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# GLOBAL ECOLOGICAL CONSEQUENCES OF THE 1982–83 EL NINO–SOUTHERN OSCILLATION

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## SEABIRDS AND THE 1982-1984 EL NIÑO-SOUTHERN OSCILLATION

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## ABSTRACT

Duffy, D.C., 1989. Seabirds and the 1982-1984 El Niño-Southern Oscillation

The 1982-1984 El Niño and associated events affected seabirds in the Pacific and Atlantic oceans. Effects ranged from extralimital dispersal to nest desertion and adult mortality, and appeared most severe in the eastern Pacific upwellings off Peru and California, and in the central Pacific. Up to 85% of seabirds died in Peru. In contrast, effects were mild in the Caribbean Sea. Other areas such as the North Atlantic and Indian Oceans were apparently unaffected. El Niño appears to be an important force shaping life-histories only for seabirds in the Peruvian upwelling, where El Niño events are both frequent and severe. In other areas, with milder or less frequent events, responses to normal environmental variability, such as deferred breeding, readiness to abandon nesting efforts, and low reproductive effort, may be sufficient to buffer seabirds against all but the most severe El Niño events. On an evolutionary scale, El Niño, by generating massive extralimital dispersals or by exterminating colonies, may have caused disjunct ranges or even speciation in Pacific seabirds. Our ability to study the effects of El Niño on seabirds is limited by the lack of long-term, intensive studies of seabird populations. Without such studies, our knowledge is likely to remain anecdotal and superficial. We also lack information on the environmental features to which seabirds respond during El Niño. These may include sea and air temperature, rainfall, food abundance or parasite loads.

## 1 INTRODUCTION

Much of the early work concerning El Niño-Southern Oscillation (ENSO) resulted from efforts to protect Peruvian guano production from periodic decreases in yields caused by the emigration and mortality of guano-producing seabirds during such events (e.g. Murphy, 1925; Vogt, 1942; Schweigger, 1964; Jordan and Fuentes, 1966). ENSO was seen as an isolated, climatic aberration, unique to Peru (but see Vogt, 1940 for an early discussion of effects in other areas). More recently, after El Niño events in 1972-1973 and 1982-1984, a global perspective has linked ENSO with a mosaic of devastating droughts, floods, and changes in storm-tracks and commercial fish stocks far beyond the borders of Peru (Quinn et al., 1978; Glantz and Thompson, 1981; Rasmusson 1985). Such events have received increased attention with the aim of understanding their global consequences and forecasting future occurrences (cf. Glantz, 1981).

Although seabirds are no longer the reason for most ENSO research, they remain important indicators of the effects of such events at upper trophic

levels in marine systems (e.g. Jordan and Fuentes, 1966; Duffy et al., 1984; Schreiber and Schreiber, 1984). This paper summarizes the world-wide effects on seabirds of the events of 1982-1984 and examines the implications of these effects for the evolution of seabird life histories.

Two sets of events are documented: 1) those in the Pacific and Atlantic directly linked to changes in wind circulation and internal, marine waves (El Niño), and 2) 'teleconnections', shifts in global atmospheric circulation responding to the main event in the Pacific (Cane, 1983; Rasmusson and Wallace, 1983; Hansen, this volume). The overall event is referred to as El Niño-Southern Oscillation (ENSO hereafter). Since our understanding of ENSO is only at its initial stages, some of the apparent effects on seabirds may prove to be coincidences. But, by casting a wider net, I hope to stimulate ENSO research, much as investigation of guano bird mortality in the past provoked research on El Niño in Peru.

## 2. RESULTS

### 2.1 The Pacific Ocean

Within the Pacific Basin, oceanographic events during ENSO are triggered by three main forces that result from changes in atmospheric circulation: surface-water moving eastward along, or polewards from, the Equator; subsurface waves that displace cold water downwards, leading to the upwelling of warm water, poor in usable nutrients; and teleconnections.

(i) Central Pacific During the 1983 ENSO, the usually dry islands of the equatorial central Pacific experienced heavy rainfall, storms, and high winds as warm surface-water moved eastward past them (Rasmusson and Wallace, 1983).

Schreiber and Schreiber (1984, 1986) reported nearly total reproductive failure and a mass exodus of adult seabirds from Christmas Island (01°52'N, 157°20'W). Beginning in November 1982, burrowing and ground-nesting species such as shearwaters and petrels suffered flooding, either from heavy rains or from unusually high sea-levels. Arboreal nests of Black Noddies Anous minutus and Greater Frigatebirds Fregata minor were destroyed by rain. Nestling Lesser Frigatebirds F. ariel and Masked Boobies Sula dactylatra weighed less than in normal years. By October 1983, many species had resumed nesting but in greatly reduced numbers, suggesting that adult mortality or emigration had occurred, although at least one species, Crested Tern Sterna bergii, was unaffected (Ainley et al., 1988), perhaps because its inshore foraging environment suffered less change than offshore areas. Other species, such as Sooty Terns Sterna fuscata, apparently increased their subsequent breeding numbers. This may have resulted from greater synchronization of breeding efforts in the subsequent breeding season (Ainley et al., 1988). Such synchronization could

have arisen if most of the birds, having been prevented from breeding during ENSO, simultaneously found conditions suitable for reproduction.

