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Population Trends

SEABIRD POPULATION TRENDS ALONG THE WEST COAST OF NORTH AMERICA: CAUSES AND THE EXTENT OF REGIONAL CONCORDANCE

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Abstract. We compared trends in breeding population size among cormorants, gulls, alcids, and others, among the Farallon Islands, and sites in northern California and Washington, Gulf of Alaska, and Bering Sea, but in most cases only during the last two decades. For a given species, trends were usually concordant within the same oceanographic domain, except for the Rhinoceros Auklet which increased across all domains in its northeastern Pacific range. Overall, humans and their domestic animals have had severe negative impacts to individual islands, but recent restoration efforts have had spectacular results. On the other hand, the California Current and the eastern Bering Sea now seem unable to support historic populations of natural, top-trophic predators. The major factor responsible appears to be overfishing by humans of important seabird prey, especially, in a period when climate has been unstable. Notable trends indicating these general patterns were as follows: 1) The Ashy Storm-Petrel on the Farallon Islands, where 80% of this species breeds, may have decreased in response to the increase of gulls in the storm-petrel breeding habitat. 2) Brandt's and Pelagic cormorants in the central California Current declined radically owing to El Niño and anthropogenic factors in the early 1980s, and have since failed to recover, contrary to trends in the 1970s; farther north, populations fluctuated slightly but at low levels during this period. 3) Large *Larus* gulls have increased. 4) Common Murres in the central and northern portions of the California Current exhibited a marked decline during the early 1980s and have since failed to recover. 5) Most Common Murre populations in the Gulf of Alaska appear to be stable; whereas those in the eastern Bering Sea are decreasing. 6) Rhinoceros Auklet has increased throughout its range and has (re-)colonized new sites in the southern portion of it. 7) Tufted Puffin has ceased recovery in the California Current, but in Alaska it has continued to recover from former negative, anthropogenic impacts. 8) Cassin's Auklet has declined in the central California Current region.

Key Words: Alaska; California; climate stability; ecological scale; feral animals; Oregon; population trends; resource depletion; seabirds; Washington.

A review of trends in seabird populations of western North America is a difficult task due to the paucity of information. On the one hand, the avifaunal richness of the Farallon Islands, California, in close proximity to the large metropolis of San Francisco, has attracted the attention of ornithologists for over 100 years. Consequently, much is known of population trends for several species there since the 1850s (Ainley and Lewis 1974, Ainley and Boekelheide 1990). Because the Farallon populations contributed the majority of breeding birds to the marine avifauna of the central California Current, and to a lesser extent still do, their history takes on regional significance. On the other hand, such an historical perspective for a seabird fauna has few equals in western North America (Nisbet 1989, Wooller et al. 1992). Comparable is the information available for the Brown Pelican (*Pelecanus occidentalis*) in southern California, where long-term censusing and research has documented recent population growth (summarized in Ainley and Hunt 1991). Thus, comparison of seabird population trends elsewhere along the West Coast is difficult, at best, except for data collected during the past 20 years and discussed herein.

We will use the Farallon data as a focal point by first updating by ten years the information in Ainley and Boekelheide (1990) and by then making comparisons with populations of similar species in Northern California/Oregon, Washington, the Gulf of Alaska and Alaskan coast of the Bering Sea

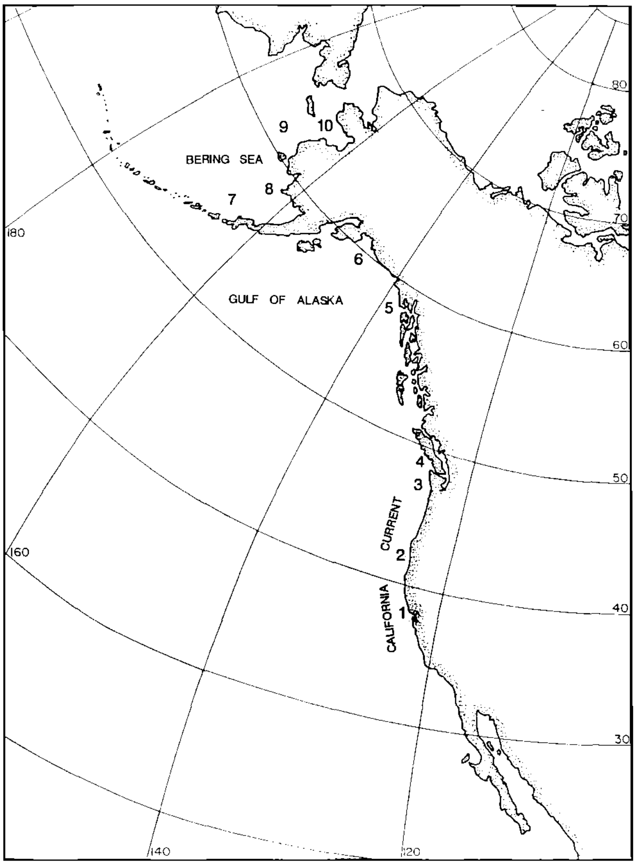

FIGURE 1. Map of the northeastern Pacific Ocean and Bering Sea showing localities discussed in the text: 1, Farallon Islands; 2, Islands near California/Oregon border; 3, Outer coast islands in Washington; 4, Islands in the Strait of Juan de Fuca; 5, Forrester Island; 6, Middleton Island; 7, St. Paul and St. George islands; 8, Cape Peirce; 9, St. Matthew Island; 10, Bluff, Alaska.

