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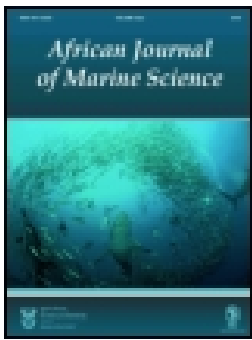
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TOP PREDATORS IN THE BENGUELA ECOSYSTEM — IMPLICATIONS OF THEIR TROPHIC POSITION

R. J. M. CRAWFORD*, L. G. UNDERHILL†, C. M. RAUBENHEIMER*,
B. M. DYER* and J. MARTIN*

Many top predators in the Benguela ecosystem feed on prey species targeted by commercial fisheries. Their roles as indicators of the state of exploited prey resources, as competitors with commercial fisheries for resources, and as susceptible to impact from commercial fishing on those resources are briefly considered. Trends in the occurrence of anchovy *Engraulis capensis* and pilchard *Sardinops ocellatus* in the diet of Cape gannets *Morus capensis* off South Africa's west coast are related significantly to survey estimates of the abundance of these fish species, and they provide useful confirmation of those estimates. In the 1980s, anchovy decreased in the diet of Cape gannets, but pilchard increased. In both the northern and southern portions of the Benguela system, ground-fish were thought to eat most (66–73%) of the total quantity of cephalopods and vertebrates consumed by predators and man in the 1980s. South African fur seals *Arctocephalus pusillus pusillus*, predatory pelagic fish and man removed roughly equal amounts, with squids, seabirds and cetaceans having a smaller impact. In the 1980s, man and seals removed about two million tons live mass more than in 1930. Indices of the rate of natural mortality of anchovy and pilchard attributable to Cape gannets are not related to biomass of the prey species. That for anchovy was high in 1989 when a poor anchovy year-class was formed. Decreased abundance of anchovy led to poor breeding by Cape cormorants *Phalacrocorax capensis* in 1989 and 1990. A model linking the Cape cormorant population with anchovy is used to explore the impact of possible exploitation strategies for anchovy on Cape cormorants.

Baie spitspredatore in die Benguela-ekostelsel vreet prooispesies wat ook die teiken van kommersiële visserye is. Hul rol as indikatore van die stand van ontginde prooihulpbronne, as mededingers met kommersiële visserye om hulpbronne, en as kwesbaar vir die invloed van kommersiële bevissing op daardie hulpbronne word kortliks oorweeg. Tendensies in die voorkoms van ansjovis *Engraulis capensis* en sardyn *Sardinops ocellatus* in die dieet van Kaapse malgasse *Morus capensis* teenoor Suid-Afrika se weskus vertoon 'n beduidende verband met ramings uit opnames van die talrykheid van hierdie visspesies, en hulle bied nuttige bevestiging van hierdie ramings. In die 1980s het ansjovis in die dieet van Kaapse malgasse verminder, maar sardyn het toegeneem. In sowel die noordelike as die suidelike deel van die Benguelastelsel is gemeen dat bodemvis die meeste (66–73%) van die totale hoeveelheid koppotiges en werweldiere verbruik deur roofdiere en die mens, gevreet het in die 1980s. Suid-Afrikaanse pelsrobbe *Arctocephalus pusillus pusillus*, pelagiese roofvis en die mens het omtrent gelyke hoeveelhede verwyder, maar tjokka, seevoëls en setaseë minder. In die 1980s het die mens en robbe sowat twee miljoen ton lewende massa meer verwyder as in 1930. Indekse van die koers van natuurlike mortaliteit van ansjovis en sardyn wat toegeskryf kan word aan Kaapse malgasse het nie verband gehou met die biomasses van die prooivisspesies nie. Ansjovis s'n was hoog in 1989 toe 'n swak ansjovisjaarklas tot stand gekom het. Verminderde talrykheid van ansjovis het daartoe gelei dat die trekduiker *Phalacrocorax capensis* in 1989 en 1990 swak gebroei het. 'n Model wat die bevolking van die trekduiker met ansjovis koppel, word aangewend om die uitwerking op die trekduiker van moontlike ontginningstrategieë vir ansjovis te ondersoek.

Top predators in the Benguela ecosystem have been the subject of much research related to their trophic position. This research has had three major objectives. One has been investigation of the usefulness of predators as monitors of the abundance (or availability) of species on which they prey. A second has been quantification of the impact of predators on their prey. The third has been study of the consequences of changes in prey resources for predators, which in some instances are species of conservation concern.

In this paper, progress made towards these objectives,

each of which is of major interest primarily because many of the prey species fed upon by the predators are also targets of major commercial fisheries, is considered briefly. Information that can be gained from predators on the status of fish stocks has potential use for managing those stocks. The predators compete with fisheries for resources, and hence they may be detrimental to the fisheries or, alternatively, themselves adversely influenced by the fisheries. In this paper, any animal that preys on cephalopods or vertebrates is considered to be a top predator.

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PREDATORS AS INDICATORS OF PREY POPULATIONS

Awareness that predators may provide useful information on trends in the abundance of the fish species on which they prey came from realization that major changes in the production of seabird guano, at islands and platforms off south-western Africa where the seabirds breed, matched trends in the abundance of their prey, notably pilchard *Sardinops ocellatus* (Crawford and Shelton 1978, Siegfried and Crawford 1978, Newman and Crawford 1980). The local pilchard has recently been reclassified by Parrish *et al.* (1989) as being the same species as the Californian sardine. However, as most researchers in South Africa and Namibia (where the species was thought to be endemic) still refer to it as the pilchard *Sardinops ocellatus*, those common and scientific names are retained for this paper.

In the 1950s, pilchard dominated the diet of some guano-producing seabirds off Namibia, contributing 93–99 per cent by mass of the diet of Cape gannets *Morus capensis* and 89–90 per cent of that of Cape cormorants *Phalacrocorax capensis* (Matthews 1961, Matthews and Berruti 1983). Its abundance decreased markedly in the 1960s, to be followed by a greatly reduced production of guano off both Namibia and South Africa (Crawford *et al.* 1987). This led to guano harvests being used as a surrogate index of pilchard abundance in assessment of the Namibian sardine resource (Troadec *et al.* 1980). Off South Africa, numbers of foraging Cape cormorants were shown to reflect trends in the strength of pilchard year-classes in the mid 1950s (Crawford *et al.* 1983a). A relatively abundant year-class spawned in 1982/83 was prominent in the diet of Cape gannets in Algoa Bay and off western South Africa between 1983 and 1985 (Armstrong *et al.* 1987).

