in mind. Marine resources vary spatially and temporally. While seasonal patterns occur with a certain level of predictability, environmental stochasticity means that from the breeding seabird's perspective there will be good years and poor years. Population viability analyses reveal that populations of sea birds can be particularly susceptible to catastrophic events. One such cause of reduced breeding performance can be El Niño and La Niña events, which often result in a reduction of available prey or necessitate a switch to poorer-quality alternative prey.

Such environmental uncertainty could be expected to impact upon reproductive life histories. Increases in foraging distances and conservation of breeding life span may be expected. That is, selection should favor offshore foraging strategies that enlarge the potential feeding zone and maximize life span to take advantage of as many good years as possible. Hence, in determining the efficacy of offshore foragers in particular, data from single-season studies are unlikely to be sufficient. Conversely, inshore foragers, which tend to rely on a locally abundant and predictable food supply, are the species most likely to be affected by human activities (e.g., emission of greenhouse gases) that increase environmental stochasticity.

Conclusions

The breeding of seabirds is dictated by life history strategies that have evolved principally in response to food supply. In that sense, David Lack was correct. However, the situation is more complex than he envisaged. At opposite ends of a continuum there are two broad strategies adopted by seabirds: the James Bond strategy of the inshore foragers (breed fast, die young, and have a good-looking corpse) and the more conservative strategy of the offshore foragers that seeks to maximize lifetime reproductive output by withholding and adjusting investment as necessary to maximize breeding life span. As we learn more about seabirds, we discover that their reproductive behavior is not fixed but can be relatively plastic, adjusting just where they are on that continuum in response to environmental conditions and food availability.

See also

Laridae, Sternidae and Rynchopidae. Seabird Foraging Ecology. Seabird Overview.

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SEABIRD RESPONSES TO CLIMATE CHANGE

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doi:10.1006/rwos.2001.0237

Introduction

This article reviews examples showing how seabirds have responded to changes in atmospheric and marine climate. Direct and indirect responses take the form of expansions or contractions of range; increases or decreases in populations or densities within existing ranges; and changes in annual cycle, i.e., timing of reproduction. Direct responses are those related to environmental factors that affect the physical suitability of a habitat, e.g., warmer or colder temperatures exceeding the physiological tolerances of a given species. Other factors that can affect seabirds directly include: presence/absence of sea ice, temperature, rain and snowfall rates, wind, and sea level. Indirect responses are those mediated through the availability or abundance of resources such as food or nest sites, both of which are also affected by climate change.

Seabird response to climate change may be most apparent in polar regions and eastern boundary currents, where cooler waters exist in the place of the warm waters that otherwise would be present. In analyses of terrestrial systems, where data are in much greater supply than marine systems, it has been found that range expansion to higher (cooler but warming) latitudes has been far more common than retraction from lower latitudes, leading to speculation that cool margins might be more immediately responsive to thermal variation than warm margins. This pattern is evident among sea birds, too. During periods of changing climate, alteration of air temperatures is most immediate and rapid at high latitudes due to patterns of atmospheric circulation. Additionally, the seasonal ice and snow cover characteristic of polar regions responds with great sensitivity to changes in air temperatures. Changes in atmospheric circulation also affect eastern boundary currents because such currents exist only because of wind-induced upwelling.

Seabird response to climate change, especially in eastern boundary currents but true elsewhere, appears to be mediated often by El Niño or La Niña. In other words, change is expressed stepwise, each step coinciding with one of these major, short-term climatic perturbations. Intensive studies of seabird populations have been conducted, with a few exceptions, only since the 1970s; and studies of seabird responses to El Niño and La Niña, although having a longer history in the Peruvian Current upwelling system, have become commonplace elsewhere only since the 1980s. Therefore, our knowledge of sea-bird responses to climate change, a long-term process, is in its infancy. The problem is exacerbated by the long generation time of seabirds, which is 15–70 years depending on species.

Evidence of Sea-bird Response to Prehistoric Climate Change

Reviewed here are well-documented cases in which currently extant seabird species have responded to climate change during the Pleistocene and Holocene (last 3 million years, i.e., the period during which humans have existed).

Southern Ocean

Presently, 98% of Antarctica is ice covered, and only 5% of the coastline is ice free. During the Last Glacial Maximum (LGM: 19 000 BP), marking the end of the Pleistocene and beginning of the Holocene, even less ice-free terrain existed as the ice sheets grew outward to the continental shelf break and their mass pushed the continent downward. Most likely, land-nesting penguins (Antarctic genus *Pygoscelis*) could not have nested on the Antarctic continent, or at best at just a few localities (e.g., Cape Adare, northernmost Victoria Land). With warming, loss of mass and subsequent retreat of the ice, the continent emerged.

