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Historical variations in food consumption by breeding seabirds of the Humboldt and Benguela upwelling regions

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Introduction

Estimates of food consumption by seabirds are necessary for the management of many commercially important fish species and the ecosystems in which they live. Cohort or Virtual Population Analysis (VPA) (Ricker, 1975), widely used to estimate the sizes of fish stocks, is dependent on estimates of mortality caused by natural predators such as seabirds. The results of VPA are sensitive to even relatively small alterations in the estimates of natural mortality (e.g. Armstrong *et al.*, 1983).

For most marine predators, such as marine mammals, squid, or predatory fish, estimates of populations and their food consumptions are either unavailable or are accurate to only one or two orders of magnitude. Seabirds are one of the few groups for which, despite the often formidable problems of censusing populations and assessing diets, reasonably accurate estimates of food consumption can be provided. These estimates can be used to 'calibrate' or rank vaguer estimates for other predators in relation to seabirds. Fluctuations in avian consumption levels can also signal changes in the total natural mortality of fish, which may have major implications for VPA estimates, although the possibility of such changes appears to have received relatively little attention (but see Schaefer, 1967, 1970; MacCall, 1983).

Estimates of the amounts of food consumed by seabirds are also essential where multi-species management is necessary, either because of legal or treaty requirements as in the California Current (Green, 1978) and the Southern Ocean (Mitchell & Sandbrook, 1980), or because a suite of

commercially important fish species may alternate in dominance within a marine ecosystem (Ahlstrom, 1966; Daan, 1980; Newman & Crawford, 1980; Skud, 1982) so that the ecosystem can only be managed by understanding the competitive milieu, including predators, of the fish species (May *et al.*, 1979). This appears to be the situation in both the Benguela upwelling ecosystem off southwestern Africa (Shannon, Crawford & Duffy, 1984) and the Humboldt or Peruvian upwelling ecosystem off the west coast of South America (Serra, 1983; Zuta, Tsukayami & Villanueva, 1983).

Finally, seabirds, in addition to being potentially useful as monitors of fish stocks, are in themselves important economic resources as guano producers in Peru, South Africa and Namibia, and as tourist attractions in Galapagos and many places in Europe and North America. For economic and conservation reasons, it is desirable to know how much food is necessary to maintain these populations.

As a result of these and other needs, numerous studies have estimated consumption by seabirds in different marine environments, with varying degrees of apparent precision and accuracy (e.g. Vogt, 1942; Hutchinson, 1950; Davies, 1958; Schaefer, 1967, 1970; Sanger, 1972; Wiens & Scott, 1975; Furness, 1978; Croxall & Prince, 1982, 1984; Furness & Cooper, 1982; Schneider & Hunt, 1982; see also Chapter 11). Most of these studies have provided single values for food consumption by seabirds. Both the Benguela and Humboldt ecosystems are characterised by long- and short-term spatial and temporal variability (e.g. Hutchinson, 1950; DeVries & Schrader, 1981; Hendey, 1981; Shannon *et al.*, 1984). Given the natural variability of seabird populations (reviewed by Drury, 1979) and of marine ecosystems (e.g. Smith, 1978; Walsh, 1978), as it may affect seabirds (Myres, 1979), single estimates for consumption are likely to have only transitory value or to even be dangerous, if they imply existing or potential competition with a commercial fishery. Inflated consumption figures have been used by politicians and commercial fishermen in Peru (Nelson, 1978), South Africa (Jarvis, 1971), Namibia (Green, 1950) and elsewhere to support attempts to cull large numbers of seabirds in the belief that this would increase fish stocks available for commercial exploitation.

In this chapter we use guano production to estimate the food consumption of seabirds in the Southern Benguela and the Humboldt or Peruvian coastal current ecosystems at different stages of the commercial exploitation of their fish stocks. Peru and the west coast of South Africa have been chosen because relatively little is known about seabird population sizes off Chile or fluctuations in the abundance of seabirds breeding off

Namibia. We compare the extent and variability of consumption between years and between decades. Finally, for the Peruvian ecosystem, we examine the possibility that the importance of seabird predation may be in terms of its timing rather than total consumption.

Methods

We have confined our analysis to the major breeding populations of seabirds of each ecosystem: the Guanay Cormorant *Phalacrocorax bougainvillii*, Peruvian Booby *Sula variegata*, and Peruvian Brown Pelican *Pelecanus thagus* in the Humboldt ecosystem; and the Jackass Penguin *Spheniscus demersus*, Cape Gannet *Sula (Morus) capensis*, and Cape Cormorant *Phalacrocorax capensis* in the Benguela ecosystem.