(Fig. 1). Besides the review itself, another goal is to determine the degree and geographic scale of concordance in trends among sites and regions. If trends agree above the coarse or local scale, patterns may indicate responses to climate change or other large-scale factors. We will not elaborate on census methods, except as described in figure captions; interested readers may consult the original studies. The changing status of the Double-crested Cormorant (*Phalacrocorax auritus*) is being reviewed elsewhere by H. Carter and collaborators. In addition, the trends and status of this and several other species have been detailed recently in Vermeer et al. (1993). Hatch (1993) has reviewed historical information, mostly anecdotal accounts, in Alaska dating back to the 1800s.

SEABIRD POPULATION TRENDS IN THE CENTRAL CALIFORNIA CURRENT

Population growth among Farallon seabirds over the past two decades exhibits great annual variability, a pattern characteristic of marine avifaunas in eastern boundary currents (Duffy 1983, Ainley and Boekelheide 1990). At longer temporal scales other patterns are discernible. During the 1970s many species were showing recovery from human activities, such as disturbance from over-population of these islands (e.g., >200 persons housed in more than two dozen buildings during WW II), introduction of exotic vertebrates, oil spills, commercial egging, and changes in prey availability (Ainley and Lewis 1974). In the Gulf of the Farallones region many of these detrimental impacts had diminished significantly by the beginning of the 1970s, leading to increased numbers of virtually all Farallon species (Ainley and Boekelheide 1990). More recently, however, startling changes have occurred.

The Ashy Storm-Petrel (*Oceanodroma homochroa*), an endemic species to the California Current, is more abundant at the Farallones than elsewhere (80% of the world population) but is also at the extreme northern edge of its breeding range (Ainley and Boekelheide 1990). One line of evidence indicates a severe decline from the early 1970s to the late 1980s. Two mark-recapture, mist-netting studies showed a decrease in the adult population of about 50% (cf. Ainley and Lewis 1974, Carter et al. 1992). On the other hand, annual (semi-quantitative) observations in Monterey Bay, 80 km south, where perhaps the entire world population of Ashy Storm-Petrel congregates during autumn, have not indicated such a radical change, if any, during the past 15 years (R. Stallcup, pers. comm.).

In eastern boundary currents (e.g., the California Current), breeding populations of cormorants, especially, can fluctuate dramatically year-to-year in response to fish availability (Ainley and Boekelheide 1990). The Brandt's Cormorant (*P. penicillatus*) population at the Farallones, in the center of a range confined largely to the California Current, varied between 15,000 and 25,000 breeders until the early 1980s (Fig. 2A), when El Niño 1982–1983 severely restricted food resources, reproduction failed, and many birds died (Ainley et al. 1986, Ainley and Boekelheide 1990). To date, the breeding population has shown little recovery, and now ranges from 3000 to 10,000 birds.

An even more erratic pattern is evident in the Pelagic Cormorant (*P. pelagicus*; Fig. 2B), which at the Farallones is in the southern portion of its distribution. In this species, the entire population may forgo breeding as a response to restricted food (Ainley and Boekelheide 1990). Maximum popu-

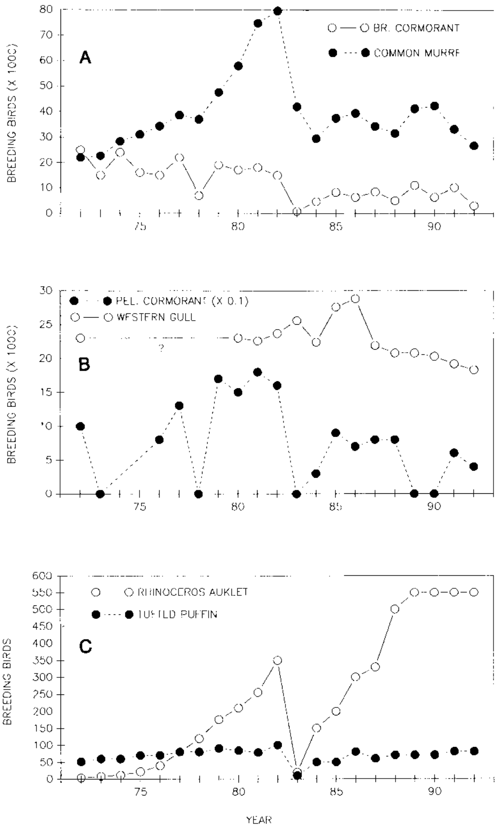

FIGURE 2. Trends in seabird breeding populations at the South Farallon Islands, 1972–1992; see Ainley and Boekelheide (1990) for details on census techniques. A) The number of breeding Brandt's Cormorants and Common Murres. The murre estimates for 1972–1979 are based on extrapolations from a single reference colony and back calculations of annual growth rate from the 1980 census figure when all murres on the island were counted (see Ainley and Boekelheide 1990, fig. 8.1). An island-wide census conducted in 1972 (see Ainley and Lewis 1974) counted 20,500 murres compared to the back-calculated estimate of 22,049. Counts after 1979 are based on island-wide censuses. B) The number of breeding Pelagic Cormorants and Western Gulls. Counts for cormorants are inflated by a factor of ten so that the scale, suitable for the gull numbers, does not hide fluctuations in the cormorant population. No gull censuses were made between 1972 and 1980; the population varied little during this period (Ainley and Boekelheide 1990). C) The number of Rhinoceros Auklets and Tufted Puffins breeding on the South Farallon Islands, 1972–1992.

lation size increased from about 1000 breeding birds in 1971 to 1600 by the early 1980s, then, following El Niño 1982–1983 dropped by half and is still decreasing.

