THE HISTORY OF FARALLON ISLAND MARINE BIRD POPULATIONS, 1854–1972

DAVID G. AINLEY AND T. JAMES LEWIS

Point Reyes Bird Observatory
Bolinas, California 94924

The marine bird populations of the Farallon Islands, California, have long been of great interest to ornithologists. In fact, the first scientific information on the status of these populations dates back to a series of publications that, in the 1850s, marked the very beginnings of modern ornithology in western North America: the *Reports, of Explorations and Surveys, to Ascertain the Most Practicable and Economic Route for a Railroad from the Mississippi River to the Pacific Ocean.* Since those *Reports*, more than 70 articles and books have been published that describe the wildlife, and mainly the birds, of the Farallones. The reasons for all the interest are readily evident. On this group of rocky islands, situated just 43 km out to sea from San Francisco, is not just the largest concentration of breeding marine birds in the United States outside of Alaska and Hawaii, but it is a diverse avifauna as well. Represented are 12 of the 16 species of marine birds known to breed on the U.S. Pacific Coast including some that are adapted to pelagic, offshore, inshore, and intertidal ways of life. The overall result of the many reports is a documentation of an avian community over a time span probably unsurpassed in the Western Hemisphere.

There has never been a complete review of the history of this community. We now present such a review with a time perspective of almost 120 years. That entire period has been marked by intense disruption of the populations by human activities on or near the islands, but in 1972 protection of the breeding grounds became nearly complete. For this reason, it now seems especially appropriate to review the populations during those 120 years. In addition to discussing the effects that human activities have had, we present hypotheses on the probable roles two major oceanographic events have played in shaping the history of the populations, one event being an extended period of unusual ocean conditions in an early time and the other being the complete disappearance of a major fish population (a prey species) in a later time.

THE FARALLON ISLANDS

The Farallones are a group of five granitic islands and associated rocks that lie at the edge of the continental shelf off Central California, due west of San Francisco (fig. 1). This paper and almost all previous reports concern South Farallon Island which, with its accompanying offshore rocks, is about 44 ha in area and is the largest of the group. The North Farallon Islands lie about 8 km NW of South Farallon, and together are probably less than 1 ha in area. Hence, the number of birds they support is small. They are practically inaccessible to humans because of their sheer cliffs. The remaining islets of the Farallon group are either continually or often awash by the sea.

METHODS

The methods used to determine present-day population sizes differed according to species. Storm-petrels were the most difficult to estimate because of their nocturnal activity and their habit of nesting in cavities within talus slopes. We estimated the Ashy Storm-Petrel (*Oceanodroma homochroa*) breeding population by computing a Lincoln index for birds mist-netted at night; where the population $(N) = Mn/m$, and M is the number originally banded and released, n is the total marked and unmarked birds caught during the recapture period, and m is the number of that total that were marked (Mosby 1963:107). A night-vision scope (on loan from the U.S. Army) allowed us to determine petrel distributions on the island and to select good mist-net locations. Petrel calls played on a tape recorder attracted birds to nets from a wide area. Immatures were separated from breeding birds by differences in incubation patch characteristics, molt, and wing lengths (unpubl. data). For the Lincoln index in 1972, M was 921 birds, m was 145, and n was 394 for the recapture period 15 July to 21 September. During the recapture period, most immature, nonbreeding birds that were marked earlier were not recaptured. They apparently did not visit the island during the late summer. This resulted in an overestimation of the breeding population since about 15% of the birds banded in 1972 (M) were immatures. Therefore we lowered the estimate from the Lincoln index by 15% to arrive at a less biased figure. To calculate the size of the breeding population for the entire island we multiplied the modified estimate by two since the area in which we netted birds in 1972 represented about half the population's distribution on the island. Although we trapped almost the same number of Ashy Storm-Petrels in 1971 (981) in the other half of their distribution, our efforts during the recapture period were neither regular nor frequent enough to attempt calculation of an estimate. There was little movement by adults between the 1971 and 1972 capture areas.

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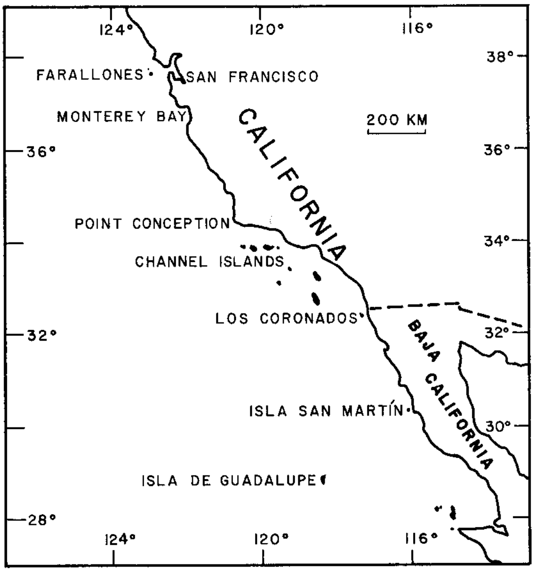

FIGURE 1. The Pacific coast of California and Baja California, showing islands and other geographic names mentioned in the text. The cold California Current moves parallel to the coast. At Point Conception it begins to swing gradually westward flowing along the western shores of the northern Channel Islands as it does so.

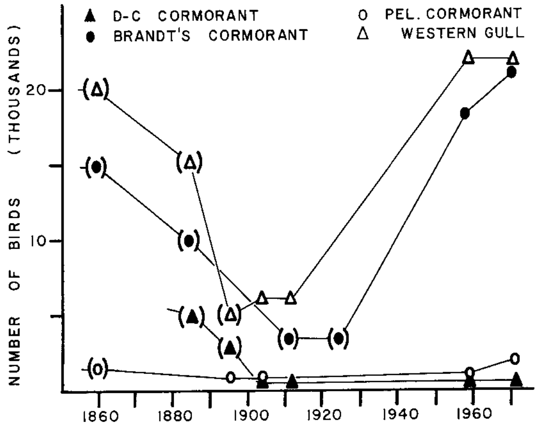

FIGURE 2. A graphic summary of the history of population changes in four marine bird species (nonalcid) on the Farallones. Symbols in parentheses estimates determined as explained in the methods. Other symbols were placed according to the information presented in the tables.

We used the same estimation technique and mist-net sites for Leach's Storm-Petrels (*O. leucorhoa*). For the Lincoln index, *M* was 378, *m* was 47, and *n* was 169. We again reduced the result by 15% to compensate for nonbreeding immatures. In the 1971 capture area, we caught only 83 birds, indicating that the species is more concentrated in the 1972 capture area. Confirming this conclusion is the fact that few Leach's Storm-Petrels could be heard calling in the 1971 area compared to the 1972 area. To arrive at an estimate for the whole island we increased the 1972 modified result by 0.25 (roughly 83/378) to include the population in the 1971 capture area.

