On the scientific basis for reducing the South African seal population

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The South African government has accepted a recommendation by the Diemont Commission of Inquiry into the Allocation of Quotas for the Exploitation of Living Marine Resources that the South African seal population needs to be reduced. The scientific basis of the rationale offered in the Commission's Report for this recommendation is critically examined. Many of the Report's statements are found to be erroneous or misleading. It is argued that there is currently no scientific basis upon which to predict whether such reduction would have a positive or negative impact on sustainable yields of commercial fish species, nor is such a prediction likely to be possible in the immediate future. The detrimental effects of operational seal-fishery interactions may provide a rationale for a population reduction, but these have yet to be quantified adequately by scientific assessment.

Die Suid-Afrikaanse regering het die Diemont-kommissie oor die Toebedeling van Kwotas vir die Ontginning van lewende Mariene Hulpbronne se aanbeveling aanvaar dat die Suid-Afrikaanse robbebevolking verminder moet word. Die wetenskaplike beredenering van die aanbeveling in die kommissie se Verslag word krities ondersoek. Heelparty bewerings in die Verslag is as foutief of misleidend uitgewys. Die outeurs voer aan dat daar tans geen wetenskaplike basis is waarop voorspel kan word of so 'n vermindering in robbegetalle 'n positiewe of negatiewe uitwerking op volgehoue opbrengste van handelsvissoorte sal hê nie, en ook nie of so 'n voorspelling in die nabye toekoms gemaak sal kan word nie. Die nadelige gevolge van die rob-vissery-interaksie wat tans geld, sal miskien grondslae vir die vermindering van die robbebevolking lewer, maar die getalle moet nog deur afdoende wetenskaplike evaluering bepaal word.

Commercial exploitation of the South African fur seal, *Arctocephalus pusillus pusillus*, began early in the 17th century. Harvesting by European and South African sealers was periodically intensive and generally indiscriminate. By the time formal legal authority over sealing in the Cape was established in 1893, over 20 island colonies had been extirpated, and back projections suggest that the total population had been reduced to less than 50 000 animals. Since then, harvesting has been restricted to pups and bulls and the quotas introduced from 1974 have been set with a view to exploiting the seal population on a sustainable basis. By 1983, the population, whose breeding colonies extend from Cape Cross in Namibia to Black Rock in Algoa Bay, South Africa, is estimated to have recovered to a level producing 310 000 (standard error 30 000) pups annually.[1] This corresponds to an average total population size over the year of about 1,4 million animals (see Appendix 1).

In 1983, however, the international market for seal pelts collapsed, removing much of the commercial incentive for harvesting

seals (specifically the pups). This served to focus attention on the question of whether seal numbers needed to be controlled or reduced (probably by culling programmes) because of their alleged deleterious effect on fish stocks and fishing operations. In 1983 this matter was considered by the Scientific Committee of Enquiry into the Exploitation of Pelagic Fish Resources of South Africa and South West Africa. This body, known as the Alant Committee, was chaired by Dr T.G. Alant and included eight other scientists. Recommendation 10.15 of the Committee[2] reads: 'Seals, seabirds and other predators on commercially important pelagic shoal-fish should not be culled if the principal objective for doing so is to attempt to make more fish available to the industry.' This recommendation was accepted by the South African government.[3]

In contrast, the 1986 White Paper[4] on the Report of the Commission of Inquiry into the Allocation of Quotas for the Exploitation of Living Marine Resources[5] states that the South African government accepts the Commission's recommendation 8.70.1: 'That the control and reduction of the huge seal herds have become issues of major importance in the Fishing Industry and culling must be undertaken by the State'. This Commission, known as the Diemont Commission, was chaired by Justice M.A. Diemont, and included no marine resource scientists.

In the following, we examine the scientific basis for statements made regarding seals, and the rationale offered for recommendation 8.70.1, in the Diemont Commission Report.[5] This is done under the headings: Population Demography, Consumption by Seals, Ecosystem Considerations, and Fishery Interactions. The quotations that begin each sub-section are taken from sections 8.61 to 8.68 of the Diemont Commission Report.

Population demography

Age at first parturition

> 'cubs . . . grow rapidly and by their second year are able to reproduce'

This statement is probably derived from a study of the sequence of closure of skull sutures,[6] from which it was estimated that female fur seals reached sexual maturity (i.e. came into breeding condition for the first time) at 21 to 27 months of age, giving birth 12 months later. However, some data from animals of known age[7] indicate that females do not reach first parturition until at least age 4. Captive *A. pusillus* females of known age have conceived for the first time at ages 2 to 5 (Table 1). In the Australian population of *A. pusillus*, females normally first give birth at age 5 or later, although a few apparently give birth at age 4.[8]

The age at puberty of male *A. pusillus* has been established from tagged animals in the Australian population as 4 to 5 years,[8] and in captivity in South Africa has ranged also from 4 to 5 years (Table 1). However, such males might normally have restricted access to receptive females in the wild, and harem-master status may be reached only much later.

The statement in the Diemont Commission Report[5] therefore seriously underestimates the age at which fur seals are able to reproduce.