The Farallon breeding population of the Western Gull (*Larus occidentalis*), another California Current endemic in the center of its range, was stable at about 23,000 birds from the 1960s until El Niño 1982–1983 (Ainley and Boekelheide 1990; Fig. 2B). Numbers then fluctuated until El Niño 1986, after which they began to decline. Overall in California, however, the population remained stable, because many small colonies have been newly founded in the San Francisco Bay Area (see Carter et al. 1992).

The Common Murre (*Uria aalge*), another species at the southern extreme of its range, showed the pattern similar to that exhibited by the cormorants (Fig. 2A). Murres in the PRBO census increased annually by 7.8% through the 1970s until 1982–1983 (Ainley and Boekelheide 1990). Suffering simultaneously from El Niño restrictions on food supply, oil spills, and intense gill netting, which was then greatly restricted (Salzman 1989), the murre breeding population crashed in 1983 to its 1972 level, and two small colonies south of the Farallones virtually disappeared (Takekawa et al. 1990). Since then the Farallon population has increased by only 1–2% per yr.

The Cassin's Auklet (*Ptychoramphus aleuticus*), a small, cavity-nesting species, which at the Farallones is within the southern third of its range, decreased by 50% between 1971 (Manuwal 1974) and 1989, when Carter et al. (1992) estimated 40,000 breeding birds. Because methods and personnel differed between the two estimates, we are uncertain about the magnitude of the decrease. That a significant decrease has occurred is indicated by a severe contraction in extent of nesting habitat used since the early 1970s (PRBO, unpub. data). This is significant because 30% of auklets in California nest on the Farallones, the only breeding population along a 600 km stretch of coast between San Miguel Island and islands near the Oregon/California border (Carter et al. 1992).

Finally, contrasting rates of increase were exhibited by the two "puffins," Rhinoceros Auklet (*Cerorhinca monocerata*) and the Tufted Puffin (*Fratercula cirrhata*), both at the southern extreme of their breeding ranges. During the early 1970s, the Tufted Puffin increased gradually from 50 to 80 breeding birds (Fig. 2C), but after 1977, the population remained stable. The Rhinoceros Auklet recolonized the islands in 1972, following the extermination of cavity dwelling, feral hares (*Oryctolagus cuniculatus*) (Ainley and Lewis 1974). Subsequently, auklet numbers exploded at a rate of about 50% per yr, a pattern interrupted only by El Niño 1982–1983. Numbers stabilized at about 550 breeding birds by 1988.

TRENDS IN SEABIRD POPULATIONS OF THE NORTHERN CALIFORNIA CURRENT

Waters from northern California to central Washington comprise the northernmost portion of the California Current. Carter et al. (1992) suggested that Brandt's and Pelagic cormorant populations for northern California were slightly lower in 1989 than in 1980, but the lack of annual census data makes comparison risky. Wilson (1991, unpub. data) noted a slight increase among Brandt's Cormorants in Washington, in a series of censuses 1979–1992, but total population size is so small (153–265 nests, 1979–1985; 132–578 nests, 1986–1992) that the trend has little regional significance. Wilson's unpublished data for Pelagic Cormorants along Washington's outer coast indicate an increase from 1200 nests in 1985 to 2200 in 1992. On the inner coast (i.e., Strait of Juan de Fuca), numbers of Pelagics fluctuated between 800 and 1200 nests, 1983 to 1992. With a longer time scale, Speich and Wahl (1989) summarized all available census data in Washington over the past few decades, and found no consistent trends among Pelagic or Brandt's cormorants.

For Common Murres, five major California colonies near the Oregon border (ca. 550 km north of the Farallones) during five non-consecutive years 1979–1989, showed similar but less extreme trends as did Farallon murres (cf. Figs. 2, 3; Takekawa et al. 1990, Carter et al. 1992). Northern California populations did not experience oil spills or intense gill-netting, which probably explains why their decrease during El Niño 1982–1983 was minimal. The Farallon pattern of crash-and-no-recovery, however, was repeated farther north among all murre colonies in Washington (to 1000 km north of the Farallones). There, a series of oil spills coincided with El Niño 1982–1983 (Wilson 1991, unpub. data; Fig. 3).

Rhinoceros Auklet populations increased markedly in Oregon during the 1970s (Scott et al. 1974), and in central and northern California during the 1980s, including the founding of 22 new colonies (Carter et al. 1992). The increase was coincident with recolonization on the Farallones, indicating a regional expansion. In Washington, populations also increased to the extent that nesting habitat may have been saturated on Destruction Island (26,000–32,000 birds, Speich and Wahl 1989), though perhaps not Protection Island. Beginning in the late 1960s, the population on Protection Island increased 4–5 fold to about 31,400 birds by the late 1970s (Wilson and Manuwal 1986) and 40,600 birds by 1983 (Thompson et al. 1985). Unused nesting habitat remains (Wilson, unpub. data). During the same period, Tufted Puffins in Washington have been gradually declining (Speich and Wahl 1989); in the Juan de Fuca Strait and in the San Juan Islands the decline has been precipitous, from 1070 birds in the 1950s to about 100 at present (Wilson, unpub. data).

