S. Afr. J. mar. Sci. 21: 145–156
1999

COMPARISON OF TRENDS IN ABUNDANCE OF GUANO-PRODUCING SEABIRDS IN PERU AND SOUTHERN AFRICA

R. J. M. CRAWFORD and J. JAHNCKE†*

The abundant guano-producing seabirds in Peru and southern Africa feed mainly on the large populations of anchovy *Engraulis* spp. and sardine *Sardinops sagax* supported by the Humboldt and Benguela upwelling systems. Numbers of guanay cormorants *Phalacrocorax bougainvillii* in Peru and the breeding population of Cape cormorants *P. capensis* in South Africa are significantly related to the biomass of anchovy. For both species, reproductive success decreases in periods of anchovy scarcity, and there may also be substantial adult mortality. There has been long-term stability in numbers of Peruvian boobies *Sula variegata,* whereas the numbers of Cape gannets *Morus capensis* decreased as sardine decreased in southern Africa. Numbers of Peruvian pelicans *Pelecanus* (*occidentalis*) *thagus* are significantly related to the combined biomass of anchovy and sardine in Peru. They have been stable in the long-term. There have been ongoing severe decreases in populations of the Humboldt penguin *Spheniscus humboldti* and the African penguin *S. demersus*, both of which are now Vulnerable. Common causes for the decreases have been collection of eggs, loss of habitat through exploitation of accumulated deposits of guano and competition with fisheries for food. Short-term decreases in guanay cormorants, Peruvian boobies, Peruvian pelicans and Humboldt penguins have followed *El Niño* events. Time-series of indices of the abundance of guano-producing seabirds date from 1908 in Peru and 1896 in southern Africa. They are significantly, negatively correlated in the period prior to the development of intensive fisheries on sardine and anchovy, suggesting that the out-of-phase nature of the anchovy and sardine populations in the Peru and Benguela systems pre-dated commercial exploitation of these fish resources.

There is a similarity in the marine avifaunas of the Humboldt upwelling system off western South America and the Benguela upwelling system off western southern Africa. Each system has an abundant, endemic cormorant, sulid and penguin, each of which feeds primarily on the large populations of sardine *Sardinops sagax* and anchovy *Engraulis* spp. that are found in the two systems (e.g. Jordán and Fuentes 1966, Crawford and Shelton 1981, Crawford *et al*. 1991a). These endemic birds are the guanay cormorant *Phalacrocorax bougainvillii*, the Peruvian booby *Sula variegata* and the Humboldt penguin *Spheniscus humboldti* in the Humboldt system, and the Cape cormorant *P. capensis*, Cape gannet *Morus capensis* and African penguin *S. demersus* in the Benguela system. Additionally, the Peruvian pelican *Pelecanus (occidentalis) thagus* is abundant in the Humboldt system, where it also feeds mainly on sardine and anchovy (Jordán and Fuentes 1966, Paulik 1971). The eastern white pelican *P. onocrotalus* is found in smaller numbers in the Benguela system, but its diet is not dominated by sardine and anchovy (Berry 1976, Crawford *et al.* 1991a, 1995a).

The large numbers of seabirds in the Humboldt and Benguela systems produced large, accumulated deposits of seabird guano that were harvested in the mid and late 19th century and early 20th century (Hutchinson 1950, Tovar *et al.* 1987b). Thereafter, seabird guano was collected on an annual basis at the end of the seabird breeding season. The two systems are at present the only regions in the world where seabird guano is harvested annually.

In both the Humboldt and Benguela systems, there have been sustained and large decreases in the numbers of penguins (Crawford *et al*. 1990, 1995b, Luna-Jorquera 1998) and large variations in the numbers of other seabirds (Jordán 1967, Crawford 1987, 1991, Tovar *et al.* 1987b, Guillén 1992).

There have also been large fluctuations in the abundance of sardine and anchovy in the Humboldt and Benguela systems, and elsewhere in the world's oceans (Lluch-Belda *et al.* 1989, 1992). Many recent fluctuations have been co-incident, leading to the opinion that they have been influenced by climate operating at a global scale (Kawasaki 1983). Catches of anchovy in the Humboldt system were significantly, positively related to those of sardine in the Benguela system two years earlier, indicating a possible link between the two systems. However, the significance was attributable to peak catches before, and low catches after, stock collapses, which may have resulted from overfishing (Crawford *et al.* 1991b).

In this paper, the use of indices of bird abundance as surrogates of fish abundance in Peru is explored by

---

* Marine & Coastal Management, Private Bag X2, Rogge Bay 8012, Cape Town, South Africa. E-mail: crawford@sfri.wcape.gov.za
† Point Reyes Bird Observatory, Stinson Beach, CA 94970 California, USA; formerlyInstituto del Mar del Peru, Esq. Gamarra y Gral. Valle s/n, Chucuito, Callao, Peru. E-mail: prbo@seismo.berkeley.edu

Manuscript received: March 1998

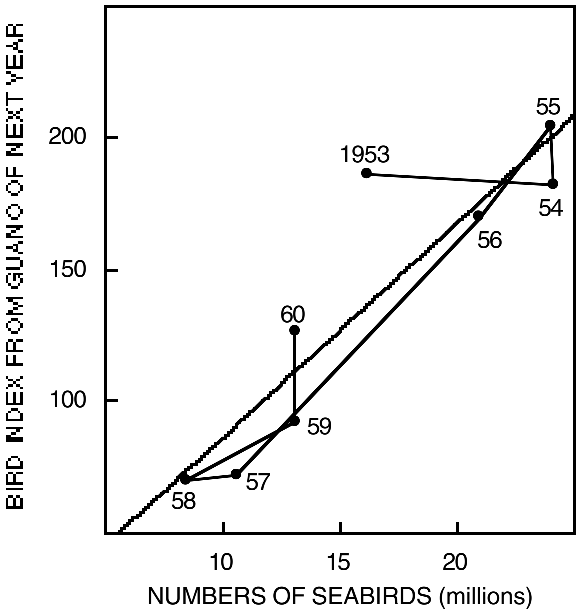

Fig. 1: Relationship between the combined number of guanay cormorants, Peruvian boobies and Peruvian pelicans and an index of seabird numbers obtained from the harvest of guano at islands and headlands in Peru in the following year, 1953–1960. The estimated regression line is shown

Table I: Models used to generate prewhitened residuals for time-series subject to cross-correlation. AR(*x*) signifies autoregressive of Order *x*

Data series	Fitted model	Period of residuals
Number of birds (adults)		
Guanay cormorant	AR(1)	1954–1997
Peruvian booby	AR(1)	1954–1997
Peruvian pelican	AR(1)	1954–1997
Peruvian seabirds*	AR(1)	1909–1997
Fish biomass		
Peruvian anchovy	AR(1)	1954–1996
Peruvian sardine	AR(1)	1979–1993
Peruvian anchovy and sardine	AR(1)	1979–1993
Guano harvest		
South African islands	AR(2)	1898–1995
Namibian islands	AR(2)	1898–1995
Namibian platforms	AR(2)	1931–1995
Southern African islands	AR(2)	1898–1995
Southern African total	AR(2)	1898–1995

* Sum of guanay cormorant, Peruvian booby and Peruvian pelican extended using guano harvests

comparing estimates of bird and fish abundance in this system. Indices of bird abundance have been used as measures of fish abundance in the Benguela system (Crawford and Shelton 1978, Troadec *et al.* 1980). The possibility of linkage between the Humboldt and Benguela systems is further explored by comparing trends in indices of bird abundance in these systems. The relationship between indices of abundance of different seabirds in the Peruvian system is examined, and comment is made on factors influencing trends in numbers of seabirds that feed mainly on anchovy and sardine.