Colony growth rates

> 'undisturbed colonies expand with astonishing rapidity'; 'the seals breed fast'

The growth rates at the two largest seal colonies at Atlas Bay and Kleinsee are both estimated to have been about 10% per annum from 1971 to 1983.[1] Both these colonies were subjected to pup harvesting over that period, and it is probable that these growth rates may partly reflect immigration from other colonies.

Atlas Bay and Kleinsee are mainland colonies; they and three of the four other mainland colonies are estimated to have increased over the period from 1971 for which census data are available. Over the same period of 1971 – 1983, however, 13 of the 17 island colonies are estimated to have decreased in size.[1] Combining results from all the colonies gives a net annual increase rate of about 4% (standard error 1%) for the total population from 1971 to 1983. This is a relatively modest rate when compared with the population of fur seals (*A. gazella*) at South Georgia, for which an annual increase from 1958 to 1972 of 17% has been reported.[9]

Migration patterns

> 'there is, according to the evidence, steady recruitment from Cape Cross and other colonies on the South West African coast' [to South African colonies]

We have been unable to trace published evidence to support this statement. Although immigration may have played a role in the rate of increase of the large colonies at Kleinsee (in South Africa) and Atlas Bay (in Namibia), there is no indication of the origin of such immigrants.

Most tagging and sealing operations to date have been directed at animals in their first year, so that it is difficult to follow shifts in the population as inferred in the Diemont Commission Report.[5] A report[10] on the movements of 14 pups tagged on Seal Island, False Bay, reveals that 10 were found at Cape Cross (i.e. in the reverse direction to that proposed). As these were still in their first or second year when killed, however, they would not necessarily still have been resident in Namibian waters when they reached breeding age.

In evidence presented to the Alant Committee, the movements of seals tagged as pups and recovered at sea (mostly in fishing gear) up to 10 years later were documented.[11] These showed that of the 13 pups tagged south of the Orange river, 4 (all males) were recovered in Namibian waters, while of the 9 pups tagged north of the Orange river (6 males, 3 females) none was recovered south of the Orange (see Figs 1 and 2). This evidence does not support the contention of the Diemont Commission Report[5] that there has been steady migration from Namibian to South African colonies.

Consumption by seals
Consumption rate

> 'Assuming, as it is often said, that a seal eats its weight of fish in a day'

No direct measurements of the energy requirements of Cape fur seals have yet been made. Per capita food requirements depend greatly on the caloric density and digestibility of the prey, and without knowledge of how these vary seasonally or geographically, simple calculations of the amount of food eaten on a simple basis of percentage of body mass may be misleading.[12] Nevertheless, a review[13] of published estimates of daily food intake for other pinnipeds shows that these generally fall within the range of 2 to 10% of body mass for a maintenance diet, with values as high as 20% for lactating and growing fur seals. The food requirements of *A. pusillus* therefore probably lie between 5 and 20% of body mass per day.

Average seal mass

> 'accepting that an average seal weighs 100 kg (a bull may weigh 400 to 500 kg)'

No detailed mass-at-age data have been published for the South African fur seal. The average mass of seals shot at sea during scientific seal-feeding surveys is about 50 kg, and this figure (somewhat arbitrarily increased to 60 kg to account for the under-representation of large males in such samples) is used in recent estimates of consumption by seals.[13] The actual mass of an 'average seal' to be used in such calculations depends on the component of the population to which it is to be applied. Appendix 1 presents details of a calculation of 54 kg as the effective average feeding mass of a seal in relation to the total seal population numbers (including pups) at the beginning of the year. The equivalent average mass of the animals actually foraging over the year (which excludes pups) is estimated to be 72 kg. The calculation uses published data[14] on the mass-at-age by sex for the Northern fur seal, *Callorhinus ursinus*. The maximum recorded mass of a South African bull seal is 316 kg, with the average asymptotic mass averaged over the year probably only a little greater than 200 kg (see Appendix 1).

Total consumption

> 'seals on Seal Island (False Bay) . . . 3 500 000 kg of fish consumed in a day'; 'Seals . . . were described . . . as "the biggest quota holders on the coast" ' [quoting Mr P.J. Retief, Manager of the North Bay Canning Company at Doring Bay]; 'Not only are they (seals) said to eat great quantities of rock lobster, but they have learnt that where a seine is cast there is food.'

Appendix 2 details a calculation of the total average daily consumption by seals at Seal Island, False Bay. The result is 120 000

Table 1. Ages of captive *A. pusillus* at the time of first conception. Data from Port Elizabeth and Durban oceanaria.