CAUSES OF SEABIRD POPULATION TRENDS IN THE CALIFORNIA CURRENT

The population trends at the Farallones and at other sites in the central and northern California Current were concordant for a number of species.

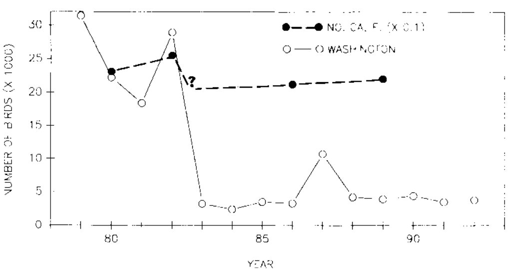

FIGURE 3. The number of breeding Common Murres in five California colonies near the Oregon border (data from Takekawa et al. 1990, Carter et al. 1992) and 28 colonies on the outer coast of Washington, 1979–1990 (data from Wilson 1991, unpub. data). California counts are reduced by a factor of 10 to complement the y-axis scale, fitted to the Washington counts.

The Rhinoceros Auklet was the only nonlarid seabird species that significantly increased during the past 30 years. The increase in Washington (and farther north; see below) preceded that in California (see Speich and Wahl 1989), indicating that populations in the Pacific Northwest were the source of southward dispersal. The floating population (i.e., adults that do not breed because space is lacking; *sensu* Manuwal 1974), was so large near the Farallones, as evidenced by the remarkable rate of increase, the quick recovery from El Niño 1982–1983, and the high densities of this species at sea in central California (Briggs et al. 1987, Ainley and Allen 1992), that the species rapidly took over the deserted rabbit warrens. This invasion may have blocked, or at least severely slowed, the recovery of Tufted Puffins at the Farallones, as both "puffins" are cavity-nesting species of similar size and each is aggressive toward the other (Ainley and Boekelheide 1990). The Tufted Puffins at the Farallones were recovering from impacts attributed to humans, but recovery had been slow due to the presence of rabbits and, perhaps, changes in the food web, i.e., loss of an important prey, the Pacific sardine (*Sardinops coerulea*; Ainley and Lewis 1974). At the Farallones, the availability of cavities suitable for both puffins apparently reached saturation in 1988. In Washington, the decline of Tuft-

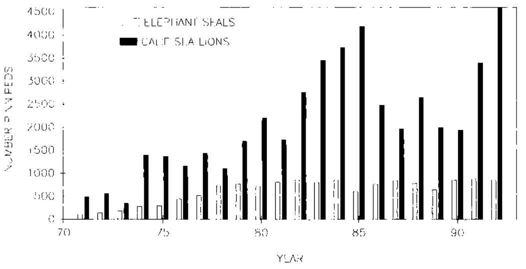

FIGURE 4. The number of California Sea Lions and Northern Elephant Seals hauling out on the South Farallon Islands during April and May, the seabird egg-laying and incubation periods, 1971–1992; data are based on censuses conducted weekly year round (PRBO, unpub. data).

ed Puffins is likely the result of human disturbance to nesting islands: farming, real estate development, Coast Guard activities, and feral animals.

In contrast, other factors affected trends in other seabird species. Predation and interference by Western Gulls may be responsible for the decrease among Ashy Storm-Petrels on the Farallones. In the early 1970s, few gulls nested in the optimal storm-petrel nesting habitat. Gulls are now spread everywhere and, besides eating storm-petrels, often nest in the sheltered positions at the entrance to petrel burrows. A dense, exotic grass introduced in the 1800s, appears to be spreading over the talus and also blocks crevice entrances.

By the early 1980s, the Western Gulls had colonized densely all available terrain on the island and a "floating" gull population was evident (Spear et al. 1987). The decrease in recent years, beginning about 1986, involves at least two factors: 1) a large increase in numbers of Elephant Seals (*Mirounga angustirostris*) and California Sea Lions (*Zalophus californianus*) along the seaward edges of the islands (Fig. 4; fig. 1.4 in Ainley and Boekelheide 1990), and 2) increased mortality due to disease (Spear et al. 1987; PRBO, unpub. data). The fact that the total California population did not change between 1980 and 1989 indicates that emigration from the huge population on the Farallones may also have increased.

The decrease in Cassin's Auklets on the Farallones may also involve several factors. 1) Different census methods could be involved, as discussed above, especially as cavity-nesting seabirds are difficult to estimate. Yet, auklets clearly nest less densely than they did in the early 1970s. 2) Predation by Western Gulls and Peregrine Falcons (*Falco peregrinus*) may have increased. Wintering falcons "recolonized" the island in the early 1970s, reaching maximum numbers (ca. 5) about 1980 (Pyle and Henderson 1990). Auklets are so numerous, however, that a measurable population effect seems unlikely, in contrast to effects among the many fewer auklets on Tatoosh Island, Washington (see Paine et al. 1990). 3) Most importantly, oceanographic factors may have changed food availability. In the early 1970s, a large floating population was evident (Manuwal 1972) and it may have been maintained by double-brooding, a rare phenomenon among seabirds. Since the mid-1970s, however, warm-water conditions have prevailed leading to a switch in diet composition, perhaps lower breeding success and certainly no second chicks fledged successfully (Ainley and Boekelheide 1990; PRBO, unpub. data). Ainley and Lewis (1974) noted that auklets were also much reduced in number during the late 19th century when another prolonged warm-water period occurred.

