nest site tolerances, however, given that we discovered nests in 2000–2002 on the east side of Alcatraz in human-made structures, and where tourism- and maintenance-related activities occur during the breeding season.

The rapid growth of the Western Gull population on Alcatraz during 1998–2002 is especially notable because the nearby SEFI population experienced a concurrent decline. The proximity of Alcatraz to urban areas affords Western Gulls the possibility of feeding on refuse, but during chick rearing, this behavior may lead to reduced reproductive output (Pierotti & Annett 1987). The high reproductive rate of Western Gulls on Alcatraz relative to birds on SEFI suggests that many Alcatraz birds do not rely exclusively on poor-quality foods such as refuse during the nesting phase (Annett & Pierotti 1989)—although refuse may be an important dietary supplement (Brown 1997). Annual productivity of 1.3–1.6 chicks per pair, similar to productivity on Alcatraz during this study, was achieved by Western Gulls on SEFI during 1985–1989 (Sydeman *et al.* 1991), but since then a substantial reduction has occurred (Sydeman *et al.* 2001). This decline has been attributed to changes in the prey base of SEFI gulls, as well as to a corresponding increase in intraspecific predation on the island (Sydeman *et al.* 2001). We have not observed severe intraspecific predation on Alcatraz and theorize that, as with Brandt's Cormorants, Western Gulls have a reliable prey base in and around San Francisco Bay that has facilitated productivity and fueled population growth, especially during the second half of our study period.

Despite NPS and federal protection, Alcatraz seabird populations face numerous potential anthropogenic hazards. The close proximity of humans to breeding seabirds presents special management issues on Alcatraz. Western Gulls often build nests in locations that conflict with tourism operations, and the seasonal closure of breeding areas reduces opportunities for island visitors. Alcatraz is located in a major, narrow shipping channel, making it particularly sensitive to oil or chemical spills. A dredge disposal site is located immediately adjacent to the island, raising concern over possible pollutant mobilization from contaminated dredge spoils (Ohlendorf & Fleming 1988). Seabirds on Alcatraz must also contend with almost constant aircraft overflights and near-shore boat traffic.

Regularly-disturbed seabird colonies may persist only if the advantages for seabirds to stay at the colony outweigh the disadvantages. Consequently, the active protection and management of seabird breeding habitat on Alcatraz Island is critical to the observed growth and maintenance of Alcatraz seabird populations. Without portions of the island being closed to staff and visitors during the breeding season, most seabird species on Alcatraz would not have sufficient habitat to breed and produce young.

Understanding the effects of the surrounding urban environment on Alcatraz seabirds is not straightforward. Colonial seabird species have shown habituation to regular and predictable human presence (Dunlop 1996, Nisbet 2000); however, different species likely have different aptitudes for habituation. Brandt's and Pelagic Cormorants in particular are sensitive to human disturbance (Ainley & Lewis 1974, Carter *et al.* 1984, Boekelheide & Ainley 1989, Boekelheide *et al.* 1990). Although breeding seabirds on Alcatraz appeared fairly resilient to disturbance events on a case-by-case basis during our study, cumulative effects of chronic, varied disturbance to seabird breeding colonies are unknown.

Additionally, environmental conditions may outweigh disturbance in terms of effects on seabird productivity (Carney & Sydeman 1999, Fraser & Patterson 1997). For instance, predictable or high levels of prey availability near Alcatraz may prompt breeding seabirds to tolerate some level of disturbance.

The success of the Alcatraz breeding seabirds despite chronic human disturbance warrants further investigation, especially as the marine climate changes. Seabirds are indicators of prey availability, and as top predators, they may serve as a proxy for ecosystem status (Kushlan 1993, Furness & Camphuysen 1997, Sydeman *et al.* 2001). We hope that the results of this study may be used as a baseline for measuring the health of San Francisco Bay and associated seabird populations, and for evaluating the efficacy of future seabird management decisions.

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REFERENCES

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

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

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

ANNETT, C.A. & PIEROTTI, R.J. 1989. Chick hatching as a trigger for dietary switching in the Western Gull. *Colonial Waterbirds* 12: 4–11.

BAXTER, R. 1999a. Cottidae. In: Orsi, J. (Ed). Report on the 1980–1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Technical Report 63. Stockton, CA: California Department of Fish and Game. pp. 249–278.

BAXTER, R. 1999b. Pleuronectiformes. In: Orsi, J. (Ed). Report on the 1980–1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Technical Report 63. Stockton, CA: California Department of Fish and Game. pp. 369–442.

BAXTER, R., HIEB, K., DE LEÓN, S., FLEMING, K. & ORSI, J. 1999. Appendix A–D. In: Orsi, J. (Ed). Report on the 1980–1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Technical Report 63. Stockton, CA: California Department of Fish and Game. pp. 419–503.