The marine-based West Antarctic Ice Sheet (WAIS) may have begun to retreat first, followed by the land-based East Antarctic Ice Sheet (EAIS). Many Adélie penguin colonies now exist on the raised beaches remaining from successive periods of rapid ice retreat. Carbon-dated bones from the oldest beaches indicate that Adélie penguins colonized sites soon after they were exposed. In the Ross Sea, the WAIS receded south-eastward from the shelf break to its present position near Ross Island approximately 6200 BP. Penguin remains from Cape Bird, Ross Island (southwestern Ross Sea), date back to 7070 ± 180 BP; those from the adjacent southern Victoria Land coast (Terra Nova Bay) date to 7505 ± 230 BP. Adélie penguin remains at capes Royds and Barne (Ross Island), which are closest to the ice-sheet front, date back to 500 BP and 375 BP, respectively. The near-coast Windmill Islands, Indian Ocean sector of Antarctica, were covered by the EAIS during the LGM. The first islands were deglaciated about 8000 BP, and the last about 5500 BP. Penguin material from the latter was dated back to 4280–4530 BP, with evidence for occupation 500–1000 years earlier. Therefore, as in Victoria Land, soon after the sea and land were free from glaciers, Adélie penguins established colonies.

The study of raised beaches at Terra Nova Bay also investigated colony extinction. In that area several colonies were occupied 3905–4930 BP, but not since. The period of occupancy, called 'the penguin optimum' by geologists, corresponds to one of a warmer climate than at present. Currently, this section of Victoria Land is mostly sea-ice bound and penguins nest only at Terra Nova Bay owing to a small, persistent polynya (open-water area in the sea ice).

A study that investigated four extinct colonies of chinstrap penguin in the northern part of the Antarctic Peninsula confirmed the rapidity with which colonies can be founded or deserted due to fluctuations in environmental conditions. The colonies were dated at about 240–440 BP. The chinstrap penguin, an open-water loving species, occupied these former colonies during infrequent warmer periods indicated in glacial ice cores from the region. Sea ice is now too extensive for this species offshore of these colonies. Likewise, abandoned Adélie penguin nesting areas in this region were occupied during the Little Ice Age (AD 1500–1850), but since have been abandoned as sea ice has dissipated in recent years (see below).

South-east Atlantic

A well-documented avifaunal change from the Pleistocene to Recent times is based on bone deposits at Ascension and St Helena Islands. During glacial maxima, winds were stronger and upwelling of cold water was more pronounced in the region. This pushed the 23°C surface isotherm north of St Helena, thus accounting for the cool-water seabird avifauna that was present then. Included were some extinct species, as well as the still extant sooty shearwater and white-throated storm petrel. As the glacial period passed, the waters around St Helena became warmer, thereby encouraging a warm-water avifauna similar to that which exists today at Ascension Island; the cool-water group died out or decreased substantially in representation. Now, a tropical avifauna resides at St Helena including boobies, a frigatebird not present earlier, and Audubon's shearwater. Most recently these have been extirpated by introduced mammals.

North-west Atlantic/Gulf of Mexico

Another well-documented change in the marine bird fauna from Plio-Pleistocene to Recent times is available for Florida. The region experienced several major fluctuations in sea level during glacial and interglacial periods. When sea level decreased markedly to expose the Isthmus of Panama, thus, changing circulation, there was a cessation of upwelling and cool, productive conditions. As a result, a resident cool-water avifauna became extinct. Subsequently, during periods of glacial advance and cooler conditions, more northerly species visited the area; and, conversely, during warmer, interglacial periods, these species disappeared.

Direct Responses to Recent Climate Change

A general warming, especially obvious after the mid-1970s, has occurred in ocean temperatures especially west of the American continents. Reviewed here are sea-bird responses to this change.

Chukchi Sea

The Arctic lacks the extensive water–ice boundaries of the Antarctic and as a result fewer seabird species will be directly affected by the climate-related changes in ice edges. Reconstructions of northern Alaska climatology based on tree rings show that temperatures in northern Alaska are now the warmest within the last 400 years with the last century seeing the most rapid rise in temperatures following the end of the Little Ice Age (AD 1500–1850). Decreases in ice cover in the western Arctic in the last 40 years have been documented, but the recent beginnings of regional ornithological research precludes examining the response of birds to these changes.