Populations of Pelagic and Brandt's cormorants and Common Murre at the Farallones and in Washington have recently begun to fluctuate within levels lower than those previous to El Niño 1982–1983. These species are largely piscivorous, feeding principally on juvenile rockfish (*Sebastes*) during the breeding season (Ainley and Boekelheide 1990). The principal prey that sustains *reproduction* is the juvenile shortbelly rockfish (*S. jordani*), which during mid-summer settles to depths beyond the foraging capabilities of seabirds. During the non-breeding season, these seabirds then feed on the early year-classes of other rockfish (those that settle to shallow depths) and of Pacific whiting (*Merluccius productus*), as well as all year-classes of anchovies (*Engraulis mordax*), Pacific herring (*Clupea harengus*), market squid (*Loligo opalescens*) and euphausiids (Baltz and Morejohn 1977, PRBO, unpub. data). Historically, when one prey species has been unavailable the seabirds have been able to switch to alternative species (Ainley and Boekelheide 1990). Seabird populations at the Farallones (and farther north) are depressed enough from historical levels (see Ainley and Lewis 1974, Ainley and Boekelheide 1990) that the spring surge in availability of rockfish juveniles is sufficient to produce high chick production (PRBO, unpub. data, see also Sydeman et al. 1991). Declines in reproductive success are too small to explain the trends (PRBO, unpub. data), in contrast to resource levels during the non-breeding season and effects on adult survival, juvenile recruitment or both.

The pattern exhibited by the three piscivores is closely similar to that shown by Peruvian guano birds before the crash of their prime prey species, the anchovetta (*Engraulis ringens*) (cf. Tovar et al. 1987). Documented since the time of the Incas, over a 30-year period beginning in the 1950s the guano birds recovered from successive El Niño events to lower and lower population levels concomitant with the increase in the commercial harvest of anchovetta. Ultimately, the anchovetta was lost due to over-fishing of a climatically stressed resource (Glantz and Thompson 1981). The birds and the fishery have yet to recover.

Similarly, commercial fisheries in California, except for anchovies and euphausiids, have been expanding greatly. In central and northern California, expansion of both pelagic (Fig. 5) and groundfish fisheries (Fig. 6) duplicates the pattern elsewhere in the California Current (see Pacific Fisheries Management Council 1992, and previous annual reports). Although the seabirds do not eat the adult groundfish (i.e., rockfish and whiting), reduction in spawning biomass of adults and curtailment of strong year-classes by the fisheries (or other factors), indirectly reduces the abundance of young fish available to seabirds and other predators. At present, no fishery exists for Shortbelly Rockfish, but proposals for development have been made. Among the pelagic fisheries, which compete directly with the birds, only the small one for anchovies has not greatly expanded (due to market conditions; Fig. 5A). Anchovies are abundant in southern California, where they are important to seabirds and other top-trophic predators (e.g., Anderson et al. 1982, Antonellis and Fiscus 1980, Hunt and Butler 1980); in central and northern California, anchovies are relatively unimportant to seabirds, except during summer (Ainley and Boekelheide 1990). In contrast, pelagic fisheries for Pacific herring (Fig. 5B) and market squid (Fig. 5C), centered in central California, have grown enormously.

We hypothesize that growth of fisheries for seabird prey species has been so dramatic, extensive, and coincident in time and region to the decrease in seabirds that a cause-effect process is involved. Prey switching may no longer be a viable alternative to seabirds (or individual fishermen) as virtually the entire suite of important prey species are now fished to their maximum. Annually extracting from this food web the amount and type of fish now accomplished by commercial fisheries cannot occur without consequences to the food web, and especially top carnivores (see Ludwig et al. 1993). Indeed, commercial catch rates for individual species have declined, specific fisheries in the California Current region recently have been closed (e.g., willow rockfish *S. entomelas,* Pacific Fishery Management Council 1992; Pacific herring, Calif. Dept. Fish and Game, results of 1993 Fish Commission hearings), and others have been severely restricted (e.g., rockfish, Pacific Fisheries Management Council 1992). For both reasons (fewer fish and more restrictions), commercial catches have declined (Fig. 6A). Moreover, as discussed above, the physical environment has been changing,