BOEKELHEIDE, R.J. & AINLEY, D.G. 1989. Age, resource availability, and breeding effort in Brandt's Cormorants. *Auk* 106: 389–401.

BOEKELHEIDE, R.J., AINLEY, D.G., MORREL, S.H. & LEWIS, T.J. 1990. Brandt's Cormorant. In: Ainley, D.J. & Boekelheide, R.J. (Eds). Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling system community. Palo Alto, CA: Stanford University Press. pp. 163–195.

BOARMAN, W.I. 1989. The breeding birds of Alcatraz Island: life on the rock. *Western Birds* 20: 19–24.

BROWN, M.E. 1997. Breeding success of Western Gulls (*Larus occidentalis*) on Alcatraz Island: the effects of experience, sex and condition [unpublished PhD thesis]. West Lafayette, IN: Purdue University.

CAIRNS, D.K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261–271.

CARNEY, K.M. & SYDEMAN, W.J. 1999. A review of human disturbance effects on nesting colonial waterbirds. *Waterbirds* 22: 68–79.

CARTER, H.R. & HOBSON, K.A. 1988. Créching behavior of Brandt's Cormorant chicks. *Condor* 90: 395–400.

CARTER, H.R., HOBSON, K.A. & SEALY, S.G. 1984. Colony-site selection by Pelagic Cormorants (*Phalacrocorax pelagicus*) in Barkley Sound, British Columbia. *Colonial Waterbirds* 7: 25–34.

CAUGHLEY, G. 1977. Analysis of vertebrate populations. New York: Wiley.

DUNLOP, J.N. 1996. Habituation to human disturbance by breeding Bridled Terns *Sterna anaethetus. Corella* 20: 13–16.

FLEMING, K. 1999. Northern Anchovy. In: Orsi, J. (Ed). Report on the 1980–1995 fish, shrimp, and crab sampling in the San Francisco Estuary, California. Technical Report 63. Stockton, CA: California Department of Fish and Game. pp. 167–178.

FRASER, W.R. & PATTERSON, D.L. 1997. Human disturbance and long-term changes in Adélie Penguin populations: A natural experiment at Palmer Station, Antarctic Peninsula. In: Battaglia, B., Valencia, J., and Walton, D.W.H. (Eds). Antarctic communities: species, structure and survival. Cambridge, UK: Cambridge University Press. pp. 445–452.

FURNESS, R.W. & CAMPHUYSEN, C.J. 1997. Seabirds as monitors of the marine environment. *ICES Journal of Marine Science* 54: 726–737.

HALL, C.S. & KRESS, S.W. 2004. Comparison of Common Tern reproductive performance at four restored colonies along the coast of Maine. *Waterbirds* 27: 424–433.

HOTHEM, R.L. & HATCH, D. 2004. Reproductive success of the Black-crowned Night Heron at Alcatraz Island, San Francisco Bay, California, 1990–2002. *Waterbirds* 27: 112–125.

HOWELL, J.A., LACLERGUE, D., PARIS, S., BOARMAN W.I., DEGANGE, A. & BINFORD, L.C. 1983. First nests of Heermann's Gull in the United States. *Western Birds* 14: 39–46.

HUNT, G.L. 1972. Influence of food distribution and human disturbance on the reproductive success of Herring Gulls. *Ecology* 53: 1051–1061.

KUSHLAN, J.A. 1993. Colonial waterbirds as bio-indicators of environmental change. *Colonial Waterbirds* 16: 23–251.

LEMMETYINEN, R. 1973. Clutch size and timing of breeding in the Arctic Tern in the Finnish archipelago. *Ornis Fennica* 50: 18–26.

NISBET, I.C.T. 2000. Disturbance, habituation, and management of waterbird colonies. *Waterbirds* 23: 312–332.

NUR, N. & SYDEMAN, W.J. 1999. Survival, breeding probability, and reproductive success in relation to population dynamics of Brandt's Cormorants *Phalacrocorax penicillatus. Bird Study* 46: 92–103.

OHLENDORF, H.M. & FLEMING, W.J. 1988. Birds and environmental contaminants in San Francisco and Chesapeake bays. *Marine Pollution Bulletin* 19: 487–495.

PIEROTTI, R. & ANNETT, C.A. 1987. Reproductive consequences of dietary specialization and switching in an ecological generalist. In: Kamil, A.C., Krebs, J.R. & Pulliam, H.R. (Eds). Foraging behavior. New York: Plenum Press. pp. 417–442.

SYDEMAN, W.J., HESTER, M.M., THAYER, J.A., GRESS, F., MARTIN, P. & BUFFA, J. 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current system, 1969–1997. *Progress in Oceanography* 49: 309–329.

SYDEMAN, W.J., PENNIMAN, J.P., PENNIMAN, T.M., PYLE, P. & AINLEY, D.G. 1991. Breeding performance in the Western Gull: effects of parental age, timing of breeding and year in relations to food availability. *Journal of Animal Ecology* 60: 135–149.