Interactions Between Breeding Seabird and Pelagic Fish Populations in the Southern Benguela Region

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ABSTRACT: A bioenergetics model was used to estimate the quantity of pelagic fish eaten and the energy consumed by 3 species of breeding seabirds in the Saldanha Bay fishing ground in the Southern Benguela Region off the west coast of South Africa. The 3 species – jackass penguin *Spheniscus demersus*, Cape gannet *Sula capensis*, and Cape cormorant *Phalacrocorax capensis* – were estimated to consume a total of 16,500 t of fish yr^{-1}, of which 11,800 t were anchovy *Engraulis capensis* Gilchrist. This represented a total consumption of 1.3×10^8 Kj. Annual consumption of fish by the 3 seabird species was estimated to represent 30 % of the mean annual catch in the Saldanha Bay fishing ground, based on a mean commercial fishery landing of 55,000 t per year. This figure is similar to that estimated for several other oceans where breeding seabirds and a commercial fishery coexist.

INTRODUCTION

Increasing exploitation of pelagic fish populations throughout the world has led to a focusing of attention on the management of marine ecosystems, rather than of single isolated populations of fish. Predation of pelagic fish by seabirds is one aspect requiring study before fish populations can be effectively managed. Also, development of commercial fisheries can affect seabird populations. For example, seabird numbers decreased by more than an order of magnitude during the development of the Peruvian anchovy *Engraulis ringens* Jenyns fishery, apparently because, under conditions of reduced fish population size, they were unable to rear sufficient chicks to balance the irregular adult mortality caused by periodic oceanographic perturbations (Jordán and Fuentes, 1966; Nelson, 1978).

Recent studies have shown that seabirds may consume 22 to 29 % of the fish production each year (Wiens and Scott, 1975; Furness, 1978). Detailed investigations of the correlations between seabird and pelagic fish populations in the Benguela region off the west coast of South Africa (Crawford and Shelton, 1978, in press) have revealed clear relationships between fluctuations in seabird and fish populations, and recent tendencies for overfishing to result in decreasing seabird numbers. Application of a model

similar to that of Furness (1978) to the major breeding seabird populations of the Benguela region would therefore be of particular interest in further defining these relationships. In this paper we use a bioenergetics model to estimate the food consumption of populations of jackass penguins *Spheniscus demersus*, Cape gannets *Sula capensis* and Cape cormorants *Phalacrocorax capensis* in the Saldanha Bay fishing ground (defined in Crawford, 1981a) in the southern Beguela region (Fig. 1). This system is particularly amenable to analysis: the 3 large diurnal species comprise over 95 % of the breeding seabird biomass of the area (JC. unpubl.), and data are available on their diets, breeding biology and foraging ranges (e.g. Cooper, in press), as well as on biomass and size distribution of their fish prey (e.g. Crawford, 1980a, b, 1981a, b, c, d, e, f). More bioenergetics equations are now available from studies of a wider variety of species (Kendeigh et al., 1977), further improving the accuracy of these energy budget calculations.

METHODS

Annual energy requirements of the jackass penguin, Cape gannet and Cape cormorant populations were estimated using a bioenergetics model adapted from
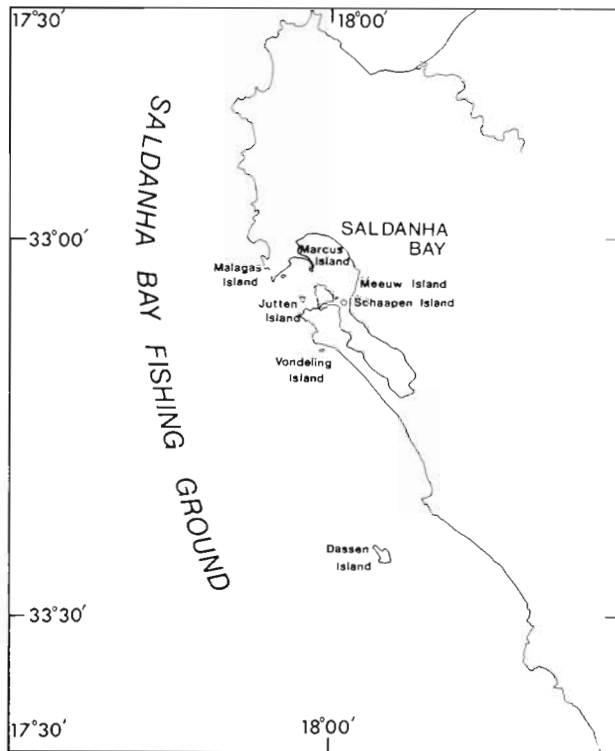
Fig. 1. Saldanha Bay fishing ground, Southern Benguela region, South Africa showing the seabird breeding islands