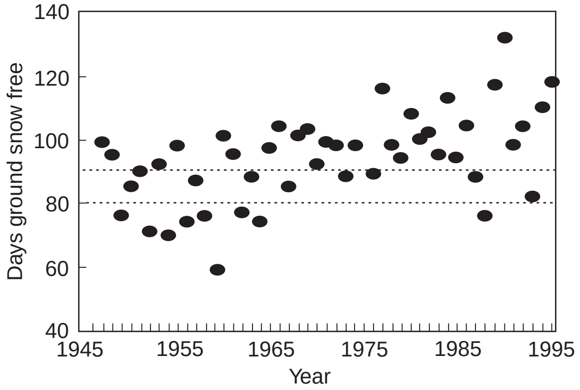

Figure 1 Changes in the length of the annual snow-free period at Barrow, Alaska, 1947–1995. Dashed lines show the number of days that black guillemots and horned puffins require a snow-free cavity (80 and 90 days, respectively). Black guillemots first bred near Barrow in 1966 and horned puffins in 1986. (Redrawn from Divoky, 1998.)

Changes in distribution and abundance related to snow cover have been found for certain cavity-nesting members of the auk family (Alcidae). Black guillemots and horned puffins require snow-free cavities for a minimum of 80 and 90 days, respectively, to successfully pair, lay and incubate eggs, and raise their chicks(s). Until the mid-1960s the snow-free period in the northern Chukchi Sea was usually shorter than 80 days but with increasing spring air temperatures, the annual date of spring snow-melt has advanced more than 5 days per decade over the last five decades (**Figure 1**). The annual snow-free period now regularly exceeds 90 days, which reduces the likelihood of chicks being trapped in their nest sites before fledging. This has allowed black guillemots and horned puffins to establish colonies (range expansion) and increase population size in the northern Chukchi.

California Current

Avifaunal changes in this region are particularly telling because the central portion of the California Current marks a transitional area where subtropical and subarctic marine faunas meet, and where north–south faunal shifts have been documented at a variety of temporal scales. Of interest here is the invasion of brown pelicans northward from their 'usual' wintering grounds in central California to the Columbia River mouth and Puget Sound, and the invasion of various terns and black skimmers northward from Mexico into California. The pelican and terns are tropical and subtropical species.

During the last 30 years, air and sea temperatures have increased noticeably in the California Current region. The response of seabirds may be mediated by thermoregulation as evidenced by differences in the amount of subcutaneous fat held by polar and tropical seabird species, and by the behavioral responses of seabirds to inclement air temperatures.

The brown pelican story is particularly well documented and may offer clues to the mechanism by which similar invasions come about. Only during the very intense El Niño of 1982–83 did an unusual number of pelicans move northward to the Columbia River mouth. They had done this prior to 1900, but then came a several-decade long period of cooler temperatures. Initially, the recent invasion involved juveniles. In subsequent years, these same birds returned to the area, and young-of-the-year birds followed. Most recently, large numbers of adult pelicans have become a usual feature feeding on anchovies that have been present all along. This is an example of how tradition, or the lack thereof, may facilitate the establishment (or demise) of expanded range, in this case, compatible with climate change.

The ranges of skimmers and terns have also expanded in pulses coinciding with El Niño. This pattern is especially clear in the case of the black skimmer, a species whose summer range on the east coast of North America retracts southward in winter. On the west coast, almost every step in a northward expansion of range from Mexico has coincided with ocean warming and, in most cases, El Niño: first California record, 1962 (not connected to ocean warming); first invasion *en masse*, 1968 (El Niño); first nesting at Salton Sea, 1972 (El Niño); first nesting on coast (San Diego), 1976 (El Niño); first nesting farther north at Newport Bay and inland, 1986 (El Niño). Thereafter, for Southern California as a whole, any tie to El Niño became obscure, as (1) average sea-surface temperatures off California became equivalent to those reached during the intense 1982–83 El Niño, and (2) population increase became propelled not just by birds dispersing north from Mexico, but also by recruits raised locally. By 1995, breeding had expanded north to Central California. In California, with warm temperatures year round, skimmers winter near where they breed.

The invasion northward by tropical/subtropical terns also relates to El Niño or other warm-water incursions. The first US colony (and second colony in the world) of elegant tern, a species usually present off California as post-breeders (July through October), was established at San Diego in 1959, during the strongest El Niño event in modern times. A third colony, farther north, was established in 1987 (warm-water year). The colony grew rapidly, and in 1992–93 (El Niño) numbers increased 300% (to 3000 pairs). The tie to El Niño for elegant terns is confused by the strong correlation, initially, between numbers breeding in San Diego and the biomass of certain prey (anchovies), which had also increased. Recently, however, anchovies have decreased. During the intense 1997–98 El Niño, hundreds of elegant terns were observed in courtship during spring even farther north (central California). No colony formed.