The remaining species of breeding birds were easier to estimate. Many of our counts were made through binoculars or spotting scopes. Population sizes of Double-crested and Brandt's Cormorants (*Phalacrocorax auritus* and *P. penicillatus*) were determined by counting active nests. This was done on foot in September just after the young had fledged. Intensive observation of a colony from a blind provided criteria for judging active nests. Pelagic Cormorants (*P. pelagicus*) were counted pair-by-pair on several evenings in May during peak egg-laying. At that time all birds were present at their nests.

Black Oystercatchers (*Haematopus bachmani*) were counted on their feeding and breeding territories and when flocked together during storms. The Western Gull (*Larus occidentalis*) breeding population was estimated by dividing the island among several observers who then simultaneously made counts in their areas. This was done on 3 consecutive days in June at peak egg-hatching, with the observers taking different areas each day. The results were averaged and corrections were made to allow for fluctuation in gull numbers relative to time of day (unpubl. data).

Common Murres (*Uria aalge*) were counted bird-by-bird in their colonies. Colonies too large to count each bird were blocked off visually into groups of 50, using natural reference points whenever possible. Most counts were made from the land using a spotting scope but a few were made from a boat using binoculars. Pigeon Guillemots (*Cepphus columba*) were counted one evening in May just prior to the onset of egg-laying. At that time of year both members of each pair sit by their nest entrances in the evenings. Tufted Puffins (*Lunda cirrhata*) were counted as they sat at burrow entrances in the mornings just prior to egg-laying. Rhinoceros Auklets (*Cerorhinca monocerata*) were counted in the waters near the island in the evenings. They tended to be diurnal (!) in their nest visits, and they were counted at that time, too. Cassin's Auklet (*Ptychoramphus aleuticus*) numbers are quoted from the reports of recent detailed studies (Sibley and Robert, unpubl. data; Manuwal 1972).

Finally, figures 2 and 3 are reconstructions of the trends in populations as we have best been able to interpret them. The early reports only occasionally presented numerical records of populations but often presented rankings of species by abundance. Estimations of early population levels for the purpose of these figures and this paper were done with the few numerical data, the rankings, and the descriptions by Emerson (1904) of colony locations in various years. After about 1900, most reports included numerical estimates of populations. Figure 2 depicts population trends for nonalcids and figure 3 does the same for alcids.

RESULTS

A SUMMARY OF HUMAN ACTIVITY ON SOUTH FARALLON

Doughty (1971) has provided a useful summary of human activities. American and Russian sealers occupied South Farallon from 1807 until the end of the 1830s. They exterminated the elephant seal (*Mirounga angustirostris*), the fur seal (*Arctocephalus philippi* or *Callorhinus ursinus*), and the sea otter (*Enhydra lutris*). The sealers' impact

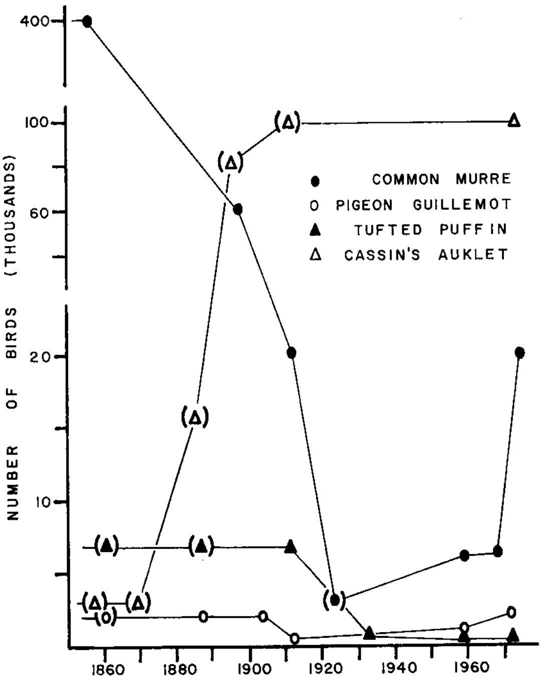

FIGURE 3. A graphic summary of the history of population changes in four alcid species on the Farallones. Placement of symbols is explained in figure 2. Note the discontinuity in the vertical scale to allow for the rather large changes in murre and auklet numbers.

on the bird populations is not known, but they did use birds and eggs for food. In 1848, eggs were taken commercially and by 1855 the "Farallon Egg Company" was founded to supply eggs to the growing human populations of Gold Rush California. The egging was carried out each year from April through June by a dozen persons. In 1881 the company was disbanded; however, fishermen and lighthouse keepers continued the egging into the early 1900s in spite of a prohibition instigated by the A.O.U. Committee on Bird Protection and declared in 1896 by the Lighthouse Board. The number of murre eggs taken in 45 years was well over 14 million. There was no regard for a sustained yield harvest, and no protection was extended to other species. Cormorants fled their nests ahead of the eggers, leaving their eggs to scavenging gulls. Gull eggs and young were stepped on in an effort to reduce the gull population and thereby to reduce competition for murre eggs.

In 1855 the first lighthouse also began operation. Until 1965 it was attended by four keepers and their families (15–20 people). The families kept dogs, cats, hogs, and a mule. During World War II, about 50 people were present to operate gun emplacements. In 1965 the U.S. Coast Guard removed families but continued with a crew of four keepers. In December 1972 the aids-to-navigation equipment was automated and the keepers were removed. Since the 1960s, helicopters have been used to transfer Coast Guard personnel or equipment to the island when boat transportation was not possible. Until 1972 these aricraft usually flew at low altitude over much of the island on each visit.

Besides disturbance of nesting by human residents, a new problem beset the avian populations in the early 1900s: oil pollution. From 1900 into the 1940s oil tankers, on their way into one of the busiest ports in the world, routinely flushed their tanks close to the island before entering San Francisco Bay. Dawson (1911) reported island shores strewn with oiled bird carcasses, and the keepers' logs often reported oil slicks with oiled murres, puffins, and cormorants as being common. During this period two major oil spills also occurred in the area. Written accounts of the 1937 incident, resulting from a wrecked tanker at the mouth of San Francisco Bay, reported thousands of alcids oiled and dead on mainland beaches. In the last two decades the bird populations have escaped major oil pollution incidents, but this has sometimes been miraculous as in 1971 (Smail et al. 1972).

In 1909, North and Middle Farallon (the large rocks located 8 and 4 km N of South Farallon) were made a National Wildlife Refuge; and in 1969 South Farallon was included. In 1972 the Bureau of Sport Fisheries and Wildlife contracted the Point Reyes Bird Observatory (PRBO) to be caretaker of the islands. In 1968 PRBO established a year round research station on South Farallon and since then one or two PRBO biologists plus assistants have been present at all times. In addition, each year scientists from other institutions have conducted their own research. Beginning in 1968, PRBO closed breeding colonies (by fairly successful persuasion) to the wanderings of resident personnel other than active researchers. Beginning in 1971, West End and several other important breeding areas were closed even to research. In 1972 PRBO removed the last domestic cat (there were five in 1967). In late 1972 a helicopter flight pattern was worked out with the Coast Guard that succeeded in reducing aircraft disturbance almost to zero. Part of the plan restricts helicopter use, except in extreme circumstances, to the period September through March when no species are breeding.