Seal	Date of capture or birth	Age at capture (yr)	Date of birth of first pup	Birth status	Age at sexual maturity (first parturition) (yr)
Females					
Binkie	Jul./Aug. 1977	~1,5	16.11.79	Live	3 (4)
Sally	6.11.82	0	– 01.86	Live?[1]	2 (3)
Siggi	8.11.75	~2,0	3.05.79	Live	5 (6)
Males					
Helmut	18.11.76	0	6.11.82	Live	5[2]
Dougal	8.11.75	~1,0	3.05.79	Live	4
Ben	16.11.81	0	21.11.86 / 21.11.86	Live / Stillborn	4

[1] Pup said to have been killed by other seals almost immediately after birth.
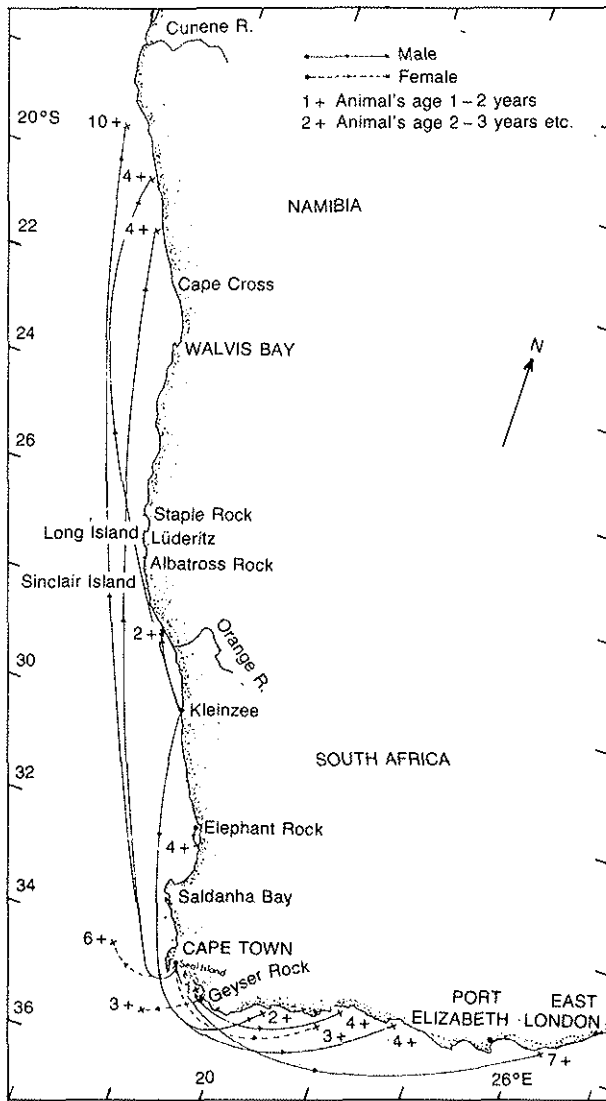
[2] Adult male also present until 17.2.81.

Fig. 1. Recoveries at sea of seals tagged as pups in the colonies south of the Orange river. (Solid lines—males; broken lines—females; animal's age 1 – 2 years shown as 1 +, 2 – 3 years as 2 +, etc.)
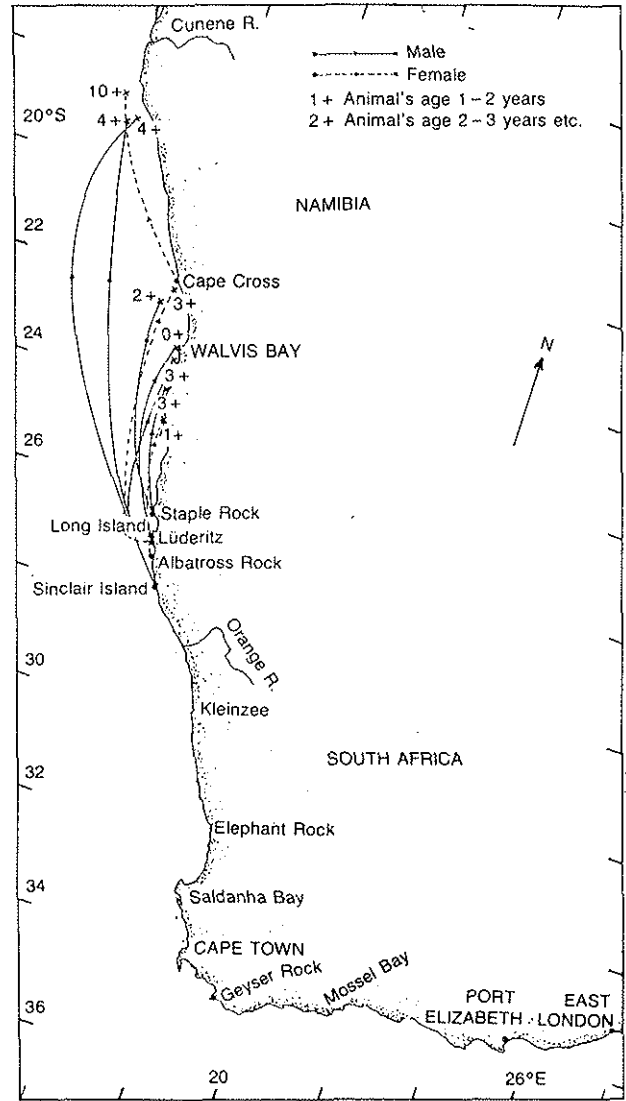

Fig. 2. Recoveries at sea of seals tagged as pups in the colonies north of the Orange river. (Notation as in Fig. 1.)

to 480 000 kg per day (3 to 14% of the estimate quoted above), where the range reflects the extent of experimental estimates of the consumption rate of seals. It should also be borne in mind that not all of this consumption comprises species sought by commercial or recreational fishermen.