Such findings led to the establishment of programmes aimed at monitoring various parameters of the seabird populations. These have been discussed by Berruti (1985) and Berruti *et al.* (1989). In this paper one of the programmes is considered, the monthly monitoring by South Africa's Sea Fisheries Research Institute of the diet of Cape gannets at two islands off western South Africa — Bird Island at Lambert's Bay since December 1977, and Malgas Island in Saldanha Bay since September 1978.

Usually 50 gannet regurgitations are collected at each island every month, although on occasion the sample size has been smaller or greater. For both localities, the monthly percentage contributions (by mass, by number and by frequency of occurrence) of various prey organisms to the overall diet of Cape gannets have been computed. Additional information on sam-

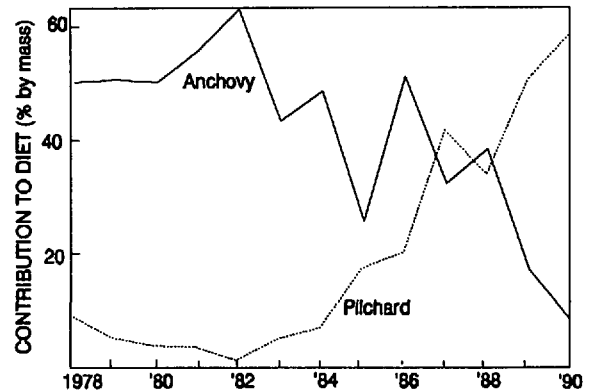


Fig. 1: Trends in the contribution of anchovy and pilchard to the diet of Cape gannets off western South Africa, 1978–1990

pling techniques and on the intensity of sampling is reported elsewhere (Berruti 1987, Berruti *et al.* in prep.). Annual indices of the contribution by mass of pilchard and anchovy *Engraulis capensis* to the diet of Cape gannets off western South Africa were derived by weighting months (January–December) and the

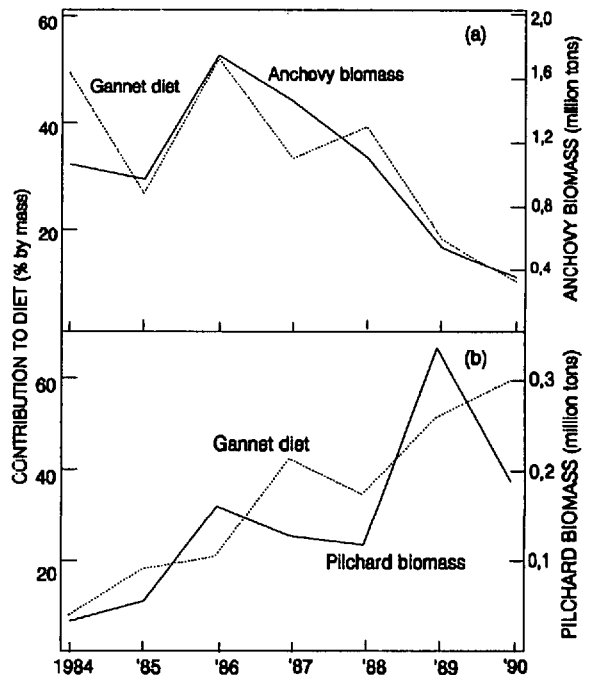


Fig. 2: Comparison of trends in the contribution of (a) anchovy and (b) pilchard to the diet of Cape gannets off western South Africa, with acoustic estimates of the biomass of these prey species, 1984–1990

two localities equally. The indices reveal a fluctuating downward trend of anchovy in the diet since 1982, but an increase in the contribution of pilchard over the same period (Fig. 1).

When the monitoring of gannet diet commenced in 1977, estimates of the abundance of anchovy and pilchard were based on catch statistics (Newman and Crawford 1980). Later, it became apparent that the fishing fleet was sampling only a portion of the stocks of these fish species and that the techniques that had been used to age anchovy and pilchard in the catches were in error (Thomas 1985). The assessments were therefore regarded as unreliable. From 1984, direct surveys were introduced to estimate abundance of anchovy and pilchard off South Africa (Hampton 1987).

The change in assessment procedure resulted in time-series of abundance estimates for anchovy and pilchard that are shorter than those of the two species in the diet of Cape gannets. For the period for which estimates of abundance are available, trends in the quantity of both anchovy and pilchard in the diet match trends in the spawner biomass of these two species measured acoustically during direct surveys (Hampton 1987, Shannon *et al.* 1992) reasonably well (Fig. 2). An exception is in 1990 for pilchard, when the contribution to the diet increased but the estimate of spawner biomass decreased.

The contribution of anchovy and pilchard to the diet of Cape gannets was modelled by means of standard univariate techniques (Box and Jenkins 1970) to remove systematic time-series effects and to obtain series of so-called "prewhitened residuals". No such systematic effects were detected in acoustic estimates of biomass of anchovy and pilchard. For anchovy, prewhitened residuals of contribution to the diet were strongly positively correlated with biomass estimates ($n = 7$, $r = 0.93$, $p < 0.01$). This suggests that the contribution of anchovy to the diet of gannets in the 1980s was a reasonable indicator of anchovy abundance. For pilchard, the correlation was not significant ($n = 7$, $r = 0.31$). Coefficients of variation for acoustic estimates of pilchard biomass obtained on direct surveys are high (20–87%, Borchers 1991), possibly influencing the result. An alternative index of pilchard abundance is the fraction of stations at which pilchard eggs are detected during surveys (Borchers *op. cit.*). Prewhitened residuals for this index were correlated with those for the contribution of pilchard to the diet of gannets at a low level of significance ($n = 7$, $r = 0.69$, $p < 0.10$).

It would be expected that the contribution of a particular prey item to the diet of Cape gannets will be influenced by the availability of alternative prey. When this is borne in mind, the correlations obtained between diet and abundance for both anchovy and pilchard are unexpectedly good. They suggest that the contributions of these species to the diet of Cape gan-

nets may provide useful information on trends in the abundance of both fish species. If this is so, they will have value in confirming estimates obtained from direct surveys. Precision of hydroacoustic estimates of pilchard abundance decreases at low stock size (Borchers 1991), and the diet index would be especially useful at such low biomass.