In the late 1800s Old World rabbits (*Oryctolagus cuniculus*) were introduced to

TABLE 1. The history of Leach's Storm-Petrel.

Date	Status	Source
1896	Present	Loomis 1896
1897	Present	Barlow 1897
1904	Could not find	Ray 1904
1911	Present	Dawson 1911
1959	100–200 birds	Thoresen unpubl. data
1972	ca. 1400 birds	This study

South Farallon. They compete with the larger species of burrowing alcids for nesting cavities; and their grazing results in a depauperate flora. For these reasons extermination measures are now underway, and hopefully will be completed by the end of 1973. House mice (*Mus musculus*) were introduced at some unknown time, possibly in the feed for the island mule. They have no effect on the breeding birds. Luckily, no rats are present.

BIRD POPULATIONS

The numbers of Leach's and Ashy Storm-Petrels have probably changed little over the years, but the difficulty in observing them makes this uncertain (tables 1 and 2). In fact, it was not until 1896 that Leach's Storm-Petrels were discovered on the Farallones (Loomis 1896). The petrels' pelagic feeding areas, their nocturnal island activities, and the inaccessibility of their nests—in narrow crevices and under rocks deep within stone walls and talus slopes—have undoubtedly been helpful in their avoidance of humans and domestic animals. In 1959 Thoresen (unpubl. data) estimated 3000–4000 Ashy Storm-Petrels and our estimate in 1972 is similarly about 4000 breeding birds. Thoresen estimated that 100–200 Leach's Storm-Petrels were breeding on the island in 1959; and this was our estimate in 1971. However, in 1972 we revised this estimate following discovery of a dense concentration of this species high on Lighthouse Hill. The revised estimate is 1400 breeding birds.

TABLE 2. The history of Ashy Storm-Petrel.

Date	Status	Source
1862	Present	Coues 1862
1886	Rare	Taylor 1887
1886	Seventh in abundance	Bryant 1888
1895	More than in 1885	Barlow 1897
1896	Abundant all parts of island	Loomis 1896
1904	Present	Ray 1904
1911	Second in abundance	Dawson 1911
1959	3000–4000 birds	Thoresen unpubl. data
1972	ca. 4000 birds	This study

TABLE 3. The history of Double-crested Cormorant.

Date	Status	Source
1859	Present; late egg-laying	Heermann 1859
1862	Present	Gruber 1884
1886	Present	Taylor 1887
1886	Second most abundant cormorant	Bryant 1888
1896	Not as abundant as expected	Loomis 1896
1903	At least three colonies gone	Emerson 1904
1904	Only 20 nests; all on Maintop	Ray 1904
1911	35 pair	Dawson 1911
1959	33 pair on Maintop	Thoresen unpubl. data
1972	40 pair on Maintop	This study

Both species concentrate their nesting to the southeast quarter of the island where there are areas of few or no nesting gulls (fig. 4). Up until 1965 many Ashy Storm-Petrels nested in stone walls and building foundations in that area (E. James-Veitch, unpubl. map in litt.). Since then, the Coast Guard destroyed many of these structures. In 1971 and 1972 we rebuilt a few walls to encourage return of the petrels to these areas. Coulter and Risebrough (1973) detected high pesticide levels and egg-shell thinning in Farallon Ashy Storm-Petrels, but our breeding biology studies have not yet disclosed any adverse effects of the thinning.

Three species of cormorants breed on the island: Double-crested, Brandt's, and Pelagic. Throughout the 1800s and into the early 1900s, observers found no cormorant eggs until late

TABLE 4. The history of Brandt's Cormorant.

Date	Status	Source
1859	Present; no eggs or chicks in in June	Heermann 1859
1862	Present	Gruber 1884
1886	Most numerous cormorant; 400 nests in largest colony	Taylor 1887
1886	Most numerous cormorant	Bryant 1888
1896	No chicks and few entire clutches in June	Barlow 1897
1896	In July: 1–2 eggs per nest, no chicks	Loomis 1896
1903	Two largest colonies gone; 187 nests in largest colony	Emerson 1904
1904	Most numerous cormorant	Ray 1904
1911	Most numerous cormorant; 600 birds on slope of Maintop	Dawson 1911
1924	Hundreds vs. thousands of gulls	Chaney 1924
1959	18,000–20,000 birds	Thoresen unpubl. data
1972	22,000 birds; 1000+ nests in two largest colonies	This study

TABLE 5. The history of Pelagic Cormorant.

Date	Status	Source
1859	Present; eggs, no chicks in late June	Heermann 1859
1862	Present	Gruber 1884
1886	Present; not most numerous cormorant	Taylor 1887
1886	Least numerous cormorant	Bryant 1888
1892	Least numerous cormorant	Blankinship and Keeler 1892
1896	Not as numerous as expected	Loomis 1896
1897	Least numerous cormorant	Barlow 1897
1903	At least one colony gone	Emerson 1904
1904	Largest colony of 20 nests	Ray 1904
1911	Present	Dawson 1911
1959	700–800 birds	Thoresen unpubl. data
1972	2000 birds; largest colony of 100 nests	This study

June. This is quite different from the present. In 1971 and 1972 the Double-crested began laying in March, the Brandt's in late April, and the Pelagic early May. Late laying in the past probably resulted from the intense disturbance. Cormorants are the most timid birds on the island, and will flee their nests if a human shows himself within 50–100 m. During the egging years, human activity probably kept them from their nests until after the harvest ended. They may have been either prevented from breeding early or the gulls may have eaten the early eggs. Early observers also reported unusually small clutches; perhaps as an effect of late breeding. Another expected effect of late breeding would be greater mortality of chicks and fledglings. In any case, populations declined (fig. 2).

Double-crested Cormorants once numbered in the thousands and were the second most abundant cormorant species (table 3). Emerson (1904) noted the disappearance of at least three colonies since his 1887 visit. Ray (1904) estimated a total of 70 birds all in one colony on Maintop. The size and location of that colony has remained the same; and Western Gulls now nest sparsely in the areas where other colonies once existed. Brandt's Cormorants have always been the most common cormorant, but they too experienced a great population decrease (table 4). By the turn of the century, there were only a few thousand birds, and their largest colony was 187 nests. With the end of egging they began to recover, and by 1959 we estimated 22,000 breeding birds were present in several colonies each having over 1000 nests. Finally, Pelagic Cormorants were the least abundant cormorants prior to the egging (table 5). Like the other cormorants, they were at their lowest numbers by the end of egging when at most only a few hundred birds were present. They then began to increase in numbers very slowly so that by 1959, Thoresen counted 700–800 birds. Since then, they have increased further to 1000 individuals. In some areas they are still increasing.

TABLE 6. The history of Black Oystercatcher.