Diemont[15] states that the figure of 3 500 000 kg per day quoted in the Diemont Commission Report[5] was intended as a hypothetical example to illustrate the question: Is the quota being fairly divided between the 35 boat owners at Kalk Bay and the 35 000 seals on Seal Island? The only commercial fishery based at Kalk Bay is for line fish, and the catches of this fishery are not limited by quotas. Furthermore, the percentage of line fish in the diet of fur seals is very small, comprising less than 5% by volume of all fish consumed.[10] The vicinity of Seal Island is in fact a recognised line-fishing ground in False Bay (Fig. 3).

In addition, within three months of giving birth, adult female seals are indulging in feeding trips averaging 4 days in duration, which may extend to 7 to 8 days by the end of the year.[16] This time enables them to forage widely, and adult females have been caught at sea from 70 to 240 nautical miles from their natal colony[11] (see Figs 1 and 2). Female Northern fur seals have been tracked to feeding locations about 100 nautical miles from their breeding rookeries during round trips of 5 days' duration.[17] Animals that have no social ties to their breeding colony for the

majority of the year (such as non-nursing juveniles and adult males) may range even farther afield, as shown by the recoveries of male *A. pusillus* at sea up to 970 n. miles from their natal colony[11] (see Figs 1 and 2). The inference that the Seal Island population feeds mainly or exclusively within the confines of False Bay is thus misleading.

The consumption of anchovy by seals off the South African coast has been estimated by David[13] to be about 125 000 tons per annum. [Strictly, David's estimates should be amended, taking into account the revised foraging/pup ratio of $\theta^{**} = 3,55$ and associated average mass $\bar{w}^{**}$ (SA) = 72,2 kg calculated in Appendix 1—David used values of $\theta^{**} = 3,0$ and $\bar{w}^{**}$ (SA) = 60 kg, respectively. The resultant increase of 42% in David's estimate (to 178 000 tons per annum), however, makes no marked qualitative difference to the conclusions that follow.] This compares with annual anchovy landings by the industry in the neighbourhood of 300 000 tons from 1979 to 1986. A recently developed anchovy stock assessment technique[18] provides an estimate (see Appendix 5) of about 2 million tons of anchovy lost to natural mortality each year (the technique can also be used to show that the standard error for this estimate is some 1 million tons). The dominant contributors to this mortality are probably squid, hake and snoek; the seal contribution is only some 6%.

Rock-lobsters constitute 7% of the overall diet of seals along

Fig. 3. Line-fishing boats near Seal Island, False Bay on 23 January 1987.

the South African west coast, but are almost absent from their diet along the south coast and off Namibia.[13] This corresponds to an estimate of the total annual consumption of rock-lobsters by seals that exceeds the industry's quota. For various reasons,[13] however, the estimate is probably positively biased. The main biasing factor is that samples were taken mostly close to the coast where the lobsters are prevalent, whereas seals forage to much greater distances from the shore. In any case the impact of such consumption must be assessed in terms of arguments (developed in a subsequent section relating seal predation to commercial fisheries) which cast doubt on the validity of simplistic reasoning about the consequences of biological seal – fishery interactions.

Counts of the number of seals attending trawlers and purse-seiners indicate that offal from these vessels may support up to 20 000 seals,[13] or approaching 2% of the population. The great majority of the population therefore forages independently of fishing operations.

Ecosystem considerations
Exclusion of birds by seals

'Seal Island in False Bay was at one time inhabited by birds and no seals; today there is a colony of 35 000 seals and no birds.'

A recent review[19] of the history of seal and seabird populations on Seal Island, False Bay, reports that from an 'original' mixed community of seals and seabirds in 1687, the island became a pure seabird colony from 1830 to about 1910, was a mixed community again for the next 35 years, but is now dominated by seals. The composition of the seabird population of the island has not remained constant either, the dominant species changing from gannets in the seventeenth century to penguins in the late nineteenth century and cormorants in the first half of this century. Similar faunal changes seem to have occurred at several other islands off the Cape and Namibia, so that island communities now tend to be composed either entirely of seals or entirely of seabirds, whereas historically some at least bore mixed seal and seabird populations.

The reasons for these changes are complex, and include the possibility of natural fluctuations. It seems more likely, however, that the principal role has been played by a combination of human interference factors comprising sealing, guano scraping, egg collection, over-fishing of prey populations (particularly pilchard and hake) and (more recently) oil pollution. The review[19] concludes that it is unlikely that the fauna of each island would revert to its 'original' status even if harvesting of seals and seabird products were to cease. Similarly, there is no guarantee that artificial reduction of the seal population would necessarily result in a 're-stocking' of Seal Island with seabirds such as penguins, whose numbers may ultimately be controlled by the availability of pelagic fish.