Abundance of birds

We have little idea of the abundance of migratory seabirds in the Humboldt ecosystem (cf. Murphy, 1936; Brown, 1981; Duffy, 1981) or of seasonal variation in the abundance of migrants in the Benguela ecosystem (Summerhayes, Hofmeyr & Roux, 1974; Abrams & Griffiths, 1981). Hence migratory species which do not breed in our regions are excluded from our calculations.

To examine annual and decadal changes in the abundances of resident breeding species, we used guano production from nesting and roosting islands to estimate bird numbers. Since the early 1900s guano, as a renewable resource, has been collected annually and biennially, which should reflect bird abundance since the last collection (Murphy, 1925; Green, 1950; Hutchinson, 1950; Jordan & Fuentes, 1966*a,b*). Jordan & Fuentes (1966*a,b*) estimated numbers of adult guano birds in Peru between 1909 and 1964 by dividing guano collections by the average amount of guano deposited per adult bird per year (= 15.9 kg; Vogt, 1942). For the period 1960 to 1981, we used estimates of Peruvian guano bird numbers calculated by Tovar (1983).

For the South African seabird population, we calculated numbers of birds from guano production and an estimate made by Jarvis (1971) that each Cape Gannet deposits 8.7 kg guano per year on its breeding island. This was obtained by dividing average guano production (457.6 tonnes) on Malagas Island (33° 03'S, 17° 56'E) during 1950–60 by the estimated maximum population of Cape Gannets on the island (Jarvis, 1971). Although nestlings also contributed to the guano, their numbers are not included in these estimates. Estimates of guano deposition per bird are lower for the slightly larger Benguela species, because there is much more

rain, and wind speeds are higher off the South African coast than off Peru and thus there is more run-off of guano into the sea. In our analyses we included all Peruvian guano collections between 1909 and 1980 and all South African collections made at islands between Bird (Penguin) Island, Lambert's Bay (32° 05'S, 18° 17'E), and Dyer Island (34° 14'S, 19° 25'E) before 1975.

Energy requirements of birds

We assumed that all Peruvian guano birds had the energetic requirements of the Guanay Cormorant (mass = 1.8 kg), rather than the lighter Peruvian Booby (mass = 1.3 kg) or the heavier Peruvian Brown Pelican (mass = 6.0 kg), based on data from Duffy (1980). The average mass of a Benguela seabird was assumed to be 2.65 kg, equivalent to that of the Cape Gannet, rather than that of the Jackass Penguin (3.00 kg) or the Cape Cormorant (1.22 kg), based on data in Furness & Cooper (1982). This assumption was necessary, because we have data on the relative abundances of the three species only since 1960 in Peru (Tovar, 1983) and 'complete' data for the entire Benguela region for only three years (1956, 1967, 1978) (Crawford & Shelton, 1981). The 'average' bird masses calculated from these figures do not differ much from those of the Guanay Cormorant (1.80 kg *versus* 1.81 kg), assuming that Guanay Cormorants, Peruvian Boobies and Brown Pelicans account for 83%, 15% and 2%, respectively, of the total Humboldt population (Jordan & Fuentes, 1966b), or Cape Gannet (2.65 kg *versus* 2.43 kg), assuming that Jackass Penguins, Cape Gannets and Cape Cormorants account for 57%, 14% and 29%, respectively, of the total population for the Saldanha Bay area in the Benguela region (Furness & Cooper, 1982).

We used the equation of Lasiewski & Dawson (1967) to calculate the SMRs (Standard Metabolic Rates) of the Guanay Cormorant and Cape Gannet. These were multiplied by 2.5 (Cooper, 1978; Kooyman *et al.*, 1982; Nagy, Siegfried & Wilson, 1984) to estimate the energy requirements of a single Guanay Cormorant or Cape Gannet per day and per year, and by 4.186 to convert calories to joules.

Food consumption by birds Estimates of daily annual energy requirements were converted to mass (wet weight) of anchovy *Engraulis* spp. by dividing by a conversion factor of 6.37 kJ g⁻¹ (22.35 kJ g⁻¹ × 0.285 dry/wet weight, derived from Cooper, 1978) for Cape Anchovy *Engraulis capensis*. We multiplied this by 1.33 to allow for a 75% assimilation efficiency (Dunn, 1975; Cooper, 1978). The birds also eat other species, such as sardines *Sardinops* spp. and horse mackerels *Trachurus* spp. (Murphy,

1925; Rand, 1959, 1960a,b; Crawford & Shelton, 1981; Cooper, 1984), which have differing energetic values (Nagy *et al.*, 1984).