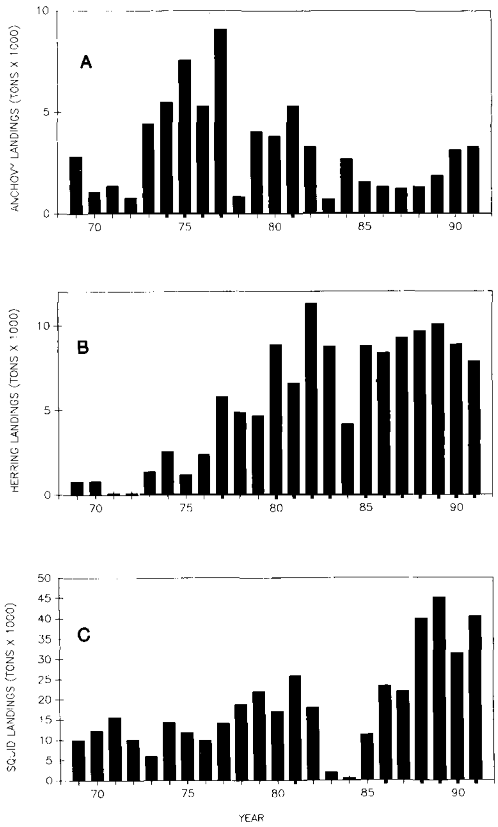

FIGURE 5. Annual landings (tons × 1000) in central and northern California of principal seabird prey by human, "pelagic" fisheries (i.e., mid-water species) over the previous few decades: A) northern anchovy; B) Pacific herring; and C) market squid, with about 40% of the squid landings from central California and the remainder from the vicinity of the northern Channel Islands (data from McAllister 1975, 1976; Oliphant 1979; Oliphant et al. 1990; Pinkas 1974, 1977).

but fishery management has been too slow to respond to the change; since 1976, sea temperatures have been warmer and annual variability of climate has been more severe than at any period in historical times (Kerr 1985, 1992). Many of the fish prey species have a zooplankton diet similar to the Cassin's Auklet, whose diet and population size have changed likely in response to oceanographic anomaly. Thus, the same phenomena that wrecked the Peruvian anchovy fishery appear to be in place: intense fishing coincident with climatic stress.

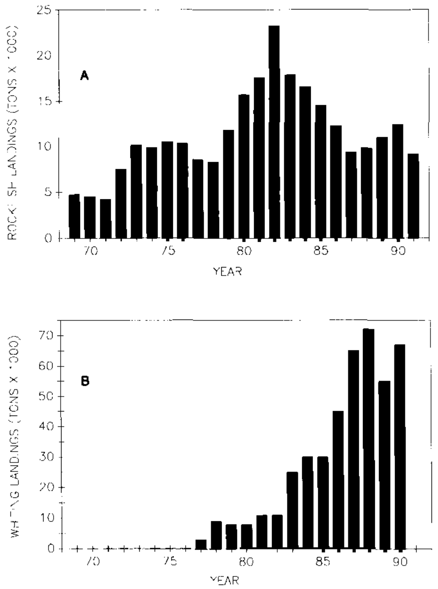

FIGURE 6. Annual landings (tons × 1000) of principal seabird prey by human fisheries in California waters over the previous few decades—groundfish whose juveniles are pelagic (although seabirds also eat year-old fish): A) rockfish, all species, with most of the catch taken in central and northern California; B) Pacific whiting, with most of the total taken in northern California (data from Calif. Dept. Fish and Game 1992); (McAllister 1975, 1976; Oliphant 1979; Oliphant et al. 1990; Pinkas 1974, 1977; Calif. Dept Fish & Game, R. Lea, pers. comm.).

The increase in California Sea Lions in the central and northern part of the California Current (Fig. 4) may in a way represent still another "fishery" competing indirectly with seabirds. The sea lions feed heavily on Pacific whiting older than one year and, when such prey are not available, rockfish and anchovies (Jones 1981, Bailey and Ainley 1981/1982, Antonellis et al. 1983). Like the human fishery, the sea lions may reduce the spawning biomass and ultimately the availability of one-year-old and younger fish. Growth rates of this sea lion's population have changed in concert with harvest levels of whiting (Ainley et al. 1982). Overall population levels, however, may or may not have reached their historical levels, following recovery from persecution (Boveng 1988). In the 1800s, the same or a greater number of sea lions and, with the Farallon history as a gauge (Ainley and Lewis 1974), a population of seabirds an order of magnitude greater than now co-existed in the California Current. For what ever reason, the system no longer appears capable of supporting close to the former levels of upper trophic-level predators.

SEABIRD POPULATION TRENDS IN THE GULF OF ALASKA AND BERING SEA

The major oceanographic region north of the California Current is the Gulf of Alaska (Subarctic Current system) and father north, separated by a series of complex currents among the Aleutian Islands, is the Bering Sea Gyre (Favorite et al. 1977). As a result of the Outer Continental Shelf Environmental Assessment Program (OCSEAP) established in 1975, permanent plots at a number of sites in the Gulf of Alaska, Bering Sea and Chukchi Sea, have been censused periodically. The result is a time series of censuses spanning 15+ years for a few common and easily-studied species.

On Middleton Island, in the Gulf of Alaska, a large colony of Pelagic Cormorants (2000–4500 pairs) has fluctuated widely since 1974, but on average is much larger now than in 1956 (Rausch 1958, pers. comm). In Chiniak Bay (Kodiak Island), censuses of 13 mixed colonies of Pelagic and Red-faced cormorants (*P. urile*) between 1975 and 1991 indicate stable populations (D. R. Nysewander and D. B. Irons, unpub. data). No data are available in the Bering Sea, but at Cape Thompson, southeastern Chukchi Sea, Pelagic Cormorants decreased in the late 1970s to a level 20% lower than in the early 1960s (Springer 1993).