On the other hand, where seals now begin to 'invade' established seabird breeding colonies (such as at Lamberts Bay and Mercury Island), it would seem reasonable to attempt to limit their expansion in such local areas, while investigating the causal factors behind such 'invasions'.

Correction of ecological 'imbalance'

'To restore the balance a large number of seals will have to be destroyed annually on the West Coast'

The most straightforward interpretation of the growth of the South African seal population over the twentieth century is that of the recovery of a heavily exploited resource towards its pre-exploitation level. The possible counter-argument that present-day colonies at sites apparently not occupied in earlier times (e.g. Kleinsee, Wolf and Atlas bays) suggest that the population is increasing beyond its pre-exploitation level is not conclusive; note that many of the historical sites (including the large Dassen, Possession and Robben islands) have never been recolonized, so that the new sites may represent merely a displacement of the population.

Unfortunately there is no basis at present upon which to estimate the pre-exploitation population level of seals. A compilation of harvest levels from the seventeenth to the nineteenth centuries has not yet been made and may well be impossible to complete. Analysis of 1971 – 1983 colony census data showed no significant evidence of density dependence in the overall population growth rate,[1] from which it might have been possible to calculate the carrying capacity value.

There is thus no biological basis for a categorical conclusion that the present overall seal numbers or population growth rate are inappropriately high (presumably the principal reason for the suggestion of an 'imbalance'). Ecological imbalance is unfortunately a term frequently used without a clear definition of what is meant. At the semantic level, an ecosystem is never in a static equilibrium state (or 'balance') because, in part, of seasonal trends and environmental fluctuations from year to year. The variations in the population trajectories of component populations can nevertheless be considered as fluctuations about some stable multi-species equilibrium state. Human intervention could then be viewed as causing 'imbalance' if it resulted in increasing the amplitude of these fluctuations to levels regarded as undesirable for some reason, or caused the system to move into the attraction zone of some alternative stable equilibrium state (again considered less desirable in some context).

The analysis of such possibilities, however, is no more than a very distant possibility at present, because of the absence of reliable estimates of even the most basic demographic parameters and variables (such as population trajectories) of many of the principal constituent populations of the region (e.g. squid, snoek). Accordingly, no framework exists within which hypotheses of ecological imbalance in this sense could be tested, so that their advancement would seem to serve little purpose.

Fishery interactions
The Norwegian experience quoted

'In Norway 80% of the seal population was exterminated; this led to much public criticism, but the Fishing Industry was restored.'

Dr T. Oritsland, senior seal biologist of the Institute of Marine Research in Bergen, Norway, comments (in litt. 16/12/86) that ' "extensive research" has failed to reveal the source of the statement', and that the statement is 'utterly misleading'.

It is unclear to which species of seal the statement refers: presumably not to the stocks of harp (*Phoca groenlandica*) and hooded seals (*Cystophora cristata*) in the North Atlantic, which have been recovering from overexploitation in the 1950s, and of which the Barents Sea harp seal stock is showing a declining rate

of increase. Rather, it seems likely that the reference is to coastal colonies of common (*Phoca vitulina*) and grey seals (*Halichoerus grypus*). The primary concern about these seals, however, is not necessarily that they cause damage to gear or an alleged reduction of fish stocks (the factors argued in the South African case), but rather that they act as hosts for part of the life-cycle of the parasitic cod-worm, which markedly reduces the value of landed fish catches (there is no analogous problem in South Africa). Oritsland (*op. cit.*) advises that a programme was instituted to halt the increase of these species by culling about 50% of the minimum population estimate over a five-year period; however, it has not as yet proved possible to measure any resultant effect on either the seal stocks or the fisheries.

On a wider front, we are unaware of any proven link between any seal population reduction and a consequential increase in yield to any fishery world-wide. The Royal Commission on seals and sealing in Canada,[20] although acknowledging strong evidence that seals can have an effect on the abundance of fish stocks and the size of catches, states that they 'are not aware of any instance in which a known and measured change in the abundance of seals has had a measurable effect on fish catches'.

The impact of consumption by seals on commercial fisheries
'The White Fish Industry, the Pelagic Industry and the Rock Lobster Industry are all put in jeopardy by the growing herds.'

The underlying basis for much of the rationale offered in sections 8.61 to 8.68 of the Diemont Commission Report[5] for the ultimate recommendation 8.70.1 that the seal herds be culled, is that fewer seals would eat less fish, so that the fish 'saved' would become available for commercial exploitation. Is this assumption justified? There are two ways in which it can be examined: theoretically and empirically. In the former respect, consider for simplicity that man and seals are 'in competition' for the anchovy resource. Appendix 3 details some simple Lotka-Volterra predator – prey model characterizations of this situation. In the simplest man – seal – anchovy system, reducing the seal numbers does indeed produce a higher potential sustainable yield of anchovy for man. However, suppose a further predator (such as squid) is interposed between the seals and anchovy. The seals eat both squid and anchovy, while the squid eat anchovy. The man – seal – squid – anchovy model of Appendix 3 then indicates that reducing the seal numbers would lead (eventually) to a *decreased* potential sustainable yield of anchovy for man. Essentially this occurs because the lower predator pressure on squid allows them to increase and consume more anchovy. A similar analysis could be applied to the man – seal – octopus – rock lobster interaction.

