EL NIÑO AND THE BIRDS: A RESOURCE-BASED INTERPRETATION OF CLIMATIC FORCING IN THE SOUTHEASTERN PACIFIC

EL NIÑO Y LAS AVES: UNA INTERPRETACIÓN BASADA EN EL USO DE RECURSOS FRENTE AL FORZAMIENTO CLIMÁTICO EN EL PACÍFICO SUDORIENTAL

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ABSTRACT

Through a review, we attempt to identify what aspects of El Niño-Southern Oscillation (ENSO) determine the availability of resources that affect avian ecology in the southeastern Pacific. We recognized three functional bird types: seabirds, waterbirds, and landbirds (the latter separately treated as granivorous, insectivorous, carnivorous). The evidence shows that El Niño affects seabirds by reducing their food base. Seabirds feeding on fish, or fish plus squid, generally decrease their population abundance, as a combined result of adult mortality and reproductive failure. Omnivorous seabirds negotiate El Niño periods with modest declines, while those including fishery wastes in their diets show minimal changes during such periods. Waterbirds in the southeastern Pacific benefit from precipitation that accompanies El Niño, which enlarges their wetland habitats. Finally, landbirds are favored by El Niño-driven precipitation, which fires up primary productivity fuelling arthropod and mammal increases. Granivorous birds react promptly to peaks in seed output, while insectivores respond similarly to arthropod abundance. Carnivorous birds take somewhat longer to react to increases in mammal populations. We conclude that (a) Food shortage may be an important key factor for bird populations in the southeastern Pacific, but its effects depend on diet breadth, prey switching, and life history parameters. (b) Seasonal patterns of productivity determine distribution and abundance of resident birds, but variations imposed by occurrences of El Niño and La Niña phases determine the presence and abundance of migratory birds. (c) The dichotomy El Niño versus La Niña or versus 'normal' years is artificial and non conducive. (d) Long-term monitoring is needed to understand the connection between climate and birds.

Key words: seabirds, waterbirds, landbirds, food shortage, seasonal patterns, dichotomy El Niño/ La Niña, long-term monitoring.

RESUMEN

Mediante una revisión exhaustiva, tratamos de identificar qué aspectos del fenómeno El Niño-Oscilación Sur (ENOS) determinan la disponibilidad de recursos que afectan a la ecología aviar en el sudeste del Océano Pacífico. Hemos distinguido tres tipos funcionales de aves: marinas, acuáticas y terrestres (este último grupo subdividido en granívoros, insectívoros y carnívoros). La evidencia muestra que El Niño

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afecta a las aves marinas mediante la reducción de su sustento alimenticio. Las aves marinas que se alimentan exclusivamente de peces, o peces sumados a calamares, por lo general disminuyen su abundancia poblacional, como resultado combinado de la mortalidad de adultos y del fracaso reproductivo. Las aves marinas omnívoras franquean los períodos de El Niño con descensos poblacionales moderados, mientras que aquellas aves que incluyen en su dieta residuos de la industria pesquera muestran cambios mínimos. Las aves acuáticas en el sudeste del Pacífico se benefician de la precipitación que acompaña a El Niño, al ver ampliados sus hábitats de humedales. Por último, las aves terrestres se ven favorecidas por el incremento en la precipitación asociado al fenómeno El Niño, que conlleva un incremento de la productividad primaria y por consiguiente de la abundancia de artrópodos y mamíferos. Las aves granívoras reaccionan con rapidez a los máximos de la producción de semilla, mientras que las aves insectívoras responden de manera similar a la abundancia de artrópodos. Las aves carnívoras tardan un poco más en responder a los aumentos en las poblaciones de mamíferos. Concluimos que: (a) La escasez de alimento es un factor clave para las poblaciones de aves en el sudeste del Pacífico, pero sus efectos dependen de la amplitud de la dieta, la alternancia de presas, y los parámetros de historia de vida. (b) Los patrones estacionales de productividad determinan la distribución y abundancia de aves residentes, pero las variaciones impuestas por las fases alternas El Niño y La Niña determinan la presencia y abundancia de aves migratorias. (c) La dicotomía El Niño versus La Niña o versus "años normales" es artificial e inconducente. (D) El seguimiento a largo plazo es necesario para entender la conexión entre el clima y las aves.

Palabras clave: aves marinas, aves acuáticas, aves terrestres, escasez de alimentos, patrones estacionales, dicotomía El Niño/La Niña, seguimiento a largo plazo.

INTRODUCTION

There is plenty of anecdotal information that El Niño affects different aspects of avian ecology, ranging from individual to population to community aspects. Most of the evidence is qualitative and correlational at most, with few attempts to relate emerging patterns to underlying causes (see reviews by England 2000, Jaksic 2001, 2004). Pioneer exceptions were the publications by Jordan (1964)[1] and Tovar (1983, 1987) on guano birds in Peru, Boersma (1978) on Galapagos penguins in Ecuador, Harris (1979) on flightless cormorants in Ecuador, Graybill & Hodder (1985) on seabirds in Oregon USA, and Hays (1986) on Humboldt penguins in Peru. A benchmark was the publication of the proceedings of the 'Symposium on birds and the El Niño Southern Oscillation' (convened by R. W. Schreiber and D. C. Duffy in 1986), which concentrated on El Niño 1982-83 and examined its effects on Peruvian, Caribbean and Atlantic seabirds (Duffy *et al.* 1988), on North and South Pacific seabirds (Ainley *et al.* 1988), and on landbirds of North and South America (Hall *et al.* 1988). Foresightedly, Schreiber & Schreiber (1988) prefaced that such symposium was meant, among other things "...to encourage ornithologists to carry out long-term studies that will shed further light on the interactions between global atmospheric cycles, oceanographic phenomena, and avian populations."

But not much heed was paid to that recommendation. Most of the blame may be placed on the fact that the following El Niño's were much weaker (and less spectacular) than that of 1982-83. Indeed, those of 1986-87 and 1991-92 failed to elicit interest from ornithologists (see Anderson 1989, Lindsey *et al.*1997, for exceptions). Only with the advent of the strong El Niño of 1997-98 was there a renewed thrust on trying to understand this phenomenon with regard to birds in general (England 2000, Jaksic 2001, 2004). These latter three studies suffered some shortcomings: the first because it did not show any data, the second because it was broadly scoped, briefly touching on birds, and the third because it showed preliminary data delivered as a plenary lecture at a meeting. Thus, it seems timely to address this issue again, with emphasis on quantitative data.

Here, we attempt to remedy the lack of synthesis on the putative effects of El Niño on birds, through a review of accumulated evidence. We attempt to determine which aspects of El Niño (an oceanographic/atmospheric phenomenon) determine the availability of resources (food and habitat)

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[1]Jordan, R. 1964. Las emigraciones y mortandad de aves guaneras en el otoño e invierno de 1963. Informe del Instituto de Investigaciones en Recursos Marinos 27, 1-31.

that in turn affect avian ecology in the southeastern Pacific. We found that El Niño has contrasting effects, some positive and some negative, depending on the types of birds considered, and on the types of responses measured.

MATERIAL AND METHODS

We concentrated our literature search on the southeastern fringe of the Pacific Basin (including the Galapagos Archipelago), an area with which we are familiar and where most of the known effects of El Niño on birds have been reported. Nevertheless, we also considered results from the equatorial Pacific (Kiritimati Island, also known as Christmas Island but not located in the Indian Ocean) and northeastern Pacific (French Frigate Shoals, 500 km northwest of Hawaii), where seabirds have been particularly well studied. We searched the primary literature for quantitative, or at least categorical, data on bird abundance (and migration), mortality (or survival) and reproduction (or lack thereof), in connection with fluctuations in prey and habitat resources. We recognized three functional bird types: seabirds, waterbirds, and landbirds, regardless of systematic affinities.