At French Frigate Shoals (23°45'N, 166°10'W) and Jarvis Island (00°23'S, 160°02'W), Fefer (in Ainley et al., 1988) found a variable response to ENSO within the seabird community. Grey-backed Terns Sterna lunata and Masked Boobies abandoned nests but returned in pre-ENSO numbers the following year. Sooty Tern breeding numbers dropped by half. Black Noddy numbers did not decrease, but they fledged fewer and lighter young during ENSO. Nestling Red-footed Boobies Sula sula were also lighter. Breeding populations of Black-footed Diomedea nigripes and Laysan D. immutabilis albatrosses, Red-footed Booby, Brown Anous stolidus and Black noddies and White Terns Cygis alba were not affected during or after the 1983 ENSO, perhaps because ENSO conditions are not very different from those in their normal foraging habitats.

(ii) Galapagos Islands Earlier studies during ENSO events in Galapagos suggested that nesting failure occurred, but that adult mortality did not (Maridueña, 1977; Boersma, 1978; Harris, 1979). Coverage of the event in 1982 was sparse; however, observations during 1983 suggested a far more devastating event than any previously documented. Heavy rainfall, rapid vegetation growth, and flooding from higher sea-levels physically damaged nesting efforts (e.g. Rechten, 1985; Gibbs et al., 1987), while food apparently became less available, as suggested by adult mortality (Sosa, 1985) and decreased sizes of foraging aggregations (Duffy and Merlen, 1986). Numbers of two endemic species, Galapagos Penguin Spheniscus mendiculus and Flightless Cormorant Nannopterum harrisi, decreased to 23% and 51%, respectively, of 1980 levels (Valle, 1984). By 1985, cormorant numbers had recovered completely, and penguin numbers, although still only 38% of 1980 counts, were increasing (Valle, 1986; Valle and Coulter, 1987).

Other species experienced breeding failure: Waved Albatross Diomedea irrorata (Rechten, 1985), Greater Frigatebird (Hernandez and de Vries, 1985), Brown Pelican Pelecanus occidentalis, Blue-footed S. nebowxi and Masked S. dactylatra boobies (Gibbs et al., 1987), and Swallow-tailed Creagrus furcatus and Lava Larus fuliginosus gulls (Valle, 1985). Many individuals of these species apparently emigrated or died, since they were not seen elsewhere in the islands (Valle, 1985) or in adjacent waters (Duffy and Merlen, 1986). Adult mortality was reported (Sosa, 1985; Valle, 1985), but its extent was unknown. The rapid increase of birds in sea-transects following the 1983 ENSO (Duffy and Merlen, 1986) suggests that, rather than dying, many of the birds dispersed and returned.

In contrast to the negative effects, Magnificent Frigatebirds F. magnificens were relatively unaffected, with approximately half their

population breeding through the event (cf. Valle, 1985). Red-footed Boobies also bred without interruption (Merlen, 1985, but see Valle, 1985). These species normally feed in low productivity warm water areas, so that ENSO conditions might represent an extension of normal foraging habitat.

Breeding success of Dark-rumped Petrels Pterodroma phaeopygia increased in 1983 compared to 1981, but growth was slower, and birds took longer to fledge (Cruz and Cruz, 1985). Nest and burrow destruction, primarily by flooding or collapse, rose from 20% to 60%, but this was counterbalanced by the success of a rat control program that reduced predation from 24% to zero (Cruz and Cruz, 1985). The apparent increase in overall success may have had little to do with ENSO. High nesting success in 1984 (Cruz et al., 1984) supports this interpretation.

Many species resumed nesting in October 1983 (Valle, 1985), returning to their colonies as early as June 1983 (Merlen, 1985). The thermocline was re-established at its normal depths in June 1983 (Halpern, 1984), and the heavy rainfall characteristic of ENSO ended in July 1983 (Merlen, 1985).

Increased vegetation caused by the 1982-83 ENSO reduced available nesting space for Blue-footed Boobies on Isla Daphne Major until at least January 1986 and apparently limited Masked Booby nesting space as well (Gibbs et al., 1987). The growth of lantana (Lantana camara) during ENSO also reduced nesting space for Dark-rumped Petrels on Isla Floreana (Cruz et al., 1986).