Climate change, and El Niño as well, may be involved in the invasion of Laysan albatross to breed on Isla de Guadalupe, in the California Current off northern Mexico. No historical precedent exists for the breeding by this species anywhere near this region. First nesting occurred in 1983 (El Niño) and by 1988, 35–40 adults were present, including 12 pairs. Ocean temperatures off northern Mexico are now similar to those in the Hawaiian Islands, where nesting of this species was confined until recently. In the California Current, sea temperatures are the warmest during the autumn and winter, which, formerly, were the only seasons when these albatross occurred there. With rising temperatures in the California Current, more and more Laysan albatross have been remaining longer into the summer each year. Related, too, may be the strengthening of winds off the North American west coast to rival more closely the trade winds that buffet the Hawaiian Islands. Albatross depend on persistent winds for efficient flight, and such winds may limit where albatrosses occur, at least at sea.

Several other warm-water species have become more prevalent in the California Current. During recent years, dark-rumped petrel, a species unknown in the California Current region previously, has occurred regularly, and other tropical species, such as Parkinson's petrel and swallow-tailed gull have been observed for the first time in the region.

In response to warmer temperatures coincident with these northward invasions of species from tropical and subtropical regions, a northward retraction of subarctic species appears to be underway, perhaps related indirectly to effects of prey availability. Nowadays, there are markedly fewer black-footed albatross and sooty and pink-footed shearwaters present in the California Current system than occurred just 20 years ago (**Figure 2**). Cassin's auklet is becoming much less common at sea in central California, and its breeding populations have also been declining. Similarly, the southern edge of the breeding range of common murres has retreated north. The species no longer breeds in Southern

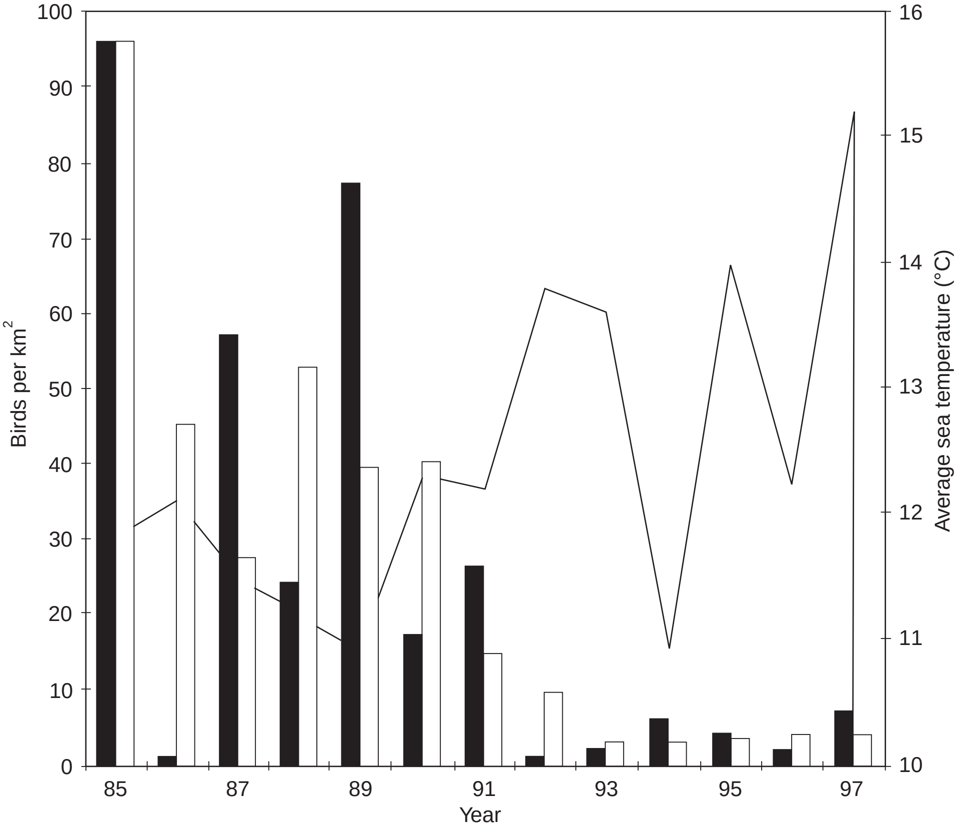

Figure 2 The density (■) (plus 3-point moving average, □) of a cool-water species, the sooty shearwater, in the central portion of the California Current, in conjunction with changes in marine climate (sea surface temperature, (—)), 1985–1997.