With respect to seabirds, when enough references were available (*e.g.*, Ashmole & Ashmole 1967, Castro & Phillips 1996, Duffy 1983b), we characterized their main prey for four regions: Kiritimati Island, French Frigate Shoals, Galapagos Archipelago, and Peru. Following the methods of Shealer (2002), a Jaccard presence/absence coefficient of similarity (Jaccard 1901, Sneath 1957) was used to analyze similarity in diet composition of the seabirds living in each region. The pattern of similarity was contrasted using a cluster diagram of the Jaccard coefficients calculated for each species. The cluster was constructed using un-weighted average linkage methods (Wilkinson *et al.* 1996) and the significant level of similarity was estimated using the distribution of the Jaccard coefficients, calculated after bootstrapping 1000 times the prey matrix (Clarke 1993). To test the hypothesis that El Niño effects depend on diet preferences of seabirds, for each region we summarized reported changes in abundance and reproduction of the species belonging to every dietary group. For each group (cluster) we proceeded as follows: for any change in abundance,

the reported percentage was registered using negative values for decreases (due to increased mortality or emigration) and positive value for increases (usually associated with immigration). Similarly, any decrease in reproduction (nesting, clutch size, brood size, chick size, or survival) was denoted by its reported percentage in negative values and any increase by positive values. For our analysis we considered a threshold of 5% for a detected change. That way, in cases when changes on abundance or reproduction were mentioned but no percentage was given, we assumed a minimum effect of ± 5%. In cases when no change was mentioned we assumed 0%. We then averaged all the effects reported for each species, calculating the twice-standard error for each dietary group (data in tables 1 and 2).

Seabird species are referred to by common names throughout the text, but their scientific names may be found in table 1.

For waterbirds, all information that was available was so limited, that there was no need to use screening procedures, and therefore we analyzed all that was available. In this case, all usable data came from Chile.

For landbirds, we further divided this category among granivorous, insectivorous and carnivorous birds, because there were enough data to address these avian consumers separately. Most of the usable data came from the Galapagos Archipelago, Chile, and Argentina.

RESULTS
Seabirds

In the Pacific region, occurrences of El Niño-Southern Oscillation (ENSO) are associated with dramatic changes in seabird geographic distribution, population abundance, survival, and reproductive success (Arntz & Fahrbach 1996). Although a direct link between oceanographic events and seabird breeding failures and die-offs has been observed since long ago (Murphy 1926, 1936, Vogt 1942[2]), there is no clear determination of the mechanisms responsible. One of the most severe El Niño events occurred during 1982-83, and several studies gathered information about the changes on southeastern Pacific Ocean seabird populations. Below we document those responses.

[2] Vogt, W. 1942. Aves guaneras. Boletín de la Compañía Administradora de Guano del Perú. 18, 127-167.

Effects on migration, abundance and distribution

Murphy (1925, 1926) first noted massive migrations of resident seabirds away from Peruvian waters during El Niño events. Ainley *et al.* (1988) reported that in association with the 1982-83 El Niño, in February 1983, over 7,000 Peruvian Boobies and 10,000 Blue-footed Boobies appeared suddenly at the Bay of Panama. The occurrence of atretic follicles in Peruvian Boobies suggested that their reproductive cycles had been cut off sharply just prior to laying. The two species began to lose weight when fish disappeared in May. By August 1983, many Peruvian Boobies had died and Blue-footed Booby populations decreased by 50%. On June 1984, no Peruvian Boobies and only 75 Blue-footed Boobies remained in the Bay of Panama (Ainley *et al.*1988).

Distributions of seabirds are known to shift with movements of their preferred water temperatures (Ainley 1976, Spear *et al.* 2001). The 1982-83 El Niño confirmed this phenomenon. Duffy & Merlen (1986) compared bird counts in the Galapagos Archipelago during and after El Niño and reported species-specific changes in occurrence. Some species left (Audubon's Shearwater, Wedge-rumped Storm-petrel, Red-billed Tropicbird, Blue-footed Booby, Frigatebirds, Northern Phalarope, Swallow-tailed Gull, Brown Noddy and Galapagos Penguin), some arrived (Dark-rumped Petrel, *Oceanites* sp. Storm-petrel), while others remained in the Archipelago (Waved Albatross, White-vented Storm-petrel, Band-rumped Storm-petrel, Brown Pelican, Masked Booby and gulls). In central and northern California, Briggs et al. (1983) and Massey et al. (1992) reported that at the beginning of autumn 1982, cool-water species were noticeably less abundant, and warm-water species more abundant, than expected. By mid- to late 1983, even greater adjustments in California marine avifaunas occurred, when species normally not present in the northern part began to appear (Ainley *et al.*1988). Later, warm-water species such as Black-vented Shearwater, Black Storm-Petrel, Craveri's Murrelet and Brown Booby appeared at Farallon Islands and in some cases remained through the winter of 1984-85. These occurrences were preceded by the unusually early arrival and late departure of large numbers of Brown Pelicans and Heermann's Gulls. The same happened during the El Niño 1972-73 (Anderson & Anderson 1976). In the central subarctic Pacific, Wahl *et al.* (1989) re-ported higher than expected numbers of cool-water species in 1983, as if individuals had spread out, rather than concentrated in the more productive eastern margin as they usually do.

Effects on mortality and reproduction

Mortality of Peruvian guano birds as a result of El Niño is well known (Murphy 1925, 1936, Vogt 1942[2], Jordan & Fuentes 1966[3], Duffy 1983a, Ainley *et al.* 1988). During the 1982-83 El Niño, large numbers of dead and dying birds were observed at several places throughout the eastern Pacific (Ainley *et al.* 1988): boobies and Brown Pelicans in the Galapagos Archipelago and in Panama; cormorants, Common Murres and Pigeon Guillemots in California; murres and guillemots in Oregon; Short-tailed Shearwaters and Black-legged Kittiwakes in Alaska and the Bering Sea.

The absence of, or the decrease in, adults attempting to nest during 1983 meant a lower reproductive output for eastern Pacific seabirds. Schreiber & Schreiber (1984) reported low nesting success of most Sooty Terns at Kiritimati Island in 1983, although the few individuals of other species that attempted to breed were generally successful. At French Frigate Shoals, only 51% of Black Noddy pairs successfully fledged young, compared with 65% in 1981, and 69% in 1984. The asymptotic weight of Black Noddy chicks in 1982 and 1983 was only 108± 2 g (mean ± standard deviation), compared with 112 ± 2 g in 1980 and 115 ± 2 g in 1981. Asymptotic weights of Red–footed Booby chicks were also lower in 1982 (1178 ± 50 g) and 1983 (1165 ± 20 g) as compared with 1980 (1207 ± 20 g) and 1981 (1222 ± 20 g). Similarly, the weight of Dark-rumped Petrel chicks in the Galapagos Archipelago showed an effect of El Niño: At age 45 days they weighed 290 ± 69 g in 1983 compared with the 1981, 1984 and 1985 mean of 415 ± 52 g (Ainley *et al.* 1988). By the time chicks fledged, the between-year weight disparity had disappeared. The shape of the growth curve was unusual in 1983: it lacked the pre-fledging maximum typical of petrels. Chicks required longer fledging in 1983 (119 ± 6 days) than in other years (108 ± 6 to 113 ± 5 days).

It seems reasonable to relate the reproductive failure and high mortality that occurred at some localities with the arrival of El Niño 1982-83. Some nesting populations such as Flightless Cormorant

[3]Jordan, R. & H. Fuentes 1966. Las poblaciones de guaneras y su situación actual. Informativo del Instituto del Mar del Callao 10, 1-31.

in the Galapagos Archipelago, Graybacked Tern at French Frigate Shoals, Masked Booby at Jarvis Islands, Red-tailed Tropicbird at Kiritimati Island, and Brown Pelican in the Gulf of California, almost disappeared during 1983 and returned only after 1984. In some cases, the apparent stability of population sizes could be an artifact of recruitment from 'floating' populations. This was evident from a dramatic turnover among banded, breeding individuals, and the much lower numbers of non-breeding adult and sub-adult birds observed among Western Gull and Cassin's Auklet at the Farallon Islands (Ainley *et al.* 1988; see also Schreiber 1994 for Red-tailed Tropicbirds, and Ludwig *et al.* 2000 for Black-footed Albatross).