(iii) Southeastern Pacific The effects of ENSO on the Peruvian and Chilean upwelling ecosystems are well known (e.g. Glantz and Thompson, 1981; Bernal et al., 1982; Arntz, 1986; Hansen, this volume). The onset of ENSO is marked by the arrival of eastward-moving subsurface waters on the west coast of South America, depressing the thermocline. Upwelling continues, but the cool nutrient-rich water that normally serves as the water-source is overlain by warm, nutrient-poor water (Smith and Huyer, 1983). Cold patches of water may remain along the coast, concentrating the marine fauna typical of upwelling. Successive cold-water patches of surviving prey are overwhelmed by southward-moving internal waves (Arntz, 1986). Prey such as "anchoveta" Engraulis ringens and mackerel Scomber japonicus move southward, offshore to deeper water, or die (Vogt, 1942; Zama et al., 1984; Arntz, 1986). Anchovy and the herring Clupea betincki typically experience reduced reproductive success during ENSO, but the reverse is true of the "sardina" Sardinops sagax (Tsukayama and Alvarez, 1981; Ware and Tsukayama, 1981; Bernal et al., 1982; Veloso and Arrizaga, 1985). Occurring at approximately 3.8-year intervals (Quinn et al., 1978, 1987), ENSO causes adult mortalities and nesting failure of the resident seabirds, especially the Guanay Cormorant Phalacrocorax bougainvillii, Peruvian Booby Sula variegata and Peruvian Brown Pelican Pelecanus occidentalis thagus (Vogt,

1942; Jordan and Fuentes, 1966; Duffy, 1983). Effects occur sequentially down the coast (Vogt, 1940; Jordan and Fuentes, 1966), apparently as cold-water refuges are swamped by southward-moving warm water (Duffy, 1983).

During the most recent ENSO event, Peruvian sea-surface temperatures began to rise in early October 1982, indicating the arrival of the subsurface wave (Smith, 1983). Emigration and mortality of guano birds started as early as October 1982 in northern Peru, but not until March 1983 in southern Peru (Tovar and Cabrera, 1985). Large numbers of Guanay Cormorants and Peruvian and Blue-footed boobies occurred in Ecuador in April-May 1983, presumably having emigrated from northern Peru or Galapagos (Herdson, 1984). Both booby species were present in Panama in April 1983 (Aid et al., 1985). Mortality of these species subsequently occurred in both areas (Herdson, 1984; Ainley et al., 1988; Smith, this volume). Blue-footed Boobies were also reported from northern Chile (22-23° S) in February 1983, along with an influx of warm-water fish (Guerra, 1983).

In southern Peru, southward movement of guano birds peaked during November 1982 - February 1983 (Fig. 1; after Hughes, 1985). Increased numbers, probably coinciding with a northward return of pelicans and cormorants, occurred from October onward in 1983. In Chile, an unquantified but large die-off of Guanay Cormorants, Peruvian Brown Pelicans and Peruvian Diving Petrels Pelecanoides garnoti took place from December 1982 to February 1983 in the vicinity of Arica, ca. 18°S (M. Pinto, via B. Araya, pers. comm.). At 21°S, Guerra and FitzPatrick (ms.) found that Grey Gulls Larus modestus shifted their molt patterns and did not breed during 1982-1984. Guano birds experienced a major influx from the north, then an 84% mortality. Local breeding of pelicans was disrupted by the influx of guano birds and of sea lions Otaria byronia. Pelicans were able to exploit larger prey than did the other guano birds, feeding on sardines Sardinops sagax moving in from the north, and did not experience food shortages as did the Guanay Cormorant and Peruvian Booby that require smaller prey.

Duffy et al. (1988) calculated a mean mortality of 0.22 - 0.25 birds/m along the Peruvian coast at the height of the 1982 - 1983 ENSO, based on data from Tovar and Cabrera (1985). The initial Peruvian guano bird population in March 1982, at the end of the breeding season, was six million adults and 2.9 million juveniles (Tovar and Cabrera, 1985). Toward the end of the event, in May 1983, only 330,000 birds remained in Peru (Fuentes, 1984) and numbers declined further to reach 110,000 by June (Tovar and Cabrera, 1985). By March 1984, ten months after the end of the ENSO, about 1.2 million birds were present in the area 12° - 18°S (Fuentes, 1984) (birds north of 12°S were not counted), suggesting a maximum mortality of approximately 87%, one of the highest ENSO mortalities recorded (cf. Jordan and Fuentes, 1966; Duffy, 1983).

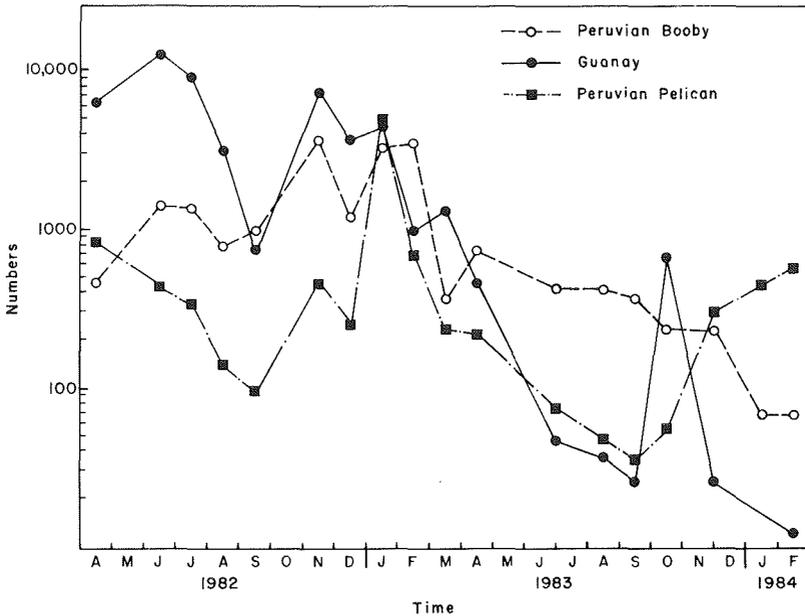


Fig 1. Numbers of birds passing north or south offshore from Mollendo, Peru, 17°S, April 1982 - February 1984 (after Hughes, 1985).