California (Channel Islands) and numbers have become greatly reduced in Central California (**Figure 3**). Moreover, California Current breeding populations have lost much of their capacity, demonstrated amply as late as the 1970s, to recover from catastrophic losses. The latter changes may or may not be more involved with alterations of the food web (see below).

Northern Bellingshausen Sea

Ocean and air temperatures have been increasing and the extent of pack ice has been decreasing for the past few decades in waters west of the Antarctic peninsula. In response, populations of the Adélie penguin, a pack-ice species, have been declining, while those of its congener, the open-water dwelling chinstrap penguin have been increasing (**Figure 4**). The pattern contrasts markedly with the stability of populations on the east side of the Antarctic Peninsula, which is much colder and sea-ice extent has changed little.

The reduction in Adélie penguin populations has been exacerbated by an increase in snowfall coincident with the increased temperatures. Deeper snow drifts do not dissipate early enough for eggs to be laid on dry land (causing a loss of nesting habitat and eggs), thus also delaying the breeding season so that fledging occurs too late in the summer to accommodate this species' normal breeding cycle. This pattern is the reverse of that described above for black guillemots in the Arctic. The penguin reduction has affected mostly the smaller, outlying subcolonies, with major decreases being stepwise and occurring during El Niño.

Similar to the chinstrap penguin, some other species, more typical of the Subantarctic, have been expanding southward along the west side of the Antarctic Peninsula. These include the brown skua, blue-eyed shag, southern elephant seal and Antarctic fur seal.

Ross Sea

A large portion (32%) of the world's Adélie penguin population occurs in the Ross Sea (South Pacific sector), the southernmost incursion of ocean on the planet (to 78°S). This species is an obligate inhabitant of pack ice, but heavy pack ice negatively affects reproductive success and population growth. Pack-ice extent decreased noticeably in the late 1970s and early 1980s and air temperatures have also been

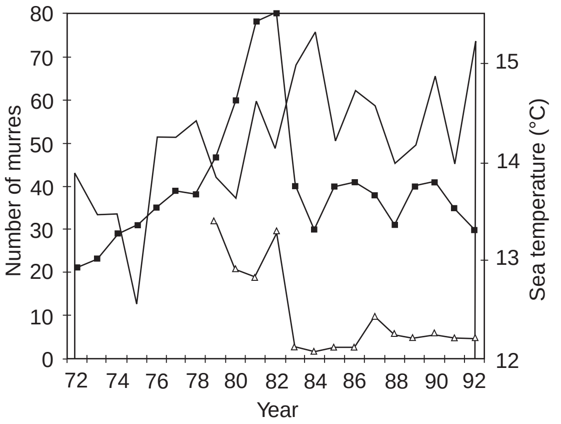

Figure 3 Changes in the number of breeding common murres in central (California, ■) and northern (Washington, △) portions of the California Current during recent decades. Sea surface temperature (—) from central California shown for comparison. During the 1970s, populations had the capacity to recover from reductions due to anthropogenic factors (e.g., oil spills). Since the 1982–83 El Niño event and continued higher temperatures, however, the species' capacity for population recovery has been lost (cf. **Figure 5**).

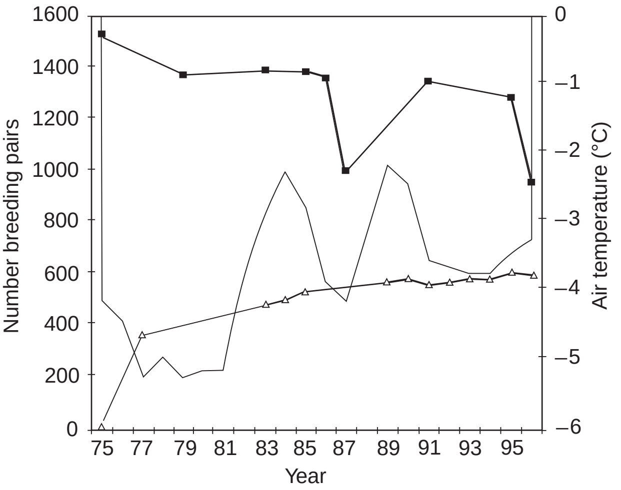

Figure 4 Changes in the number of breeding pairs of two species of penguins at Arthur Harbor, Anvers Island, Antarctica (64°S, 64°W), 1975–1996. The zoogeographic range of Adélie penguins (■) is centered well to the south of this site; the range of chinstrap penguins (△) is centered well to the north. Arthur Harbor is located within a narrow zone of overlap (200 km) between the two species and is at the northern periphery of the Adélie penguins' range.

rising. The increasing trends in population size of Adélie penguins in the Ross Sea are opposite to those in the Bellingshausen Sea (see above; **Figure 5**). The patterns, however, are consistent with the direction of climate change: warmer temperatures, less extensive pack ice. As pack ice has become more dispersed in the far south, the penguin has benefited.