that described by Furness (1978). In that model a major limitation to the precision of population energy estimates was the wide confidence intervals associated with the bioenergetics equations of Kendeigh (1970). In this study these equations have been replaced by more recent ones based on considerably more extensive data (Kendeigh et al., 1977). Existence energy requirements of full grown birds were estimated using their equations for non-passerines in 15 h photoperiods and interpolating linearly between the value at 0 °C ($M = 17.33\ W^{0.5444}$) and 30 °C ($M = 4.47\ W^{0.6637}$), where M = metabolic requirement in Kj day^{-1}; W = mass in g. For flapping flight, metabolic costs are increased by $M = 1.395\ W^{0.67}$ Kj h^{-1} over existence requirements, while gliding flight is estimated to be an additional $M = 2.186\ W^{0.7347}$ Kj d^{-1}. Energetic costs of underwater and surface swimming are taken to be the same as flapping and gliding flight, respectively, and we have had to assume that the thermal insulation of the birds is adequate to allow us to ignore any differences between water and air temperatures to which the birds are exposed while foraging. Chick daily energy requirements are obtained from $M = 5.661$ $W^{0.814}$ Kj d^{-1} (Kendeigh et al., 1977). Energy costs of moult are calculated assuming that this increases daily existence metabolism by a factor of 10 to 50 % depending on the rate of moult (Kendeigh et al., 1977, p. 177).

Energy costs of egg production are given by $M = 5.439$ (egg weight) $\times \frac{100}{73}$ Kj egg^{-1} and all energy costs were multiplied by 1.25 to account for digestive losses (Furness, 1978).

Mean monthly air temperatures for the area were taken from Schulze (1972). Chick masses were input as growth equations fitted according to the method of Ricklefs (1967), using data from field studies by members of the FitzPatrick Institute. Numbers of breeding adults were obtained from colony counts published in Rand (1963), Frost et al. (1976), Crawford and Shelton (1978), Crawford et al. (in press a, b) and JC (unpubl.). Numbers in immature age classes were estimated by constructing a life table for a stable population using available or estimated values of adult survival, age at first breeding, clutch size, hatching and fledging success. Breeding biology statistics were taken from published literature or unpublished data belonging to the FitzPatrick Institute. As a first approximation it was assumed that all members of the populations remained within the Saldanha Bay fishing ground throughout the year. Where counts of non-breeders showed deviations from this assumption owing to migrations outside the breeding season, estimates obtained from life tables have been replaced by field estimates of numbers. This was necessary only for Cape cormorants, where numbers in Saldanha Bay often greatly exceeded expectation (JC, unpubl.) due presumably to immigration of non-breeders from further afield into this sheltered area.

MODEL INPUT

Counts of moulting jackass penguins at Saldanha Bay islands in 1977–1978 gave a population estimate of 52,400 adults, of which 6,857 were 1 yr old (JC, unpubl.). Assuming that all members of the population moulted within Saldanha Bay, and confounding effects of population growth or decrease can be ignored, this implies an annual adult mortality of 13 %, similar to the mortality rate of the yellow-eyed penguin *Megadyptes antipodes* (13 %; Lack, 1966) and of the little penguin *Eudyptula minor* (14 %; Reilly and Cullen, 1979). Although Jackson et al. (1976) assume that jackass penguins first breed when 2 yr old, very few have been recorded breeding before three years of age (R. M. Randall, pers. comm.; JC, unpubl.). Taking an age of first breeding of 3 yr and assuming all older birds breed, a mean of 1.8 eggs laid per pair per year, 70 % hatching and 40 % fledging success (Frost et al., 1976; Jackson et al., 1976) a first year survival of 68 % is required to balance an adult mortality rate of 13 %. This seems quite within the bounds of expectation, so