MATERIAL AND METHODS

Estimates of numbers of adult guanay cormorants, Peruvian boobies and Peruvian pelicans at islands and headlands in Peru are available for each month between January 1953 and December 1982 for the coast between 6 and 14°S (Tovar *et al.* 1987b) and between January 1984 and December 1989 for the entire Peruvian coast (Guillén 1992). For those years, the mean abundance of the three seabird species was calculated, and taken to be an estimate of annual population size. In 1983, estimates of the number of adults of the three seabirds were available for March, May, June and July (Tovar and Cabrera 1985). For the years 1990–1997, estimates were available for March or April, July and November (J J unpublished data). Again, mean values for those years were calculated. To ensure comparability of data over the period 1953–1997, only estimates of abundance for the coastline between 6 and 14°S were used. In most years, most of the populations of guanay cormorant, Peruvian booby and Peruvian pelican occur in that region (Guillén 1992). Estimates of abundance were derived from maps indicating the areas occupied by breeding and non-breeding birds at islands and headlands and estimates of the densities of these birds. The areas of occupation were measured using a planimeter (Tovar *et al.* 1987b).

For the period 1909–1960, it has been assumed that the overall number of guanay cormorants, Peruvian boobies and Peruvian pelicans was proportional to their production of guano at islands and headlands (Jordán and Fuentes 1966, Duffy 1983). For the years 1953–1960, the numbers of these three species of seabird between 6 and 14°S are known (Tovar *et al.* 1987b). They were totalled and regressed against the quantity of guano collected in the following year. The resulting relationship was used to estimate the overall number of these seabirds in this region of the coast from 1908 to 1952. Guano was not collected at each island each year, but in the period 1953–1960 harvests at islands were undertaken in most years.

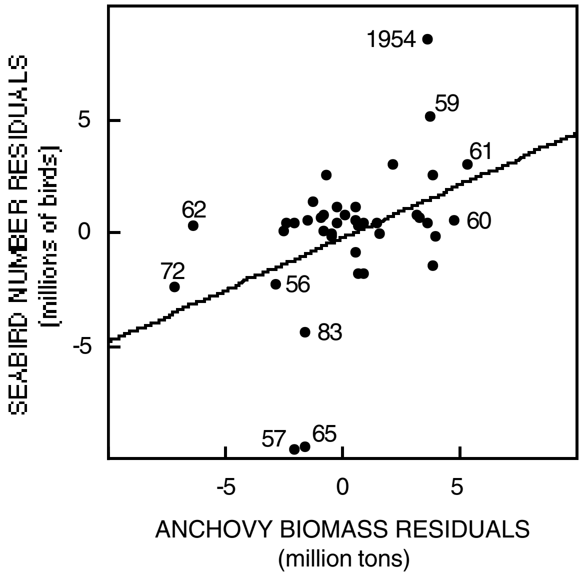

Fig. 2: Relationship between residuals for combined numbers of guanay cormorants, Peruvian boobies and Peruvian pelicans and for the biomass of anchovy in Peru, 1954–1996. The estimated regression line is shown

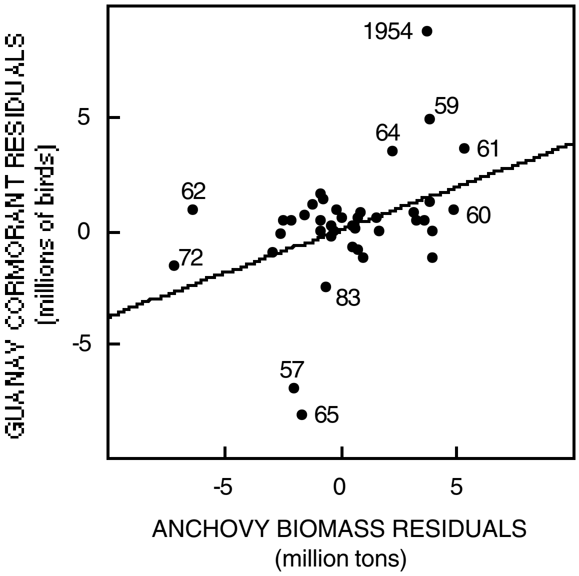

Fig. 3: Relationship between residuals for numbers of guanay cormorants and for the biomass of anchovy in Peru, 1954–1996. The estimated regression line is shown

Records of harvests of seabird guano at islands and platforms in southern Africa are available since 1896 (Best *et al.* 1997). The platforms are on the central Namibian coast. At these, harvests of guano are almost entirely attributable to Cape cormorants (Rand 1963b, Berry 1976). These platforms were built between 1930 and 1971, with the bulk of the construction completed by 1963 (Cooper *et al.* 1982). Guano deposited at islands in southern Africa is mostly attributable to Cape cormorants and Cape gannets (Rand 1963a, b, Cooper *et al.* 1982, Crawford *et al.* 1983). From the 1890s until 1975, guano at islands off South Africa and Namibia was collected annually by the South African government. From 1976 until the 1990s, the collection of guano was leased out to private enterprise (Best *et al.* 1997). This resulted in a different approach to harvesting guano, with guano sometimes being left to accumulate at islands over several years.

Purse-seine fisheries in the Peruvian and Benguela systems commenced after World War 2 and developed rapidly during the 1950s (Crawford *et al.* 1987, Pauly *et al.* 1987). These changes in the exploitation of the food base of the seabirds and in the management of the southern African guano harvests, and the fact that estimates of numbers of different seabirds in Peru date from 1953, made it useful to compare indices of seabird abundance for Peru and southern Africa not only over their full extent, but also for the periods 1909–1953, 1954–1975 and 1976–1995. Guano production in the Benguela system was considered as a whole, as well as for platforms, for islands off Namibia and for those off South Africa. Comparisons were undertaken for the same year, and with each series leading the other by one and two years.

Annual estimates of the biomass off Peru of anchovy aged six months or older are available from 1961/62 to 1996 (Csirke *et al.* 1996, Instituto del Mar del Peru unpublished data). Monthly estimates of biomass of anchovy off Peru are available from January 1953 to December 1961 (Pauly *et al.* 1987). In those years, mean values were used as estimates of annual abundance. Estimates are available of the biomass off Peru of sardine aged three years or older from 1978–1993 (Csirke *et al.* 1996).