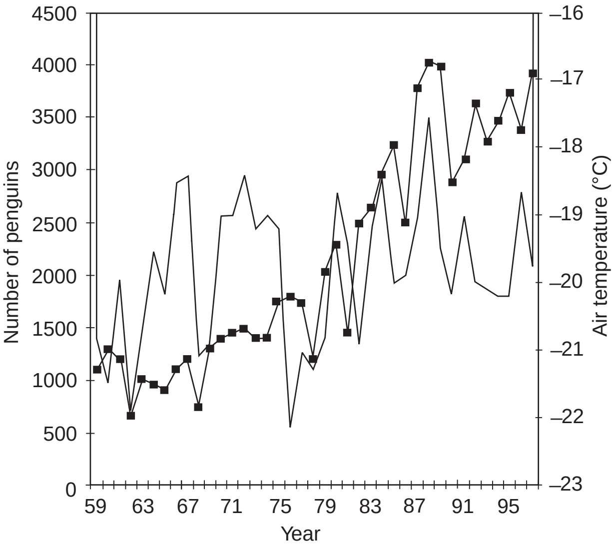

Figure 5 Changes in numbers of breeding pairs of Adélie penguins (■) at Cape Royds, Ross Island, Antarctica (77°S, 166°E), during the past four decades. This is the southernmost breeding site for any penguin species. Although changes in sea ice (less extensive now) is the major direct factor involved, average air temperatures (—) (indirect factor) of the region are shown.

As with the Antarctic Peninsula region, subantarctic species are invading southward. The first brown skua was reported in the southern Ross Sea in 1966; the first known breeding attempt occurred in 1982; and the first known successful nesting occurred in 1996. The first elephant seal in the Ross Sea was reported in 1974; at present, several individuals occur there every year.

Indirect Responses to Recent Climate Change

California Current

The volume of zooplankton has declined over the past few decades, coincident with reduced upwelling and increased sea-surface temperatures. In response, numbers of sooty shearwaters, formerly, the most abundant avian species in the California Current avifauna, have declined 90% since the 1980s (**Figure 2**). The shearwater feeds heavily on euphausiids in the California Current during spring. The decline, however, has occurred in a stepwise fashion with each El Niño or warm-water event. Sooty shearwaters are now ignoring the Peru and California currents as wintering areas, and favoring instead those waters of the central North Pacific transition zone, which have been cooling and increasing in productivity (see below).

The appearance of the elegant and royal terns as nesting species in California (see above) may in part be linked to the surge in abundance in northern anchovy, which replaced the sardine in the 1960s–1980s. More recently, the sardine has rebounded and the anchovy has declined, but the tern populations continue to grow (see above). Similarly, the former breeding by the brown pelican as far north as Central California was linked to the former presence of sardines. However, the pelicans recently invaded northward (see above) long before the sardine resurgence began. Farthest north the pelicans feed on anchovies.

Central Pacific

In the central North Pacific gyre, the standing crop of chlorophyll-containing organisms increased gradually between 1965 and 1985, especially after the mid-1970s. This was related to an increase in storminess (winds), which in turn caused deeper mixing and the infusion of nutrients into surface waters. The phenomenon reached a maximum during the early 1980s, after which the algal standing crop subsided. As ocean production increased, so did the reproductive success of red-billed tropicbirds and red-footed boobies nesting in the Leeward Hawaiian Islands (southern part of the gyre). When production subsided, so did the breeding success of these and other species (lobsters, seals) in the region. Allowing for lags of several years as dictated by demographic characteristics, the increased breeding success presumably led to larger populations of these seabird species.

Significant changes in the species composition of seabirds in the central Pacific (south of Hawaii) occurred between the mid-1960s and late 1980s. Densities of Juan Fernandez and black-winged petrels and short-tailed shearwaters were lower in the 1980s, but densities of Stejneger's and mottled petrels and sooty shearwaters were higher. In the case of the latter, the apparent shift in migration route (and possibly destination) is consistent with the decrease in sooty shearwaters in the California Current (see above).