Date	Status	Source
1859	One breeding pair in June	Heermann 1859
1862	Not reported	Gruber 1884
1903	A few present, not breeding	Kaeding 1903
1944	No longer breeding	Grinnell and Miller 1944
1956	Two seen in spring	Cogswell and Stallcup 1956
1956	Eight seen in October	Craig and Cogswell 1956
1959	16 present May to August	Thoresen unpubl. data
1972	52 present, including 20 breeding pair	This study

The Black Oystercatcher has had an interesting history on the island (table 6). It disappeared in the 1860s, probably as a result of too much disturbance from humans and domestic animals. From our experience, eggs and newly hatched chicks are easy prey for gulls if adults are kept long from their nests. Other than a few birds present in 1903, but not included in a list of breeding species, they were next reported in 1956. The observers at that time (Cogswell and Stallcup 1956; Craig and Cogswell 1956) apparently did not realize the significance of their records. The species increased to 16 birds by 1959, and they now number 52 with 20 breeding pairs. Unless present feeding territories can be further compressed, the breeding population has perhaps reached maximum.

Western Gulls had also declined to their lowest numbers at the turn of the century (table 7). This was probably the result of disturbance from humans and domestic animals but more so from the extermination measures of the eggers. In 1904 Emerson reported their disappearance from five areas since his 1887 visit. In 1903 they nested mostly on inaccessible cliff ledges, not the optimal habitat for this species. In 1911 Dawson estimated 6000 gulls present, which may have been an increase from a few years earlier. Since then, their numbers have increased further. By 1959, 23,000 breeding gulls were present and the number of breeding birds has remained at that level. They are perhaps more numerous now than ever before due to increased

TABLE 7. The history of Western Gull.

Date	Status	Source
1859	Present	Heermann 1859
1862	Second most numerous species	Gruber 1884
1886	Second most numerous	Taylor 1887
1886	Nest in colonies of 10 pair	Bryant 1888
1895	Breed on flat at West End	Barlow 1897
1896	Downy young and well-incubated eggs 8–16 July	Loomis 1896
1903	Gone from five colonies	Emerson 1904
1904	Breed on West End and a few other places	Ray 1904
1911	6000 birds	Dawson 1911
1959	22,000–23,000 birds	Thoresen unpubl. data
1972	23,000 birds	This study

survival in the winter resulting from new food sources in the form of garbage and fish offal, and due to the availability of nesting habitat once occupied by fur seals. At present there seems to be a growing surplus population, now about 1000 adult plumaged birds, that form several "clubs."

In the 1850s Common Murres numbered about 400,000 birds (fig. 3; table 8). This estimate is based on the number of eggs taken then in a single year (Hutchings 1856), and the fact that a female can lay only two (often fewer) replacement clutches (Tuck 1960). By the end of egging just after 1900, they had been reduced to 60,000 birds, and with the advent of oil pollution, they began to decline further. In 1959 there were only 6000 murres. Since then, they have escaped major oil slicks and have enjoyed increasing protection from human disturbance. A noticeable increase in their numbers has resulted, with 20,500 birds currently present, and they continue to increase rapidly. Gress et al. (1971) discovered shell-thinning in murre eggs on the Farallones, but our studies of their breeding biology have not yet revealed detrimental effects.

TABLE 8. This history of Common Murre.

Date	Status	Source
1854	ca. 400,000 birds	Nordhoff 1874
1856	Myriads; on every peak	Hutchings 1856
1859	Countless numbers	Heermann 1859
1862	Most numerous species	Gruber 1884
1886	Most numerous species	Taylor 1887
1886	Outnumbers all others combined	Bryant 1888
1895	Most numerous species	Barlow 1897
1896	60,600 birds; only in inaccessible places	Loomis 1896
1903	Gone from some areas; reduced elsewhere	Emerson 1904
1904	Outnumbers all others combined	Ray 1904
1911	20,000 birds	Dawson 1924
1923	Counted by tens vs. gulls by thousands	Chaney 1924
1959	6000–7000 birds	Thoresen unpubl. data
1972	20,500 birds	This study

TABLE 9. The history of Tufted Puffin.

Date	Status	Source
1856	Numerous	Hutchings 1856
1859	Present	Heermann 1859
1862	Present	Gruber 1884
1886	Rather common	Taylor 1887
1886	Fifth most numerous species; 50 easily accessible nests	Bryant 1888
1895	A veritable rookery on West End	Barlow 1897
1896	Second most numerous diurnal bird	Loomis 1896
1903	Status unchanged from 1887; many West End and main island	Emerson 1904
1904	Many West End and main island; saw 43 at one time	Ray 1904
1911	Several thousand	Dawson 1911
1933	300 birds	Smith 1934
1959	26 birds	Thoresen unpubl. data
1972	50–60 birds entire island	This study

In contrast to the murres, Tufted Puffins apparently declined little if any during the egging years (table 9). They were protected by their deep nest cavities and a reputation for giving painful bites. With the arrival of oil pollution, however, their numbers dropped suddenly from an estimated several thousand in 1911 to 300 by 1933. In the last 15 years, at least, their numbers have been stable at 50–60 birds. The Pigeon Guillemot, another burrow-nesting alcid, also was apparently unaffected by the earlier disturbance and began to decline only after the coming of oil

TABLE 10. The history of Pigeon Guillemot.

Date	Status	Source
1859	Present	Heermann 1859
1862	Present	Gruber 1884
1886	Present	Bryant 1888
1895	Present	Barlow 1897
1896	Common	Loomis 1896
1903	Gone from one area; same elsewhere as in 1887	Emerson 1904
1904	Present	Ray 1904
1911	about 200 birds	Dawson 1911
1959	750–1000 birds	Thoresen unpubl. data
1972	2000 birds; nest in same areas as in 1903	This study

TABLE 11. The history of Rhinoceros Auklet.

Date	Status	Source
1859	Present and breeding	Heermann 1859
1862	Breeding; rarest species	Gruber 1884
1927	No longer breeding; disappeared in 1860s	Grinnell 1926
1971	Four to five birds present spring and summer; possible breeder	This study
1972	Two to three pair; probable breeder	This study

TABLE 12. The history of Cassin's Auklet.

Date	Status	Source
1859	Present in winter but not summer	Heermann 1859
1862	Rare; present in winter	Gruber 1884
1886	Present and breeding	Taylor 1887
1895	Common; on all parts of the island	Barlow 1897
1896	Abundant	Loomis 1896
1903	Same as in 1887	Emerson 1904
1904	Abundant; thousands	Ray 1904
1911	Most abundant species; 100,000–200,000 birds	Dawson 1911
1971	105,000–120,000 birds	Manuwal 1972 Sibley and Robert unpubl. data

pollution (table 10). Emerson (1904) noted the disappearance of only one small colony since his 1887 visit and added that the status of this bird had changed little. Pigeon Guillemots were common and, as mapped, nested in the same areas where they nest today (see below). By 1911, however, Dawson counted only 200 birds, indicating that a sudden decline in numbers had occurred during the first decade of the 1900s. After the oil pollution lessened, they began to increase. By 1959 the population had reached 1000 birds. Since then, they have increased further to number about 2000 birds at present, and they again nest in the areas described by Emerson for 1887 and 1903. Their population is probably close to maximum since most suitable crevices are now occupied except in the immediate vicinity of the human quarters. The population of rabbits introduced in the late 1800s will hopefully soon be removed with one intended result being to release a few more nesting cavities for guillemots and puffins.