With regard to fish, the term 'population' in this paper refers to the total sum of interbreeding individuals of a species, whereas the term 'stock' is that proportion of the population that is exploitable by commercial fishing. Fish that are too large, too small, or otherwise unavailable for commercial fishing are considered part of the population but not part of the stock. Population estimates of Anchoveta *Engraulis ringens* stocks were taken from Csirke (1980) and commercial fishing landings from Schaefer (1970) and Idyll (1973). For South African fish stocks, we used estimates from Armstrong *et al.* (1983).

Estimating variability of food consumption We investigated variability of food consumption by seabirds over time by calculating the coefficient of variation (CV) for increasing intervals of years since 1909 in Peru and 1905 in South Africa. Variability should increase slowly and at a relatively constant rate if the population remains stable but should show sharp increases at short time intervals when major changes occur. We tested the theory that decreases in avian predation on young fish in Peru result in increases in recruitment to the commercial fish stock, using data on the strength of annual recruitment of Anchoveta (Csirke, 1980) before and after 1965.

Results

Guano as a measure of seabird populations

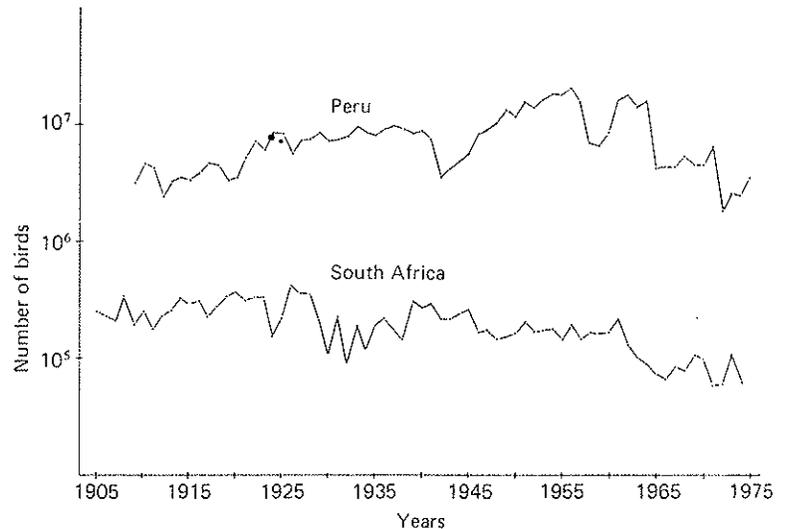
Comparisons of direct counts of seabirds, usually by aerial surveys or sketches of occupied areas, with guano yields produced Spearman rank correlations (Siegel, 1956) of 0.66 for Peru ($P < 0.05$; $n = 10$), based on data from Jordan & Fuentes (1966a,b) and Tovar (1978), and 0.60 for South African islands on which Gape Gannets nest ($P < 0.05$; $n = 14$), using data from figure 2 of Crawford & Shelton (1978). Randall & Ross (1979), however, reported no relation between guano production and area occupied by Cape Gannets during two decades ($n = 3$) at Bird Island (33° 50'S, 26° 17'E) off the south coast of South Africa. On the other hand, Valdivia (1960) showed a significant correlation between Peruvian guano collections and areas occupied by guano birds ($r_s = 0.73$; $P < 0.05$; $n = 16$). On balance, therefore, guano does apparently reflect the abundance of breeding seabirds in both ecosystems, suggesting that change in guano yields can be used to investigate the extent and variability of food consumption by seabirds.

Population trends

In Peru, seabird populations, based on guano production, rose from approximately 4 million birds during 1909–20 to about 8 million in the 1930s, before decreasing sharply in the 1940s (Fig. 14.1). The increase was the result of better protection of the birds and their nesting islands (Jordan & Fuentes, 1966*b*). The decrease in the mid-1940s was the result of a series of El Niño oceanographic events which killed off large numbers of birds by making their main prey, the Anchoveta, scarce or unavailable. The subsequent recovery of the avian predators in the 1950s led to populations of up to 20 million birds, considerably above levels in the 1930s. This was probably a response to an increase in nesting space, following the walling off of coastal headlands with predator-proof concrete fences (Jordan & Fuentes, 1966*b*; Duffy, 1983*b*). The sharp decreases in the late 1950s and during 1965 were again the results of El Niño events. The avian population never recovered fully from the 1965 El Niño, probably because heavy commercial fishing for the Anchoveta reduced the birds' food supply, leading to a large non-breeding population and reduced rates of increase (Tovar, 1978, 1983; Duffy, 1983*a*).

Except for a peak in the 1920s, bird populations resident off the west of South Africa showed no long-term trends until the 1960s when heavy

Fig. 14.1. Estimated numbers of breeding seabirds in the Peruvian (1909–81) and South African (1905–74) sectors of the Humboldt and Benguela ecosystems, respectively.