High correlation between two time-series, each having autocorrelation structure, may be entirely spurious. However, once the structure has been removed from both series to obtain two series of so-called "prewhitened residuals", these may be validly cross-correlated. Data series used in the present analysis were modelled by standard univariate techniques (Box and Jenkins 1970) using the package MicroTSP (Hall *et al.* 1990). Prewhitened residuals were generated by subtracting model estimates from the original time-series. The regression between bird numbers and guano harvests in Peru was based on the original

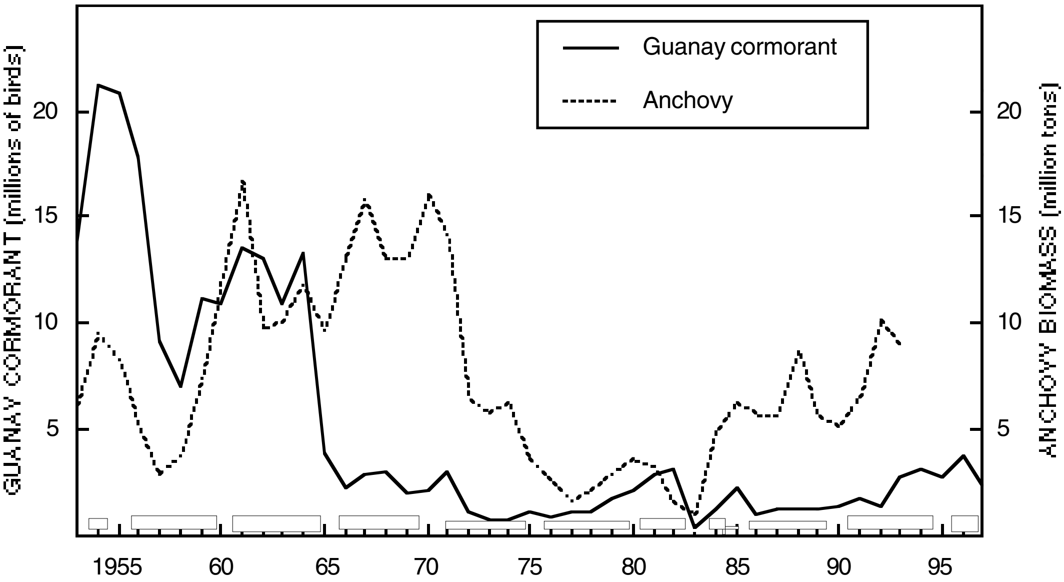

Fig. 4: Numbers of guanay cormorants (between 6 and 14°S) and biomass of anchovy in Peru, 1953–1997

data rather than prewhitened residuals as the intention was to back-calculate bird numbers from early guano harvests.

Numbers of guanay cormorants were modelled using the equation

$$N_t = aN_{t-1} + bA_t - cC_{t-1} \quad ,$$

where a, b and c are constants, N_t is the average number (millions) of guanay cormorants in year *t*, *A* is the average biomass (million tons) of anchovy off Peru and *C* is the catch (million tons) of anchovy off Peru. Residuals were generated by subtracting model estimates from observed numbers.

RESULTS

Models used to generate prewhitened residuals for the time-series subject to cross-correlation analysis are shown in Table I. Much of the autocorrelation structure in the time-series was removed by use of an autoregressive model of Order one. In some instances it was necessary to employ an autoregressive model of Order two. Estimates of numbers of guanay cormorant, Peruvian booby and Peruvian pelican in Peru between 6 and 14°S are given in Table II.

Seabird numbers and guano harvests in Peru

There was a close relationship between the combined number of guanay cormorants, Peruvian boobies and Peruvian pelicans during the period 1953–1960 and the harvest of guano off Peru in the following year ($r = 0.903$, $p = 0.002$, Fig. 1).

Seabird numbers and fish biomass in Peru

From 1954–1996, overall numbers of guano-producing seabirds in Peru (guanay cormorants, Peruvian boobies and Peruvian pelicans) were significantly correlated with the biomass of anchovy off Peru in the same year ($r = 0.355$, $p < 0.02$, Fig. 2), as were the numbers of guanay cormorants ($r = 0.392$, $p < 0.01$, Fig. 3).

Numbers of guanay cormorants are compared with the biomass of anchovy in Figure 4. The numbers of guanay cormorants were best fitted by the equation

$$N_t = 0.763N_{t-1} + 0.397A_t - 0.508C_{t-1} \quad .$$

This model accounted for 86% of the observed

Table II: Estimates of numbers of guanay cormorant, Peruvian booby and Peruvian pelican (millions) in Peru between 6 and 14°S, 1953–1997 (from Tovar and Cabrera 1985, Tovar *et al.* 1987b, Guillén 1992, JJ unpublished information)

Year	Guanay cormorant	Peruvian booby	Peruvian pelican
1953	13.82	1.99	0.36
1954	21.28	2.40	0.44
1955	20.81	2.71	0.49
1956	17.78	2.73	0.40
1957	9.13	1.32	0.14
1958	7.00	1.18	0.21
1959	11.22	1.46	0.43
1960	10.96	1.80	0.36
1961	13.51	1.80	0.28
1962	13.04	1.99	0.25
1963	10.85	1.70	0.28
1964	13.27	1.88	0.22
1965	3.86	1.15	0.30
1966	2.27	1.14	0.21
1967	2.82	1.04	0.34
1968	2.98	1.16	0.30
1969	1.91	1.30	0.15
1970	2.09	1.30	0.20
1971	3.02	1.50	0.18
1972	1.08	0.76	0.18
1973	0.70	0.90	0.50
1974	0.76	1.32	0.20
1975	1.03	1.35	0.09
1976	0.89	1.34	0.11
1977	1.13	1.53	0.12
1978	1.11	2.33	0.26
1979	1.77	1.80	0.28
1980	2.08	1.71	0.18
1981	2.78	1.96	0.14
1982	3.14	1.83	0.16
1983	0.27	0.14	0.07
1984	1.17	1.20	0.23
1985	2.24	1.08	0.30
1986	0.96	1.28	0.39
1987	1.15	1.36	0.34
1988	1.20	1.54	0.51
1989	1.25	1.47	0.38
1990	1.36	1.02	0.15
1991	1.76	1.73	0.15
1992	1.30	1.34	0.18
1993	2.74	1.84	0.44
1994	3.09	2.08	0.46
1995	2.69	1.49	0.15
1996	3.69	2.64	0.47
1997	2.33	1.76	0.21

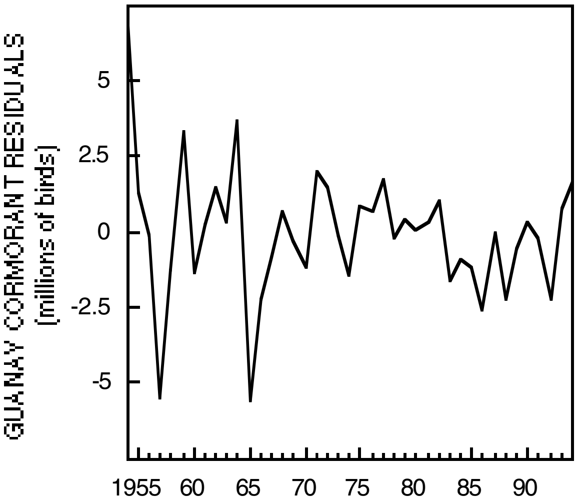

Fig. 5: Residuals generated by subtracting model estimates of numbers of guanay cormorants in Peru from observed values, 1954–1994

variation in numbers. Residuals obtained by subtracting model estimates from observed numbers are shown in Figure 5. The largest residuals were in 1954, 1957 and 1965.

Using a significance level of 0.05 over the period 1954–1996, numbers of Peruvian boobies and Peruvian pelicans were not correlated with the biomass of anchovy off Peru in the same year. For the years 1979–1993, numbers of guanay cormorants, Peruvian boobies and Peruvian pelicans were also not correlated with biomass of sardine off Peru in the same year at this level of significance. However, numbers of Peruvian pelicans were significantly correlated with the combined biomass of anchovy and sardine in the previous year ($r = 0.570$, $p < 0.05$, Figs 6, 7).

Numbers of Peruvian seabirds

Prewhitened residuals of numbers of guanay cormorants were positively correlated with those of Peruvian boobies ($r = 0.541$, $p < 0.001$, Fig. 8). The relationships between guanay cormorants and Peruvian pelicans ($r = 0.327$, $p < 0.05$) and Peruvian boobies and Peruvian pelicans ($r = 0.487$, $p < 0.001$) were also positively correlated. There were large fluctuations in average numbers of Peruvian boobies and Peruvian pelicans between 1953 and 1997, with no clear trend (Fig. 9).