Table 1. Demographic data and life tables used to estimate seabird population sizes from census data (see text for explanation)

Category		Jackass penguin	Cape gannet	Cape cormorant
Breeding adults		1,000	1,000	1,000
Eggs laid		900	500	1,500
Chicks hatched		630	400	1,050
Chicks fledged		252	380	735
Recruits required (= adults dying)		130	100	200
4 yr olds		–	100	–
3 yr olds		130	111	200
2 yr olds		149	123	250
1 yr olds		171	137	313
Necessary first year		$\frac{171}{252}$	$\frac{137}{380}$	$\frac{313}{735}$
survival				
Assumed first year				
survival		68%	36%	43%
Breeding pairs:	Saldanha	21,200	10,000	6,000
	Dassen	28,000	0	10,000
Immatures:	Saldanha	10,000	7,400	18,000
	Dassen	13,200	0	3,500

the numbers of pre-breeders and breeding pairs have been calculated from this life table (Table 1). The number of adult jackass penguins on Dassen Island was estimated at 70,000 (Frost et al., 1976) which is equivalent to 28,000 breeding pairs assuming the same life table statistics (Table 1).

The Saldanha Bay Cape gannet population was estimated to be 39,000 adults in 1956 (Rand, 1963), 34,000 in 1967, 32,000 in 1969 (Crawford and Shelton, 1978), 16,000 breeding birds in 1977–1978 (JC, unpubl.) and 32,000 adults in November 1978 (Crawford et al., in press a). Assuming an age of first breeding of 4 yr, adult survival of 90% fledging success (Jarvis, 1971; Nelson, 1978) a plausible first year survival of 36% is required to balance adult losses. The Saldanha Bay gannet population of the 1970s was estimated to number 27,400 birds comprising, according to these life table statistics, 10,000 breeding pairs and 7,400 immatures.

Rand (1960 a, 1963) calculated a population estimate of 87,400 Cape cormorants on the islands in Saldanha

Bay in 1956. Cooper (unpubl.) estimated that 11,880 Cape cormorants bred on the Saldanha Bay islands in 1977–1978, but also counted up to 60,000 roosting non-breeders at Marcus Island alone. Rand's figure for Dassen Island was 23,500 adults in 1956, while Crawford et al. (in press b) counted 13,800 nests in 1978 on Dassen Island. From their figures we have taken the values presented in Table 1 to represent the populations in the 1970s. We assume an age of first breeding of 3 yr as adult plumage is acquired when 2 yr old (Berry, 1976), an adult survival of 80%, a mean clutch size of 2.8 with 8% of pairs losing and replacing clutches so 3.0 eggs are laid per pair per year, 70% hatching and 70% fledging success (Berry, 1976 and estimates based on data from studies of other species of cormorant). With these data, constructing a life table requires a 43% survival of first year birds to balance adult mortality.

Species statistics required for energetics calculations (Table 2) were extracted from Rand (1960a, b), Jarvis (1971), Berry (1976), Cooper (1977, 1978, unpubl.), Nel-

Table 2. Species statistics used in model (see text for sources and further details)

Species	Mean adult mass (g)	Mean egg mass (g)	Mean incubation period (d)	Mean laying date	Standard deviation of laying dates (d)	Chick growth input data	Moult duration (d)	Moult cost (xEM)	Mean h foraging d⁻¹ diving	Mean h foraging d⁻¹ swimming	Mean h foraging d⁻¹ gliding	Mean h foraging d⁻¹ flapping
Jackass Penguin	2994	106	38	uniform throughout the year		$W = 2900e^{-3.6958e^{-0.0449t}}$	18	0.5	0.5	5	0	0
Cape Gannet	2649	98	43	15 Nov.	20	$W = 3300e^{-3.825e^{-0.054t}}$	150	0.1	0	0	6	2
Cape Cormorant	1219	38	23	13 Dec.	20	$W = 1500e^{-4.0558e^{-0.0795t}}$	150	0.1	0.25	3	0	1.25