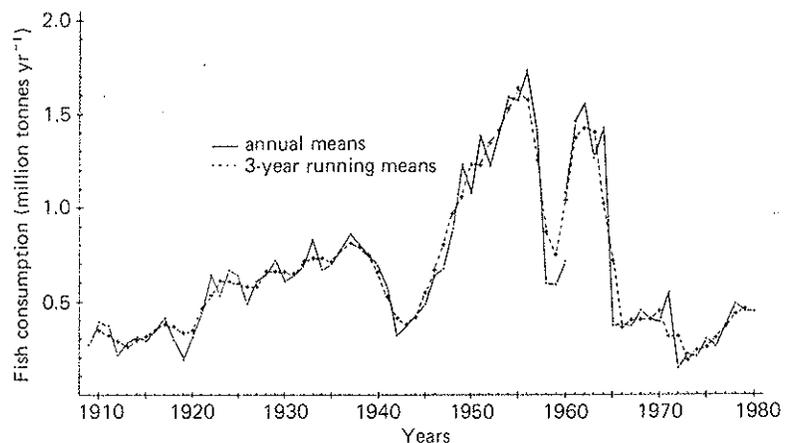


commercial fishing caused a population decrease (Fig. 14.1; Crawford & Shelton, 1981).

Consumption and availability of food Based on an estimated energy expenditure of $1657.7 \text{ kJ day}^{-1}$, a Cape Gannet requires $0.346 \text{ kg day}^{-1}$ and 126.0 kg yr^{-1} of Cape Anchovy. A Guanay Cormorant expends $946.0 \text{ kJ day}^{-1}$ and requires $0.197 \text{ kg day}^{-1}$ and 71.5 kg yr^{-1} of Anchoveta.

In Peru, population estimates for the Anchoveta exist since 1960 (Csirke, 1980). In the first years of heavy fishing (1960–62), the stock was as large as 20.1–25.8 million tonnes. Between 1963 and 1971, the Anchoveta stock fluctuated greatly from 21.6 million tonnes in 1967 to 10.0 million tonnes in 1971. In 1972, the stock collapsed to 1.5 million tonnes and has subsequently remained at about 4–5 million tonnes, supposedly replaced by the *Sardina Sardinops sagax* (Walsh, 1981). If values of 20–25 million tonnes represent the size of the unexploited stock, then consumption of Anchoveta by the seabird population was $< 5\%$ in the early 1960s (Fig. 14.2). Even during the peak of 20 million birds in 1956, only 1.73 million tonnes or 6.9–8.6% of the Anchoveta stock was consumed by breeding seabirds. The greatest proportionate consumption by seabirds occurred in 1963–65 when they apparently took up to 11% of the Anchoveta stock during a short decrease in the fish population (Fig. 14.3). Frequent El Niños appear to have kept the avian population at levels

Fig. 14.2. Consumption of food by breeding Peruvian seabirds (1909–80). Solid lines represent annual estimates; broken lines, 3-year means.



below what is necessary for the consumption of a relatively large proportion of the Anchoveta population.

In South Africa, stock estimates for the Cape Pilchard *Sardinops ocellata* are available since 1950 but Cape Anchovy values are only available since 1963 (Shannon *et al.*, 1984). The Cape Anchovy is believed to have replaced the Cape Pilchard during the 1960s, following commercial over-exploitation of the latter. In the late 1950s, the Cape Pilchard stock was as large as 2 million tonnes but in the mid-1960s it decreased to < 0.5 million tonnes. Cape Anchovy stocks appeared to be increasing rapidly when they were first exploited in the early 1960s, rising from 0.3 million tonnes or less to over 1.0 million tonnes during 1974 and since 1979. Assuming that, before the collapse of the Cape Pilchard stock following commercial over-exploitation, seabirds ate only Cape Pilchards and that this species' pre-exploitation population was about 1 million tonnes, then even the greatest bird consumption (0.050 million tonnes in 1926) accounted for only about 5% of the Cape Pilchard's biomass (Fig. 14.4). Consumption was approximately half this level in most years. If the Cape Anchovy was also common during this period, then the proportionate consumption of Cape Pilchard was even lower.

Fig. 14.3. Consumption of food by breeding Peruvian seabirds, as a percentage of fish stocks and of the commercial fishery landings.