Peru Current

The Peruvian guano birds – Peruvian pelican, piquero, and guanay – provide the best-documented example of changes in seabird populations due to changes in prey availability. Since the time of the Incas, the numbers of guano birds have been strongly correlated with biomass of the seabirds' primary prey, the anchoveta. El Niño 1957 (and earlier episodes) caused crashes in anchoveta and guano bird populations, but these were followed by full recovery. Then, with the disappearance of the anchoveta beginning in the 1960s (due to over-fishing and other factors), each subsequent El Niño (1965, 1972, etc.) brought weaker recovery of the seabird populations.

Apparently, the carrying capacity of the guano birds' marine habitat had changed, but population decreases occurred stepwise, coinciding with mortality caused by each El Niño. However, more than just fishing caused anchoveta to decrease; without fishing pressure, the anchoveta recovered quickly (to its lower level) following El Niño 1982–83, and trends in the sardine were contrary to those of the anchoveta beginning in the late 1960s. The seabirds that remain have shifted their breeding sites southward to southern Peru and northern Chile in response to the southward, compensatory increase in sardines. A coincident shift has occurred in the zooplankton and mesopelagic fish fauna. All may be related to an atmospherically driven change in ocean circulation, bringing more subtropical or oceanic water onshore. It is not just breeding seabird species that have been affected, nonbreeding species of the region, such as sooty shearwater, have been wintering elsewhere than the Peru Current (see above).

Trends in penguin populations on the Galapagos confirm that a system-wide change has occurred off western South America (**Figure 6**). Galapagos penguins respond positively to cool water and negatively to warm-water conditions; until recently they recovered after each El Niño, just like the Peruvian guano birds. Then came El Niño 1982–83. The population declined threefold, followed by just a slight recovery. Apparently, the carrying capacity of the habitat of this seabird, too, is much different now than a few decades ago. Like the diving, cool-water species of the California Current (see above), due to climate change, the penguin has lost its capacity for population growth and recovery.

Gulf of Alaska and Bering Sea

A major 'regime' shift involving the physical and biological make-up of the Gulf of Alaska and Bering Sea is illustrated amply by oceanographic and fisheries data. Widespread changes and switches in populations of ecologically competing fish and invertebrate populations have been underway since the mid-1970s. Ironically, seabird populations in the region show few geographically consistent patterns that can be linked to the biological oceanographic trends. There have been no range expansions or retractions, no doubt because this region, in spite of its great size, does not constitute

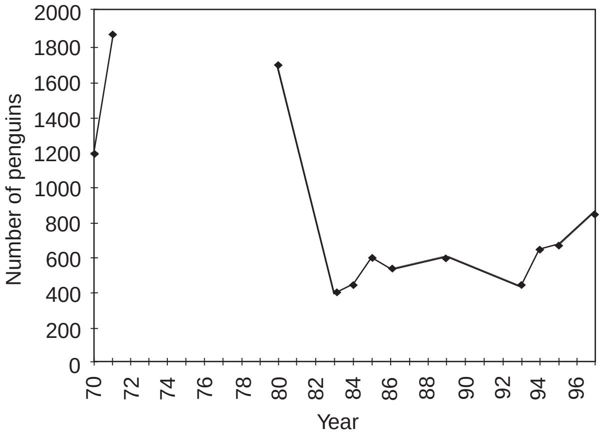

Figure 6 Changes in numbers of breeding Galapágos penguins, 1970–1997. With the 1982–83 El Niño event, the species lost the capacity to recover from periodic events leading to increased mortality. Compare to **Figure 3**, which represents another cool-water species having a similar life-history strategy, but which resides in the other eastern Pacific boundary current (i.e., the two species are ecological complements in the Northern and Southern Hemispheres).

a faunal transition; and from within the region, species to species, some colonies have shown increases, others decreases, and others stability. Unfortunately, the picture has been muddled by the introduction of exotic terrestrial mammals to many seabird nesting islands. Such introductions have caused disappearance and serious declines in seabird numbers. In turn, the subsequent eradication of mammals has allowed recolonization and increases in seabird numbers.