Effects on food web structure and rainfall regime
By comparing the effects of El Niño 1982-83 on seabirds of Peru and the Atlantic Ocean, Duffy *et al.* (1988) developed the idea that migration and mortality (or survival) of seabird populations could be associated with alterations of the marine food web, while changes in reproduction could be related with alterations of atmospheric circulation and with increased rainfall. These authors proposed that changes in the marine food web, mainly associated with a replacement of primary producers -from dino-flagellates to diatoms-, and of primary consumers -from copepods to chaetognaths- (Arntz & Fahrbach 1996) produced the migration to deeper water of the main secondary consumers -anchovies and sardines-, the preferred prey of seabirds. Hence, the massive migrations and die-offs of Peruvian seabirds was especially evident among surface feeders, including divers, pursuit plungers, and deep plungers, which require fairly reliable food sources (Shealer 2002), including Peruvian Boobies, Peruvian Pelicans, and Guanay Cormorants. Other birds turned to unusual food sources: Brown Pelicans and Inca Terns went to fishing terminals and ports; Guanay Cormorants, flock feeders specializing on pelagic fish species, fed inshore on mullet *Mugil* sp. (Arntz 1985), or died while attacking fish in nets (Herdson 1984). Arntz & Fahrbach (1996) reported that the main cause of changes observed during El Niño 1982-83 on seabird populations of Kiritimati Island and Galapagos Archipelago was shortage of food due to migration of pelagic prey (mostly fishes and squid) toward deeper water. But concurrent changes such as a higher plant cover due to increased rainfall,

and flooding of seabird reproductive grounds due to increased sea level, were also important causes of reproductive failures.

For Kiritimati Island, Schreiber & Schreiber (1984) determined the breeding chronology and reproductive attempts of the local seabird assemblage during 1982-83. Most seabirds on these islands have the following breeding characteristics: one large egg, long incubation period, extended parental care, post-fledging feeding of juveniles, deferred maturity, and long life span. These features are assumed to indicate pelagic food habits based on distant and ephemeral food supplies of small fish and squid. These pelagic birds depend on predatory fishes and marine mammals to drive smaller fishes and squid up toward the ocean surface. Therefore, these seabirds are thought to be limited by food availability. Data from Kiritimati Island collected from the 1940s to June 1982 revealed no reproductive failure of any species during that long period, when fishes and squid were the primary food source. But in November 1982, there was a total reproductive failure of all species present and a virtual disappearance of all individuals from the islands (Schreiber & Schreiber 1984). This situation was maintained until the end of 1983. Of 18 seabird species, 16 showed severe reductions of their population sizes while two (Crested Tern and Black Noddy) remained at their normal numbers. All the species but Crested Terns showed reproductive failures. Several of these failures were associated with increased rainfall. For example, despite populations being reduced by only 1 or 2% of normal levels, Great Frigatebirds nested, but all nests were either empty or were destroyed by rain. Black Noddy remained at normal population sizes but all nests were washed out of trees by rain. Schreiber & Schreiber (1984) concluded that in addition to the reduction of the already low primary productivity levels, the high sea level accompanying the heavy rains caused extensive flooding, and adult birds were either flooded out of nests or their breeding activity was inhibited by rain.

For the Galapagos Archipelago, Valle *et al.* (1987) presented a detailed report on seabird population responses to El Niño 1982-83. These authors showed that the El Niño event began when higher than normal sea surface temperatures and heavy rains were recorded. Observations of seabird breeding colonies indicated low or no reproductive

effort from July to September 1983. Ten species temporarily interrupted their breeding cycles, deserting young or eggs or not even attempting to breed: Galapagos Penguin, Flightless Cormorant, Waved Albatross, Audubon's Shearwater, Wedged-rumped Storm Petrel, Brown Pelican, Blue-footed Booby, Masked Booby, Red-footed Booby and Swallow-tailed Gull. Five other species bred during their normal period, but reproductive success was low: Dark-rumped Petrel, Red-billed Tropicbird, Great Frigatebird, Magnificent Frigatebird, and Lava Gull. Of 15 seabird species, 10 gave up breeding, while 5 continued breeding with low reproductive success. In general, seabirds feeding closer to shore (Galapagos Penguin, Audubon's Shearwater, Brown Pelican, Blue-footed Booby and Flightless Cormorant) were the most affected. This was particularly apparent in those species normally feeding in cold, upwelled waters (penguin and cormorant). These waters were displaced during El Niño 1982-83. Valle *et al.* (1987) and Cruz & Cruz (1990) pointed out that the slower growth rate and the death of large chicks observed in some species (Dark-rumped Petrel and Great Frigatebird), which did not abstain from breeding, could be associated with a severe decrease in food abundance, but also with rainfall collapsing burrows of the ground-nesting Dark-rumped petrel, and with increased plant cover on Frigatebird nesting places, which made the movements of this species more difficult. These effects were most evident in the case of Waved Albatross nesting on Española Island, where all nesting grounds were flooded and covered by plants. It is worth mentioning that the only successful breeders were species with scavenging habits. Those species with population decreases, as well as with low or no reproduction, comprised inshore and pelagic foragers apparently unable to shift to alternative foods.

Effects of fisheries

The largest decreases of seabird populations along Peruvian and Chilean coasts since 1909 have been associated with El Niño events (Arntz & Fahrbach 1991). Due to their dependence on anchovies, which usually disappear during El Niño, Peruvian Booby, Guanay Cormorant and Peruvian Pelican are highly sensitive to the occurrence of El Niño, but also to anthropogenic activities such as guano exploitation and fisheries. For instance, by the end of the 1950s, and partly due to artificially increased nesting facilities (Jordan & Fuentes 1966)[3] these three seabird species increased their abundances almost five times, reaching a total of 20 million individuals.

Fisheries became important in the early 1960s, when anchovies (*Engraulis ringens*) began to be processed into fishmeal. The industry grew spectacularly, from less than 1 million metric tones in 1955 to 12.3 million metric tones in 1970. Overfishing and the El Niño 1972-73 led to a dramatic reduction in catches, to the point that the record catch has never again been approached. Instead, the fishery switched to sardines (*Sardinops sagax*) in Peru and to the Peruvian horse mackerel (*Trachurus murphyi*) in Chile. El Niño events have always had a negative influence on guano bird populations, but severe crashes have only been apparent since fishing activities intensified (Duffy et al. 1984). A possible explanation is that the anchovy fishery took up the superabundance of food on which the seabirds depended to cope with the crashes induced by oceanographic perturbation (Duffy 1983a, Arntz & Fahrbach 1991, Crawford & Jahncke 1999). Another explanation is that anchovies and sardines alternate in abundance over decadal scales and that anchovies are able to sustain higher seabird populations than do sardines or mackerels (Chávez *et al.* 2003).

Mechanisms invoked

El Niño 1982-83 affected species living in four areas of the South Pacific in different ways. On Kiritimati Island, Schreiber & Schreiber (1984) reported that 16 of 18 seabird species suffered nesting failures ranging from 70% to 100%. Black Noddy populations showed a reduction of 100% in chick survival, while Crested Tern did not show changes in either reproduction or survival. With regard to mechanisms involved, Schreiber & Schreiber (1984) mentioned that reproductive failures of the Great Frigatebird and the Black Noddy were due to the effect of rain, which flooded or destroyed their nests. But no mechanistic explanation was offered for the failures of other species.

At French Frigate Shoals, Ainley *et al.* (1988) reported a reduction of 10% in the reproductive output of two species: Black Noddy and Red-footed Booby. In this case, no mention was made of any causal mechanism for these effects.