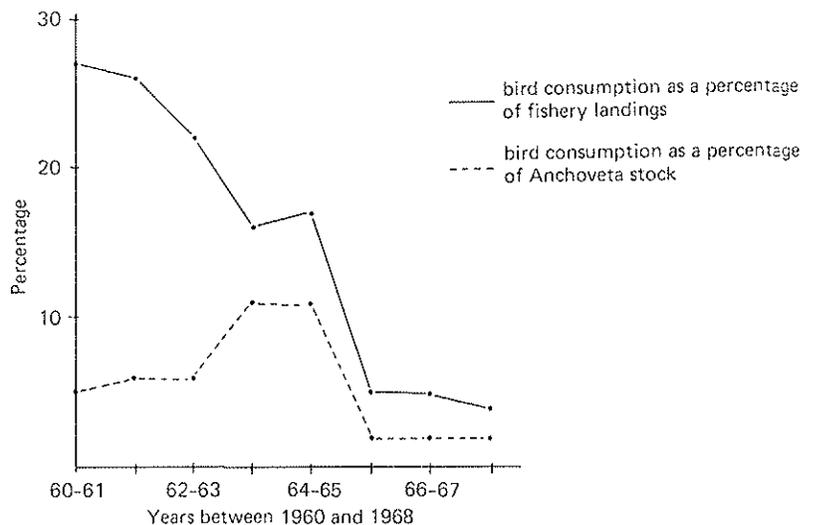


Fig. 14.4. Consumption of food by breeding South African seabirds (1905-74). Solid lines represent annual estimates; broken lines, 3-year running means.

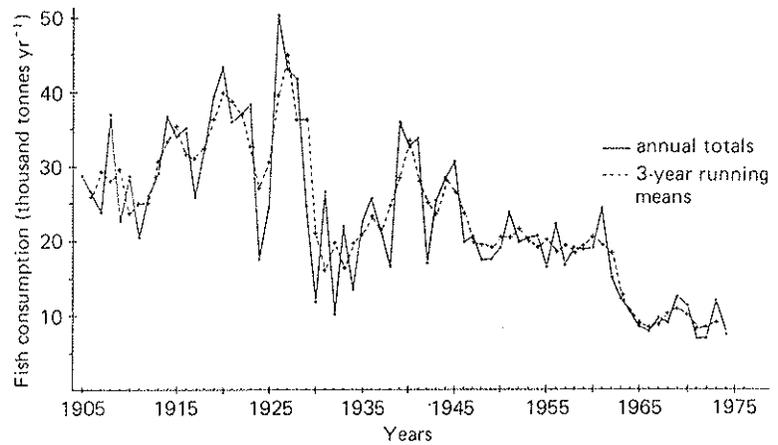
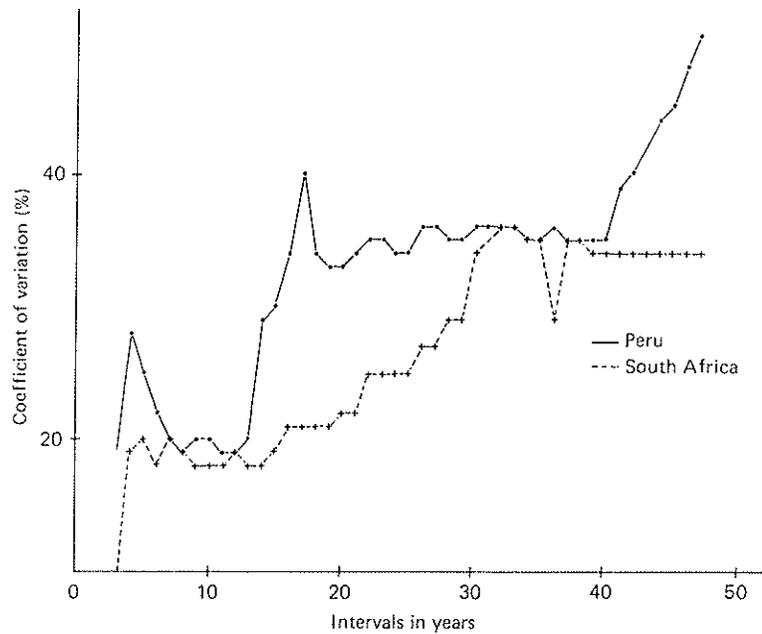


Fig. 14.5. Cumulative coefficients of variation for abundance of breeding populations of seabirds (and their food consumption) as a function of increasing number of years since 1909 in Peru and 1905 in South Africa.