Humboldt Penguin *Spheniscus humboldti* numbers were reduced severely, with only 2,100 - 3,000 individuals surviving a 65% die-off of the initial population (Hays, 1986). Juveniles constituted 76% of 21 penguins found dead on beaches (Hays, 1986) and mortality was heavier (80%) in the northern part of Peru (5° - 12°11'S) than in the center (64%: 12°11'S - 15°30'S). Similarly, in Chile, Araya (pers. comm.) found that Humboldt Penguins in the northern part of the country (Tarapaca, Antofagasta, and northern Atacama) experienced a greater population decrease than did penguins farther south.

Scavengers such as Turkey Vultures *Cathartes aura*, and Kelp *Larus dominicanus* and Band-tailed *L. belcheri* gulls increased, apparently attracted to the dead birds (Arntz, 1986). In Paracas Bay, Black Skimmers *Rynchops niger*, inshore foragers in sheltered bays, appeared unaffected, whereas Chilean Flamingoes *Phoenicopterus chilensis* increased, presumably as a result of emigrants escaping the concurrent drought in the Andean altiplano (Arntz, 1986).

(iv) Central Eastern Pacific Central America experiences drought during ENSO events (Rand and Rand, 1982; Vega, 1987), linked to similar conditions in the Caribbean (Rasmusson, 1985). Effects of ENSO events are best documented for

landbirds (e.g. Foster, 1977; Wheelwright, 1986).

In 1982, the rainy season was drier and shorter than usual and drought conditions persisted into June 1983, caused by strong easterly winds that prevented the build-up of the cumulus clouds characteristic of the rainy season (Vega, 1987).

A colony of 400-500 pairs of Brown Pelicans at Isla Guayabo, Gulf of Nicoya, Costa Rica deserted in March 1982 and did not nest at all in 1983 (M. McCoy, pers. comm.). Pelicans breed during the dry season (Stiles, 1984), extending from December to April, when the Gulf of Nicoya is wind-mixed as a result of strong northerly winds (Peterson, 1960) spawned by polar cold-fronts (Hasenrath, 1966; Coen, 1983).

In Panama, Peruvian guano birds, including Peruvian Booby (see above), Guanay Cormorant, and Inca Tern Larosterna inca, occurred during the ENSO event (Smith, this volume).

(v) Northeastern Pacific Although 'warm events' in the northeastern Pacific have occurred in the past and are frequently synchronous with Peruvian events (Sette and Isaacs, 1960; McLain et al., 1985; Dayton and Tegner, this volume), this is not always the case (cf. Chelton et al., 1982).

The California Countercurrent strengthens during ENSO conditions (McLain and Thomas, 1983), transporting warmer water and planktonic warm-water organisms northward (cf. Hubbs, 1948; Radovich, 1961). Pacific mackerel experience increased reproductive success during ENSO events (Sinclair et al., 1985), and pelagic red crabs Pleuroncodes planipes are swept north by the countercurrent (McLain and Thomas, 1983). Anderson (1973), Ainley and Lewis (1974) and Ainley (1976) report on some effects of the 1972 ENSO on seabirds.

In 1983, large-scale warming along the North American west coast began in January; temperatures were above normal from Mexico to Alaska; and sea-levels rose to values higher than those reported in the previous severe ENSO of 1957-1958 (Lynn, 1983). The countercurrent reversed inshore in February - March 1983 and off northern California by April (Lynn, 1983), suggesting a return to more typical oceanographic conditions. Warm waters (anomalies in excess of 2°C) were present in the Gulf of Alaska from April through October 1983 (Royer and Xiong, 1984).

Among seabirds, changes in their distribution began in the boreal autumn of 1982, with fewer cold-water and more warm-water species in northern California waters (Ainley et al., 1988). Unusual warm-water species such as Black-vented Shearwater Puffinus opisthomelas, Black Storm-Petrel Oceanodroma melania, Craveri's Murrelet endomychura craveri, and Brown Booby Sula leucogaster began to occur near the Farallon Islands, off northern California, in early to mid 1983; the murrelet and storm-petrel having disappeared from their normal ranges

in the Gulf of California, Mexico (Ainley et al., 1988). Adult mortality included cormorants in California, murres and guillemots in California and Oregon, and Short-tailed Shearwaters Puffinus tenuirostris and Black-legged Kittiwakes Larus tridactyla in Alaska and Kamchatka (Nysewander and Trapp, 1984; Graybill and Hodder, 1985; Hodder and Graybill, 1985; Hatch, 1987; Ainley et al., 1988). Many breeding sites were deserted during the 1983 ENSO. Post-event populations were 50% lower for Tufted Puffins Lunda cirrhata on the Farallons (Ainley et al., 1988) and 19% lower for Pigeon Guillemots Cepphus columba in Oregon (Hodder and Graybill, 1985). Although some populations showed no decrease after the 1983 ENSO, Ainley et al. (1988) suggest that this apparent stability could have resulted from an influx of non-breeders.