In the Galapagos Archipelago, 22 seabird

species were studied during the 1982-83 El Niño. Eleven of the species showed a decrease in nesting success; three species had reduced chick size and survival, and nine species showed decreased abundances -due to mortality or migration-. On the other hand, seven species showed no significant changes in abundance or reproduction, while two species (Dark-rumped Petrel and an *Oceanites* sp. Storm Petrel) increased their abundances. The Dark-rumped Petrel also showed higher nesting densities, but with chicks of smaller size. In terms of mechanisms invoked, food shortage was associated with the reduction in size of Dark-rumped Petrel chicks as well as with the reduction of Great Frigatebird chick survival. Due to the unusual amount of rainfall, coastal vegetation increased considerably. This phenomenon was associated with the increase in Dark-rumped Petrel nesting and with the reduction in nesting success of Waved Albatross and Blue-footed Booby. Despite the high number of species affected, no other mechanisms were mentioned to explain the observed effects.

In the Peruvian coast, eight of 11 species showed decreased abundances (ranging from 50% to 100%) due to massive die-off and migration. Three species displayed no changes in abundance, but Cormorants, Inca Terns and Brown Pelicans shifted diets. For all cases food shortage was mentioned as the main cause.

Trophic ecological effects

Diet studies on breeding seabirds abound so that more is known about what seabirds eat than any other aspect of their ecology. The prey type that seabirds select can have important fitness consequences, particularly during the chick-rearing period (Pierotti & Annett 1990). Diets of breeding seabirds usually consist of a very limited range of taxa: primarily pelagic fishes, squid and crustaceans (krill and euphausiids) (Montevecchi & Myers 1996). Nevertheless, the composition of such diets is not static between years, seasons, or even weeks. Changes in diet more likely reflect changes in the marine prey base, or shifts in foraging habitat, than they reflect inherent changes in seabird preference (Ainley & Boekelheide 1990, Ainley *et al.* 1993, 1995, Montevecchi *et al.* 1995, 1996, Ainley & Divoky 2001, Spear *et al.* 2007, Ainley & Tukenian 2010). Thus, diet studies are used as indicators of

the health of the marine ecosystem, because prey harvest often is correlated with prey abundance at a variety of scales (Montevecchi & Myers 1995), and changes in seabird diet often reflect variations in the prey base (Montevecchi *et al.* 1998, Crawford & Jahncke 1999, Jahncke & Goya 2000). Baird (1990) suggests that surface feeders are more vulnerable than subsurface feeders to environmental changes, but this is opposite to much of the evidence (Duffy 1983b, D.C. Duffy pers. comm. 2005, Ainley & Tukenian 2010).

In terms of its exploitation, the ocean represents a challenge for seabirds. The problem of finding enough food to survive and reproduce in this realm has generally been solved in one of three ways. Coastal or inshore species, such as most gulls and terns, gather to feed in areas where prey are abundant or where they are forced to the surface. Diving seabirds, including penguins and alcids, can exploit a greater range of depths to obtain food. Pelagic species, such as albatrosses, shearwaters, and some petrels, soar over vast expanses of the ocean surface at a relatively low energy cost in search of widely dispersed surface prey. Seabirds may feed either during daylight hours (diurnally) or at night (nocturnally). Presumably these diel habits are a response to the behaviour of their primary prey. Nevertheless, some species such as Red-footed Boobies and Red-tailed Tropicbirds may forage during both day and night (Schreiber & Schreiber 1993).

During periods of reduced food availability, such as El Niño years, seabirds may be forced to switch their diet from foods that enable them to survive and reproduce (Pierotti & Annett 1990, Jahncke & Goya 2000). During these periods seabirds can maximize the chances of their own survival by not breeding rather than by attempting to breed and risk death of both adult and offspring (Goodman 1974, Harris *et al.* 1998). Based on these ideas it has been proposed that seabirds with a restricted dietary range and with no chances to effect prey switching, will suffer reproductive failures during periods of reduced food availability. Depending on how severe and long is the period of reduced food, seabirds may suffer high mortality (Pierotti & Annett 1990). On the other hand, seabirds with a broad dietary range and able to switch prey, may display no changes in reproduction and survival, or may even improve their reproductive rate during periods of food shortage of

their usual food (Stewart *et al.* 1984).

To explore these ideas we analyzed information available in 10 studies on the effects of the 1982-83 El Niño on seabird populations in four areas of the South Pacific Ocean (Table 1). At Kiritimati Island for a total of 18 species, 17 suffered reproductive failures ranging from 40% (Lesser Frigatebird) to 100% (Audubon's Shearwater, Brown Booby, Brown Noddy and Sooty Tern). At French Frigate Shoals there is information on two species that suffered reduction from 10 to 20% on their chick body sizes. The Galapagos Archipelago showed the most diverse array of effects: Among 22 species, four suffered reductions in both their abundances and reproductive activities, five solely in their abundances, eight in their reproductive activities, three did not show any alteration, one increased in abundance (White-throated Storm Petrel), and one in reproductive activities (Lava Gull). In the case of Peru, among eight species, six experienced reductions in their abundance (ranging from 50 to 90%) and two displayed no changes at all (Flightless Cormorant and Inca Tern).

We characterized the diet of 41 seabird species (Table 2). At Kiritimati Island all the species were piscivorous but due to the inclusion of squid in their diet, two different dietary groups (Fig. 1a) were recognized: piscivorous and fish+squid consumers. In these islands the averaged effect of El Niño over the species in this feeding group (Table 1) was a general reduction of -82% ± 6.26, this value being -78 ±17.0% for the piscivorous group and -85 ± 4.9 % for the fish+squid eaters. Most of the birds in the Galapagos Archipelago consumed fishes, crustaceans and squid, but due to the inclusion of sea lion wastes and fishery wastes, two main dietary groups were recognized in this archipelago (Fig. 1b). The averaged El Niño effect over the species in this feeding group (data in Table 1) on the Galapagos birds was -27 ± 6.2% , which corresponded to -31 ± 6.7% for fish, crustacean and squid eaters, and to -2 ± 3.3% for consumers of fish+crustacean+squid+sea lion waste +fishery waste. In Peru, two dietary groups (Fig. 1c) were identified: fish consumers (7 species) and fish+squid consumers (Inca terns). The averaged effect of El Niño (Table 1) on these birds was -57 ± 14.1%, corresponding to -80 ± 12.7% for fish consumers and +5 ± 0.0% for Inca terns. Our results show that in general there is an inverse relationship between El Niño events and the breadth
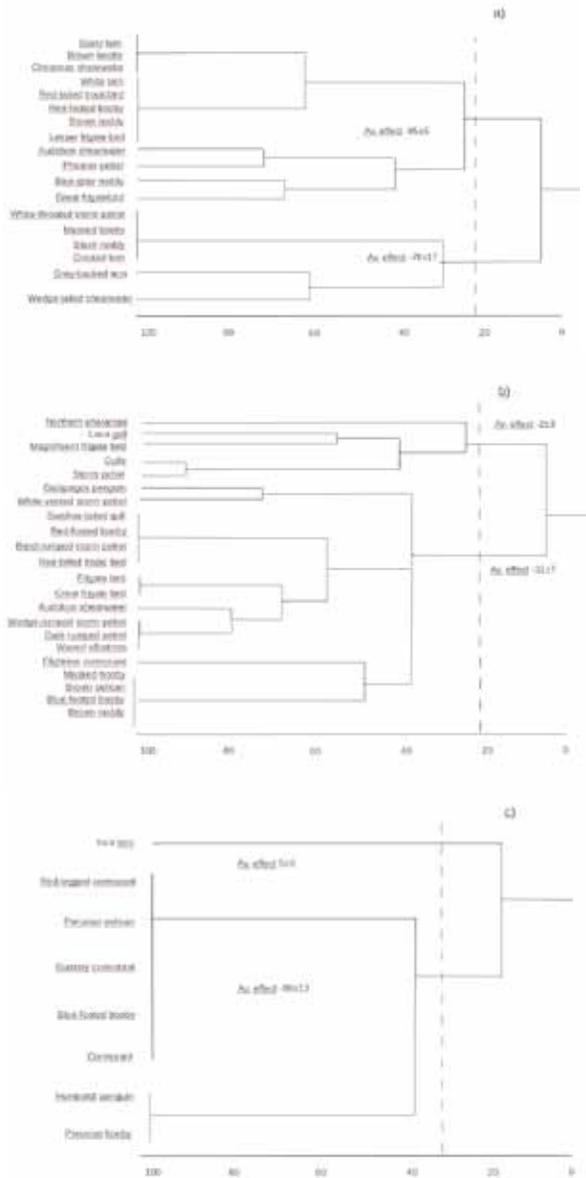