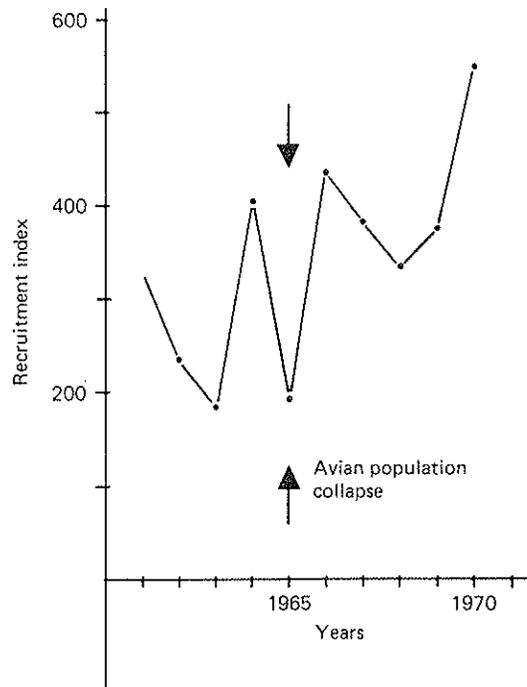


Variability of consumption Variability in consumption data differed considerably between the two areas (Fig. 14.5). Peruvian data showed an early peak then low variability until the 15-year interval when the coefficient of variation (CV) increased rapidly to a plateau of about 35%. There appeared to be a regular fluctuation until the 40-year interval when the CV began to increase sharply again.

Although the South Africa CV data showed an initial sharp increase, the subsequent increase was much slower than in Peru. The plateau was not reached until the 30-year interval, twice as long as in Peru.

Regulating anchovy recruitment The mean Recruitment Index (an arbitrary number) of Anchoveta before the El Niño of 1965 was 291.5 (1960–65) (S.D. = 108.49; $n = 6$) but afterwards it rose to 398.4 (Fig. 14.6) before the stock began to collapse (1966–70) (S.D. = 75.69; $n = 5$) (Csirke, 1980). The means were not significantly different ($F = 2.137$; $P > 0.05$).

Fig. 14.6. Recruitment indices and stock size before and after the 1965 collapse of the Peruvian guano bird population (data from Csirke, 1980).



suggesting that recruitment was not increased by the reduction in the population of guano birds. Stock estimates did not increase following 1965 (Csirke, 1980).

Discussion

Guano as a measure of seabird populations

Using information on guano yields to estimate the abundance of seabird populations has major advantages not available from conventional census methods. Long runs of historical data exist, beginning in the early 1900s. Population estimates derived from guano data also provide a summation of bird activity on an island throughout an entire breeding season or year. These data can be used to supplement more exact estimates based on single counts. Both methods have disadvantages. For example, conventional population estimates based on one or more actual counts of birds are subject to a series of potentially serious biases, especially for species with extended or continuous breeding seasons such as occur in both the Benguela and Humboldt avian communities. Even counts made at peak breeding times may seriously under-estimate numbers of breeders if other individuals nest at other times during the year, as do Jackass Penguins and Peruvian Boobies. The accuracy of single counts depends on the time of day and on weather conditions, because these may affect the number of birds absent from their nests (Frost, Siegfried & Cooper, 1976). Ground censuses of individuals or nests are not practical when attempting to count colonies of tens or hundreds of thousands of birds in Peru and South Africa. Replication of counts to obtain confidence limits would be out of the question, even for much smaller colonies. Inter-observer biases would further complicate matters. Aerial photographs have the advantage that a permanent record exists (Nelson, 1978), but counts from photographs are subject to counting bias (Harris & Lloyd, 1977; Shelton *et al.*, 1982).

Counting problems can be avoided by measuring areas used for nesting, on a photograph, and multiplying by a nesting density (e.g. Randall & Ross, 1979). This assumes accuracy in identifying nesting areas (Barrett & Harris, 1965; Shelton *et al.*, 1982) and a relatively constant nesting density. Estimating numbers of nests for species such as the Cape Gannet and Guanay Cormorant may be possible with this method but Jackass Penguin nesting densities are very variable. Even for the Cape Gannet, estimates of nest density vary from 2.25 to 4.54 nests per square metre between islands and from 2.34 to 3.08 nests per square metre on one island (Randall & Ross, 1979). Jackass Penguins also nest in burrows

which presents problems in interpreting aerial photography (Frost *et al.*, 1976).

On the other hand, population estimates from guano yields can be biased by three main sets of factors: (1) the estimation of guano deposition per bird per year; (2) the percentage of non-breeders not present on the islands; and (3) economic and environmental factors which may affect the size of the guano collection. Although we have fairly reliable data on the accuracy of guano deposition as an index of the abundance of Peruvian guano birds (see Hutchinson (1950) for a review), similar information is meagre for field conditions in South Africa. More accurate estimates of guano production are needed to refine South African data presented here.

Data on the abundance of seabird populations, as derived from guano production, are probably under-estimates, since pre-breeding immature birds and non-breeding adults may spend most of their time at sea. This problem also affects other census methods. Numbers of pre-breeders can be estimated from calculations of life history tables (e.g. Furness & Cooper, 1982) but these usually involve major assumptions such as population stability, constant reproductive success and fixed longevity. None of these applies to Peruvian seabirds (Nelson, 1978), and they are unlikely to be valid for Benguela species.