Reduced nesting success occurred in a wide variety of birds. Pelagic P. pelagicus and Brandt's P. pencillatus cormorants and Common Murre Uria aalge produced fewer young in Oregon in 1983 compared to 1982, but Pigeon Guillemot and Western Gull Larus occidentalis success was not affected (Hodder and Graybill, 1985; Bayer, 1986). At the Farallon Islands, six of seven species (Brandt's and Pelagic cormorants, Western Gull, Common Murre, Pigeon Guillemot, and Cassin's Auklet Ptychoramphus aleuticus, but not Ashy Storm-petrel Oceanodroma homochroa), had their lowest nesting success in 1983, compared to data from 1981-1985 (Ainley et al., 1988). In Alaska, Black-legged Kittiwakes experienced nesting failure in 1983 (Ainley et al., 1988), but desertions have also been common in recent, normal years (Hatch, 1987). Common and Thick-billed U. lomvia murres and Horned Puffins had normal or improved breeding success in 1983, suggesting that diving species were less affected by ENSO, compared to surface-feeding kittiwakes (Hatch, 1987).

(vi) Southwestern Pacific During ENSO events, New Zealand and Australia are protected from eastward-moving cold-fronts by a 'blocking high' pressure area between eastern Australia and New Zealand, resulting in drought in Australia and unusually cold water off New Zealand (van Dijk et al., 1983). Beached-bird surveys (Veitch, 1975, et seq.; Powlesland, 1983, et seq.) showed few dead birds during the 1972, 1977, and 1983 ENSO events, but counts were higher in years following such events (Fig. 2). There was a major invasion and beach-wreck of southern ocean species in New Zealand, Australia, and Tasmania in 1984 (Carter, 1984; Powlesland, 1986). The absence of fronts, blocked by the high pressure area during ENSO events, would have resulted in calmer conditions, less likely to cause mortality of seabirds. The subsequent increase in counts of dead birds may reflect especially vigorous circulation in the Southern Ocean following ENSO events.

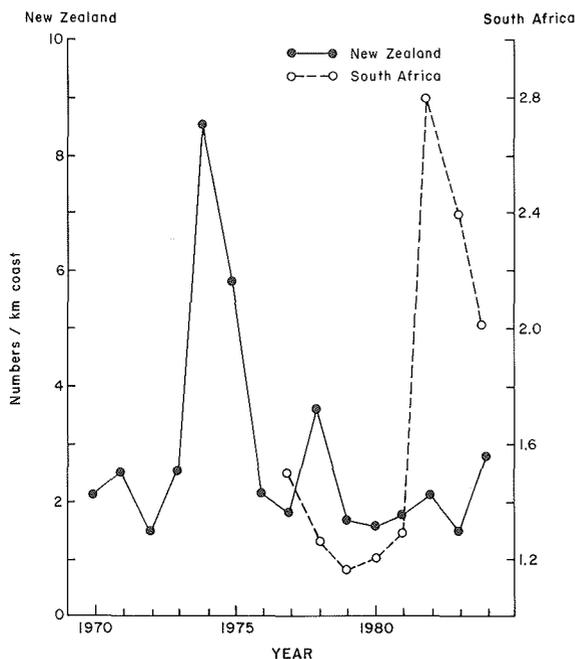


Fig 2. Annual number of beached birds/km coast for South Africa (1977 - 1983) and New Zealand (1970 - 1983), after Veitch (1975; et seq.); Powlesland (1983, 1984, 1985); and Avery (1985; pers. comm).

## 2.2 Atlantic Ocean

(i) South-west Atlantic The northward-moving shelf-waters off Argentina are sub-antarctic in origin, with an influx of water from the Straits of Magellan (Carreto et al., 1986). Local winds are strong from the west and southwest, especially in summer (Charpy and Charpy, 1977), resulting in coastal upwelling and productive inshore communities. Offshore, conditions are determined by the relative strengths of the warm, southward-flowing Brazil Current and the cold, northward-flowing Falkland Current; increased penetration by the Brazil Current and warmer conditions occur in summer (de Ciechomski and Sanchez, 1983).