Fig. 1. Percent dietary similarities on seabird species of three southeastern Pacific Ocean regions: (a) Kiritimati Island, (b) Galapagos Archipelago, (c) Peru. Dashed line defines the limit of similarity for the dietary groups (∝ < 0.05). The averaged effect of El Niño 1982-83 for each recognized dietary group is shown (based on data in tables 1 and 2).

of seabird diets. Seabirds with a narrow dietary breadth (e.g., those eating fish and fish larvae) were the most severely affected by El Niño 1982-83, while species eating more than four different prey items

(species from the Galapagos Archipelago) were less affected. In addition, it appears that the inclusion of crustaceans, and specially fishery wastes or carrion (sea lion wastes), in the diet alleviated the shortage of food. Seabirds with the ability to switch and use these food types (*i.e.*, Inca tern in Peru) were basically not affected by El Niño.

Waterbirds

The distribution and area of wetlands are highly variable and depend on climate conditions, especially rainfall. Any change in these variables has the potential to impact strongly on birds dependent on such habitats. Analyses of El Niño effects on waterbird populations are scarce. In the southeastern Pacific, no reports were issued on this group of birds during the 1982-83 event, but three studies (Vilina & Cofré 2000,Vilina *et al.* 2002, Schlatter *et al.* 2002) were developed in Chilean wetlands during El Niño 1997-98.

Vilina & Cofré (2000) analyzed the presence, seasonal abundance, and habitat associations of four grebe species: White-tufted Grebe (*Rollandia rolland*), Silver Grebe (*Podiceps occipitalis*), Great Grebe (*Podiceps major*) and Pied-billed Grebe (*Podilymbus podiceps*), in a central Chilean wetland. They found a positive correlation between spring abundance of all these species and total rainfall the previous year. Rain fell chiefly during the winter and spring of the El Niño year (1997); grebe populations increased during the summer (beginning of 1998), and peaked during the spring of 1998. Further, the Silver Grebe bred in the wetland studied only during the El Niño and post-El Niño years.

Vilina *et al.* (2002) analyzed the relationship between the 1997-98 El Niño event, rainfall, and changes in abundance, breeding and local distribution of an endemic bird of southern South America, the Black-necked Swan (*Cygnus melancoryphus*), in a central Chilean wetland. During and after the El Niño event, Black-necked Swan increased in abundance, breeding success, and time of presence (from seasonal to year-around) in the wetland studied. Based on Vilina *et al.*'s (2002) observations it seems logical to predict that during the alternate phase of El Niño (that is, La Niña), which brings drought conditions, a reduction in Black-necked Swan abundance and possibly increased migration to southerly wetlands may occur.

In the context of waterbird migration, Schlatter *et al.* (2002) developed the idea that Black-necked Swan populations in a wetland of southern Chile fluctuated within years due to seasonal rainfall patterns and between years due to El Niño events. They hypothesized that because of migration from northern wetlands (with unstable water levels), populations in the south peaked during dry years associated with La Niña. Their results showed that numbers of swans more than doubled during the La Niña period of 1996 to mid-1997. These periods coincided with a regional drought that forced northerly wetland swans to move nomadically toward the south, where Rio Cruces is a water stable wetland and a likely population source for Black-necked Swans for all of Chile.

Thus, waterbirds seem to benefit from precipitation that accompanies El Niño, which enlarges the water surface of marshes, coastal lagoons, and other waterbodies. Increased wetland habitat then affords more opportunities for building adequate nests and obtaining sufficient food.

Landbirds

Landbirds are affected by El Niño in two contrasting ways: Negatively, because when El Niño arrives, excessive precipitation may result in nesting failure and increased chick mortality due to nest flooding, thus lowering reproductive success. The subsequent drought years that follow El Niño (usually the reverse phase of La Niña) further decimate bird populations because of the depletion of food resources, which may trigger reduced allocation of energy to breeding. These negative effects have been reported in the Galapagos Archipelago (Gibbs & Grant 1987, Grant & Grant 1987, 1993, Hall *et al.* 1988), Snares Islands of New Zealand (Miskelly 1990), Hawaii (Lindsey *et al.* 1997), and continental Argentina (Masello & Quillfeldt 2003). On the other hand, El Niño-driven precipitation fires up primary productivity (aboveground plant biomass and seed crop), which in turn fuels arthropod and mammal increases in semiarid regions of South America, thus positively affecting bird populations.

Granivorous birds

There is information on the response of granivorous birds to seed availability for three sites, presented here in chronological sequence. On Daphne Island, Ecuador, seed abundance (mass in the soil) increased strongly with the El Niño year of 1983, and remained high in 1984 (Fig. 2). Finch abundance
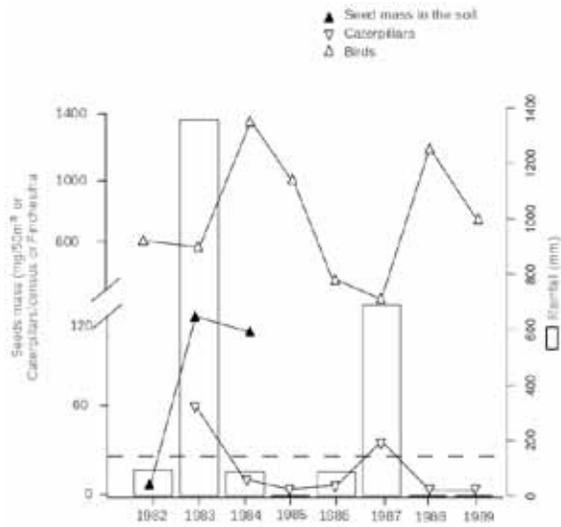
Fig. 2. Yearly course of finch abundance (1982-1989), total seed biomass (1982-1984) and caterpillar abundance (1983-1989), together with rainfall (1982-1989) in Daphne Island, Galapagos Archipelago. Mean annual rainfall is shown as dashed line. El Niño events occurred in 1982-83 and 1987.
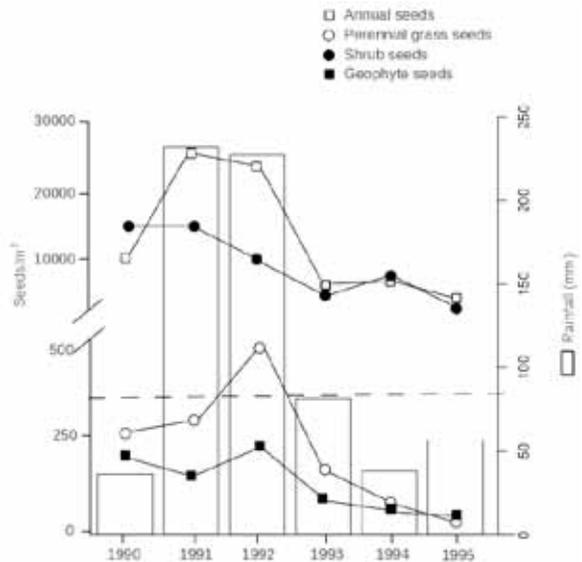