son (1978) and observations of the foraging activity budgets of these species made by the authors. Of the input data in Table 2 the estimated hours of each daily foraging activity are poorly known. These may be in error by as much as ± 50 %. Egg laying dates were assumed to be normally distributed in Cape gannets and Cape cormorants but are clearly not in the jackass penguin population, where laying occurs with irregular peaks several times of year (Cooper, 1980; Randall and Randall, in press). For this model jackass penguin laying was taken to occur uniformly throughout the year.

ENERGY COSTS AND FISH CONSUMPTION

Estimated annual energy costs of adult existence, feeding activity (additional to existence costs), moult, egg production and chick daily energy budget (growth plus existence) were calculated for the populations of each species in Saldanha Bay (Table 3) and at Dassen Island. Adult existence costs represented 51 to 72 % of the total population budget, while costs of moult and egg production together accounted for less than 3 % of any species' total (Table 3). A sensitivity analysis (Furness, 1978) indicated that in this model population energy estimates were particularly sensitive to errors in estimates of seabird population size, rather less so to

errors in the input hours of flapping flight or swimming under water per day, while the likely errors in other parameters or the model equations themselves all contribute relatively little to the total inaccuracy of the output.

Total population annual energy requirements need to be increased by a factor of 1.25 to allow for a digestive efficiency of 80 %. The resulting annual consumption by each population is shown in terms of energy in Table 4.

Energy requirements can be converted to fish consumption from a knowledge of the diets of these species in the Saldanha Bay area in the period 1977–1979 (Crawford and Shelton, in press; Cooper, in press). Percentage composition is given in terms of numbers of fish of each species. Individuals of demersal species in the diet tend to be larger than the pelagic ones but have a considerably lower energy value, so the average energetic content of a fish of each species is likely to be similar. For this reason we have simply converted energy intake to grams of fish in proportion to the frequency of each species in the diet (averaged over the year), assuming that 1 g of fish is equivalent to 8 Kj. This is approximately the energy value of anchovy (Cooper, 1978), the main species in the diet of all 3 seabirds. Diets and consumption figures are given in Table 5. Pelagic fish species, particularly anchovy, predominate. The category 'other species' consists

Table 3. Saldanha Bay seabird population energy requirements for adult existence, additional costs of foraging, moult, egg production, and chick existence plus growth. Values are annual totals before allowance has been made for digestive efficiency

Category	Jackass Penguin		Cape Gannet		Cape Cormorant	
	Population requirement $(kj \times 10^8)$	Percentage of total population requirement	Population requirement $(kj \times 10^8)$	Percentage of total population requirement	Population requirement $(kj \times 10^8)$	Percentage of total population requirement
Adult existence	229.4	71.4	101.9	50.7	72.1	63.6
Adult foraging	62.4	19.4	72.7	36.1	32.3	28.5
Chick existence + growth	24.6	7.6	22.2	11.0	6.2	5.4
Moult	4.9	1.5	4.3	2.1	2.8	2.5
Egg production	0.4	0.1	0.1	0.1	0.05	0.0
Population total	321.7	100 %	201.2	100 %	113.4	100 %

Table 4. Annual energy consumption by seabird populations in the Saldanha Bay fishing ground

Species	Annual energy consumption $(kJ \times 10^8)$		
	Saldanha Bay islands	Dassen Island	Saldanha fishing ground (total)
Jackass Penguin	402.1	424.9	827.0
Cape Gannet	251.5	0.0	251.5
Cape Cormorant	141.8	94.4	236.2
Total	795.4	519.3	1314.7

Table 5. Diet and consumption of major seabird populations in the Saldanha Bay fishing ground

| Species | Jackass Penguin | | Cape Gannet | | Cape Cormorant | | Total |
	Diet (%)	Tonnes consumed per year	Diet (%)	Tonnes consumed per year	Diet (%)	Tonnes consumed per year	Tonnes consumed per year
Anchovy	80	8,270	60	1,887	55	1,624	11,781
Round Herring	10	1,034	0	0	30	886	1,920
Pilchard	5	517	15	472	5	148	1,137
'Other species'	5	517	25	786	10	295	1,598
Total		10,338		3,144		2,953	16,435

largely of demersal species scavenged from trawlers by Cape gannets (Sinclair, 1978; Cooper, in press) and squid eaten by jackass penguins.