IMPACT OF PREDATORS ON PREY RESOURCES

The South African (Cape) fur seal *Arctocephalus pusillus pusillus* and various seabirds that breed off southern Africa are conspicuous predators and are often thought to consume large quantities of fish that might otherwise be caught commercially. For this reason they are a perceived threat to the interests of commercial fishermen. For example, in 1930, the Deputy Mayor of the Strand is reported to have stated that ". . . the fishermen's livelihood was being taken away from them by the seals" (Crawford and Payne 1989). In 1953, a motion was moved in the senate "That in view of serious depredations carried out by certain birds and animals on the food resources . . . in the seas around our coasts, this House urgently requests the Government to introduce legislation for the control of these pests . . ." (Davies 1955). In 1983, an investigation into the state of the purse-seine fisheries off South Africa and Namibia noted that fishermen often hated seals (Alant *et al.* 1983). In 1990, a committee was appointed to advise South Africa's Minister of Environment Affairs *inter alia* on ". . . the scientific basis for culling as a method of reducing the seal population in order to reduce seal impacts on commercial fish . . ." (Anon. 1990).

In 1989, a workshop to investigate consumption and production in the Benguela ecosystem was held under the auspices of the Benguela Ecology Programme (Field *et al.* in prep.). Although there is uncertainty regarding much of the information presented at that workshop (e.g. Crawford *et al.* 1991), its compilation makes possible a preliminary comparison of the quantities of various resources that are consumed by different predators. As far as fishermen are concerned, consumption of cephalopods and vertebrates is of primary concern. In the 1980s, almost seven million tons (live mass) of these resources were estimated to have been taken annually by predators and man in the southern portion of the Benguela system, including the Agulhas Bank (29°S to 28°E, coast to 500 m depth contour), and nearly eight million tons in the northern portion (15–29°S, coast to 500 m depth contour). In both regions, groundfish are considered to be the major consumers of cephalopods and fish, with consumption by seals and pelagic

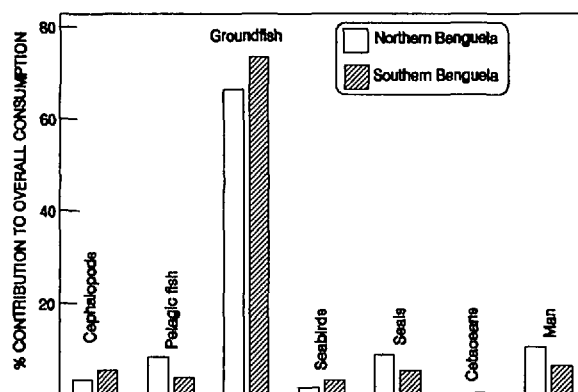


Fig. 3: Proportions of the overall quantity of cephalopods and vertebrates thought to have been removed from the northern and southern Benguela ecosystem by various groups of predators and by man in the 1980s (from information in Field *et al.* in prep.)

fish considerably less and each approximately equivalent to the catch by man (Fig. 3). Squids, seabirds and cetaceans are of lesser importance as predators.

For three groups of land-based predators — seals, abundant locally breeding seabirds (Cape gannets, Cape cormorants and African penguins *Spheniscus demersus*), and man — it is possible to estimate the quantities of cephalopods and vertebrates extracted from the sea in two earlier years: 1930 and 1956. Estimates of seal abundance in these years are provided by Butterworth and Wickens (1990), and of numbers of seabirds by Rand (1963), Frost *et al.* (1976), Crawford (1987) and Crawford *et al.* (1991). It was assumed that *per capita* food requirements for seals and seabirds were equivalent to those used in the 1980s. Historical catches have been documented by Crawford *et al.* (1987).

In 1930, seabirds were probably the most important predator of the three groups considered (Fig. 4). Subsequently, substantial decreases in the numbers of Cape gannets (Crawford *et al.* 1983b) and African penguins (Shelton *et al.* 1984, Crawford *et al.* 1990) have resulted in decreased consumption of resources by seabirds. Conversely, the seal population has grown (Butterworth and Wickens 1990) and catches by man have increased. The overall result is that the three land-based groups of predators are now probably taking about two million tons (live mass) more cephalopods and vertebrates than they did in 1930. This increase amounts to about 14 per cent of the total consumption (by predators and man) of cephalopods and vertebrates estimated for the 1980s (Field *et al.* in prep.). Either the Benguela system is now more productive than formerly, or less food is now being utilized by other predators. The latter would be the case if the size of some other predator populations had decreased, as have

some of the land-based seabirds. Fishing is thought to have reduced some groundfish populations substantially (Payne 1989), which would have decreased consumption by the larger piscivorous size-classes of those populations.

In models used to assess the status of exploited fish populations and to calculate the yields that can be taken from them, the rate of natural mortality M is an important parameter. In the absence of information about changes in M with time, this parameter is often assumed constant or to vary randomly about a constant level (Bergh and Butterworth 1987). Monitoring of the abundance of Cape gannets off western South Africa (Crawford *et al.* 1983b, Berruti 1987, Sea Fisheries Research Institute unpublished data), of the contribution of various prey items to their diet (see earlier), and of the abundance of anchovy young-of-the-year and pilchard spawners (Hampton 1987, Shannon *et al.* 1992), when coupled with assumptions concerning the *per capita* consumption of Cape gannets (Crawford *et al.* 1991), makes it possible to estimate annual changes in the rate of natural mortality of anchovy and pilchard attributable to the gannets. For this purpose, it was assumed that anchovy eaten by Cape gannets are only young-of-the-year. Most anchovy in gannet regurgitations at Lambert's Bay and Malgas Island have a caudal length L_c of <11.1 cm (Berruti *op. cit.*), their approximate size at one year of age (Prosch 1986).

M is computed as $-\ln(1 - D/X)$ where X is the biomass of the appropriate portion of the fish stock and D is the mass of that portion of the stock eaten by Cape gannets. D is the product of the abundance of Cape gannets, the annual food requirement of each gannet, and the annual proportional contribution by mass of the prey item to the diet of Cape gannets.

For both anchovy and pilchard, there is no clear relationship between M and biomass, and there is considerable interannual fluctuation in M (Fig. 5). Of interest is the higher rate of mortality estimated for pilchard — approximately double that estimated for anchovy. This result lends support to the hypothesis of Berruti (1987) that pilchard are the preferred prey of Cape gannets. A high rate of mortality was computed for anchovy in 1989, when a poor year-class was formed; it resulted in a substantial drop in anchovy spawner biomass (Shannon *et al.* 1992). If all predators inflicted a similarly high rate of mortality, this may have contributed to the poor year-class.