In the Bering Sea, changes in the population biology of seabirds have been linked to decadal shifts in the intensity and location of the Aleutian Low Pressure System (the Pacific Decadal Oscillation), which affects sea surface temperatures among other things. For periods of 15–30 years the pressure (North Pacific Index) shifts from values that are above (high pressure state) or below (low pressure state) the long-term average. Kittiwakes in the central Bering Sea (but not necessarily the Gulf of Alaska) do better with warmer sea temperatures; in addition, the relationship of kittiwake productivity to sea surface temperature changes sign with switches from the high to low pressure state. Similarly, the dominance among congeneric species of murres at various sympatric breeding localities may flip-flop depending on pressure state. Although these links to climate have been identified, cause–effect relationships remain obscure. At the Pribilof Islands in the Bering Sea, declines in seabird numbers, particularly of kittiwakes, coincided with the regime shift that began in 1976. Accompanying these declines has been a shift in diets, in which lipid-poor juvenile walleye pollock have been substituted for lipid-rich forage fishes such as sand lance and capelin. Thus, the regime shifts may have altered trophic pathways to forage fishes and in turn the availability of these fish to seabirds. Analogous patterns are seen among the seabirds of Prince William Sound.

Chukchi Sea

Decrease of pack ice extent in response to recent global temperature increases has been more pronounced in the Arctic than the Antarctic. This decrease has resulted in changes in the availability of under-ice fauna, fish, and zooplankton that are important to certain arctic seabirds. The decline of black guillemot populations in northern Alaska in the last decade may be associated with this pack ice decrease.

North Atlantic

The North Atlantic is geographically confined and has been subject to intense human fishery pressure for centuries. Nevertheless, patterns linked to climate change have emerged. In the North Sea, between 1955 and 1987, direct, positive links exist between the frequency of westerly winds and such biological variables as zooplankton volumes, stock size of young herring (a seabird prey), and the following parameters of black-legged kittiwake biology: date of laying, number of eggs laid per nest, and breeding success. As westerly winds subsided through to about 1980, zooplankton and herring decreased, kittiwake laying date retarded and breeding declined. Then, with a switch to increased westerly winds, the biological parameters reversed.

In the western Atlantic, changes in the fish and seabird fauna correlate to warming sea surface temperatures near Newfoundland. Since the late 1800s, mackerel have moved in, as has one of their predators, the Atlantic gannet. Consequently, the latter has been establishing breeding colonies farther and farther north along the coast.

South-east Atlantic, Benguela Current

A record of changes in sea-bird populations relative to the abundance and distribution of prey in the Benguela Current is equivalent to that of the Peruvian upwelling system. As in other eastern boundary currents, Benguela stocks of anchovy and sardine have flip-flopped on 20–30 year cycles for as long as records exist (to the early 1900s). Like other eastern boundary currents, the region of concentration of prey fish, anchovy versus sardine, changes with sardines being relatively more abundant poleward in the region compared to anchovies. Thus, similar to the Peruvian situation, seabird populations have shifted, but patterns also are apparent at smaller timescales depending on interannual changes in spawning areas of the fish. As with all eastern boundary currents, the role of climate in changing pelagic fish populations is being intensively debated.

See also

Benguela Current. California and Alaska Currents. Canary and Portugal Currents. El Niño Southern Oscillation (ENSO). Polynyas. Seabird Foraging Ecology. Sea Ice: Overview. Sea Level Change. Upwelling Ecosystems.

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SEABIRDS AND FISHERIES INTERACTIONS

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doi:10.1006/rwos.2001.0235

Introduction

Of the ~9000 species of birds in the world, only about 350 may be classified as seabirds (**Table 1**). The exact number of species depends on the definition of a 'seabird' and on recent taxonomic conventions. Here, in addition to the four orders that are generally considered as seabirds (all Sphenisciformes, all Pelecaniformes, all Procellariiformes, and some Charadriiformes), also divers or loons (Gaviiformes) and seaducks (members of the much larger order of Anseriformes) are included. Following this selection, it is apparent that only 4% of all species of birds utilize the greater part of the world's surface: the oceans. Seabirds prey upon fish, squid, and other marine organisms and the productivity of the oceans and regional variations in food availability determine the distribution, breeding success, and ultimately the numbers of seabirds on our planet. Most seabirds are largely piscivorous, but, particularly in the penguins, petrels and storm petrels, and northern auks, many species are planktivorous. Some seabirds exploit marine resources only outside the breeding season and shift to terrestrial feeding during nesting. Several species of seaduck exploit shellfish resources in shallow seas and these may shift to fish prey only under exceptional conditions.

Seabirds vary substantially in size and morphology. From the smallest of the storm-petrels (the least petrel *Halocyptena microsoma*, ~20 g) to the largest of the albatrosses (wandering albatross *Diomedea exulans*, up to 11 kg with a wingspan of up to 3.5 m) or penguins (emperor penguin *Aptenodytes forsteri*, 19–46 kg flightless), there is a great variability in capacity for flight, time spent at sea, preferred types of prey, and foraging techniques. Seabirds are wide-ranging organisms and they can be both predators and scavengers of marine