Guano harvests can be affected by a number of economic and environmental factors. Government control would tend to buffer the guano industry against free-market economic forces, and provide a continuity which would be less likely under private management. Apparently, guano extraction and management of the birds in both South Africa and Peru have altered little since descriptions by Murphy (1925) and Green (1950). However, in the last decade, in both regions, islands which have been almost deserted by nesting birds or are difficult to supply no longer have watchmen stationed on them. Moreover, the collecting of guano has recently been prohibited on those South African islands where guano is produced primarily by Jackass Penguins. Finally, the guano industry in South Africa has been operated by private companies since 1976, although management and protection of the islands remain the responsibility of the South African government (Sea Birds and Seals Protection Act, 1973). In Peru and South Africa, the collection of guano may not be undertaken during years of poor reproduction by the birds. Hence, guano is allowed to accumulate for more than one year in order to justify its collection. On the other hand, in years of good recruitment and an abundance of birds, it may be impossible to collect all the guano, so the excess is left for the

next year. Three-year running means (which we have also used here) should reduce the effects of these factors on population estimates.

Rainfall might affect guano deposits, especially during anomalous conditions such as El Niño in the Pacific (Murphy, 1936; Hutchinson, 1950; Jordan & Fuentes, 1966a) and similar, but less severe, events in South African waters (Hutchinson, 1950; Duffy *et al.*, 1984). However, most Peruvian islands receive very little rainfall, even during El Niño years when the coastal desert may be flooded (Vogt, 1940, 1942). Thus, their guano yields are likely to be relatively unaffected by rainfall compared to the loss of guano caused by seabird breeding failures and the abandonment of islands by birds (Murphy, 1925, 1936; Vogt, 1940; Duffy, 1983a). In South Africa, where rainfall is more likely to cause run-off of guano from islands, desertions of nests and islands have also been linked to heavy rainfall and El Niño-like events (Hutchinson, 1950; Duffy *et al.*, 1984). During such events, rainfall and nesting failures would both reduce guano yields.

Additional factors, such as relative changes in seabird nesting populations on islands, might affect guano yields. Some species, such as the Guanay Cormorant and the Cape Gannet, produce more or purer guano than others (Vogt, 1942; Rand, 1952). Unfortunately, we lack quantitative information on species composition before the 1950s in Peru (Tovar 1978, 1983). Although changes are known to have occurred (Hutchinson, 1950; Cooper, 1984), we have assumed that these have had minor effects from year to year on guano production, compared to changes caused by El Niño and other environmental factors.

Food consumption

Our calculations of the birds' energy requirements are conservative, compared to other methods (Schneider & Hunt, 1982; Laugksch & Duffy, unpublished). Consumption values twice as great as those obtained here could be produced by selecting the 'correct' metabolic equations and assimilation efficiencies for the birds, and energetic values for fish. We believe, however, that our results are sufficient to show that breeding seabirds have been relatively minor consumers of fish in the two regions. Breeding Peruvian seabirds consumed two orders of magnitude more food than the Benguela birds, even though the areas of the two upwellings considered in this paper only differ by approximately a factor of two (assuming both upwellings to be approximately 100 km wide, the Peruvian coastline is 2250 km, the South African coastline, 900 km). The difference in numbers may, in part, be the result of a relative scarcity of suitable

nesting habitat in the Benguela region. Brooke & Crowe (1982) reported 15 islands with a total land area of 389 ha off the 900 km South African coastline between the Orange River (28° 35'S, 16° 27'E) and Cape Agulhas (34° 08'S, 20° 00'E). Only about 7% of this island space was occupied by nesting birds in 1956 (calculated from Rand, 1963), primarily by low-density nesting Jackass Penguins. The total area of Peruvian islands and coastal headlands is approximately 8116 ha (Gonzalez, 1952). The nesting area used by seabirds totalled as much as 332 ha (Valdivia, 1960) but averaged 196 ha (Gonzalez, 1952) along a coastline of approximately 2250 km.

The low levels of food consumption reported in this paper do not necessarily mean that total avian consumption is minor; non-breeding seabirds from the northern and southern hemispheres are abundant in both upwelling ecosystems (Murphy, 1925; Summerhayes *et al.*, 1974) and probably consume large amounts of food, including anchovy and sardines.