IMPACT OF PREY RESOURCES ON PREDATORS

In 1988, conservation of South Africa's marine ecosystems became a legislated objective of their utiliza-

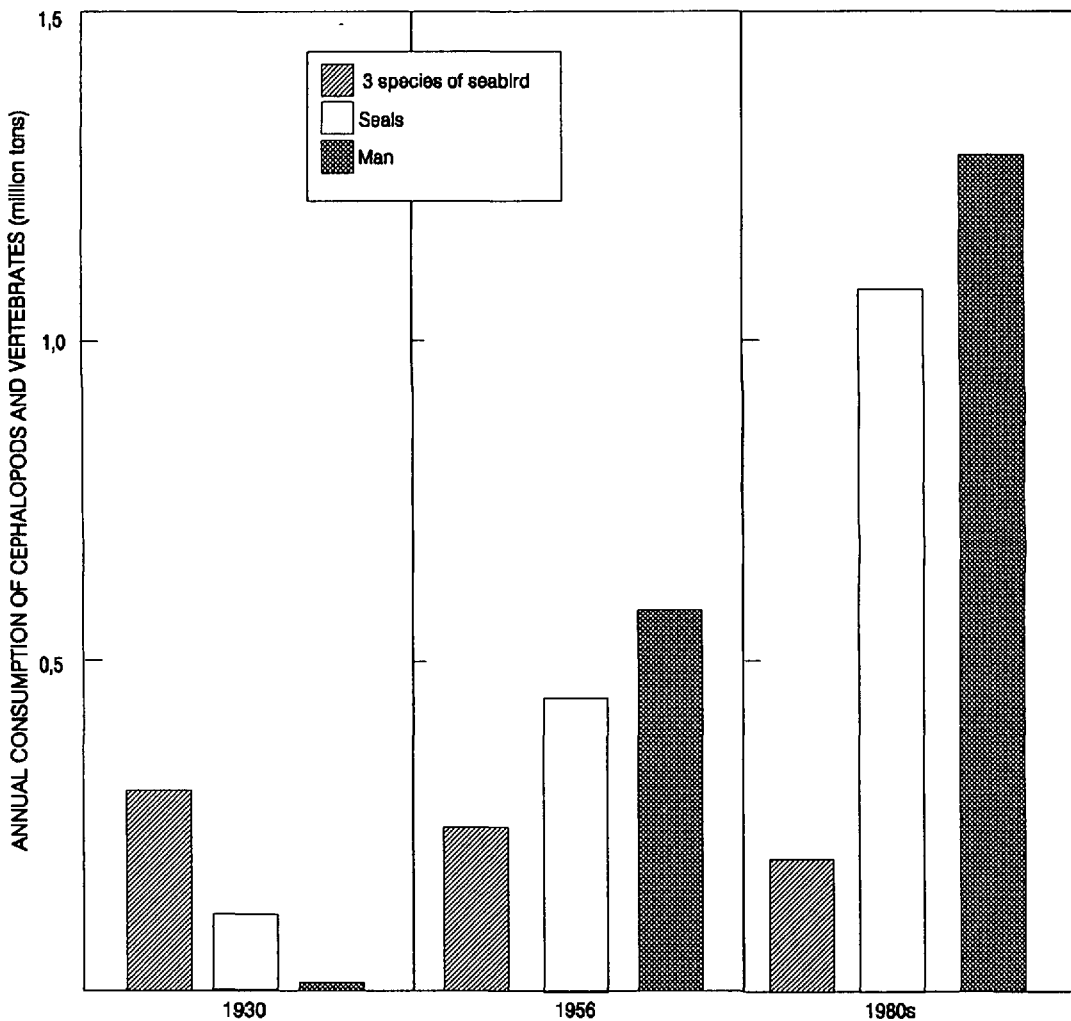


Fig. 4: Quantities of cephalopods and vertebrates removed from the Benguela ecosystem by three locally breeding seabirds, by South African fur seals and by man at three periods in the 20th century

tion (Anon. 1988). However, to date this goal has been accounted for only in the management objectives set for individual species (Crawford 1991). The impact that commercial exploitation of a resource may have on predators of that resource is not explicitly taken into consideration, even though there is strong suggestion that, in the Benguela system, a number of seabirds have been influenced adversely through competition with fisheries for food (Frost *et al.* 1976, Crawford and Shelton 1978, 1981, Crawford 1981, Crawford *et al.* 1983b, 1990, Shelton *et al.* 1984). Before the consequences for predators of harvesting a prey population can be taken into account, it is necessary to model the relationships between the prey and its predators (Butterworth 1986).

Recent years, with their large contrast in the abundance of anchovy (Fig. 2), have provided preliminary information on responses of some locally breeding seabirds to an altered abundance of anchovy. This information has been used to link a model of Cape cormorants to the model of the anchovy population currently used to advise on management of the anchovy resource (Bergh and Butterworth 1987, Cochrane and Starfield 1992). The aim was to investigate consequences of different management strategies for anchovy on the Cape cormorant population. The model for Cape cormorants and its linkage to that for anchovy are described in the Appendix. This is a first attempt, using crudely estimated parameters, at describing the predator-prey-fishery interactions for these two species

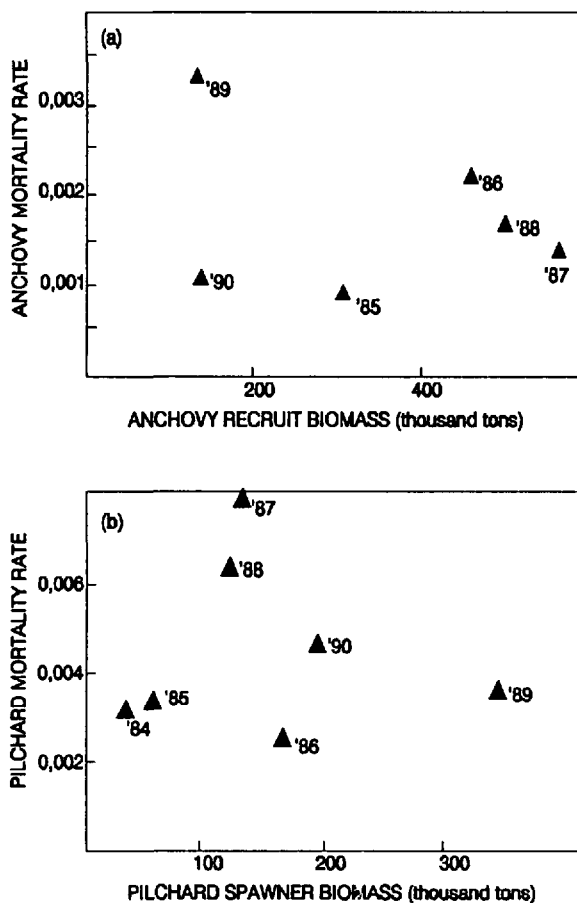


Fig. 5: Relationship between mass-specific annual rates of mortality of (a) young-of-the-year anchovy and (b) pilchard spawners, attributable to Cape gannets, and survey estimates of the abundance of these components of the fish stocks, 1984–1990

using a stochastic simulation model.