Indices of seabird abundance in Peru and the Benguela system

For the period 1909–1995, the period for which prewhitened residuals of indices of seabird abundance are available for Peru and the Benguela system, there

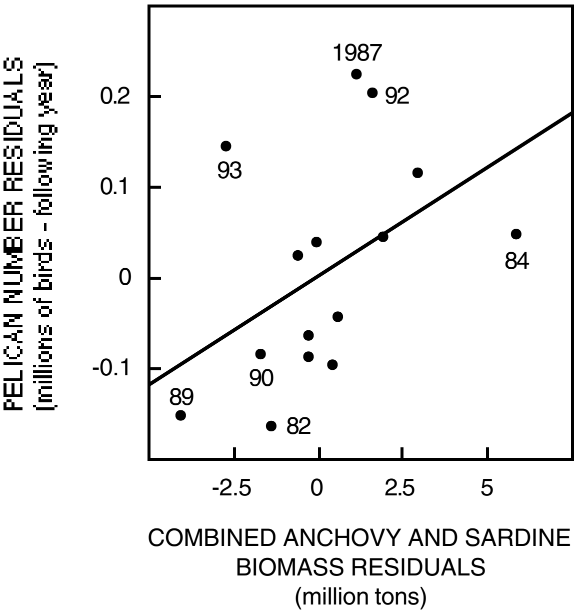

Fig. 6: Relationship between residuals for the combined biomass of anchovy and sardine in Peru and for numbers of Peruvian pelicans in the following year, 1979–1993. The estimated regression line is shown

were no significant correlations for any of the four comparisons made – the Peruvian index with guano produced in the Benguela at Namibian platforms, Namibian islands, South African islands and in total.

For the years 1909–1953, the Peruvian index was significantly negatively correlated with overall guano production in the Benguela system two years earlier ($r = -0.376$, $p < 0.01$, Fig. 10). There was no significant correlation of the Peruvian index with guano production at South African islands or at Namibian islands; and no comparison was made with the Namibian platforms, which were being built from 1930 onwards (Cooper *et al.* 1982). Trends in the Peruvian seabird index and in the production of guano in the Benguela system were in opposite directions between 1920 and 1953 (Fig. 11), and the relationship was highly significant ($r = -0.505$, $p < 0.005$).

For the period 1954–1975, the Peruvian seabird index was positively correlated with guano produced at islands off Namibia two years earlier, but not at a high level of significance ($r = 0.317$, $p < 0.20$). However, residuals of guanay cormorants were significantly correlated with those of guano produced at Namibian islands two years earlier ($r = 0.465$, $p < 0.05$). For the years 1976-1995, because of the irregular nature of harvesting guano at southern African islands, a comparison was only made between the Peruvian seabird residuals and those for guano production at

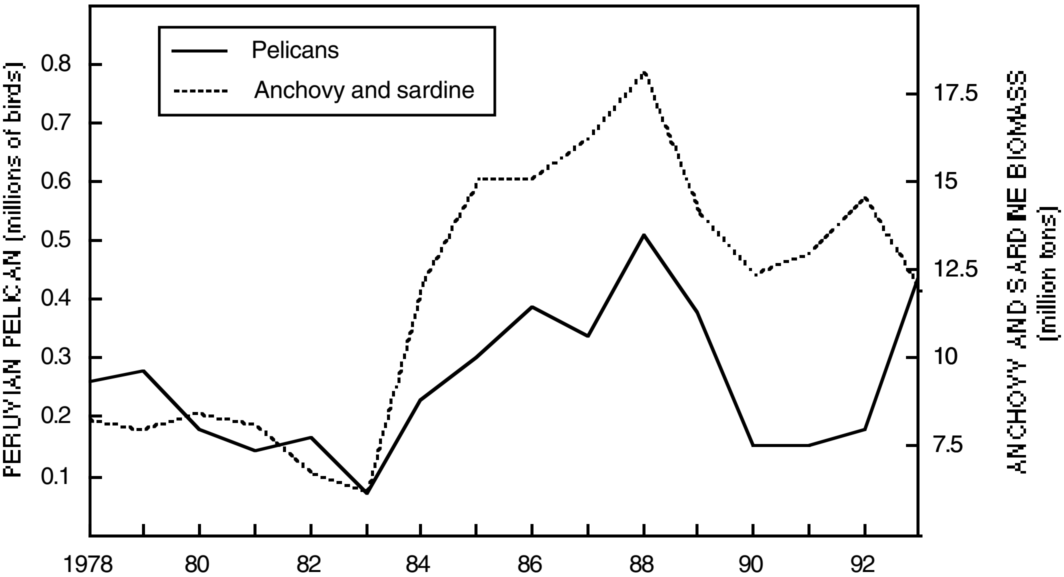

Fig. 7: Numbers of Peruvian pelicans (between 6 and 14°S) and combined biomass of anchovy and sardine in Peru, 1978–1993

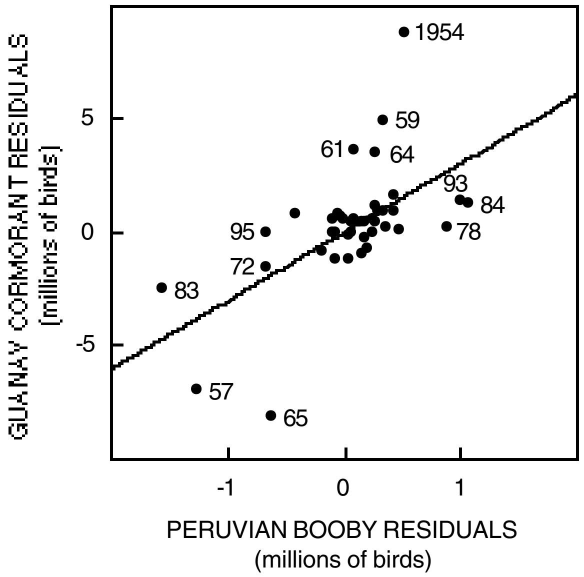

Fig. 8: Relationship between residuals for numbers of guanay cormorants and Peruvian boobies in Peru, 1954–1997. The estimated regression line is shown

Namibian platforms. The Peruvian seabird index was negatively related to guano harvested at the Namibian platforms in the following year ($r = -0.509$, $p < 0.02$), as was that for guanay cormorants ($r = -0.446$, $p < 0.05$).

DISCUSSION

Peruvian seabirds

The close correlation between seabird numbers and the harvest of guano off Peru supports a similar result obtained for the years 1943–1958 by Valdivia (1960). This made it reasonable to utilize guano harvests as an index of numbers of guano-producing seabirds off Peru for the period 1908–1952.

The model of guanay cormorants accounted for a large proportion (86%) of the observed variation in numbers of this species. Guanay cormorants had their highest recorded abundance of more than 21 million adults in 1954. This decreased to 10–14 million adults from 1959 to 1964, and to less than five million adults thereafter (Fig. 4). Much (30%) of the unexplained variation in the model is attributable to 1954, when there was a large increase in the population compared to the previous year, and 1957 and 1965, when there were large decreases (Fig. 5). These three years were also outliers in the relationships between overall numbers of seabirds and numbers of guanay cormorants and the biomass of anchovy off Peru (Figs 2, 3).