Fig. 4. Yearly course of seed abundance of different types, together with rainfall (1990-1995), in Fray Jorge, northern Chile. Mean annual rainfall is shown as dashed line. An El Niño event occurred in 1991-92

peaked one year after the rainfall and seed peak of 1983, subsequently declined, and again peaked with a one-year lag after the high-rainfall year brought by El Niño 1987. Although this time no record was kept of seed abundance, the similarity in pattern
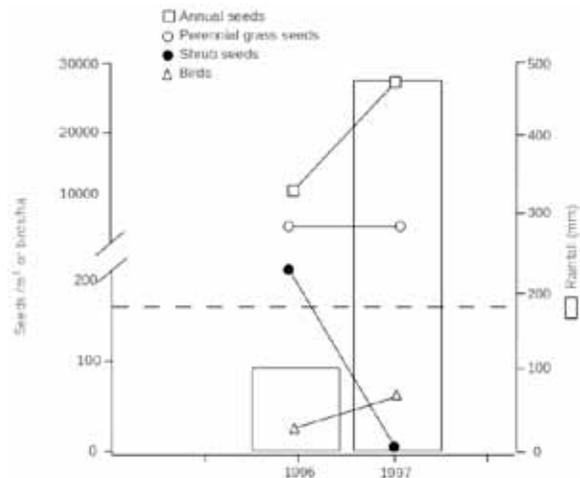

Fig. 3. Yearly course of bird abundance, seed abundance of different types, together with rainfall (1996-1997), in Auco, northern Chile. Mean annual rainfall is shown as dashed line. An El Niño event occurred in 1997.

seems beyond coincidence. It is interesting to note that caterpillars also were in high abundance during El Niño years of 1983 and 1987, and that finches

use these prey to feed their nestlings.

In Auco, semiarid Chile, the increased rainfall brought by El Niño 1997-98 resulted in an immediate increase in annual herb seeds, in a lack of response in perennial herb seeds, and in a decrease in shrub seeds. Granivorous birds increased in abundance from 26 to 58/ha by 123% (Fig. 3). A similar phenomenon was described in Fray Jorge, semiarid Chile, where the increased rainfall brought by El Niño 1991-92 resulted in an immediate increase in annual herb seeds, a slower one in perennial herb seeds, a 1-yr delayed increase in geophyte seeds, and a decrease in shrub seeds (Fig. 4). Unfortunately, no tally was kept of granivorous bird abundance.

In Ñacuñan, Monte desert of Argentina, El Niño of 1997 brought increased precipitation (but there may be other important climatic influences at play, see Compagnucci *et al.* 2002). Higher rainfall did not elicit a response from perennial herbs or forbs, but there was a marked increase in seed germination and seedling survivorship (Fig. 5). Nevertheless, bird abundance remained flat (López de Casenave 2001)[4].

The response of granivorous birds to peaks in seed output reported above is suggestive. Both in Daphne Island and in Auco there was a positive response. In Ñacuñan there was no increase in seed crop to which the birds could respond. The

[4]López de Casenave, J. 2001. Estructura gremial y organizacion de un ensamble de aves del desierto del Monte. Doctoral Thesis, Universidad de Buenos Aires, Buenos Aires, Argentina.
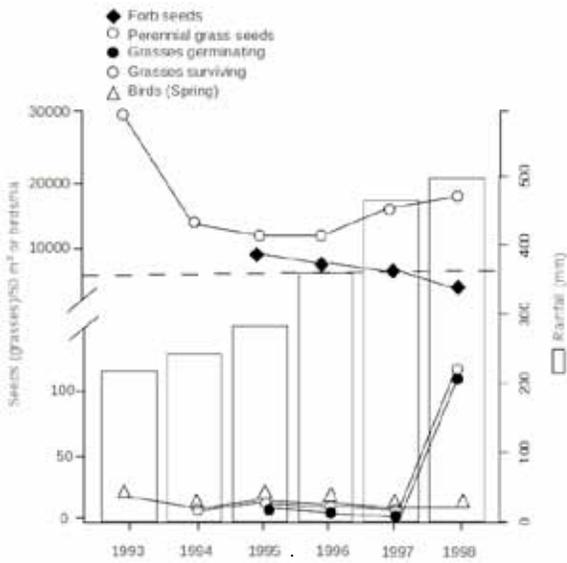
Fig. 5. Yearly course of bird abundance, seed abundance of different types, seed germination and survival, together with rainfall (1993-1997), in Ñacuñan, western Argentina. Mean annual rainfall is shown as dashed line. An El Niño event occurred in 1997.

functional response of insectivorous birds was steep at the start, but tended to saturate quickly, reaching an asymptote. Again, the response of insectivorous birds to peaks in insects reported above is suggestive, but marred by lack of consistent monitoring.

Fig. 6. Seasonal course of the abundance of insectivorous birds and arthropod prey, together with yearly rainfall (1992-2002) in Auco, northern Chile. No animal data are available 1998-2000. During winter and spring 2002 arthropods could not be sampled. Yearly rainfall corresponds to precipitation accumulated from autumn (March) to summer the following year (February). Mean annual rainfall is shown as dashed line. El Niño events occurred in 1991-92, 1997, 2002.

best database, that from Fray Jorge, did not simultaneously record bird abundance and thus did not contribute to make a better case for the coupling between seeds and birds.

Insectivorous birds

Information on the response of birds to arthropod availability exists for only two sites, presented chronologically here. On Daphne Island, Ecuador, caterpillar abundance was high during the El Niño year of 1983, and decreased thereafter until El Niño 1987, which resulted in another caterpillar peak (Fig. 2). Unfortunately, the tally kept for bird abundance considered only finches, and not true insectivores.

In Auco, semiarid Chile, insect and insectivorous bird populations decreased after the El Niño of 1991-92 until the augmented rainfall brought by El Niño 1997-98 resulted in a simultaneous increase in arthropod and bird abundance (Fig. 6). Unfortunately, the monitoring data covering the following three years disappeared, and thus the response of insects and birds to El Niño 2002 was obscured by the lack of preceding background. Nevertheless, a plot of insectivorous bird abundance against arthropod abundance yielded a diminishing return (Fig. 7). The

Fig. 7. Relationship between insectivorous bird and arthropod prey abundance in Auco, northern Chile. Each datapoint corresponds to a calendar season (n = 26). The regression line corresponds to the best fit by Vernier Graphical Analysis 3.1.
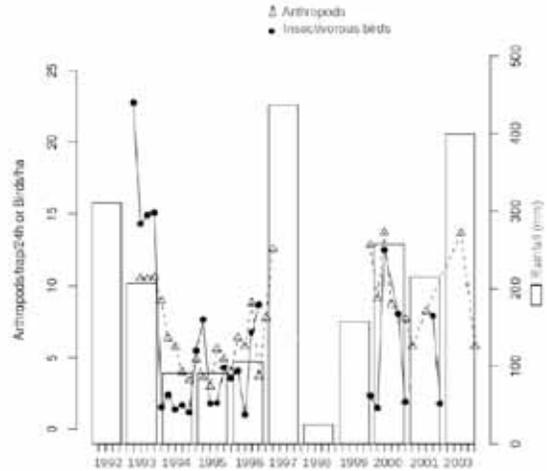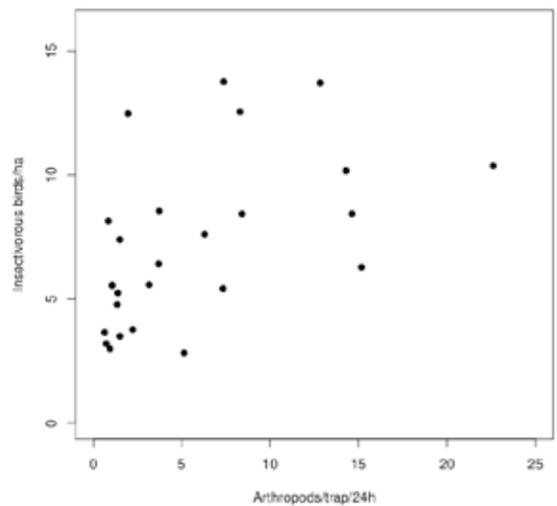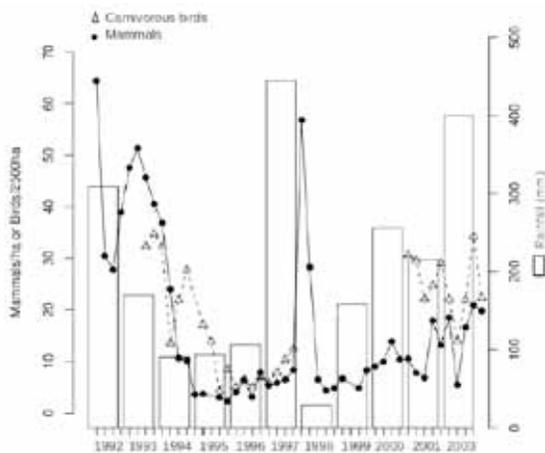
Fig. 8. Seasonal course of the abundance of carnivorous birds and mammal prey, together with yearly rainfall (1992-2002) in Auco, northern Chile. Bird sampling started in winter 1993. No bird data are available 1998-2000. Yearly rainfall corresponds to precipitation accumulated from autumn (March) to summer the following year (February). Mean annual rainfall is shown as dashed line. El Niño events occurred in 1991-92, 1997, 2002.