The model of the Cape cormorant population depends on the spawner biomass of anchovy in two ways: the number of pairs of Cape cormorants that laid eggs and the probability of hatching eggs were modelled as stochastic functions of the spawner biomass of anchovy. All other parameters in the Cape cormorant model were taken as constants, including some, such as clutch size, frequency of laying, survival from hatching to fledging, survival for the remainder of the first year, and survival of birds older than one year, that could conceivably also be dependent on anchovy spawner biomass. The little available information on these

dependencies suggests that their effects are likely to be smaller than the two effects modelled stochastically. For example, the mean clutch size of 472 nests of Cape cormorants with eggs examined at islands off South Africa in 1990, when there was a low abundance of anchovy, was 2,39, compared with the mean for 1978–1991 off southern Africa of 2,36 (Appendix). No large mortalities of fledged Cape cormorants were observed in 1990.

The coupled model for anchovy and Cape cormorants was run with 500 Monte Carlo simulations over a 25-year time horizon for seven management strategies for anchovy: a zero catch, a constant catch of 250 000 tons, a constant catch of 300 000 tons, strategies where 20 and 30 per cent of the available anchovy biomass were caught, and strategies where it was attempted to ensure escapement of 80 and 60 per cent of the unexploited biomass.

For each of the six strategies that permitted a catch, the modelled numbers of Cape cormorants alive after 25 years were significantly ($p < 0,01$ in all cases, χ^2 test) lower than for the strategy of zero catch (Fig. 6). The estimated number of Cape cormorants alive after 25 years decreased from that computed for the strategy of no catch by 42, 51, 52, 66, 60 and 77 per cent respectively for the strategies of constant catches of 250 000 tons and 300 000 tons, catches of 20 and 30 per cent of the available biomass, and catches allowing escapement of 80 and 60 per cent of the unexploited biomass. In general, regardless of the strategy adopted, the higher the mean catch over the 25-year period the lower the expected population of Cape cormorants at the end of that period (Fig. 6).

If assumptions underlying the models are correct, the results suggest that the purse-seine fishery for anchovy will have reduced the number of Cape cormorants off South Africa. This finding agrees with known decreases in some seabird populations as man's catch has increased (Fig. 4). However, there is evidence that the numbers of anchovy and Cape cormorants in the Benguela system have increased since the 1950s in spite of purse-seine fishing (Crawford 1987, Crawford *et al.* 1991). Anchovy are likely to have replaced a collapsed pilchard resource in the 1960s, and Cape cormorants are likely to have increased on account of the increased abundance of anchovy (Crawford *et al.* 1987).

Strategies aiming at a constant annual catch of 300 000 tons, a harvest of 20 per cent of the available anchovy biomass, and escapement of 80 per cent of the unexploited anchovy biomass gave similar mean numbers of Cape cormorants after 25 years (Fig. 6). Of these three strategies, the last estimated a signifi-

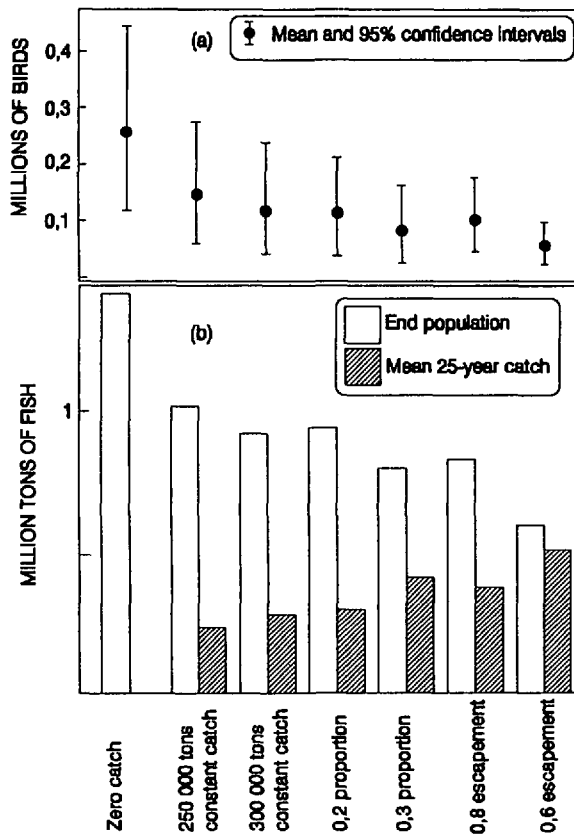


Fig. 6: (a) Model estimates of mean numbers and 95% confidence intervals of Cape cormorants alive after 25 years, and (b) mean spawner biomass of anchovy after 25 years and the mean catch of anchovy over the 25-year period, both for different management strategies for anchovy

cantly higher mean catch than either of the other two strategies ($p < 0.01$ in both cases, χ^2 test). It also provided a less variable population of Cape cormorants after 25 years, as shown by the smaller confidence interval. Therefore, in this preliminary analysis, it appears to be the preferable strategy of the three for management of the anchovy resource, at least in so far as the Cape cormorant population is concerned.

Sensitivity analysis indicates that the model of Cape cormorants is especially sensitive to the value used for survival of birds in their second or older years. Better estimates of survival probabilities, and also of the proportion of females that commence breeding at various ages, could be obtained by an expanded ringing

programme, followed by intensive fieldwork aimed at resighting and retrapping as many ringed birds as possible. It is also necessary to improve understanding of responses by Cape cormorants to altered abundance of anchovy, which at this stage is based on few data points (Appendix). It is hoped that this will be achieved by continued monitoring of the Cape cormorant population and of the anchovy resource.

Cape cormorants are just one of a number of predators that feed on anchovy. Other seabirds have different demographic parameters (Crawford and Shelton 1981), and they may respond differently from Cape cormorants under various management strategies for anchovy. Before final conclusions can be reached on the best way to achieve the objectives of the Sea Fishery Act of 1988 (Anon. 1988) with regard to exploitation of the anchovy, it would be necessary to model responses of other seabird predators of anchovy to the different strategies.