The conclusion to be drawn from this exercise is not that anchovy fishermen should welcome increases in the seal population. The real situation is considerably more complicated than any of the models of Appendix 3, some of which produced the counter-intuitive result that seals and fishermen should not be regarded as competitors for anchovy in the simplest sense. Given an age-structured multi-species model incorporating all the major species interactions in the Benguela [so-called 'multi-species virtual population analysis'[21,22] might be a start in this direction], it may be possible to predict the directions of the responses of commercial fish populations to a reduction in the seal population. But, for the reasons discussed earlier, there is no immediate prospect of developing such a model, too many of the parameters required being inestimable from current data. Thus the theoretical modelling approach cannot at present determine whether seal harvesting would have a beneficial or detrimental effect on the sustainable yield of anchovy; at the very least more data first need to be collected. An alternative approach is an entirely empirical determination of the effect by means of a controlled experiment. Appendix 4 details a feasibility study of an experiment to reduce the seals and monitor the effect on the anchovy population. It indicates that acquisition of a result statistically significant at the

5% level would require an experiment of at least about 650 years' duration—the empirical approach is thus quite impractical in this instance.

The conclusion thus follows that there is no basis at the present time (nor likely to be so in the immediate future) to determine whether reducing the seal population would have a positive or negative effect on the sustainable yields of populations of commercial fish species, and hence the quotas that could be allocated to the fishing industry.

Operational interactions
'they swarm into the net consuming fish and then, in their efforts to escape, damage costly nets.'

Undoubtedly this problem occurs, but the point at issue is its quantification. The only scientific study to date[23] concluded that 'damage caused to fishing gear by Cape fur seals does not appear to be an important problem, except in the snoek line-fishery'. This study was, however, based on a fairly small sample, and there is scope for a more extensive scientific assessment of this aspect. Consideration should also be given to operational solutions for such problems, e.g. modifying fishing gear or practices, or the use of seal deterrents such as crackers.

Conclusions

The preceding discussions throw considerable doubt on much of the information presented in paragraphs 8.61 to 8.68 of the Diemont Commission Report,[5] as well as the principal rationale advanced therein for the ultimate recommendation (8.70.1) that the seal herds be reduced. Certainly there is currently no scientific basis upon which to predict whether the reduction would have a positive or negative impact on commercial fish quotas. (A defensible argument might be made that since one cannot state conclusively that continuing growth of the seal population will not have a negative impact on sustainable yields, the population should therefore be kept at its *present* level to avoid the possibility of such an outcome. Nevertheless this argument has no relevance to a proposal to *reduce* the population.) There may be a case for reduction on the grounds of the detrimental effects of operational seal – fishery interactions; however, these have yet to be adequately quantified by scientific assessment—a necessary prerequisite to any rational management decision.

Accordingly, the South African government's White Paper response[4] accepting recommendation 8.70.1 of the Diemont Commission Report seems to us to be premature and meriting reconsideration. The Commission also recommended (8.70.2) that culling be undertaken in liaison with scientists and conservationists. We consider the White Paper response accepting this, but which also states that 'The Government . . . wishes to record that the policy objectives of a seal reduction programme and the objectives of scientists and conservationists are not necessarily reconcilable', to be somewhat unfortunate in the latter respect. While at a tactical level scientists (and conservationists) may tend to be more averse to taking risks than industrialists, nevertheless the fundamental objective of scientists in the field of marine resources is surely that management decisions be rational and objectively based. Does the government really wish to advance policy objectives inconsistent with these criteria?

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Appendix 1
The effective average mass of seals for food consumption calculations

First the ratio of total males (θ_m) and total females (θ_f) to number of pups born is calculated. The requisite formulae are:

$$\theta_m = (1 - q_f) + (1 - q_f)(1 - F) \sum_{i=1}^{4} (S_j)^i (R)^{-i}$$

$$+ (1 - q_f)(1 - F)(S_j)^4 \sum_{i=5}^{9} (S)^{i-4}(R)^{-i}$$

$$+ (1 - q_f)(1 - F)(S_j)^4 S^6 \sum_{i=10}^{\infty} (S_b)^{i-10} R^{-i}$$

$$\theta_f = q_f + q_f(1 - F) \sum_{i=1}^{4} (S_j)^i (R)^{-i}$$

$$+ q_f (1 - F)(S_j)^4 \sum_{i=5}^{\infty} (S)^{i-4}(R)^{-i} \tag{A1.1}$$

where q_f = 0,437 = fraction of pups born that are female[24]
    F = 0,371 = pup harvesting rate[1]
    R = 1,0365 = population annual increase rate (expressed as a ratio)[1]
    S_j = 0,883 = juvenile survival rate (until first parturition, which is assumed to be at 4 years of age)
    S = 0,917 = adult survival rate[1]
    S_b = territorial bull survival rate.