Among large *Larus* species north of the California Current, only the Glaucous-winged Gull (*L. glaucescens*) has been studied sufficiently. In Washington, at the transition between California Current and Gulf of Alaska systems, Glaucous-winged Gulls increased appreciably during the past few decades (Speich and Wahl 1989). Farther north, on the Alaid-Nizki island group (western Aleutians), the species increased from 200 to 1300 pairs within a few years following eradication of feral foxes in 1976 (C. F. Zeillemaker and J. L. Trapp, unpub. data). The greatest documented change occurred on Middleton Island, where this species grew from none in 1956, to 500–700 pairs by the mid-1970s, to more than 7000 pairs by 1990 (S. A. Hatch, unpub. data). Thus, the increase is consistent among widely spaced sites in the region. A decline in the Glaucous-winged Gull population of Prince William Sound since the early 1970s (Vermeer and Irons 1991, Laing and Klosiewski 1993) probably reflects the local closure of some canneries and canning regulations that have reduced availability of offal (M. E. Isleib, pers. comm.).

In recent years Common Murres have been well studied in Alaska (Byrd et al. 1993), but historic data are rare. Elliot (1881) described "hundreds of thousands" of Common and Thick-billed murres (*U. lomvia*) on Walrus Island, Bering Sea. As recently as 1953, Peterson and Fisher (1955) estimated more than 1 million murres there; yet, by 1976 almost all had vanished (Hunt 1976). In partial explanation, Steller Sea Lions (*Eumetopias jubatus*) had moved onto the island's plateau, which had formerly been dominated by murres. At other sites in the Bering Sea monitored since the 1970s, most study colonies have declined (Fig. 7), but not due to competition with pinnipeds (see below). At Cape Thompson, in the southeastern Chukchi Sea, murres have declined as well (Springer 1993). Elsewhere in Alaska, trends among Common Murre populations have been inconsistent with those in the Bering Sea Gyre. For example, in 1956 on Middleton Island, Rausch (1958) counted only about 400 murres, mostly Thick-billed. Today the island supports a similar number of Thick-billed Murres but 6000–8000 Common Murres as well (Fig. 7).

Cassin's Auklets formerly nested in abundance on Sanak Island (Bendire 1895), but foxes were introduced and the auklets became scarce by the late 1930s (Murie 1959). Murie also learned of probable declines or

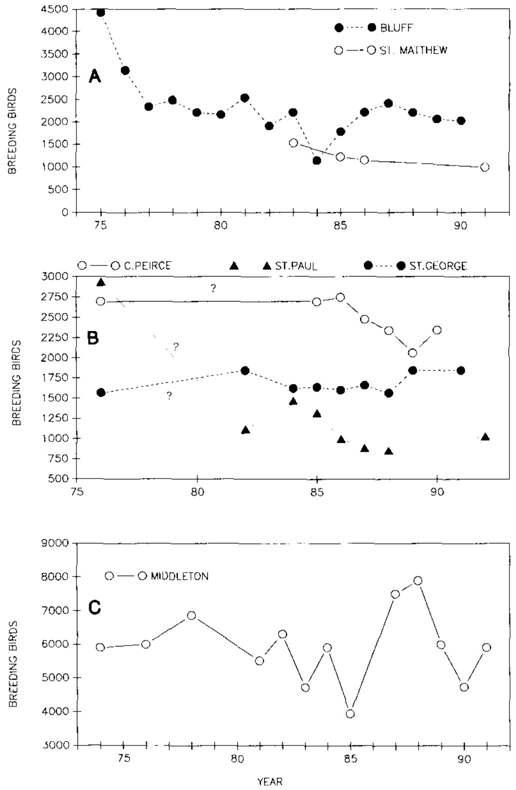

FIGURE 7. The number of breeding Common Murres at A) two reference colonies in the northeastern portion of the Bering Sea Gyre, Alaska, 1976–1991; B) three colonies in the southeastern Bering Sea Gyre, 1976–1992; and C) a colony in the Gulf of Alaska: Middleton Island, 1974–1991. Sources of the data are as follows: Middleton Island (Rausch 1958, Nysewander et al. 1986, S. Hatch, unpub. data); Cape Peirce (Haggblom and Mendenhall 1993); St. George Island (Dragoo et al. 1990, unpub. data); St. Paul Island (Dragoo et al. 1989, L. Climo, pers. comm.); St. Matthew Island (Murphy et al. 1987, A. L. Sowls, pers. comm.); Bluff (Murphy et al. 1986, Murphy 1993).

extirpations on other Aleutian Islands including Keegaloo, Adugak, Amlia (nearby islets) and Ilak.

Particularly susceptible to foxes is the Tufted Puffin. Murie (1937) recommended that Kaligagan Island should be managed as a fox farm because of the paucity of breeding seabirds (i.e., no impact evident). Foxes eventually died out, however, and today Kaligagan has one of the largest Tufted Puffin colonies in Alaska (> 100,000 birds; Nysewander et al. 1982)!

Most of the Alaskan population of Rhinoceros Auklets breeds on Forrester Island, which is likely the world's largest colony of this species (> 54,000 pairs; DeGange et al. 1977). The only site that has been closely censused, however, is Middleton Island where one of four small colonies located in 1976–1978 had increased from about 50 to more than 900 burrows by 1992 (Hatch et al. 1979, Hatch, unpub. data). Farther south in the Gulf of Alaska, in British Columbia, Rhinoceros Auklet populations also increased substantially during the past few decades (Rodway et al. 1992).