CONCLUSIONS

There are few abundant cephalopod and vertebrate populations in the Benguela system. Therefore, many of the plentiful prey populations are fed upon by a variety of predators, including man (Crawford 1987). Trends in the diet of some predators, as well as in the catches of man, are influenced by trends in the abundance of prey species. For this reason, the occurrence of a prey species in the diet is potentially useful as an indicator of its abundance. It may be affected by changes in the quantity or availability of other prey items, which would complicate interpretation of trends in the diet. However, in spite of this, contributions of anchovy and pilchard to the diet of Cape gannets have been significantly related to estimates of the abundance of these fish species off South Africa. This provides useful confirmation of trends in the estimates (see Fig. 2).

Certain conspicuous predators, particularly seals, are a perceived threat to commercial fisheries. Although the consumption of seals is roughly equivalent to man's catch, in the 1980s they were thought to account for only 5–10 per cent of the total biomass of cephalopods and vertebrates removed by predators and man (Fig. 3). Further, a substantial portion of their diet is of fish that are not sought commercially (David 1987). However, seal numbers have increased rapidly during the 20th century. Coupled with the expansion of commercial fisheries, this may mean that about two million tons less food per annum is now being consumed by other predators than in 1930.

Some populations of seabirds have decreased in abundance, possibly as a result of competition for food with commercial fisheries. Preliminary modelling suggests that the South African fishery for anchovy has influenced the abundance of Cape cormorants, and that simple multispecies models may be a useful means of accounting for the conservation objective of the Sea Fishery Act of 1988 (Anon. 1988) when selecting management strategies for prey populations. To develop such models, it is necessary to estimate parameters for predator populations and to quantify relationships between predators and their prey. Both aspects require continued monitoring of the predator populations.

ACKNOWLEDGEMENTS

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APPENDIX

Model for Cape cormorants

In a closed population, the number of seabirds at time t can be modelled as the number at some earlier time $t - 1$, augmented by the number of eggs laid, and reduced by the number of deaths to eggs and birds:

$$\sum_{i=1}^I N_{it} = \sum_{i=1}^I N_{i,t-1} + E_t - D_t, \quad (1)$$

where I is the number of age-classes, N_{it} is the number of birds in age-class i alive at time t , $i = 1 \dots I$, E_t is the

number of births (i.e. eggs laid) between times $t - 1$ and t , and D_t is the number of deaths of eggs and birds between times $t - 1$ and t .

The size of the population of Cape cormorants was modelled using Equation 1 and assuming a closed population with monogamous breeding. The number of births can then be modelled as

$$E_t = fA_t \sum_{i=1}^I c_i l_i b_i N_{it} \quad (2)$$

where f is the proportion of birds which are female, c_i is the mean clutch size of females in age-class i , assumed independent of year, l_i is the mean number of clutches laid per female in age-class i per year, assumed independent of year, b_i is the maximum proportion of females in age-class i that breed in a year, under the most favourable conditions, i.e. the proportion of females in age-class i that is reproductively mature, and A_t is the proportion of mature females that lay eggs in year t , i.e. it is a function of the spawner biomass of anchovy at time t , to be described later. (The convention is used that symbols for quantities that are fixed constants in the models are lower-case roman letters, whereas quantities that are variable are upper-case).

The number of deaths was modelled by

$$D_t = E_t(1 - S_{et}) + E_t S_{et}(1 - s_c) + \sum_{i=1}^I (1 - s_i) N_{it} \quad (3)$$

where S_{et} is the proportion of eggs surviving to hatching, modelled as a function of spawner biomass of anchovy in year t , s_c is the proportion of chicks surviving from hatching to fledging, and s_i is the proportion of birds in age-class i surviving to the end of the year, $i = 1 \dots I$. The first term on the right-hand side of Equation 3 is the number of eggs that die before hatching in year t , the second term is the number of chicks that die before fledging in year t , and the sum contains the number of birds in each age-class that die in year t .

Apart from eggs and chicks, five age-classes of Cape cormorants were distinguished in the model; first-year birds for the approximately eight-month period from fledging to one year after the egg was laid ($i = 1$), second-year birds aged from one to two years ($i = 2$), third-year birds from two to three years ($i = 3$), fourth-year birds from three to four years ($i = 4$), and birds aged four years or older ($i = 5$). Thus, for this application of the model, $I = 5$. The model was incremented on an annual basis. In each year, eggs

progressed through the chick class to that of first-year birds, with a reduction in numbers at each stage. At the end of each year, the numbers of birds surviving in each age-class were moved to the next oldest age-class. This was accomplished by means of the following equations:

$$\begin{aligned} N_{1t} &= E_t S_{et} s_c \\ N_{it} &= N_{i-1,t-1} s_{i-1}, \quad i = 2 \dots 4 \\ N_{5t} &= N_{5,t-1} s_5 + N_{4,t-1} s_4 \end{aligned} \quad (4)$$

The age at which Cape cormorants first breed is unknown. Based on information for four extralimital cormorants (Ruwet 1963, Cramp and Simmons 1977, Brothers 1985), Crawford *et al.* (1991) assumed that Cape cormorants first breed at an age of four years. Berry (1976) noted that some species of cormorant may breed successfully at three years of age. In the model it was assumed that, under favourable conditions, all Cape cormorants aged four or older, and half of the fourth-year birds, would breed, i.e.

$$\begin{aligned} b_5 &= 1,0 \\ b_4 &= 0,5 \\ b_i &= 0,0, \quad i < 3 \end{aligned} \quad (5)$$

Estimates of the number of pairs of Cape cormorants breeding at seven islands (Bird Island at Lambert's Bay, Malgas, Marcus, Jutten, Vondeling, Dassen and Dyer) off South Africa, made from maximum counts of the number of breeding pairs at these localities, have been 103 746 in 1978/79 (Cooper *et al.* 1982), about 60 000 in 1985/86, 96 000 in 1988/89, 8 000 in 1989/90 (Crawford 1991) and 46 000 in 1990/91 (Table 1). The mean number of pairs is about 63 000. A few Cape cormorants breed at other localities off South Africa (Cooper *et al.* 1982). The model was initialized with a breeding population of 70 000 pairs, or 140 000 individuals, i.e.

$$N_{50} + 0,5N_{40} = 140\,000 \quad (6)$$

The number of birds aged three, and four or older, were determined by assuming an equilibrium situation, viz.

$$N_{50} = s_4 N_{40} + s_5 N_{50} \quad (7)$$

Given values for s_4 and s_5 , Equations 6 and 7 provide

Table I: Counts of active nest sites of Cape cormorants at seven islands off South Africa, September 1989–March 1991. For details of methods employed, see Shelton et al. (1982) and Cooper et al. (1982)