In the South Georgia area, krill biomass in the upper water column during the austral winter of 1983 was considerably reduced compared to summer 1981-1982 (Heywood et al., 1985). Breeding failure of Gentoo Penguins *Pygoscelis papua* and Black-browed Albatrosses *Diomedea melanophris* occurred during the 1983-1984 summer, as it had following the 1976-1977 ENSO (Croxall and Prince, 1987). Breeding success of Grey-headed Albatrosses and Macaroni Penguins *Eudyptes chrysolophus* was also minimal, even though the former had been unaffected by the earlier event (Croxall and Prince, 1987).

In Chubut Province, King Cormorants *P. atriceps* did not breed at all during

their normal austral-summer breeding season in 1982-1983, while Rock Cormorants P. magellani had a limited and late nesting season (Boersma, in Duffy et al., 1988). In 1983-1984, both species had poor seasons.

Magellanic Penguins Spheniscus magellanicus had a relatively successful season in 1982-1983, but, in subsequent years, productivity and mean body size of young were reduced. Both these indices of breeding success are significantly and positively linked to January sea-surface temperatures. On the one hand, this suggests that warmer conditions favor penguin reproduction, while the reverse may be true for cormorants. On the other hand, Sclaro and Bodano (1986) reported an 86% mortality of fledgling Magellanic Penguins caused by heavy rains in 1984, as well as during 1976. Both these were El Niño years, suggesting that both terrestrial and marine conditions during ENSO events determine nesting success. In a limited series of counts of birds found dead during 1969-1985 along beaches at Costa Bonita, Buenos Aires, Argentina, 38°45'S, 58°50'W, Narosky and Fiameni (1986) found greatest numbers of dead Sooty Shearwaters, Slender-billed Prions Pachyptila belcheri and Magellanic and Rockhopper penguins Eudyptes chrysocome in the austral winter of 1984, coinciding with increased seabird mortalities in Australia.

Stronger than usual southward penetration by the Brazilian Current may occur during Pacific ENSO events when west winds increase because of a northward shift of the South Atlantic atmospheric high-pressure cell (Gillooly and Walker, 1984). At present, we can only speculate that this leads to increased sea temperatures and improved availability of anchovy engraulis anchoita, the major food of Magellanic Penguins (Sclaro and Bodano, 1986), and thus presumably to their increased nesting success.

(ii) Southeastern Atlantic The southwestern coast of Africa is a productive, upwelling system analogous to that off Peru. In the far south, upwelling occurs primarily during summer, whereas off Namibia upwelling occurs throughout the year, with some seasonal variation (Shannon, 1985). The southern upwelling is controlled by the South Atlantic high-pressure cell that moves south in summer, blocking eastward-moving cold fronts and producing southeast trade winds that result in coastal upwelling. In winter, the cell moves north, allowing fronts to penetrate, leading to onshore winds and cessation of upwelling (Andrew and Hutchings, 1980).

Two separate ENSO mechanisms affected the marine environment during 1982-1984 in southern Africa. In 1982-1983, the South Atlantic high-pressure cell remained north of its usual position during much of the summer, allowing fronts to move through and leading to reduced upwelling and warmer sea-surface temperatures (Nelson and Walker, 1984). Fishery landings yielded small catches of anchovy (Shannon et al., 1984). These conditions were local, mostly

affecting the southwestern Cape Province of South Africa. In 1984, the El Niño-like event in the tropical Atlantic (Horel et al., 1986; Shannon et al., 1986) led to an intrusion of warm water, heavy rains, and subsequent reproductive failure of the anchovy Engraulis japonicus capensis off Namibia (Boyd et al., 1985).

During 1982-1983, a mass breeding failure (75-95%) of Cape Cormorants Phalacrocorax capensis occurred in Saldanha and Lambert's bays of the western Cape, but not farther south or east. The failure seemed to be caused by local food shortages that forced breeding adults to undertake very long foraging trips and to neglect their nests (Duffy et al., 1984). Dead birds, especially Cape Cormorants, on beaches were more abundant during the 1982 and 1977 ENSO events than in normal years (Avery, 1985). This may represent increased mortality or simply reflect diminished offshore transport of dead birds during reduced upwelling.

During 1982-1983, breeding success of Cape Gannets Morus capensis was normal, but post-fledging mortality was higher than in previous years. African Penguins Spheniscus demersus deserted nests at Marcus and St. Croix islands (Duffy et al., 1984). Post-molting adults may have experienced higher than normal mortality (Avery, 1985).

Unfortunately, almost no information exists on the effects of the 1984 Atlantic EN in Namibia. No ornithologist worked on Namibian seabirds during this period. In South Africa, Cape Cormorants again experienced mass reproductive failure in Saldanha Bay (approximately 10,000 nests) during November 1983 (pers. observ.), but this may have been unrelated to events farther north. Survival of post-breeding adult African Penguins from Marcus Island dropped to a six-year low of 33.3% during 1984-1985, from a mean of 61.7% (La Cock et al., 1987).