A fourth alcid, the Rhinoceros Auklet, disappeared in the early 1860s (table 11). Only a few pairs were present then, and after several birds were collected over 3 years, few if any remained (Grinnell 1926). In 1971 these auklets were present and if they did not breed, they at least scouted the island a great deal. In 1972 at least two burrows and possibly a third were used by pairs daily from May through July. They entered and departed from their burrows, to our surprise, during all daylight hours. We did not check for eggs for fear of disturbing thousands of murres and cormorants nesting near by.

The last species to be discussed, Cassin's Auklet, is easily the most abundant breeding species with present day estimates (table 12) ranging from 105,000 (Manuwal 1972) to 120,000 birds (Sibley and Robert, unpubl. data). Many extensive areas of the island surface are densely pocketed with their burrows. At night the noise of the combined singing of the total population is so loud that it can prevent sleep. The birds occupy their burrows throughout the year. They are now so ubiquitous that their history as reported is almost unbelievable. In the 1850s and 1860s they were rare and present only in the winter according to the same persons who reported nocturnal Rhinoceros Auklets and storm-petrels. By the 1880s they were common and breeding, and by the 1890s they were abundant. In 1911 Dawson estimated 100,000–200,000 birds which includes the range of present estimates. At the least, a great change in numbers occurred during the 1800s, but its exact extent is not known. The probable cause for the change is discussed later.

CHANGES IN NESTING DISTRIBUTIONS

Coincident with changes in population sizes in the past 90 years, changes have occurred in colony distributions on South Farallon. Emerson (1904) published a map comparing distributions in 1887 with those in 1903. He mainly noted many disappearances of whole colonies and reductions in others. The map later published by Bowman (1961) showed that many of the lost colonies had returned by 1958. In 1972 we again mapped breeding colonies, and shown in figure 4 are the nesting distributions for three species compared to 1958.

Common Murres have been displacing gulls and Brandt's Cormorants, and in their turn Brandt's Cormorants have been displacing gulls. Murres have displaced the much larger species through (1) their rapid expansion in numbers; (2) the expansion of their dense colonies outward from the centers (they nest shoulder-to-shoulder); and (3) their arrival to claim territories a full month before the gulls and 5 months before the cormorants (unpubl. data). The cormorants displace gulls

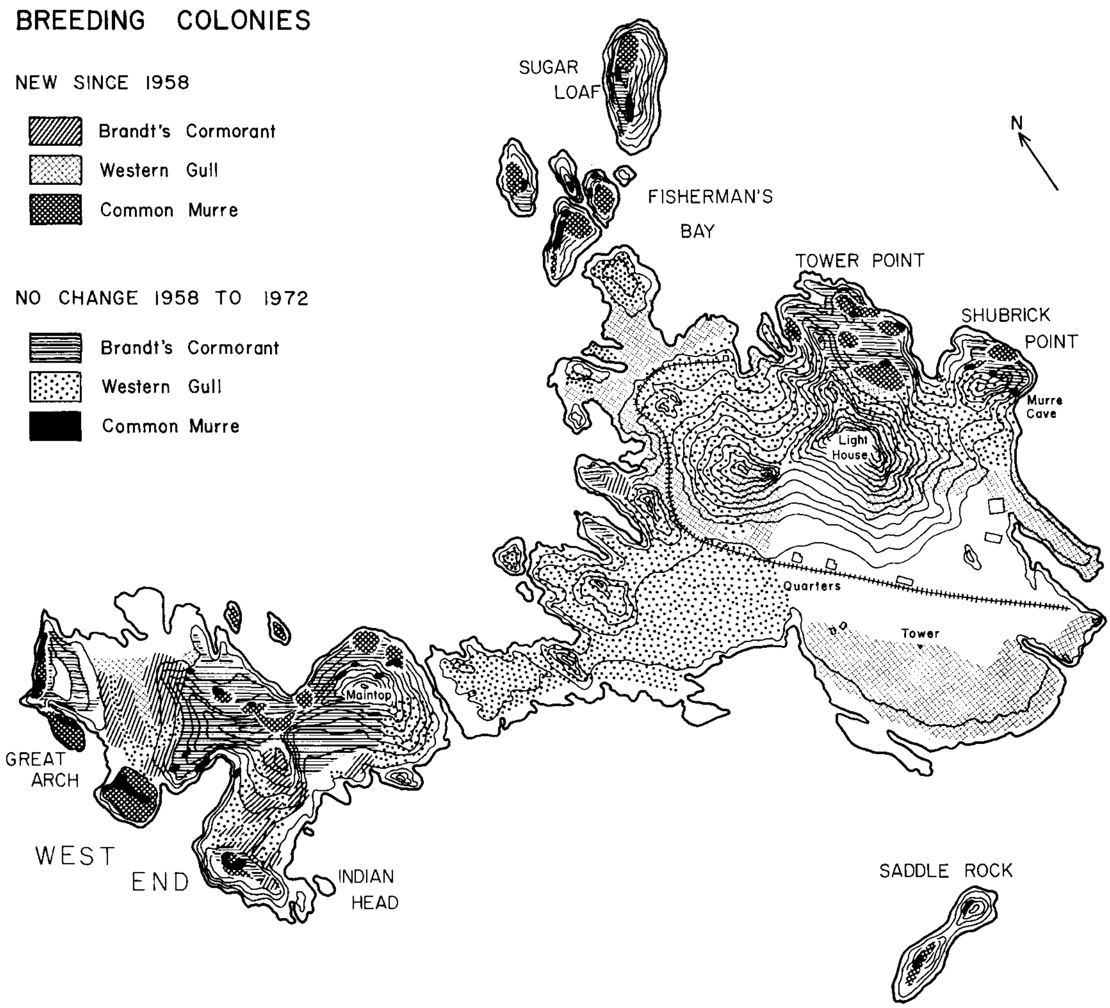

FIGURE 4. The changes in nesting distributions between 1958 and 1972 for three species of marine birds on South Farallon. The distributions for 1958 were drawn after Bowman (1961). Also shown are the areas on the island mentioned in the text and in the tables.

through (1) their denser nesting colonies (i.e., cormorants are spaced no more than pecking distance apart but gulls are usually 2–3 m apart); and (2) their sheer size advantage: many gulls nesting adjacent to cormorant colonies stand aside squawking as they lose their nests to cormorants searching for nest material. Earlier in the season, cormorants bodily displace gulls that attempt to claim territories in cormorant nesting areas. In contrast to these trends, murres have not displaced the smaller Pelagic Cormorants, the other species requiring cliff ledges for nest sites. Pelagic Cormorants are resident the year round and, on cliffs where they and murres nest, they have already occupied their sites when murres arrive. The displaced gulls have been re-establishing nests in areas close to human dwellings, and are the only birds willing to do this. Some have been forced to nest once again on cliff ledges.