Equations (A1.1) assume that the parameters are constant over all preceding years, though strictly the estimates of F, R and S apply to the period 1971 to 1983.[1] For simplicity, juvenile survival has been assumed to be independent of age, and given by

$$(\lambda/\rho q_f)^{1/4} \tag{A1.2}$$

(from Butterworth *et al.*[1] equation (13), with λ estimated to be 0,213 and the annual pregnancy rate ρ assumed equal to 0,8). The estimates[1] of S and S_j are strictly applicable to females only. Equations (A1.1) have thus assumed that the male survival rates are the same as for females, until bulls reach an age of 10 years. This is the age at which the bulls are assumed to become territorial, and results for the Northern fur seal suggest an associated 3,5-fold increase in annual natural mortality $(1 - S)$ at that time.[25] Accordingly,

$$(1 - S_b) = 3,5 (1 - S)$$
$$S_b = 0,710. \tag{A1.3}$$

For convenience of calculation, 'pseudo-survival rates' are defined which combine the effects of mortality and population increase rates:

$$\tilde{S}_j = S_j R^{-1} = 0,852$$
$$\tilde{S} = S R^{-1} = 0,885$$
$$\tilde{S}_b = S_b R^{-1} = 0,685. \tag{A1.4}$$

Equations (A1.1) can then be rewritten

$$\theta_m = (1 - q_f) [1 + (1 - F) \{ \sum_{i=1}^{4} (\tilde{S}_j)^i + (\tilde{S}_j)^4 \sum_{i=5}^{9} (\tilde{S})^{i-4}$$

$$+ (\tilde{S}_j)^4 (\tilde{S})^6 / (1 - \tilde{S}_b) \}]$$

$$\theta_f = q_f [1 + (1 - F) \{ \sum_{i=1}^{4} (\tilde{S}_j)^i + (\tilde{S}_j)^4 \tilde{S} / (1 - \tilde{S}) \}]. \tag{A1.5}$$

Substitution then yields estimates

$$\theta_m = 2,47$$
$$\theta_f = 2,30. \tag{A1.6}$$

Thus the ratio of the total population size at the beginning of the year to the number of pups born is $\theta = \theta_m + \theta_f = 4,77$. [For a stationary population $(R = 1)$ with no harvesting $(F = 0)$, the corresponding values are $\theta_m = 4,27$; $\theta_f = 4,67$ and $\theta = 8,94$.]

More appropriate values to use as representative of the average number over the whole year are provided by the ratios of mid-year numbers to pup births at the beginning of the year:

$$\theta_m^* = (1 - q_f) \, [S_j^{\frac{1}{2}} + (1 - F) \, \{ \sum_{i=1}^{3} (\widetilde{S}_j)^i S_j^{\frac{1}{2}} + (\widetilde{S}_j)^4 \, S^{\frac{1}{2}}$$

$$+ (\widetilde{S}_j)^4 \sum_{i=5}^{9} (\widetilde{S})^{i-4} S^{\frac{1}{2}} + (\widetilde{S}_j)^4 (\widetilde{S})^6 S_b^{\frac{1}{2}}/(1 - \widetilde{S}_b) \}],$$

$$\theta_f^* = q_f \, [S_j^{\frac{1}{2}} + (1 - F) \, \{ \sum_{i=1}^{3} (\widetilde{S}_j)^i \, S_j^{\frac{1}{2}} + (\widetilde{S}_j)^4 \, S^{\frac{1}{2}}$$

$$+ (\widetilde{S}_j)^4 \, \widetilde{S} \, S^{\frac{1}{2}}/(1 - \widetilde{S}) \}], \qquad (A1.7)$$

which yield

$$\begin{aligned} \theta_m^* &= 2,31 \\ \theta_f^* &= 2,18 \end{aligned} \qquad \theta^* = 4,49. \qquad (A1.8)$$

Table 2 provides masses at age for male and female Northern fur seals (*Callorhinus ursinus*) (w_i^m and w_i^f, respectively). For the moment it is assumed that these are appropriate values for the South African fur seal. It is customary to report seal population numbers either in terms of the number of pups born at the start of the year, or some multiple (θ) of this estimate corresponding to the total number of seals at that time. Accordingly, the appropriate average mass $(\bar{w})$ by which such a total population estimate should be multiplied for food consumption calculation purposes is given by

$$\bar{w}_m = \theta_m^{-1} \, (1 - q_f)(1 - F)[\sum_{i=1}^{3} (\widetilde{S}_j)^i S_j^{\frac{1}{2}} w_{i+}^m + (\widetilde{S}_j)^4 S^{\frac{1}{2}} w_{4+}^m$$

$$+ (\widetilde{S}_j)^4 \sum_{i=5}^{9} (\widetilde{S})^{i-4} S^{\frac{1}{2}} w_{i+}^m + (\widetilde{S}_j)^4 (\widetilde{S})^6 S_b^{\frac{1}{2}} w_{10+}^m/(1 - \widetilde{S}_b)],$$

$$\bar{w}_f = \theta_f^{-1} \, q_f(1 - F)[\sum_{i=1}^{3} (\widetilde{S}_j)^i S_j^{\frac{1}{2}} w_{i+}^f + (\widetilde{S}_j)^4 S^{\frac{1}{2}} w_{4+}^f$$