There were strong *El Niño* events in 1953,

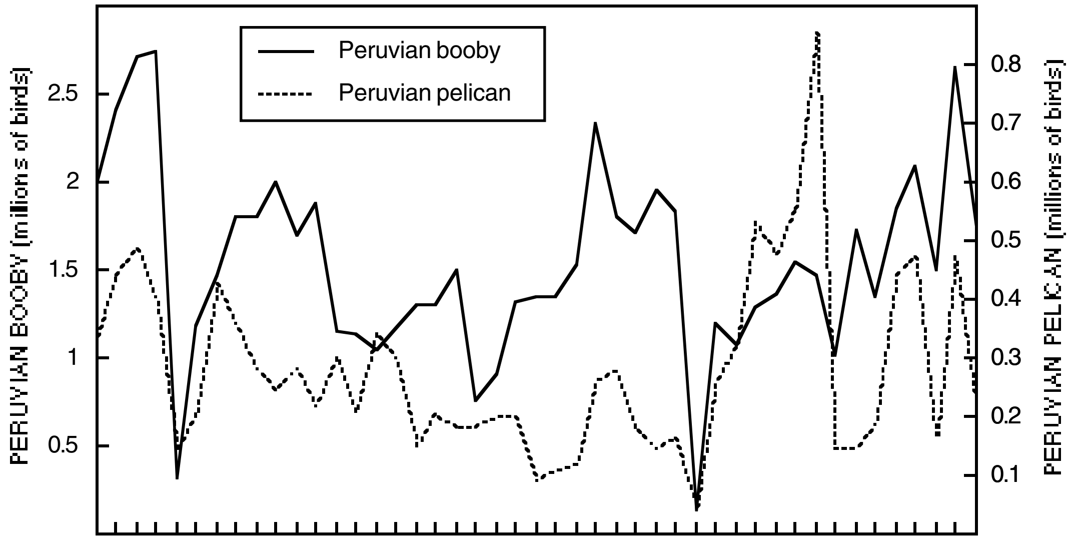

Fig. 9: Numbers of Peruvian boobies and Peruvian pelicans in Peru (between 6 and 14°S), 1953–1997

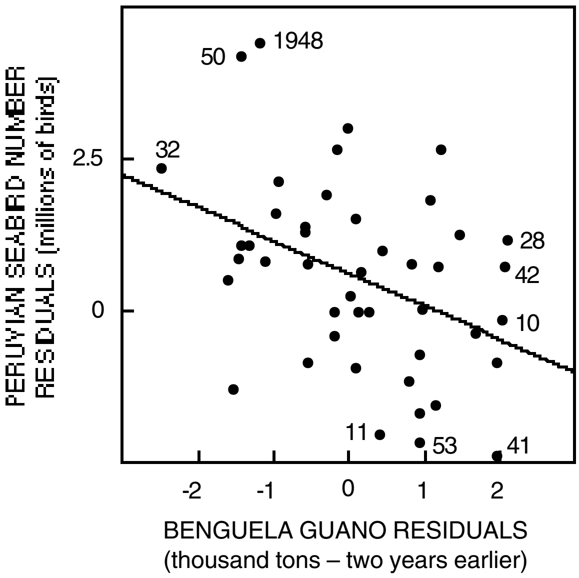

Fig. 10: Relationship between residuals for combined numbers of seabirds in Peru and the overall harvest of guano in the Benguela system two years earlier, 1909–1953. The estimated regression line is shown

1957–58 and 1965 (Quinn and Neal 1992). These all decreased numbers of guanay cormorants through mortality (Avilia 1953 as cited by Jordán 1964, Jordán and Fuentes 1966, Tovar 1983). Numbers failed to recover after 1965, as they had after 1953 and 1957–58 (Fig. 4), probably because by that stage the anchovy fishery had increased to such an extent that it reduced considerably the availability of anchovy to guanay cormorants. The Peruvian fishery caught less than two million tons of anchovy in 1959, but between 8.5 and 12.3 million tons in each year between 1966 and 1971. The biomass of anchovy then decreased markedly, until a recovery was initiated in the mid 1980s (Fig. 4).

In contrast to the significant relationship between guanay cormorants and anchovy biomass, numbers of the other two guano-producing seabirds in Peru were not significantly correlated with abundance of anchovy or sardine. However, for the period for which there are estimates of the biomass of both anchovy and sardine, numbers of pelicans were well correlated with the combined abundance of these fish species in the previous year (Figs 6, 7).

Residuals for the three Peruvian seabird species were positively related to each other, with the strongest relationship between guanay cormorants and Peruvian boobies. The large, negative residuals obtained in 1957, 1965 and 1983 (Fig. 8) may all be attributed to strong *El Niño* events in those years reducing populations of guanay cormorants and Peruvian boobies through mortality and reduced breeding (e.g. Tovar *et al.* 1987a). Numbers of Peruvian pelicans were also reduced in 1957 and 1983 (Fig. 9). Both fishing and extreme environmental conditions influence the populations of seabirds in Peru, with their relative impacts differing between the three bird species.

Links between Peru and the Benguela system

Before intensive exploitation of the fish on which the guano-producing seabirds feed during the 1950s, there was a negative relationship between indices of seabird abundance in Peru and in the Benguela system two years earlier. The significance stems in part from negative residuals for Peruvian seabirds in *El Niño* years such as 1911, 1941 and 1953 being associated with positive residuals in the Benguela system two years earlier (Fig. 10).

The lag in the relationship between the two systems is the same as, but the sign opposite to, that observed in the comparison of anchovy in the Humboldt system and sardine in the Benguela system (Crawford *et al.* 1991b). Although the Humboldt and Benguela systems have similar regimes of anchovy and sardine, these have been out of phase with each other in the latter half of the 20th century (Lluch-Belda *et al.* 1992). Sardine have been plentiful off southern Africa when anchovy have been abundant in the Humboldt system and, when anchovy have dominated the Benguela system, sardine have been abundant off Peru.

The negative relationship between seabird indices for the two systems in the early part of the 20th century may suggest that the systems were out of phase then too. This negative relationship is especially evident in the data from about 1920 to 1953 (Fig. 11). This is the period when the guano in both systems was being harvested in a sustainable manner, and before the food source of seabirds had been impacted to any great extent by fishing. Peruvian seabirds were greatly reduced by uncontrolled exploitation of guano from 1844 to 1909. Subsequently, guano islands and headlands were administered by Compañia Administradora del Guano. After 1914, this company protected the breeding seabirds and managed the exploitation of guano (Tovar *et al.* 1987b), leading to an increased abundance of seabirds (Fig. 11). If the Peruvian seabird assemblage during the years 1920–1953 was as heavily dominated by the guanay cormorant as it was from 1953 to 1964 (Tovar *et al.* 1987b), and given the significant positive relationship between numbers of