Date	Number of active nest sites	Method of counting
<i>Lambert's Bay</i>		
19.09.1989	0	Ground
24.10.1989	0	Ground
21.11.1989	0	Ground
12.12.1989	995	Ground
16.01.1990	1 468	Ground
09.02.1990	2 436 ¹	Ground
20.03.1990	1 621	Ground
23.04.1990	109	Ground
19.05.1990	59	Ground
05.06.1990	20	Ground
17.07.1990	0	Ground
14.08.1990	0	Ground
11.09.1990	610	Ground
16.10.1990	2 882 ²	Ground
28.11.1990	1	Ground
18.12.1990	0	Ground
02.01.1991	0	Ground
21.02.1991	475	Ground
29.03.1991	1 832	Ground
<i>Malgas Island</i>		
20.09.1989	0	Ground
26.10.1989	0	Ground
17.11.1989	0	Ground
14.12.1989	0	Ground
18.01.1990	0	Ground
07.02.1990	0	Ground
24.03.1990	0	Ground
30.04.1990	0	Ground
17.05.1990	0	Ground
07.06.1990	0	Ground
19.07.1990	0	Ground
16.08.1990	8	Ground
18.09.1990	391	Ground
16.10.1990	571 ³	Ground
27.11.1990	0	Ground
20.12.1990	0	Ground
23.01.1991	0	Ground
20.02.1991	0	Ground
19.03.1991	0	Ground
<i>Marcus Island</i>		
21.03.1990	0	Ground
21.10.1990	0	Ground
<i>Jutten Island</i>		
20.12.1989	133	Aerial
23.03.1990	2 548	Ground
19–21.10.1990	1 861 ³	Ground
30.11.1990	0	Ground
21.12.1990	29 819	Aerial
11–12.03.1991	0	Ground

Table I (continued)

Date	Number of active nest sites	Method of counting
<i>Vondeling Island</i>		
20.12.1989	0	Aerial
28.03.1990	200	Ground
17.10.1990	1 038 ³	Ground
30.11.1990	0	Ground
21.12.1990	0	Aerial
11.03.1991	1 500	Ground
<i>Dassen Island</i>		
27.10–01.11.1989	2	Ground
22–26.10.1990	3 078 ³	Ground
06.12.1990	0	Ground
27.03.1991	0	Ground
<i>Dyer Island</i>		
22.12.1989	3 255 ⁴	Aerial
26.01.1990	0	Ground
1–5.10.1990	8 601	Ground
21.12.1990	6 563 ⁵	Aerial
16.01.1991	812 ⁶	Ground

- ¹ Assumed successful
- ² All except one are assumed to have failed. A total of 2 427 deserted nests was counted on 28.11.1990, by which time some of the lighter nests had probably been blown away
- ³ Assumed to have failed because breeding was at an early stage and the subsequent visit revealed no sign of breeding
- ⁴ All deserted (E. Johnstone, headman, pers. comm.)
- ⁵ A recount of the same photographs gave a total of 6 864
- ⁶ In all, 812 nests were active. Additionally, 3 690 unoccupied nests were counted for which breeding had probably been completed successfully (E. Johnstone, pers. comm.)

two equations in two unknowns and can therefore be solved.

Four of the five censuses of breeding pairs of Cape cormorants were conducted in years when the anchovy spawner biomass was measured acoustically (Hampton 1987, Shannon et al. 1992). A plot of the number of Cape cormorants breeding against the anchovy spawner biomass of the same year suggests an approximately linear relationship, with c. 100 000 pairs breeding when the spawner biomass is above about 1.4 million tons and no birds breeding when there is no anchovy (Fig. 7). This is a tentative relationship, and it requires additional empirical information. For the purposes of the model it was assumed that A_t , the proportion of females laying eggs at a particular spawner biomass of anchovy, was represented by the function:

$$\begin{aligned}
 A_t &= 1 + Z_1 & X_t > 1.4 \\
 &= X_t/1.4 + Z_1 & 0 \leq X_t \leq 1.4, \quad (8)
 \end{aligned}$$

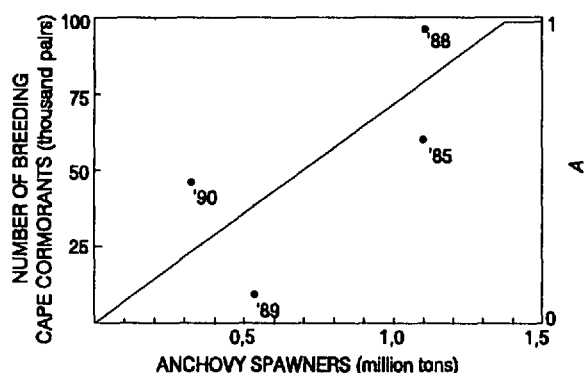


Fig. 7: Relationship between the number of breeding pairs of Cape cormorants censused off South Africa and acoustic estimates of the spawner biomass of anchovy. The relationship between the assumed mean proportion of mature birds that attempt breeding (*A*) and the spawner biomass of anchovy is shown as a solid line

where X_t is the anchovy spawner biomass (million tons) and where Z_1 has a Normal distribution, with mean zero and a standard deviation σ_1 that approximated the scatter of the four observed points about the straight line on Figure 7.

An algorithm described by Atkinson and Pearce (1976) was used to generate random numbers for a standard Normal distribution. These values were transformed, using the value applicable to the particular spawner biomass of anchovy and the assumed standard deviation σ_1 , to generate the values of Z_1 used in the model. However, A_t was truncated to take on values only in the interval zero to one inclusive.

The number of clutches laid by Cape cormorants each year is unknown. Eggs may be laid over a prolonged period (Randall *et al.* 1981). Berry (1976, p. 14) commented on a particular breeding season "Four distinct waves of breeders were observed, namely on 2 October, 10 November, 17 December and 31 January. The period between these 'waves' is 40, 38 and 46 days respectively. Thus there is an overlap between successive hatchlings because incubation lasts 22–28 days plus the nestling period of approximately 35 days." This suggests that it is different groups of birds that lay at different dates, and for the model it has been assumed that each pair of Cape cormorants produces just one clutch annually, i.e. $l_i = 1$. Some species of cormorant may lay more frequently. For example, Palmer (1962) states that *P. carbo sinensis* females replace lost clutches.

The sex ratio is assumed to be parity, so that f , the proportion of females, equals 0.5.