Comparison with previous estimates of consumption

In South Africa, Davies (1958) estimated that the Benguela populations of Jackass Penguins, Cape Gannets and Cape Cormorants together consumed 89 000 tonnes yr⁻¹ of fish in the early 1950s. This translates to a daily food consumption equal to 31% of the body weight of the Jackass Penguin and Cape Cormorant and 45% for the Cape Gannet. Comparable figures for our study would be 12.6% for the Jackass Penguin, 13.1% for the Cape Gannet and 16.1% for the Cape Cormorant. Davies' values appear to be excessively high. From studies of captive birds, Cooper (1977, 1978) estimated food consumption as 20% of body mass for both adult Cape Gannets and almost fully grown Jackass Penguin chicks. More recently, Furness & Cooper (1982) estimated total fish consumption by seabirds as 16 435 tonnes yr⁻¹ in the Saldanha Bay area which is the central part of our Benguela region. Although they used a more elaborate method of calculating energy requirements, their values for daily consumption work out as 13% of body mass for the Jackass Penguin, 19% for the Cape Gannet and 18% for the Cape Cormorant.

Davies' (1958) estimate of 89 000 tonnes would represent a consumption of 30% of the Cape Pilchard stock of about 300 000 tonnes in the early 1950s (Armstrong *et al.*, 1983). Furness & Cooper's (1982) value represents a consumption of 7–8% of the southern Benguela Cape Anchovy stock (204000–227 000 tonnes) in 1977–78 (Armstrong *et al.*, 1983). Furness & Cooper estimated that seabirds consumed 23% of the Cape Anchovy

stock in their more restricted, local study area. The stock in this area is part of a larger population which extends from at least the Orange River ($28^{\circ} 35'S$, $16^{\circ} 27'E$) to Cape Agulhas ($34^{\circ} 08'S$, $20^{\circ} 00'E$) (Duffy & Boyd, 1983). We know that a large portion of this population migrates through the Saldanha Bay area (Crawford, 1981), so that comparisons of local avian consumption with total fish stock estimates are more appropriate in attempts to assess the impact of seabirds on commercially important fish (Bourne, 1983). In other words, avian consumption should be calculated over the entire ranges occupied by fish populations, rather than over limited areas with especially high densities of breeding birds.

Variability of consumption Variability in the abundance of breeding seabirds and their food consumption is clearly much greater in Peru than in South Africa. Two factors may contribute to this: the periodic Peruvian population crashes caused by El Niño, and the expansion of Peruvian nesting space in the 1940s. In South Africa, El Niño-like events lead to nesting failures, rather than mass mortalities of adults (G.D. La Cock, unpublished). In both cases, changes in the variability of estimates of food consumption occurred in pulses rather than continually. Relatively little change occurred over several decades, followed by short periods of high variability. This suggests that estimates of food consumed by the seabirds are likely to remain valid over long periods in ecosystems not subject to commercial fishing. The variability of avian consumption in exploited ecosystems may be much more difficult to predict, because it would change in response to levels of commercial fishing.

Conclusions

Guano yields, despite the problem of calibrating precisely numbers of birds with guano produced, provide a long time-series of the kind of data needed to gain insights into the dynamics of seabird populations in upwelling areas. Our data suggest that breeding seabirds take < 5% of the populations of their principal fish prey in the Benguela and Humboldt ecosystems. These estimates could be doubled by means of 'judicious' use of selected variables, but the result would still be that these resident breeding seabirds are relatively minor predators in terms of the quantity of fish they remove from their respective ecosystems. Their populations may be limited by El Niño in Peru and by a shortage of nesting space and by milder El Niño-like events off South Africa. Culling breeding seabirds is thus unlikely to improve the landings of commercial fisheries in either area.

Seabird populations in the two ecosystems showed relatively constant

degrees of variability over long periods of time. This suggests that even with frequent environmental perturbations, the bird populations, and the communities of which they are a part, did not experience chaotic fluctuations but varied within certain limits. The relative stability of the birds suggests that other predators are also likely to show similar degrees of variability in unexploited systems. Further analysis of guano yields in both regions may provide more information on the dynamics of the avian populations and their ecosystems.

Although the resident breeding seabirds may not consume large quantities of fish in either ecosystem, they merit further study for many reasons. Their depredation, although minor in quantity, may significantly affect the populations of their prey at particularly sensitive stages in their life cycles as proposed by Schaefer (1970), even if his suggestion that seabirds limited recruitment of *Anchoveta* before 1965 is not justified by our examination of the data. Secondly, seabirds, when judiciously used, may prove highly effective for sampling and monitoring pelagic fish stocks. Seabirds can complement existing sampling methods, reducing their sources of bias (e.g. VPA estimates rely at present entirely on commercial catches). Also, seabirds in the Humboldt and Benguela ecosystems take smaller and younger fish than the commercial fisheries (personal observation). This may allow an early warning of reproductive failures of certain short-lived species, which if not heeded could lead to the extirpation of fish stocks through commercial overfishing (Paulik, 1971). Finally, guano run-off from islands may provide an important source of nutrients for plankton during temporary halts in upwelling (Murphy, 1925; Hutchinson, 1950).

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