Carnivorous birds

Only one site exists with simultaneous monitoring of carnivorous bird populations (raptors in the orders Falconiformes and Strigiformes) and of their
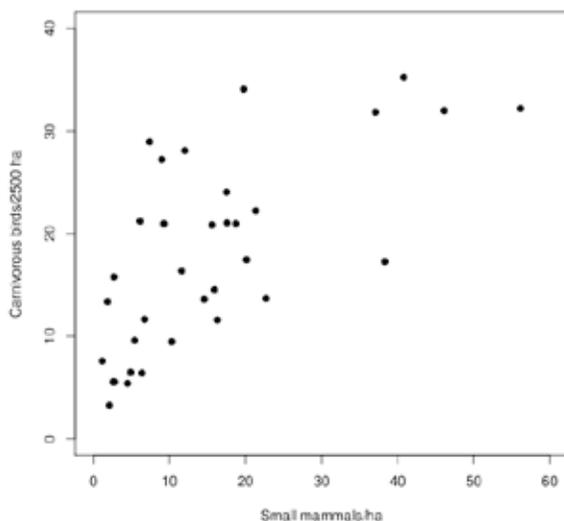

Fig. 9. Relationship between carnivorous bird and mammal prey abundance in Auco, northern Chile. Each datapoint corresponds to a calendar season (n = 28). The regression line corresponds to the best fit by Vernier Graphical Analysis 3.1.

main prey, small mammals. In Auco, semiarid Chile, mammal and carnivorous bird populations were declining after El Niño of 1991-92 until augmented rainfall brought by El Niño 1997-98 resulted in a simultaneous increase of mammal and bird abundances (Fig. 8). As mentioned above, raptor census data covering the following three years disappeared, but still the response of mammals and birds to El Niño 2002 is suggestive. Indeed, a plot of carnivorous bird abundance against mammal abundance yielded a curve of diminishing returns. As with the insectivores, the functional response of carnivorous birds was steep initially, but tended to saturate quickly, clearly reaching an asymptote (Fig. 9). In this case, there is no ambiguity in the response of carnivorous birds to their prey resources, although the missing three years of data dent an otherwise good picture.

DISCUSSION

In this section we discuss four major points that arise from the findings reported here: (a) Food shortage may be an important key factor for bird populations, but its effects depend on diet breadth, prey switching, and life history parameters of the birds involved. (b) Predictable (seasonal) patterns of productivity may determine distribution and abundance of resident birds, but variations imposed by unpredictable occurrences of El Niño and La Niña may determine the presence and abundance of migratory birds in areas affected by these anomalies. (c) The dichotomy El Niño versus La Niña phases or versus 'normal' years is artificial and leads to an impoverished view of the dynamics of bird populations and communities. (d) Long-term monitoring is needed to understand the connection between climate and birds.

Effects of El Niño depend on bird diet

It is widely recognized that El Niño produces important changes in seabird populations (Arntz & Fahrbach 1991). However, not all events have been analyzed in similar depth. The 1982-83 El Niño was the best documented, while those of 1986-87 (*e.g.* Anderson 1989) and 1991-92 (*e.g.* Lindsay *et al.* 1997) were practically ignored. During 1997-98 there was a renewed interest on the phenomenon, but most studies were directed at specific changes in particular species (*e.g.* Culik et al. 2000, Jahncke & Goya 2000, Simeone *et al.* 2002), lacking the general perspective used in the analyses of the 1982-83

event (*e.g.* Arntz & Fahrbach 1996). In spite of this, and based chiefly on information reported for the 1982-83 and 1997-98 events, the primary effects of El Niño on seabirds are related to availability of anchovy and sardine, which may be related to primary production in the marine food web and with the effects of rain and runoffs on seabird nesting grounds (Schreiber 2002). No specific mechanisms have been proposed to explain the interaction between oceanographic and atmospheric anomalies with seabird population changes. Our results show that food shortage may be an important underlying cause but that its net effects depend on seabird diet breadth and prey switching. In terms of reproduction, it has been proposed that the rapid changes in primary productivity occurring during and after El Niño events could be an important selective factor for breeding biology and life history patterns of seabirds (Luna-Jorquera *et al.* 2003). Common patterns among species with rapid recoveries after El Niño are: large clutch sizes, high body growth rates, and early reproductive ages. Luna-Jorquera *et al.* (2003) showed that, at least for the Humboldt Current system, which is frequently affected by El Niño, the seabird assemblages are dominated by species with the stated characteristics. It could further be predicted that land, and seabirds showing rapid responses to abrupt increases in primary productivity (El Niño in terrestrial habitats and La Niña in marine habitats), should display similar life history attributes (diet breadth, prey switching, large clutches, early maturity).

El Niño imposes unpredictability to bird assemblages

The structure of bird assemblages (species composition and relative abundances) may be determined by basal levels of primary productivity, but also by the seasonal and ENSO fluctuations of that variable. Hurlbert & Haskell (2003) analysed the structure of terrestrial bird assemblages in relation to fluctuations of primary productivity across the United States. They showed that basal levels of primary productivity determine resident species richness, while the range of predictable variation (seasonality) of this variable determines migrant species richness. The approach of Hurlbert & Haskell (2003) could be used in the search of general mechanisms for ENSO effects on both terrestrial and marine bird assemblages. It could be that superimposed on predictable (seasonal) changes of productivity, the range of variation imposed by unpredictable but

rather frequent occurrences of El Niño and La Niña determine geographic distribution and population abundance of the birds living in areas affected by these anomalies.

El Niño and La Niña are extremes of a wide range of variability

The occurrence (and magnitude) of El Niño is declared after some pre-defined threshold is reached, according to atmospheric and/or oceanographic indices such as sea surface temperature (SST) and southern oscillation index (SOI, Boersma 1998). Nevertheless, physical fluctuations (anomalies) are continuously occurring at different time scales. These anomalies are usually treated as departures from normality, where 'normal' (ocean/atmosphere) conditions represent either climatic means or non-El Niño/La Niña conditions. Thus, normality is not treated as a real phenomenon (a state of some system) but as the absence of extreme conditions. However, El Niño/La Niña thresholds encompass a wide range of real physical fluctuations that may have effects on bird assemblage attributes. In addition, there appears to be a weak correlation between the magnitude of El Niño/La Niña events as measured by physical indices, and the magnitude of recorded biological effects. Therefore, physical and biological dynamics do not have a direct coupling, and thus environmental signals may be filtered or processed by terrestrial and marine communities in such ways that they may resist some El Niño/La Niña events regardless of their magnitude. Both in marine and terrestrial systems, the phenomenology of community changes during El Niño/La Niña events is portrayed as an alternation between bottom-up to top-down control (*e.g.* Cury *et al.* 2000, Meserve *et al.* 2003). Nevertheless, while productivity is a central variable during those events, bottom-up effects may not preclude biological feedbacks at higher trophic levels. Conversely, decreased productivity may not necessarily lead to a strict control by predators or herbivores.