Berry (1976) recorded a range in the clutch size of

Cape cormorants breeding at platforms of 1–5 eggs, with a modal clutch of three eggs. Examination of his Figure 3.19 suggests that, for nests near the centre of colonies, the mean clutch size is 2.82 ($SD = 0.73$, $n = 100$) and for nests at the perimeter of colonies the mean clutch is 2.34 eggs ($SD = 1.00$, $n = 100$).

Between 1978 and 1991, the contents of 7 333 nests of Cape cormorants breeding between Mercury Island off Namibia and Geysers Island off the southern Cape Province were recorded by staff of the Sea Fisheries Research Institute. Of these nests, 3 176 contained only eggs, with a mean clutch size of 2.36 ($SD = 0.88$, range 1–7). It is likely that, at the time of examination of some nests, not all eggs had been laid, so that the estimate here of the mean clutch size is probably biased downwards. Unfortunately, there is no information on variation in mean clutch size in relation to age-class, and therefore c_i has been set at 2.36 for all age-classes i . This value was used in the model because it was also used to estimate egg survival (see below). The estimated rate of egg survival given here is biased upwards, with the two biases probably offsetting each other.

The mean number of downy chicks in nests of Cape cormorants during the period 1978–1991 was 2.06 ($SD = 0.71$, range 1–4, $n = 2 330$). The mean number of feathered chicks was 1.88 ($SD = 0.67$, range 1–4, $n = 269$). The maximum survival probability of eggs (i.e. in years in which there were no large-scale desertions of nests by adults), denoted by $s_{e,max}$, was estimated from the ratio of mean brood size from nests with downy chicks and mean clutch size. Similarly, the survival of chicks to fledging, s_c , was calculated from the ratio between mean brood size from nests with feathered chicks to those with downy chicks. These values were $s_{e,max} = 0.87$ and $s_c = 0.91$ respectively, higher than the value of 0.7 used by Furness and Cooper (1982) both for egg and for chick survival.

Repeated visits to some islands during the years 1989–1991 allow tentative conclusions to be drawn concerning desertions of nests by Cape cormorants in the 1989/90 and 1990/91 breeding seasons. During this period the spawner biomass of anchovy was low (a mean level of some 450 000 tons). A summary of counts of active nest sites at seven islands is given in Table I. The fate of many of the nests is unknown, but it can be assumed safely that 12 684 pairs deserted their nests as indicated. It is probable that 2 436 pairs bred successfully at Lambert's Bay in 1989/90 and 3 690 at Dyer Island in 1990/91. This means that about 32 per cent of breeding attempts whose fate can be gauged were successful. It was therefore assumed that no nests are deserted when the anchovy spawner biomass is larger than 1.4 million tons, that all nests are deserted when the spawner biomass of anchovy is zero and that intermediate values can be represented

by a linear relationship. This effect was incorporated by modelling the egg survival S_{et} in year t with the following function:

$$S_{et} = s_{e,max} + Z_2 \quad X_t > 1,4$$

$$= s_{e,max} X_t / 1,4 + Z_2 \quad 0 \leq X_t \leq 1,4, \quad (9)$$

where X_t is the anchovy spawner biomass (million tons) and Z_2 was assumed Normally distributed with mean zero and standard deviation σ_2 . S_{et} was constrained to lie between 0 and $s_{e,max}$. In the absence of information, the standard deviation σ_2 was taken to be the same as σ_1 .

The survival of Cape cormorants was regarded as constant for all birds aged one year or older. A total of 98 Cape cormorants ringed off southern Africa which had been recovered dead was available to estimate survival probabilities (SAFRING, unpublished data). The time elapsed since ringing suggested a survival rate for birds aged one year or older of 0,84 (using Haldane's method); s was used to denote this common survival probability, i.e. $s = s_2 = s_3 = s_4 = s_5$.

In comparison, a value of 0,8 was used by Furness and Cooper (1982). For other species of cormorants, survival rates have been published. For *P. carbo*, mortality was estimated as 36 per cent in the first year, 22 per cent in the second year and 16 per cent in the third year. Annual mortality of older females was estimated as 9–14 per cent and of older males as 7–12 per cent (Cramp and Simmons 1977). For *P. aristotelis*, first-year survival was estimated at 59 per cent for the Farne Islands, but higher along the south and west coasts of Britain. Thereafter, survival is estimated as 84 per cent ($SD = 5\%$, Cramp and Simmons 1977). The estimate of survival rate used here is therefore in line with results for other species of cormorant elsewhere.

The survival of young seabirds immediately after they have left the nest and attained independence is difficult to measure, but it is often thought to be low and a major factor influencing the dynamics of seabird populations (see, for example, references in Crawford

1991). Survival of first-year Cape cormorants was here selected to ensure that the population remained in equilibrium when not coupled to anchovy. This was achieved by choosing s_1 so that, when the population was in equilibrium, with the number of birds in each age-class not varying in time (i.e. $N_{it} = N_i$), the number of deaths of breeding adults was equal to the number of eggs surviving to become breeding adults.

At equilibrium (and assuming that first-year birds do not breed) the number of deaths of breeding adults is

$$\sum_{i=2}^I (1-s_i) b_i N_i, \quad (10)$$

and the number of eggs surviving to breeding age is

$$\left(f \sum_{i=2}^I c_i l_i b_i N_i \right) (s_{e,max} s_c s_1) \left(\sum_{i=2}^I \left(\prod_{j=2}^i s_j \right) b_i N_i \right). \quad (11)$$

The first term in parentheses is the number of eggs laid, the second term is the probability of the egg surviving to the end of the first year, and the third term gives the probability of becoming of breeding age at ages 2 to I .

Given the chosen values for the parameters for the biology of Cape cormorants, that $I = 5$, $f = 0,5$, $b_2 = b_3 = 0$, $b_4 = 0,5$, $b_5 = 1$, $l_4 = l_5 = 1$, $c_4 = c_5 = c$, and $s_i = s$, $i = 2 \dots 5$, Equations 10 and 11 reduce to

$$(1 - s) (b_4 N_4 + b_5 N_5), \quad (12)$$

and

$$(0,5c(0,5N_4 + N_5)) (s_{e,max} s_c s_1) (s^2 b_4 N_4 + s^3 b_5 N_5). \quad (13)$$

The resultant value of s_1 obtained from the above choice of parameters is 0,55 and may be compared with the value of 0,43 calculated by Furness and Cooper (1982). From the SAFRING data, an approximate survival rate for first-year birds was estimated to be 0,44.