DISCUSSION

Cooper (in press) showed that most breeding seabirds in the southern Benguela region fed close to the breeding colonies and coastline; 85, 95 and 70 % of jackass penguins, Cape cormorants and Cape gannets were observed less than 50 km from the coast; 75, 80 and 75 % respectively were found to be within 50 km of their Saldanha breeding colonies. It seems reasonable to compare the fish consumption statistics (Table 5) with the pelagic fish catches and stocks of the Saldanha fishing ground, since relatively few of the seabirds appear to travel beyond the limits of this region to feed. The maximum lengths of fish recorded from stomach samples of the Cape gannet, jackass penguin and Cape cormorant are 350 mm (Rand, 1959), 270 mm (Matthews, 1961) and 260 mm (Davies, 1956). Very few pelagic fish in South African waters exceed these sizes (Table 5 in Crawford and Shelton, 1978) so the majority of the pelagic fish are suitable for consumption by these seabirds. The total annual consumption of 16,500 t of fish by the 3 species in the Saldanha fishing ground represents a significant proportion compared to that taken by pelagic fishery. Almost all consumption comprises pelagic species, particularly anchovy Engraulis capensis Gilchrist (11,800 t). Since the commercial fishery has been working at or above the maximum sustainable yield for most of the pelagic species (Stander and Le Roux, 1968; Baird, 1975; Centurier-Harris, 1977; Newman et al., 1979; Crawford, 1980a, 1981a) a reduction in consumption by seabirds might lead to an increased fishing yield. However, this cause and effect relationship remains unproven. Between 1971 and 1976 catches of pelagic fish in the Saldanha Bay fishery area varied between 12,100 and 85,600, averaging 55,000 t (Crawford, 1979) so the seabird consumption in the same period equalled the fish landings in 1 yr and averaged 30 % of the mean catch.

Although some South African pelagic fish species show distinct migrations in relation to age, and occur more frequently in particular coastal areas, the seasonal pattern in commercial catch per unit effort is one reflecting a relatively constant resource within and between areas (Crawford, 1980a), particularly in the Saldanha fishing ground where the pelagic fish populations, the seabirds' food resource, show a high temporal stability (Crawford and Shelton, 1978). Between 1971 and 1976 the South African mixed-species pelagic fishery landings comprised 59 % anchovy, 22 % pilchard Sardinops ocellata Pappe, 11 % mackerel Scomber japonicus Houttuyn, 4 % round herring Etrumeus teres Whitehead, and 4 % other species in terms of biomass (Crawford, 1979). Assuming that the frequencies of these species are the same in the Saldanha fishing ground as for the whole South African fishery, one might expect the consumption by seabirds to reflect these proportions, since their diets often appear to reflect relative abundance of pelagic species (Jarvis, 1971; Crawford and Shelton, 1978). To examine this we have used the Virtual Population Analyses (VPA's) (Everhart and Youngs, 1981) for each fish species in the South African pelagic fishery and assumed that 13 % of this population is present in the Saldanha Bay fishing ground. This figure is derived from the fact that 13.7 % of the 1971–1976 catches and 15.7 % of the fishing effort occurred in the Saldanha Bay fishing ground. The catch per unit effort in this area therefore represents 92 % of the average for the whole South African pelagic fishery, suggesting that the proportion of the fish populations in this area is slightly less than the proportion of the catches made there (i.e. less than 13.7 %).