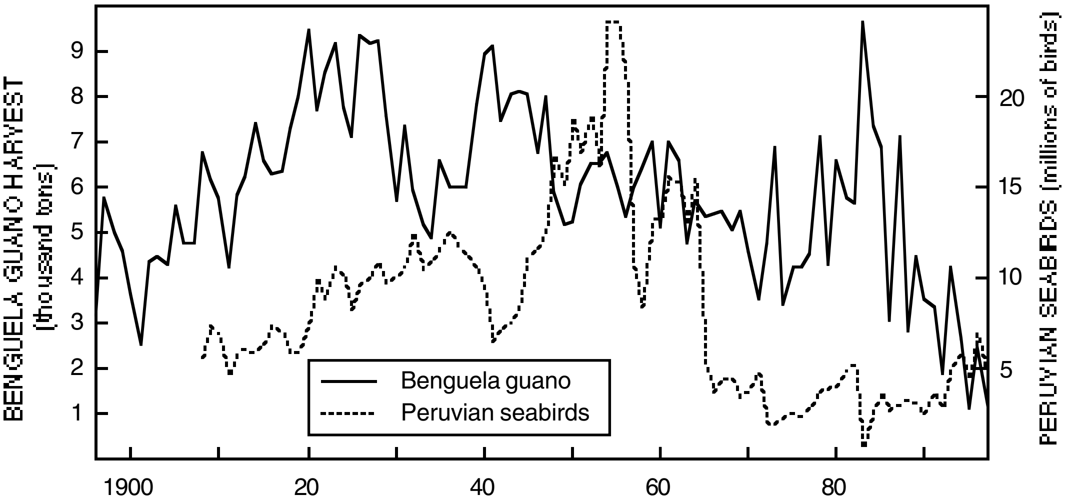

Fig. 11: Estimated numbers of seabirds in Peru (between 6 and 14°S) and the overall harvest of guano in southern Africa, 1896–1997

guanay cormorants and anchovy, the reduced number of seabirds in Peru in the early 1940s (Fig. 11) may indicate a reduced abundance of anchovy at that time. Conversely, anchovy may have been plentiful in the early 1930s.

In the Benguela system, numbers of Cape cormorants that breed are positively correlated with anchovy biomass (Crawford and Dyer 1995). Reports by the superintendent of the guano islands during the early 1930s made frequent reference to a scarcity of small fish and poor breeding by birds, especially Cape cormorants. During this period, the guano harvest decreased noticeably (Fig. 11). Comments include:

> "The scarcity of small fish during the breeding season has again considerably affected the output of guano for 1930 ..." (Jackson 1930);
>
> "... owing to the scarcity of small fish, the birds forsook the breeding flats, returning later in greatly diminished numbers." (Jackson 1931);
>
> "The prospects for the coming year, more especially as far as the guano crop is concerned, are discouraging, and it is feared that it will be one of the lowest on record, due to the fact that the birds have deserted the islands ... especially the duikers [Cape cormorants] ... For three seasons running these birds have come to the islands and the neighbouring waters at the commencement of the breeding season, for short spells only, but show a nervous tendency and do not seem inclined to settle down to breed ... scarcity of small fish in the vicinity of these islands ... is possibly the main cause." (Jackson 1932);
>
> "The duikers ... during the last three years have come to the islands in large numbers just at the beginning of the breeding season, but ... they do not appear to want to settle down, and after building their nests and in some cases laying a few eggs, they begin to take off again ..." (Jackson 1933);
>
> "The restlessness, remarked upon in previous years, was again evident during the past breeding season ..." (Jackson 1934);
>
> "The restlessness amongst the birds ... was again in evidence during the breeding season, particularly so amongst the duikers." (Jackson 1935).

A decreased proportion of Cape cormorants breeding and their early abandonment of nests are typical of years of low abundance of anchovy off South Africa (Crawford and Dyer 1995). The reports of the superintendent of the guano islands suggest poor availability of anchovy off southern Africa in the early 1930s, that may have been associated with a regime shift from anchovy to sardine. It appears from the reports that Cape cormorants were plentiful and bred successfully in the late 1920s, so anchovy was probably abundant in the Benguela system then. In Peru, anchovy was probably abundant in the early 1930s and scarce in the 1940s. If this was the case, the out-of-phase nature of the two systems would have been in place since the 1920s and perhaps earlier.

For the period 1954–1978, there was again a lag of two years in the significant relationship between the guanay cormorants and guano at Namibian islands. However, the relationship was positive, similar to that between Benguela sardine and Humboldt anchovy (Crawford *et al.* 1991b). It appears that, once intensive fisheries had developed, it was the overall abundance of fish, rather than its species composition, that regulated the seabird populations. For example, the Namibian sardine fishery collapsed in 1970, followed by the Peruvian anchovy fishery in 1972. For the period 1954–1978, large, negative residuals for Peruvian seabirds were once again associated with *El Niño* events, such as those of 1957–58, 1965 and 1972 (Quinn and Neal 1992), and positive residuals with post *El Niño* recoveries of seabird populations, e.g. 1954 and 1959. The 1965 *El Niño* was preceded by the 1963 Benguela Niño (Shannon *et al.* 1986), which gave rise to the most negative residual for guano production at Namibian islands between 1954 and 1978.

Over the period 1976–1995, Peruvian seabirds were negatively related to guano harvested at Namibian platforms in the following year. This means that the two systems were linked with no lag, because guano at platforms is produced in the summer breeding season of Cape cormorants and harvested the next year. The reason for the disappearance of a lag between the Peruvian and Benguela systems is not obvious.

In performing a large number of cross correlations where no significant relationship exists, on average one test in 20 can be expected to be spuriously significant at the 5% level, one in 50 at the 2% level, or one in 100 at the 1% level. In comparing indices for the Peru and Benguela systems, a total of 78 cross-correlations was performed. Of these, one was significant at the 1% level, two at the 2% level and four at the 5% level. In each instance, this is higher than the expected incidence of spurious correlations, but not greatly so. Clearly, the population dynamics of seabirds in the Peruvian and Benguela systems are influenced to a large extent by local phenomena, but linkage possibly occurs during extreme environmental conditions or perturbations of fish stocks. Especially during the years 1920–1953, when the systems were only lightly perturbed by fishing, linkage was apparent.

Seabird responses to ecosystem changes

Similarities in seabird trends in Peru and southern Africa were commented on earlier in the paper. Particularly noticeable have been the large declines in penguin populations, which have led to Humboldt and African penguins being classified as Vulnerable in terms of IUCN (World Conservation Union) criteria (Crawford 1998a, Luna-Jorquera 1998). Factors common to the decrease of both species have included collection of eggs, destruction of nesting habitat through guano harvests, and a decrease in food availability caused by fishing (Crawford *et al.* 1995b, Crawford 1998a, Luna-Jorquera 1998). Insufficient food may have decreased breeding success of the African penguin below that necessary to maintain the population (Crawford 1998b). The Humboldt penguin population was reduced by the *El Niño* event of 1982–83 (Hays 1986, Luna-Jorquera 1998). Extreme environmental conditions have also impacted the Galapagos penguin *Spheniscus mendiculus* population (Boersma 1978, Mills and Boersma 1998).

The guanay cormorant in Peru and the Cape cormorant in southern Africa fare best in periods of anchovy abundance (Crawford and Dyer 1995, Fig. 3). The proportion of Cape cormorants breeding in any year is significantly related to biomass of anchovy in the same year (Crawford and Dyer 1995). The reproductive success of both species of cormorant decreases in times of anchovy scarcity. In Peru, there is mortality of adult cormorants when food is exceptionally scarce, as during severe *El Niño*s (e.g. Jordán and Fuentes 1966, Tovar 1983). In South Africa, scarcity of food may have been the stress factor that precipitated high mortality of Cape cormorants from disease in 1991 (Crawford *et al.* 1992). Numbers of Cape cormorants probably increased between the mid 1950s, when sardine was the main food fish in the Benguela system, and the late 1970s, when anchovy dominated (Crawford *et al.* 1991a). Anchovy has since decreased, as have numbers of Cape cormorants off South Africa (Crawford 1999). Numbers of guanay cormorants decreased in Peru when sardine replaced anchovy as the dominant food, but have not recovered with the recent resurgence of anchovy (Fig. 4).