(iii) Caribbean Sea Events within the Caribbean and their relation with ENSO appear exceptionally complex. The 1983 ENSO coincided with a major drought (Norton, 1983a,b, 1985) that was periodically broken as fluctuations of the jet-stream brought brief periods of heavy rain (Rasmusson and Wallace, 1983; Norton, 1983b). Marine productivity would have been affected by two factors: short-term variations in inshore productivity from local freshwater run-off, and longer-term, delayed variations in regional productivity influenced by runoff from the Orinoco and other rivers on the surrounding continents (Norton, in Duffy et al., 1988).

Local effects of the 1983 ENSO were mild, with a slight die-off among young Roseate Terns Sterna dougallii during an anomalous heat wave, and a reduction in nesting success of Sooty Terns (Norton, in Duffy et al., 1988). The 1984 Atlantic EN may also have affected the Caribbean, as egg-volumes of four

inshore foragers were smaller in 1984 than in 1985, while the reverse was true for three offshore foraging species; and commercial fisheries in the Virgin Islands were greatly reduced during November 1983-March 1984 (Norton, in Duffy et al., 1988).

### 3 DISCUSSION OF EFFECTS AND EVOLUTIONARY CONSEQUENCES OF ENSO

The effects of ENSO on seabirds appear to fall into three classes of increasing biological importance: 1) extralimital dispersals and range expansions; 2) reproductive failure; and 3) adult mortality.

Extra-limital dispersal seems characteristic of ENSO events. Warm-water seabird species invaded the California upwelling; Peruvian guano birds moved south into Chile and north to Panama; and northern migrants were unusually abundant in the Galapagos. Many of the vagrants died, although enough may have survived in past events so that species occasionally established themselves in new areas. Elegant Terns *Sterna elegans* are believed to have extended their breeding range 500 km south along the California coast to San Diego following the 1957-1958 event (Schaffner, 1986). The presence of Guanay Cormorants in Argentinian Patagonia may have resulted from dispersal of this species during the 1965 or earlier ENSO events (Erize, 1972). The disjunct ranges of other species such as Blue-footed Boobies could have been caused either by dispersing birds reaching and colonizing new areas during El Niño events, or by extinctions of colonies in intervening areas. El Niño might even be a cause of speciation under such circumstances. Unfortunately, post hoc zoogeographic explanations, invoking El Niño, can never be satisfactorily tested, but changes in range and new colonizations should be watched for following future events.

Nesting failure is a characteristic of many seabirds, especially those in tropical waters (cf. Nelson, 1978). Nesting failure is also one of the commonest effects of ENSO. As one more cause of such failures, ENSO probably exerts little selective force on seabird biology, because long-lived adults can survive to breed another year. However, if ENSO conditions persist over a number of years or if ENSOs increase in frequency so that reproduction is depressed for a long period, seabird populations would decrease, as may have happened a century ago to Cassin's Auklets in California (Ainley and Lewis, 1974). ENSO may also trigger shifts between warm and cold phases in marine ecosystems, leading to longer term changes in environmental suitability for seabirds (Shannon et al., 1984).

Adult mortality may be a much more serious result of ENSO, because populations of long-lived, slowly-reproducing seabirds can require decades to recover from a single major mortality (Southwood, 1981). Unfortunately, we lack data on the extent of mortality in most seabird populations during ENSO events. Counts of unmarked seabirds at colonies are often not especially useful, as

unchanged populations after an ENSO event might reflect greater nesting synchrony or increased recruitment of non-breeders, even if extensive mortality has occurred.

Two main factors determine the importance of ENSO in shaping the breeding and population biology of seabirds: the frequency and severity of ENSO events in relation to the generation time of the birds, and the degree of density-dependent mortality during an event.

Investigating frequencies of ENSO is difficult because of the absence of long time-series of data. Even when data are available, differing intervals between ENSO events may result simply from time-series of variable lengths being recorded in different areas. Nevertheless, such comparisons serve as useful starting points for further work and may indicate the time-scales necessary for future studies.

In Peru, moderate ENSO events (approximately 17% adult mortality: Duffy, 1983) occur at approximately five-year intervals (Quinn et al., 1978) and severe ENSOs (47% adult mortality: Duffy, 1983) occur at 12.3-year intervals (Quinn et al., 1978). Off southern Africa, Shannon et al. (1986) report only two ENSO-like events since the early 1950s: 1963 and 1984, an interval of 21 years. Along the west coast of North America, major El Niño events occurred in 1940-41 (Pearcy and Schoener, 1987) and in 1957-58 (Sette and Isaacs, 1960), but little research effort was expended on seabirds. Mortality occurred in the 1972 and 1983 events (Ainley et al., 1988), suggesting the minimum time between ENSO events with adult mortality in California is likely to be on the order of 10-15 years. Milder events may have passed unnoticed because of normal, interannual variation (cf. Hatch, 1987).

In other areas, the frequency of biologically 'significant' ENSO events appears to be similar. In Galapagos, major events occurred in 1972 and 1983. In the central Pacific, 1983 appears to have been the first ENSO studied (e.g. Schreiber and Schreiber, 1984; Ainley et al., 1988). Earlier severe events would have coincided with major events in Peru, as the ENSO mechanism involves both areas (Cane, 1983).