CAUSES OF SEABIRD POPULATION TRENDS IN THE GULF OF ALASKA AND BERING SEA

In Alaska, it is clear that many local populations of seabirds have undergone marked changes during recent decades. Given the enormity and environmental complexity of the region, we can rarely posit whether any species' population is changing throughout its range. An exception is the downward trend among murre colonies in the eastern Bering Sea, where changes are concordant among widely-spaced sites.

Alaskan seabirds are killed in large numbers in high seas gill nets (DeGange et al. 1993), although effects on local breeding populations are difficult to ascertain, and oil at sea poses a significant threat, as demonstrated by the *Exxon-Valdez* spill (Piatt et al. 1990, Nysewander et al. 1992). There is little doubt, however, that the introduction of exotic animals to islands—especially foxes, but other mammals as well—has been the most potent anthropogenic factor affecting Alaskan and other seabirds during recent centuries (Croxall et al. 1984). Introduced by Russian colonists late in the 1700s, the heyday of fox farming occurred between 1885 and 1930 and included 450 islands from southeastern Alaska to the western Aleutians (Bailey 1993). Fox trappers regarded seabirds as "feed," and not surprisingly, some of our richest seabird islands supported the most successful, if short-lived, fox farms (e.g., Middleton Island). Fox introductions were locally disastrous (Murie 1959, Bailey 1993), but this damage has been reversed in most cases. Fox farming ceased in the 1930s, and today, foxes remain on only about 50 islands (Bailey 1993). Some of these islands are large, however, and impossible to rid of foxes unless restrictions on the use of toxicants are lifted.

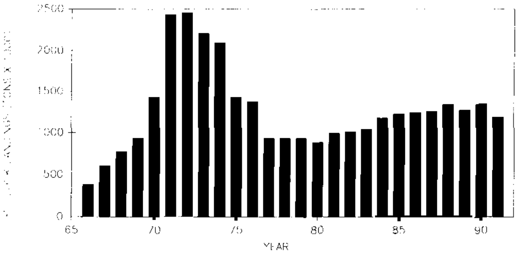

FIGURE 8. Annual landings of pollock from the eastern Bering Sea (data from Bakkala 1984; Pacific Fisheries Information Network, R. Kinoshita, pers. comm.).

The trends among sites in the eastern Bering Sea indicate other than local, coarse-scale effects as with fox introductions. The regional decline in Common Murres, as well as in pup production of Northern Fur Seals (*Callorhinus ursinus*) and adult populations of Harbor Seals (*Phoca vitulina*) and Steller Sea Lions (York and Kozloff 1987, Merrick et al. 1987, Pitcher 1990), brings to issue whether fisheries are altering the marine ecosystem to the detriment of top-trophic predators (Murphy et al. 1986, Springer 1992). Since the 1960s, walleye pollock (*Theragra chalcogramma*) have supported the world's largest single-species fishery (Lloyd and Davis 1989; Fig. 8) and are also important to pinnipeds (Lowry et al. 1989) and piscivorous seabirds (Hunt et al. 1981, Dragoo 1991). Any cause-effect explanation, however, must address both the apparent increase of planktivorous auklets (*Aethia* spp.) in the region (Pribilof Islands, St. Lawrence Island; Springer 1993) and the decline of murres and kittiwakes (*Rissa* spp.) (Pribilof Islands, St. Matthew Island, etc.; Hatch et al. 1993). Auklets presumably compete with juvenile pollock for euphausiids and other zooplankton, whereas murres and kittiwakes take juvenile pollock, especially during the breeding season (Springer and Byrd 1989). The role of fishing in this scenario is unclear, because the adult pollock (age 2+) taken in the fishery are important predators on juvenile pollock and other seabird prey such as herring, myctophids, capelin (*Mallotus villosus*), and sandlance (*Ammodytes hexapterus*; Straty and Haight 1979, Livingston 1991, Springer 1992). Thus, this fishery could theoretically benefit piscivorous birds as was the case in the large-scale fisheries of the North Sea (Furness and Barrett 1991). The issue in Alaska, as in the California Current, requires critical information on seabird demography and trophic relationships during winter. Experience has shown us (e.g., Glantz and Thompson 1981) that understanding the whole system, both prey and predators, ultimately benefits man's commercial interests in the long-term perspective (see also Cairns 1992, Ludwig et al. 1993).

CONCLUSIONS

1. Trends in population size of seabirds at breeding sites along the western coast of North America have been concordant within different oceanographic regimes, e.g., the California Current or the eastern Bering Sea Gyre (continental shelf). The best example is given by the Common Murre, a species exhibiting two sets of concordant trends, one within the California Current and the other in the eastern Bering Sea Gyre.

2. At larger spatial scales (i.e., >1000 km) less concordance was apparent, although marked changes within one species, the Rhinoceros Auklet, was consistent across oceanographic boundaries. Its spectacular increase and southward colonization appear to have been fueled by factors initially operating in the Gulf of Alaska. From there, surplus breeders dispersed southward.

3. Seabird populations along the west coast of North America have been greatly affected by two general classes of factors: encroachment of humans and especially

their animals on breeding islands, and exploitation of the prey base by human fisheries (in concert with climatic stress).

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