Natural mortality is approximately equal to fishing mortality for anchovy, pilchard and round herring (Newman and Crawford, 1980). Taking anchovy, and allowing for a constant annual natural mortality of 0.8 VPA indicates an average population of 50,700 t in the Saldanha Bay fishing ground between 1971 and 1976. An average consumption of 11,800 t by the seabirds

represents an annual cropping of 23 % of the anchovy biomass by the seabirds. VPA for the pilchard population, assuming constant annual natural mortality of 0.5, suggests a biomass of 29,000 t in the Saldanha Bay fishing ground. Seabird consumption of 1,137 t represents predation of 4 % of this population. VPA for the round herring, assuming constant annual natural mortality of 0.5, suggests a biomass of 8,000 t in the Saldanha Bay fishing ground. Seabird consumption totals 1,920 t, or 24 % of this estimated population. Seabird predation on horse mackerel, mackerel and lanternfish *Lampanyctodes hectoris* Günther populations is negligible. The first 2 species are mesopelagic for most of their life while the last is only present in small numbers (Crawford, 1980b, 1981e, f).

The impact of seabird predation on each fish population appears to differ quite widely. Possibly, pilchard are less available to seabirds than are anchovy and round herring, but it is likely that the main cause of this apparent difference is the relative abundance of the fish populations in the Saldanha Bay fishing ground compared to other South African fishing areas. If pilchard are relatively scarce and anchovy and round herring relatively more abundant in the Saldanha Bay fishing ground, then the seabirds may not be selecting between species. However, there is good evidence that seabirds breed more successfully when able to select a diet with a high energy value (Harris and Hislop, 1978), and tend to feed their young on a diet with a higher energy value than that taken by breeding adults or immatures (Furness and Hislop, 1981).

If fishing mortality equals natural mortality (Newman and Crawford, 1980) and seabird consumption averaged 30 % of the fishery catch between 1971 and 1976, then seabird predation was responsible for about 15 % of total fish mortality. As seabirds consumed about 20 % of anchovy and round herring biomass each year this implies an annual production to biomass $(P : \bar{B})$ ratio of slightly over 1 for the pelagic fish stocks. This would be compatible with $P : \bar{B}$ ratios determined for a variety of, primarily freshwater, fish species (Chapman, 1978; Craig, 1980).

Schaefer (1970) estimated from field data that each Peruvian seabird eats on average 430 g of anchovy each day. This represented an annual consumption through the early 1960s of about 2.8×10^6 t by the seabird population. At the same time the fishery landed 8×10^6 t yr^{-1} and accounted for about 60 % of the total fish mortality (Schaefer, 1970), so the seabirds were probably responsible for about 20 % of the fish mortality.

In the North Sea, overfishing of large valuable fish has led to a decrease in mean fish size, and increases in population numbers of the small and unexploited species (Anderson and Ursin, 1977). This trend is likely to have been beneficial to most seabirds, which tend to feed on the smaller fish, and in most cases their populations have increased during the 20th century. Obtaining an accurate estimate of the quantity of fish they consume has been limited by a lack of adequate data, particularly concerning species' foraging ranges from breeding colonies and their activity budgets, but also fish stock densities and productivities, and sufficiently precise bioenergetics equations for calculating costs of existence and flight metabolism. Taking the data available, Furness (1978) estimated that the seabirds of 1 colony in Shetland consumed 29 % of the fish production within a 45 km radius of the colony, with 95 % confidence limits of 11 and 63 %. A similar earlier model applied to the seabird populations of coastal Oregon suggested that these birds consume 22 % of the fish production each year (Wiens and Scott, 1975).

Thus data now available for 4 different marine ecosystems which support both seabirds and a commercial fishery suggest that seabirds consume from 17 to 29 % of annual fish production.

Since the breeding seabird populations of the Saldanha Bay fishing ground consume about one fifth of the anchovy/pilchard/round herring production each year it is not surprising that Crawford and Shelton (1978) found a close correlation between fluctuations in fish stocks and seabird breeding populations. The implications for fisheries management and seabird conservation are obvious, since commercial fisheries, seabirds, predatory fish such as snoek *Thyrsites atun,* and Cape fur seals *Arctocephalus pusillus* all depend on the pelagic fish stocks for their existence.

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