Southwood (1981) has argued that, when a species' average generation time (the years between first reproduction of an animal and of its young) is approximately equal in length to periods of favorable environmental conditions, the species will tend to lead a 'boom/bust' existence, with highly unstable populations, short generation times, high intrinsic rates of population increase, and mortality occurring irrespective of population size. In contrast, a species with a generation time shorter than typical periods of favorable environment will be long-lived, with a stable population, a low intrinsic rate of population increase, and birth rates sensitive to population densities. Conditions in Peru would appear to favor seabird species typical of the first

class of organisms, while conditions in the central Pacific islands, despite the events of 1983, favor species of the second. In neither case do birds have adaptations to survive ENSO events; they have adaptations to the environments that occur between events.

A seabird species adapted to survive Peruvian ENSOs would exhibit reduced reproductive effort to avoid depleted energy reserves that might jeopardize its survival at the onset of an ENSO. It would thus leave fewer offspring than other individuals during normal years. This might be advantageous if such 'bet-hedging' adults did indeed have a greater probability of surviving the next ENSO. If survival is mostly a matter of luck, however, the more offspring produced in good years, the greater the chance of some surviving the next ENSO. In tropical waters, adaptations to survive events that occur less than twice a century are less likely to be selected for than are adaptations to survive in the environment that occurs more than 95% of the time. Adaptations for this 'normal' environment include delayed maturity, small clutch size and frequent desertion (Goodman, 1974; Nelson, 1978). These serve to reduce the risk to adults caused by environmental variability. Such 'bet-hedging' features may also be sufficient to allow birds to survive all but the strongest ENSO events (cf. Curio, 1983).

Other marine environments may fall between the Peruvian and Pacific Island situations, with moderate mortality. Unfortunately, we usually lack the basic demographic data necessary to test this.

#### 4 CONCLUSIONS AND FUTURE WORK

The effects of ENSO on seabirds can be divided into two major themes: 1) proximate effects on breeding success and adult survival, and 2) ultimate effects on populations and the evolution of seabird species. Despite all the data presented above, we know little of either aspect.

Seabirds frequently desert their nests during an ENSO event, leaving their eggs and young to die. Some seabirds appear to anticipate the onset of an event (Vogt, 1940; La Cock, 1986; Schreiber and Schreiber, 1986). We need to investigate the forces that trigger desertions. Are desertions physically induced, by rain, high tides, anomalously high sea or air temperatures, or are food shortages and outbreaks of parasites responsible? Do desertions precede or coincide with the onset of an ENSO event? What kills adults: lack of food, parasites, diseases, or are most apparent mortalities in reality just emigrations from study areas?

The 1983 ENSO was physically one of the most severe ever recorded and seems to have affected areas usually uninfluenced by ENSO or where environmental 'noise' hides the effects of milder events (cf. Hatch, 1987, for a discussion of 'noise' and ENSO in Alaska). Nevertheless, ENSO is only one of a suite of

'cycles' that may effect seabirds and marine ecosystems (cf. Cushing, 1982; Freon, 1983). Some of the effects described here may not have been caused by ENSO alone, or even by ENSO at all. We can't be sure that the 1983 event wasn't a 40, 100, or even 1,000 year exception to normal patterns of environmental variability.

Untangling ENSO from other sources of variability will be difficult. We can start by examining the importance of different temporal scales of variability that affect seabirds (see Hunt and Schneider, 1987 for a brief discussion), as biologists have done for other marine organisms (e.g. Stommel, 1963; Lasker, 1978; Smith, 1978; Walsh, 1978). We need to work more closely with researchers studying 'teleconnections' between different parts of the globe. Our lingua franca must be time-series of quantitative data. Unfortunately, most studies of seabird populations last only a year or two. Some exceptions of relevance to ENSO studies include work on the seabirds of the Farallon Islands (Ainley and Lewis, 1974; Ainley et al., 1988) and on guano harvests and management reports from Peru and southern Africa (e.g. Jordan and Fuentes, 1966; Duffy, 1983; La Cock, 1986; Duffy and Siegfried, 1987; Schneider and Duffy, 1988). If we can't be bothered to study seabird populations at scales appropriate to their biology, we must consider whether we should study them at all.

Long-term studies ideally should include assessments of interannual variability in reproductive and life-history parameters, such as clutch size, young fledged, adult survival, age of first breeding, breeding frequency, and population size. These data will be most useful if diet and environmental parameters are sampled concurrently, at appropriate scales. We must also model populations (e.g. Leigh, 1981; MacCall, 1984). Modeling may allow us to determine whether our insights into how seabird populations work are reasonable, long before we have the data to test them directly.

Major ENSO events occur at approximately 12-year intervals (Quinn et al., 1978). The probability is high ( $p = 0.8 - 0.9$ ) of a strong event occurring by 2002 - 2003 (Glynn, 1988). Milder events, such as the one occurring in 1987, may also yield valuable data; however, if we are not to amass yet another collection of anecdotes in future reviews, we must have studies 'up and running' in time to capture events, rather than waiting until one is underway.

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