DISCUSSION

During the last 120 years, the populations of five marine bird species on the Farallones have changed in the same way: decline in numbers during the last half of the 1800s or during the first decades of the 1900s, and then recovery or approach toward recovery in more recent years (figs. 2 and 3). In extreme cases of this pattern, two other species completely disappeared and later returned. The factors shaping these patterns have been evident: prolonged low reproductive success due to disruption of nesting by human activities or prolonged high mortality from oil pollution as the causes of the declines; and then significant lessening of these stresses allowing for recovery. Not including the storm petrels whose populations have changed little, three species have exhibited patterns that differ from the one just summarized. In one case, Cassin's Auklets increased rapidly in number during the late 1800s and have since remained in high numbers (fig. 3); and in the other case, Double-crested Cormorant (fig. 2) and Tufted Puffin (fig. 3) populations declined due to disturbance and oil pollution, but unlike the other species, they have not recovered nor have they even begun to do so. Rather, they have remained stable at low numbers for many years. In the following two sections we present hypotheses to explain the last two patterns, and in the concluding section we comment on the pattern exhibited by the storm petrels.

CASSIN'S AUKLET POPULATION CHANGES

The most plausible explanation for the increased auklet population in the mid-1800s relates the change to an extended period of more than two decades when warm tropical waters moved unusually far north along the California coast. However, some discussion of warm-water periods and the oceanographic conditions of central California waters is required before a link to auklet population changes is suggested.

The annual pattern of currents off California is reviewed by Sverdrup et al. (1942). In brief, the cold, nutrient-rich waters of the California Current move south along the coast in a sluggish flow 560 km wide. The current displaces the warm, subtropical, nutrient-depleted oceanic waters that would otherwise be present. The colder waters along the coast usually reach a little beyond Point Conception (34°N), south of which they swing westward and the warming effects of the tropical waters become increasingly stronger (see fig. 1 for geographic locations). During the spring and early summer, strong prevailing northwest winds help to move the current south at full strength, and at the same time produce significant upwelling of cold, nutrient-rich waters in several places along the edge of the continent. The cold temperatures of the current are thus maintained. In the late summer and fall, the northwest winds cease or subside, causing a reduction in the strength of the current and the upwelling. As a result, warm oceanic water moves coastward and a warm, northward-flowing counter-current appears. From time to time since the early 1800s (and earlier: Hubbs 1948), circulation in the California Current has become altered with the result that especially warm waters moved unusually far north (to 37°N and beyond) for extended periods, i.e., longer than just the fall.

Hubbs (1948) presented convincing data for an intensive northward intrusion of warm waters for the unusually extended period of 1853, or earlier, to the 1870s. Exactly when the period began is not known because few data exist prior to 1853, when the Pacific Railroad Surveys began. Hubbs' data consisted of temperature records and records of warm-water animals much farther north than recorded since. Many of these organisms were notably sessile and thus required an extended period of warm water to move north. The existence of the warm-water period has since been confirmed by Robinson (1965).

The occurrence of warm waters as far north as Monterey Bay (36.7°N) was strikingly apparent during the mid-1800s, but strong intrusion to the San Francisco-Farallones area (37.7°N; only 150 km farther) was not so obvious because data both for and against this was in evidence. Since Hubbs' paper appeared, however, additional faunal records have been discovered to indicate that warm waters did affect the ocean as far as 37.7°N. First, Orr (1963) reported the skull of a tropical dolphin (*Tursiops gillii*) from San Francisco Bay, and he estimated that the individual probably died 50–100 years earlier. This probably places it well within the mid-1800s warm-water period and suggests the presence of warm water in that area. The only other verifiable record of that species north of the San Diego area is one for Monterey Bay in 1873, during the warm-water period (Banks and Brownell 1969). Second, the skull of a frigatebird (*Fregata magnificans*) was found on the Farallones in 1861 (Bryant 1888). Normally restricted to tropical waters, this species has been recorded to 37.7°N or beyond on the West Coast in only 3 other years: 1888 and 1905 (Grinnell and Miller 1944), both warm-water years (Robinson 1965), and in 1972 (DeSante et al. 1972), another warm-water year (see below). Usually, this species reaches only as far north as the San Diego area, and thus the 1861 frigatebird record for the Farallones indicates an unusually strong northward movement of warm water. Third, in 1859 during the warm-water period, the Pelagic Red Crab (*Pleuroncodes planipes*), a species normally found south of 28°N (central Baja California; Boyd 1967), was reported, and first described, in Monterey Bay. This organism was next recorded there during the years 1957–60 (Glynn 1961) when warm waters moved well north of the Farallones (Radovich 1961); and its third and latest occurrence in Monterey Bay was during the winter of 1972–73 (Baldridge, pers. comm.), when warm water again affected the ocean as far as 37.7°N (see below). Longhurst (1967) related that *Pleuroncodes* may not reach Monterey Bay with the warm waters per se but through the unusual current conditions that also bring significant intrusion of warm water. Finally, as referred to above, 1972 was indeed a year of significant warm waters in California. Dozens of warm-water fishes—especially scombrids and jacks—showed up in southern California during 1972 and 1973, but it is not known how much farther north many actually moved (Fitch, pers. comm.). Some, to be sure, did move at least as far as Point Reyes (35 km N of the Farallones), Pacific Bonito (*Sarda chiliensis*) being one example (Whitt and Ainley, pers. catch). Also indicating warm-water conditions in 1972 to be of strength similar to the mid-1800s were the pelagic crab and frigatebird records mentioned above.

How do similarities among three warm-water periods in central California relate to Farallon Cassin's Auklet populations? During the two most recent warm-water periods, auklet breeding productivity on the Farallones was lower than during years of colder sea temperatures. In 1959, the third year of a warm-water period, Thoresen (1964) recorded 0.27 chicks fledged per breeding pair (75 nests studied); and in 1972, another warm-water year, we recorded 0.58 chicks per pair (69 nests). In contrast, during 2 years of colder sea temperatures, 1970 and 1971, Manuwal (1972) recorded 0.71 and 0.62 chicks per breeding pair (234 and 201 nests). The differences are significant (Sokal and Rohlf 1969: 608) between breeding success in 1959 and each of the other years ($P < 0.001$), and between 1972 and 1970 ($P < 0.05$); but are not significant between 1972 and 1971 ($P > 0.05$) nor between 1970 and 1971 ($P = 0.05$).