The need for long-term time series

It seems obvious that without good baseline data ornithologists are doomed to be surprised by the arrival of El Niño every few years. Even when ornithologists and ecologists are at hand to take advantage of an incoming El Niño, lack of preexisting data, and of monitoring afterwards, makes it difficult

to understand responses of birds to the successive El Niño, La Niña, and "normal" years. Indeed, according to Jaksic (2001), during the last century there were 12 El Niño years and 12 La Niña years, thus leaving about 76 'normal' years in between. Thus, by heavily concentrating attention on only 12% of the time span (El Niño), and of neglecting possibly another 12% (La Niña), ornithologists are essentially ignoring what happens during 76% of the time. This situation may be remedied only as long as data are logged on a regular or continuous basis, that is, as long-term time series (Crawford & Jahncke 1999). The recipe prescribed by Schreiber & Schreiber (1988) to understand El Niño effects on birds still stands: '...carry out long-term studies that will shed further light on the interactions between global atmospheric cycles, oceanographic phenomena, and avian populations.'

TABLE 1. Effects of El Niño 1982-83 on seabird species in four localities of the southeastern Pacific Ocean Increases in abundance are coded by +% and decreases by -%. Increases in reproduction (nesting densities) are denoted by +% and decreases by –%. Decreases in chick survival are denoted by -Csurv and decreases in chick size by –Csize. Lack of changes are denoted by (=). Sources are listed in the footnote

Localities and species	Species	Abund.	Reprod.	Source
a) Kiritimati Island				
Audubon's Shearwater	*Puffinus lherminieri*		-100	7
Black Noddy	*Anous minutus*		-100	7
Blue-gray Noddy	*Procelsterna cerulea*		-95	7
Brown Booby	*Sula leucogaster*		-100	7
Brown Noddy	*Anous stolidus*		-100	7
Christmas Shearwater	*Puffinus nativitatis*		-80	7
Crested Tern	*Thalasseus bergii*	=	=	7
Gray-backed Tern	*Sterna lunata*		-99	7
Great Frigatebird	*Fregata minor*		-90	7
Lesser Frigatebird	*Fregata ariel*		-40	7
Masked Booby	*Sula dactylatra*		-98	7
Phoenix Petrel	*Pterodroma alba*		-80	7
Red-footed Booby	*Sula sula*		-70	7
Red-tailed Tropicbird	*Phaethon rubricauda*		-90	7
Sooty Tern	*Sterna fuscata*		-100	7
Wedge-tailed Shearwater	*Puffinus pacificus*		-75	7
White Tern	*Gygis alba*		-85	7
White-throated Storm Petrel	*Nesofregetta albigularis*		-100	7
b) French Frigate Shoals				
Black Noddy	*Anous tenuirostris*		-20, -Csize	1
Red-footed Booby	*Sula sula*		-10, -Csize	1
c) Galapagos Archipelago				
Audubon's Shearwater	*Puffinus lherminieri*	-5	-100	5, 9
Band-rumped Storm-petrel	*Oceanodrama castro*	=	=	5
Blue-footed Booby	*Sula nebouxii*	-5	-100	5, 9
Brown Noddy	*Anous stolidus*	-5		5

Brown Pelican	*Pelecanus occidentalis*	=	-100	5, 9
Dark-rumped Petrel	*Pterodroma phaeopygia*	+5	-42, -Csize	1, 5, 9
Flightless Cormorant	*Nannopterum harrisi*		-50	9, 10
Frigatebird	*Fregata* sp.	-5		5
Galapagos Penguin	*Spheniscus mendiculus*	-5	-77	5, 9
Great Frigatebird	*Fregata minor*		-52, -Csurv	9
Gulls	*Larus* sp.	=	=	5
Lava Gull	*Larus fuliginosus*		+5	9
Magnificent Frigatebird	*Fregata magnificent*	=	-5, -Csurv	9
Masked Booby	*Sula dactylatra*	=	-100	5, 9
Northern Phalarope	*Lobipes lobatus*	-5		5
Red-billed Tropicbird	*Phaethon aethereus*	-5	=	5, 9
Red-footed Booby	*Sula sula*		-100	9
Storm-Petrel	*Oceanites* sp.	+5		5
Swallow-tailed Gull	*Creatus furcatus*	-5	100	5, 9
Waved Albatross	*Diomedea irrorata*	=	-60	5, 9
Wedge-rumped Storm-petrel	*Oceanites tethys*	-5	-100	5, 9
White-vented Storm-petrel	*Oceanites gracilis*	=	=	5
d) Peru				
Blue-footed Booby	*Sula nebouxii*	-50		1, 3
Cormorant	*Phalacrocorax* sp.	=	=	2
Guanay Cormorant	*Phlacrocorax bougainvilli*	-80		6, 8, 4
Humboldt Penguin	*Spheniscus humboldti*	-90		6
Inca Tern	*Larosterna inca*	=	=	2, 6
Peruvian Booby	*Sula variegata*	-80		1, 6, 3, 8, 4
Peruvian Pelican	*Pelecanus thagus*	-80	=	2, 6, 8, 4
Red-legged Cormorant	*Phalacrocorax gaimardi*	-85		6

Sources: 1 = Ainley *et al.* (1988), 2 = Arntz (1985), 3 = Arntz & Fahrbach (1996), 4 = Duffy (1983a), 5 = Duffy & Merlen (1986), 6 = Duffy *et al.* (1988), 7 = Schreiber & Schreiber (1984), 8 = Tovar & Cabrera (1985), 9 = Valle *et al.* (1987), 10 = Valle & Coulter (1987).

TABLE 2. Dietary composition and similarity (clusters, see text for explanation) of seabird species in four localities of the southeastern Pacific Ocean affected by El Niño 1982-83

Main prey: 1 = Zooplankton, 2 = Fish larvae, 3 = Fishes, 4 = Eel, 5 = Octopi, 6 =Crustaceans, 7 = Squid, 8 = Sandworms, 9 = Seabirds, 10 = Turtles, 11 = Iguanas, 12 = Sealion wastes, 13 = Fishery wastes

Seabirds and prey	1	2	3	4	5	6	7	8	9	10	11	12	13
a) Kiritimati Island													
Audobon shearwater		X	X			X	X						
Blue-gray noddy			X			X	X						
Brown booby		X	X				X						
Brown noddy			X				X						
Christmas shearwater		X	X				X						
Great frigate bird			X			X	X					X	

Species													
Lesser frigate bird			X				X						
Phoenix petrel		X	X		X	X	X						
Red-footed booby			X				X						
Red-tailed tropic bird			X				X						
Sooty tern		X	X				X						
White tern			X				X						
Black noddy			X										
Crested tern													
Gray-backed tern		X	X			X							
Masked booby			X										
Wedge-tailed shearwater		X	X										
White-throated storm petrel			X										
b) French frigate shoals													
Black noddy			X										
Red-footed booby			X				X						
c) Galapagos Archipelago													
Gulls			X		X	X						X	X
Lava gull			X					X			X	X	
Magnificent frigate bird			X			X	X		X	X	X	X	
Northern phalarope	X	X				X							
Oceanites sp. Storm-petrel			X			X						X	X
Audobon shearwater		X	X			X	X						
Band-rumped storm-petrel			X				X						
Blue-footed booby			X										
Brown noddy			X										
Brown pelican			X										
Dark-rumped petrel			X			X	X						
Flightless cormorant			X	X	X								
Frigatebird			X			X	X					X	
Galapagos penguin			X			X							
Great frigate bird			X			X	X					X	
Masked booby			X										
Red-billed tropicbird			X				X						
Red-footed booby			X				X						
Swallow-tailed gull			X				X						
Waved albatross			X			X	X						
Wedge-rumped storm-petrel			X			X	X						
White-vented storm-petrel			X			X							X
d) Peru													
Inca tern			X			X							
Blue-footed booby			X										

Cormorants	X	
Guanay cormorant	X	
Humboldt penguin	X	X
Peruvian Booby	X	X
Peruvian Pelican	X	
Red-legged Cormorant	X	

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