Overall numbers of Peruvian boobies and Peruvian pelicans have been relatively robust to long-term changes in prey resources (Fig. 9). In southern Africa, the area occupied by breeding Cape gannets decreased from 8.0 ha in 1956 to 4.7 ha in 1985, and then rose to 5.1 ha in 1996 (RJMC unpublished data). There were marked changes in regional populations (Randall and Ross 1979, Crawford *et al.* 1983, Crawford 1991, Crawford and Dyer 1995). Numbers of gannets decreased in Namibia, where mesopelagic fish species as well as anchovy replaced sardine (Crawford *et al.* 1985), but increased in South Africa, where there was a clear shift from sardine to anchovy (Klages *et al.* 1992, Crawford and Dyer 1995, Crawford 1999). The overall breeding population decreased as sardine decreased, and began increasing again as sardine increased from the mid 1980s. In South Africa, gannets were able to change their diet from sardine to anchovy and back to sardine again (Crawford 1999). In the North-West Atlantic, a century-long trend for northern gannets *Sula bassana* to increase is correlated with warming surface water conditions and increased availability of mackerel *Scomber scombrus* as a prey item (Montevecchi and Myers 1997).

The Peruvian booby, Cape gannet, Cape cormorant and Peruvian pelican have coped better with the large changes in food resources in the Peruvian and Benguela ecosystems in the 20th century than the guanay cormorant and the Humboldt and African penguins. Each of the last three species have undergone severe long-term decreases, which for the penguins have also been influenced by exploitation of birds and eggs.

ACKNOWLEDGEMENTS

This paper is a product of SCOR (Scientific Committee on Oceanic Research) WG-98. RJMC thanks Sea Fisheries (Namibia), South African National Parks, Cape Nature Conservation, Eastern Cape Nature Conservation and Robben Island Museum for permission to conduct research at southern African islands. The Marine Living Resource Fund financed his travel to Peru, where the authors finalized the paper.

LITERATURE CITED

BERRY, H. H. 1976 — Physiological and behavioural ecology of the Cape cormorant *Phalacrocorax capensis*. *Madoqua* **9**(4): 5–55.

BEST, P. B., CRAWFORD, R. J. M. and R. P. VAN DER ELST 1997 — Top predators in southern Africa's marine ecosystems. In *A Century of Marine Science in South Africa*. Payne, A. I. L. and J. R. E. Lutjeharms (Eds). *Trans. R. Soc. S. Afr.* **52**(1): 177–225.

BOX, G. E. P. and G. M. JENKINS 1976 — *Time Series Analysis; Forecasting and Control, Revised Edition.* San Francisco; Holden Day: xxi + 575 pp.

BOERSMA, P. D. 1978 — Galapagos penguins as indicators of oceanographic conditions. *Science* **200**: 1481–1483.

COOPER, J., BROOKE, R. K., SHELTON, P. A. and R. J. M. CRAWFORD 1982 — Distribution, population size and conservation of the Cape cormorant *Phalacrocorax capensis*. *Fish. Bull. S. Afr.* **16**: 121–143.

CRAWFORD, R. J. M. 1987 — Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. In *The Benguela and Comparable Ecosystems.* Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 735–757.

CRAWFORD, R. J. M. 1991 — Factors influencing population trends of some abundant vertebrates in sardine-rich coastal ecosystems. *S. Afr. J. mar. Sci*. **10**: 365–381.

CRAWFORD, R. J. M. 1998a — African penguin taxon data sheet. In *Penguin Conservation Assessment and Management Plan*. Ellis, S., Croxall, J. P. and J. Cooper (Eds). Apple Valley, USA; IUCN/SSC Conservation Breeding Specialist Group: 115–129.

CRAWFORD, R. J. M. 1998b — Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources.* Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci*. **19**: 355–364.

CRAWFORD, R. J. M. 1999 — Seabird responses to long-term changes of prey resources off southern Africa. In *Proceedings of 22nd International Ornithological Congress, Durban, South Africa, 1998.* Adams, N. J. and R. Slotow (Eds). Johannesburg; Birdlife South Africa: 688–705.

CRAWFORD, R. J. M., ALLWRIGHT, D. M. and C. W. HEŸL 1992 — High mortality of Cape cormorants (*Phalacrocorax capensis*) off western South Africa in 1991 caused by *Pasteurella multocida*. *Colon. Waterbirds* **15**(2): 236–238.

CRAWFORD, R. J. M., COOPER, J. and B. M. DYER 1995a — Conservation of an increasing population of great white pelicans *Pelecanus onocrotalus* in South Africa's Western Cape. *S. Afr. J. mar. Sci*. **15**: 33–42.

CRAWFORD, R. J. M., CRUICKSHANK, R. A., SHELTON, P. A. and I. KRUGER 1985 — Partitioning of a goby resource amongst four avian predators and evidence for altered trophic flow in the pelagic community of an intense, perennial upwelling system. *S. Afr. J. mar. Sci.* **3**: 215–228.

CRAWFORD, R. J. M. and B. M. DYER 1995 — Responses by four seabird species to a fluctuating availability of Cape anchovy *Engraulis capensis* off South Africa. *Ibis* **137**: 329–339.

CRAWFORD, R. J. M., RYAN, P. G. and A. J. WILLIAMS 1991a — Seabird consumption and production in the Benguela and Western Agulhas ecosystems. *S. Afr. J. mar. Sci.* **11**: 357–375.

CRAWFORD, R. J. M., SHANNON, L. V. and D. E. POLLOCK 1987 — The Benguela ecosystem. 4. The major fish and invertebrate resources. In *Oceanography and Marine Biology. An Annual Review* **25**. Barnes, M. (Ed.). Aberdeen; University Press: 353–505.

CRAWFORD, R. J. M. and P. A. SHELTON 1978 — Pelagic fish and seabird interrelationships off the coasts of South West and South Africa. *Biol. Conserv.* **14**(2): 85–109.

CRAWFORD, R. J. M. and P. A. SHELTON 1981 — Population trends for some southern African seabirds related to fish availability. In *Proceedings of the Symposium on Birds of the Sea and Shore, 1979.* Cooper, J. (Ed.). Cape Town; African Seabird Group: 15–41.

CRAWFORD, R. J. M., SHELTON, P. A., COOPER, J. and R. K. BROOKE 1983 — Distribution, population size and conservation of the Cape gannet *Morus capensis*. *S. Afr. J. mar. Sci.* **1**: 153–174.

CRAWFORD, R. J. M., UNDERHILL, L. G., SHANNON, L. V., LLUCH-BELDA, D., SIEGFRIED, W. R. and C. A. VILLACASTIN-HERRERO 1991b — An empirical investigation of trans-oceanic linkages between areas of high abundance of sardine. In *Long-Term Variability of Pelagic Fish Populations and their Environment.* Kawasaki, T., Tanaka, S., Toba, Y. and A. Taniguchi (Eds). Oxford; Pergamon: 319–332.

CRAWFORD, R. J. M., WILLIAMS, A. J., HOFMEYR, J. H., KLAGES, N. T. W., RANDALL, R. M., COOPER, J., DYER, B. M. and Y. CHESSELET 1995b — Trends of African penguin *Spheniscus demersus* populations in the 20th century. *S. Afr. J. mar. Sci.* **16**: 101–118.

CRAWFORD, R. J. M., WILLIAMS, A. J., RANDALL, R. M., RANDALL, B. M., BERRUTI, A. and G. J. B. ROSS 1990

— Recent population trends of jackass penguins *Spheniscus demersus* off southern Africa. *Biol. Conserv.* **52**(3): 229–243.