The observed decrease in auklet productivity could result from reduced food resources during warm-water conditions. Auklets of the Farallones feed on zooplankton, and mostly euphausiids (Manuwal 1972). Warm tropical waters in the southern part of the California Current have 100 times less the biomass of zooplankton, and particularly euphausiids, than do the subarctic waters of the northern part (Aron 1960). This gradient occurs from Vancouver (48°N) to San Diego (32°N) as the influence of tropical waters increases. Additionally, the reduction in northwest winds during warm-water years results in reduced upwelling of cold, nutrient-rich waters and a further decline in productivity (Sverdrup et al. 1942). Thus an extended period of warm water and decreased food resources in the mid-1800s with resultant prolonged suboptimal production of young auklets should have resulted in a reduced population. The auklets began to increase in the 1870s, the time when the cold waters returned to the region, and by similar timing of these two events, this further links low auklet numbers in the mid-1800s to warm-water conditions. The increase in auklet numbers after the 1870s may have been a return to population levels existing prior to the warm-water period. This Banks and Brownell (1969) hypothesized for changes in dolphin distributions in the same ocean region during the return of the colder waters. They also suggested that the changes resulted from alterations in the distribution of the dolphins' prey (fish). However, for Cassin's Auklets a change in availability of food resources seems more likely since they breed on islands in warmer waters off Baja California (AOU 1957) and thus suitable prey species must be present in warmer waters.

How other Farallon marine birds were affected by the warm waters of the 1800s is not known. During the warm-water years of 1972 and 1973, most species were affected in various ways, generally to result in reduced productivity. Some were able to adapt somewhat by altering their patterns of resource exploitation, but that is an involved subject to be discussed in a future report. At the least, the added environmental stress of warm-water conditions in the mid-1800s may have rendered the birds particularly susceptible to the disturbance occurring at that time.

Another explanation for the auklet population increase relates the change to increased food availability resulting from the decrease in other Farallon wildlife. This can be ruled out since no other Farallon animals compete with the auklets for food to an appreciable degree (unpubl. data). Increased availability of nest sites due to a decrease in other species can also be ruled out, because abundant rock cavities exist that larger cavity nesters (guillemots and puffins) cannot use, and in any case, the auklets became abundant 20 years before potential nest-site competitors began to decline in number.

RECOVERY FAILURE IN DOUBLE-CRESTED CORMORANTS AND TUFTED PUFFINS

Contrasting with most other Farallon marine bird populations, Double-crested Cormorants and Tufted Puffins have failed to recover from decimation. The pattern exhibited by these two species (i.e., decline in numbers and then failure to repopulate) is not confined to the Farallon populations, however, and in addition, it is exhibited by a marine mammal of

California. Furthermore, an explanation of this pattern must account for the opposite trend in populations of some ecologically similar species. An hypothesis we wish to present relates the patterns of change in these California populations of several marine birds and mammals to the demise of the Pacific Sardine (*Sardinops caerulea*) in the California Current. The loss of the immense sardine populations was a major event in the offshore waters of California and Baja California. Such a loss should have had much broader implications than simply the disappearance of the largest human fishery in the Western Hemisphere from the 1920s through the 1940s.

First, the Double-crested Cormorant colonies south of the Farallones on the Channel Islands and on the islands off the west coast of northern Baja California have all declined since the 1920s and 1930s (Gress et al. 1973). On Los Coronados, Huey (*in* Gress et al. 1973) attributed population reductions during that time to activities of tourists; but no explanation has been offered for the decline in the immense populations farther south on Isla San Martín, and so far as known, yet farther south no apparent changes have occurred. Since 1945, populations on Los Coronados and the Channel Islands have been affected by DDT contamination (Gress et al. 1973), but not so on the Farallones (PRBO unpubl.) nor on San Martín (Gress et al. 1973). The overall pattern, then, for this species from the Farallones to Isla San Martín (northern Baja) is one of initial decimation, due in most cases to human activity, and then failure to recover.

Second, the Tufted Puffin, a species not affected much by direct human disturbance, was a common resident during the early 1900s in the northern Channel Islands (Wheelock 1904; Howell 1917). At least one of these islands is now barren of breeding puffins (Banks 1966), and if they still breed on the others, then their numbers are few (Small 1960). Tufted Puffins have also disappeared from Point Reyes (Ainley, pers. obs.). Thus, the pattern shown by the Farallon population is the same in the entire southern part of the species' range.

Third, in the northern Channel Islands the population of Steller's Sea Lion (*Eumatopias jubatus*) began a sharp decline in the 1940s that has continued to the present: from 2000 animals in 1938 to about 35 now (Bartholomew and Boolootian 1960; Odell 1971; R. DeLong, pers. comm.). These islands are at the southern extreme of this species' range, and, in fact, the breeding ranges of this sea lion and the Tufted Puffin are identical (Udvardy 1963). The Double-crested Cormorant breeds well into the north (northwest Alaska), but it also breeds farther south than these other species (AOU 1957).

In contrast to the above three species, in the same period and region, two other pinniped species and a bird have been increasing as recoveries from former decimations. The California Sea Lion (*Zalophus californianus*) breeding population of the Channel Islands increased logarithmically from 700 animals in the 1930s to almost 20,000 by the late 1950s (Bartholomew and Boolootian 1960) and have since stabilized at the last figure (Odell 1971; R. DeLong, pers. comm.). These islands (San Miguel) are the northernmost breeding area of this species. Similarly, the Northern Elephant Seal (*Mirounga angustirostris*) has been re-establishing its former breeding colonies since the 1940s. The island-by-island recolonization has moved northward from a remnant population of Isla de Guadalupe to the Farallones (Le Boeuf et al. 1974). The total population is now over 30,000 animals (Peterson and Le Boeuf 1969). Finally, the Rhinoceros Auklet, which recently re-established itself on the Farallones, has in the last 15 years established populations on other islands from British Columbia down to northern California (Scott et al., unpubl. data). This species does not breed as far north as the puffin and cormorant (AOU 1957; Udvardy 1963), but it is increasing where these others are not.

In summary, since the period 1920–40 in the region from central California to northern Baja California, the Double-crested Cormorant, Tufted Puffin, and Steller's Sea Lion populations have declined or have failed to recover from former decimation, while the Rhinoceros Auklet, California Sea Lion, and Elephant Seal populations have increased or recovered rapidly. These changes, with the possible exception of the cormorant, suggest a long-term amelioration in marine climate along the Pacific Coast. However, data on marine climate do not support this (Hubbs 1960; Robinson 1965), and neither does the recent colonization of San Miguel Island by a fur seal (*Callorhinus ursinus*) otherwise restricted to the Bering Sea (Peterson et al. 1968). In fact, since the early 1940s, ocean temperatures in the area being discussed have been colder than the few decades preceding the 1940s, with the exception of the warm-water periods mentioned previously. In the background of these faunal changes is the loss during the 1940s of the sardine population formerly centered in the same geographic region. It would be surprising if such a loss passed without other faunal repercussions, particularly to predator populations in the extremes of their respective species' ranges (cormorant excepted) where a species should be most sensitive to the ecological balance.

During the 1930s and 1940s, Pacific Sardines supported the largest human fishery in the Western Hemisphere, with its center in central California from about San Francisco to Monterey. The total fishery extended from the Pacific Northwest to central Baja California, and at its peak in the early 1940s the catch ranged up to 800,000 tons or more. A spectacular decline then began in the sardine stocks, with a simultaneous southward contraction of the population. The decline was probably a result of overfishing at a time of additional environmental stress—an extended period of cold water. By 1945, the sardine had all but disappeared from the Pacific Northwest and had become a vestige of its former abundance in central California; by 1951, it was virtually gone north of Point Conception; and now the population is centered off southern and central Baja California. As might be expected, an ecologically equivalent species, the Northern Anchovy (*Engraulis mordax*), responded to the resources vacated by the sardine. Anchovies had always been more abundant than sardines in the region, but in the last 20 years they have staged a population explosion. This has occurred, however, almost entirely in the region south of Point Conception. Both species are mid-water schooling fishes having similar life histories, ecologies, and distributions. An important difference is that the mature sardine is almost twice the size of the anchovy, adult lengths being about 38 cm and 20 cm, respectively. It was mostly the older, larger sardines that occurred off central California and farther north. This review of the recent history of sardines and anchovies was summarized from the following reports: Marine Research Committee 1952, 1953; Clark and Marr 1955; Marr 1960; Sette 1960; Ahlstrom 1966; Frey 1971; Vrooman and Smith 1971.

How might the loss of the sardine affect the populations of marine birds and mammals under discussion? Some evidence suggests that those species declining or not recovering fed on sardines to a greater degree than did those that are increasing. First, a large body of literature shows that larger predators feed on larger prey than their smaller competitors, and in that way among others, resources are partitioned (see reviews by Selander 1966; MacArthur and Levins 1969). Specifically, cormorants (Pearson 1971), puffins (including Rhinoceros Auklet; Bedard 1969), and otariids (sea lions and fur seals; Spalding 1964; Jones 1974) do divide up food resources partly in this way. It so happens that in the region under discussion, the Double-crested Cormorant is the largest cormorant (Palmer 1962; Ainley pers. obs.), the Tufted Puffin is the larger puffin (Bedard 1969), and Steller's Sea Lion is the largest otariid, while the Northern Fur Seal is the smallest (Scheffer 1969). These larger predators should have been able to exploit the larger sardine to a greater degree than could the smaller predators. Second, information on diets show, in fact, a greater use of sardines in the past by the larger animals. Double-crested Cormorants fed heavily on sardines in northern Baja (Wright 1913), and thus probably also in central California. The other cormorants did not feed much on sardines in earlier days (Loomis 1895; Bent 1922), and today they feed mostly on deep-water and benthic fish but they also take some anchovies (Hubbs et al. 1970; Ainley and Fitch, unpubl. data). Rhinoceros Auklets fed on small sardines to an unknown degree when wintering in southern California (Linton 1908); however, we know nothing of their food habits in central California today. In Washington, they prefer Sand Launce (*Ammodytes*; Richardson 1961), a species of anchovy size not common in central California, and they also feed heavily on anchovies and smelt (*Hypomesus*; Cody 1973), another anchovy-sized fish. The Steller's Sea Lion in early years fed on sardines to an unknown degree (Pike 1958), but other than being noted once in association with a school of sardines, California Sea Lions are not known to have fed on them. More importantly, the California Sea Lion, in contrast to the Steller's, feeds heavily on cephalopods (reviewed by Jones 1974), and thus the loss of sardines would not have been as important to them as to the Steller's. The Elephant Seal is specialized as a benthic or epibenthic feeder (Morejohn and Blatz 1970), and the Northern Fur Seal in central California feeds mostly on anchovies, hake (*Merluccius*), and cephalopods (North Pacific Fur Seal Commission 1969), making the loss of sardines of little direct importance to these two predators.

Two lines of evidence, a predator-size/prey-size relationship and information on diet, suggest that in the region from central California south to northern Baja California, the once abundant sardine was a more important food to certain larger members of some predator groups—cormorants, puffins and otariids—

than to those species' smaller ecological competitors. This loss, then, might have been important enough to have, at least in part, lessened the suitability of the region to the larger predators from what it was prior to the sardine's disappearance, or the loss might have given relatively greater competitive advantage to the smaller predators. Thus in marked contrast to the smaller species, the Double-crested Cormorant (also a victim of pesticides in part of the region during recent years), the Tufted Puffin, and the Steller's Sea Lion have declined or have failed to recover from decimations incurred just prior to the loss of sardines. The pattern of population change in Double-crested Cormorants and Tufted Puffins on the Farallones is part of this situation.

SUMMARY AND CONCLUSIONS

With satisfaction, we report increasing or stable populations of marine birds on the Farallon Islands, an uncommon story in many parts of today's world and even for the islands themselves during the 1800s and first half of the 1900s. Disruptive human activities from 1850 to well into the 1900s, resulting from an egging industry and operation of a four-family lighthouse station, caused sharp population loss in breeding Double-crested, Brandt's, and Pelagic Cormorants, Black Oystercatchers, Western Gulls, and Common Murres. With the end of egging, the Brandt's and Pelagic Cormorants, the oystercatchers, and the gulls began to recover; and with full protection in recent years they now have done so fully. Double-crested Cormorants have never recovered but have remained stable, and this, we hypothesize, is due at least in part to the loss of an important prey fish, the sardine. Collections of specimens around 1860 eliminated Rhinoceros Auklets from the island, but in 1972 they showed signs of recolonization.

Oil pollution caused sharp declines in the populations of Tufted Puffins and Pigeon Guillemots, both of which were not affected by human activities, beginning just after 1900, and it caused further declines in the murre population. With a lessening of the pollution in the last 20 years and with full protection at the Farallones, the murres and guillemots have been increasing. Tufted Puffins have never recovered their former numbers, and we relate this to the loss of the sardines, too. The future, however, is tenuous for all alcid populations on the Farallones. The islands are in the midst of one of the world's busiest shipping lanes, and in the region where large refineries are located, preparations are now under way to provide for the increased oil tanker traffic resulting from the exploitation of the Alaska oil fields. The existence of the populations of large alcids, including the Rhinoceros Auklet, on the Farallones depends upon the extent of the expected coincident increase in oil pollution.

Only those Farallon species "pre-adapted" to avoid contact with humans have not thus far been adversely affected by them. These species are the most pelagic, are nocturnal in their island activities, and nest in inaccessible burrows; namely, Leach's and Ashy Storm-Petrels and Cassin's Auklets. We hypothesized that an extended mid-1800 warm-water period caused a prolonged reduction in reproductive success in the auklets. This in turn resulted in population decline, and the recorded population increase from 1870 to 1890 was a response to the return of colder, more productive waters.

If the continued existence of marine birds is desirable near areas of intense human activity, as is the case for the Farallones, the need for protecting them from direct or indirect contact with that activity is well illustrated in the history of the Farallon populations. That full protection is the means to this end is amply demonstrated by the results of protection given in recent years to the Farallones.

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