CSIRKE, J., GUEVARA-CARRASCO, R., CÁRDENAS, G., ÑIQUEN, M. and A. CHIPOLLINI 1996 — Situación de los recursos anchoveta (*Engraulis ringens*) y sardina (*Sardinops sagax*) a principios de 1994 y perspectivas para la pesca en el Peru, con particular referencía a las regiones norte y centro de la costa Peruana. *Boln Inst. Mar Perú* **15**: 23 pp.

DUFFY, D. C. 1983 — Environmental uncertainty and commercial fishing: effects on Peruvian guano birds. *Biol. Conserv.* **26**: 227–238.

GUILLÉN, V. C. 1992 — Distribucion latitudinal de aves guaneras del Peru, durante 1984–89. *Boln Lima* **81**: 77–96.

HALL, R. E., JOHNSTON, J. and D. M. LILIEN 1990 — *MicroTSP User's Manual*. Irvine, California, USA; Quantitative Micro Software: no pagination.

HAYS, C. 1986 — Effects of the 1982–83 El Niño on Humboldt penguin colonies in Peru. *Biol. Conserv.* **36**: 169–180.

HUTCHINSON, G. E. 1950 — The Southwest African guano coast. In *Survey of Contemporary Knowledge of Biogeochemistry. 3. The Biogeochemistry of Vertebrate Excretion. Bull. Am. Mus. nat. Hist.* **96**: 134–157.

JACKSON, H. 1930 — A valuable asset to the farmer: guano and other island products. *Fmg S. Afr.* **5**: p. 428.

JACKSON, H. 1931 — The Government Guano Islands. *Fmg S. Afr.* **6**: p. 359.

JACKSON, H. 1932 — The Government Guano Islands. *Fmg S. Afr.* **7**: p. 380.

JACKSON, H. 1933 — Report on the Government Guano Islands. *Fmg S. Afr.* **8**: p. 519.

JACKSON, H. 1934 — Report on the Government Guano Islands. *Fmg S. Afr.* **9**: p. 581.

JACKSON, H. 1935 — The Government Guano Islands. *Fmg S. Afr.* **10**: p. 596.

JORDÁN, R. 1964 — Las emigraciones y mortandad de aves guaneras en el ontoño e invierno de 1963. *Informe Inst. Investnes Recur. Mar.* **27**: 1–31.

JORDÁN, R. 1967 — The predation of guano birds on the Peruvian anchovy (*Engraulis ringens* Jenyns). *Rep. Calif. coop. oceanic Fish. Invest.* **11**: 105–109.

JORDÁN, R. and H. FUENTES 1966 — Las poblaciones de aves guaneras y su situación actual. *Infmes Inst. Mar Perú* **10**: 31 pp.

KAWASAKI, T. 1983 — Why do some fishes have wide fluctuations in their numbers? – Biological basis of fluctuation from the viewpoint of evolutionary ecology. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983.* Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(3): 1065–1080.

KLAGES, N. T. W., WILLIS, A. B. and G. J. B. ROSS 1992 — Variability in the diet of the Cape gannet at Bird Island, Algoa Bay, South Africa. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 761–771.

LLUCH-BELDA, D., CRAWFORD, R. J. M., KAWASAKI, T., MacCALL, A. D., PARRISH, R. H., SCHWARTZLOSE, R. A. and P. E. SMITH 1989 — World-wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. mar. Sci.* **8**: 195–205.

LLUCH-BELDA, D., SCHWARTZLOSE, R. A., SERRA, R., PARRISH, R. [H.], KAWASAKI, T., HEDGECOCK, D. and R. J. M. CRAWFORD 1992 — Sardine and anchovy regime fluctuations of abundance in four regions of the world oceans: a workshop report. *Fish. Oceanogr.* **1**(4): 339–347.

LUNA-JORQUERA, G. 1998 — Humboldt penguin taxon data sheet. In *Penguin Conservation Assessment and Management Plan*. Ellis, S., Croxall, J. P. and J. Cooper (Eds). Apple Valley, USA; IUCN/SSC Conservation Breeding Specialist Group: 95–104.

MILLS, K. L. and P. D. BOERSMA 1998 — Galapagos penguin taxon data sheet. In *Penguin Conservation Assessment and Management Plan*. Ellis, S., Croxall, J. P. and J. Cooper (Eds). Apple Valley, USA; IUCN/SSC Conservation Breeding Specialist Group: 105–107.

MONTEVECCHI, W. A. and R. A. MYERS 1997 — Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change. *ICES J. mar. Sci.* **54**: 608–614.

PAULIK, G. J. 1971 — Anchovies, birds, and fishermen in the Peru Current. In *Environment: Resources, Pollution and Society*. Murdoch, W. W. (Ed.). Stamford, Connecticut; Sinauer Associates: 35–79.

PAULY, D., PALOMARES, M. L. and F. C. GAYANILO 1987 — VPA estimates of monthly population length composition, recruitment, mortality, biomass and related statistics of Peruvian anchoveta, 1953 to 1981. In *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change*. Pauly, D. and I. Tsukayama (Eds). *ICLARM Stud. Rev.* **15**: 142–166.

QUINN, W. H. and V. T. NEAL 1992 — The historical record of *El Niño* events. In *Climate since A.D. 1500*. Bradley, R. S. and P. D. Jones (Eds). London; Routledge: 623–648.

RAND, R. W. 1963a — The biology of guano-producing seabirds. 4. Composition of colonies on the Cape islands. *Investl Rep. Div. Sea Fish. S. Afr.* **43**: 32 pp.

RAND, R. W. 1963b — The biology of guano-producing seabirds. 5. Composition of colonies on the South West African islands. *Investl Rep. Div. Sea Fish. S. Afr.* **46**: 26 pp.

RANDALL, R. [M.] and G. J. B. ROSS 1979 — Increasing population of Cape gannets on Bird Island, Algoa Bay, and observations on breeding success. *Ostrich* **50**(3): 168–175.

SHANNON, L. V., BOYD, A. J., BRUNDRIT, G. B. and J. TAUNTON-CLARK 1986 — On the existence of an *El Niño*-type phenomenon in the Benguela system. *J. mar. Res.* **44**(3): 495–520.

TOVAR [S.], H. 1983 — Fluctuaciones de poblaciones de aves guaneras en el litoral peruano, 1960–1981. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(3): 957–976.

TOVAR [S.], H. and D. CABRERA 1985 — Las aves guaneras y el fenomeno *El Niño*. In *El Niño su Impacto en la Fauna Marine*. Arntz, W., Landa, A. and J. Tarazona (Eds). *Boln Inst. Mar Perú, Callao-Peru* Vol. Extraordinario: 181–186.

TOVAR [S.], H., GUILLÉN, V. [C.] and D. CABRERA 1987a — Reproduction and population levels of Peruvian guano birds. *J. geophys. Res.* **92**(C): 14445–14448.

TOVAR [S.], H., GUILLÉN, V. [C.] and M. E. NAKAMA 1987b — Monthly population size of three guano bird species off Peru, 1953 to 1982. In *The Peruvian Anchoveta and its Upwelling Ecosystem: Three Decades of Change*. Pauly, D. and I. Tsukayama (Eds). *ICLARM Stud. Rev.* **15**: 208–218.

TROADEC, J-P., CLARK, W. G. and J. A. GULLAND 1980 — A review of some pelagic fish stocks in other areas. *Rapp. P-v. Réun. Cons. perm. int. Explor. Mer* **177**: 252–277.

VALDIVIA [P.], J. 1960 — La cubicación del guano de islas y la ecuación de regresión. *Boln Compañia Adm.Guano* **36**(5): 8–10.