$$+ (\widetilde{S}_j)^4 \sum_{i=5}^{9} (\widetilde{S})^{i-4} S^{\frac{1}{2}} w_{i+}^f + (\widetilde{S}_j)^4 (\widetilde{S})^6 S^{\frac{1}{2}} w_{10+}^f/(1 - \widetilde{S})],$$

$$\bar{w} = [\theta_m \bar{w}_m + \theta_f \bar{w}_f][\theta_m + \theta_f]^{-1}, \qquad (A1.9)$$

where it has been assumed that seals do not forage during their

Table 2. Masses at age of the Northern fur seal, *Callorhinus ursinus*.[14]

Age (i) (years)	Mass (kg)	
	Male (w_i^m)	Female (w_i^f)
0	5,4	4,8
1	16,8	14,1
2	20,9	16,3
3	28,0	21,2
4	35,5	23,2
5	44,9	28,5
6	60,7	29,9
7	94,5	34,3
8	175,5	36,0
9	188,4	40,4
$\geq 10^\dagger$	195,5	43,8

[dagger] Weighted mean.

first year of life (so that for the purposes of this calculation the effective mass of 0-year-olds is zero), and where

$$w_{i+}^m = \frac{1}{2} \, (w_i^m + w_{i+1}^m)$$

$$w_{i+}^f = \frac{1}{2} \, (w_i^f + w_{i+1}^f)$$

(i.e. the mid-year masses-at-age have been assumed equal to the means of the seal's mass at the beginning and end of the year, and have been multiplied by the numbers in the corresponding age class in the middle of the year).

Substituting numerical values into (A1.9) yields

$$\begin{aligned} \bar{w}_m &= 59,3 \text{ kg} \\ \bar{w}_f &= 24,4 \text{ kg} \end{aligned} \qquad \bar{w} = 42,5 \text{ kg}. \qquad (A1.10)$$

The South African fur seal is somewhat larger than the Northern fur seal, and sexual dimorphism is not as marked. If the degree of closure of cranial sutures is used as an index of relative age (where group A represents the youngest animals and groups L or M the oldest), data[26] for females indicate that suture groups H − M have reached asymptotic length; this sample has an average mass of 74,5 kg, which is 70% greater than the corresponding value in Table 2 for the Northern fur seal. A similar analysis of data[26] for bulls (suture groups H − L) suggests an average asymptotic mass of 183,8 kg, but this estimate is negatively biased because of the absence of harem bulls in the sample. The average mass of 53 harem bulls shot on Seal Island, False Bay, is reported to be 247 kg, with a maximum of 316 kg;[27] this average would, however, provide a positively biased estimate of average mass over the year as bulls are in prime condition (maximum mass) at the start of the breeding season. Taking the mean of these two estimates provides a value of 215,4 kg for the average asymptotic mass of South African bull seals, which is 10% greater than the corresponding value for the Northern fur seal. Assuming the same proportional mass increases (70% and 10%) for other age classes provides estimates (again applicable to the total population size, including pups, at the start of the year):

$$\begin{aligned} \bar{w}_m (SA) &= 1,1 \times 59,3 = 65,2 \text{ kg} \\ \bar{w}_f (SA) &= 1,7 \times 24,4 = 41,6 \text{ kg} \end{aligned} \qquad \bar{w}(SA) = 53,8 \text{ kg}. \quad (A1.11)$$

These results can be expressed alternatively in terms of the average number of animals actually foraging over the year (assumed equal to the number, less pups, present at mid-year). The multipliers (θ^{**}) of the number of pups born are given by subtracting the contribution of pups to Equations (A1.7):

$$\begin{aligned} \theta_m^{**} &= \theta_m^* - (1 - q_f)S_j^{\frac{1}{2}} = 1,78 \\ \theta_f^{**} &= \theta_f^* - q_f \, S_j^{\frac{1}{2}} = 1,77 \end{aligned} \quad \theta^{**} = 3,55 \qquad (A1.12)$$

The average masses ($\bar{w}^{**}$) of the seals actually foraging over the year are then given by the relation $\bar{w}\theta = \bar{w}^{**} \, \theta^{**}$, i.e.

$$\bar{w}_m^{**} (SA) = \bar{w}_m (SA) \, (\theta_m/\theta_m^{**}) = 90,5 \text{ kg}$$

$$\bar{w}^{**} (SA) = 72,2 \text{ kg} \qquad (A1.13)$$

$$\bar{w}_f^{**} (SA) = \bar{w}_f (SA) \, (\theta_f/\theta_f^{**}) = 53,9 \text{ kg}$$

The current absence of age data for the South African fur seal has meant that numerous assumptions, particularly by way of analogies with the Northern fur seal, have been necessary to derive the estimates of θ and $\bar{w}(SA)$ above. Ageing studies of the South African fur seal are in progress; the results should allow direct estimates of mass-at-age and age-specific survival rates for this species. These in turn will enable the estimates above to be improved.

Appendix 2
The average daily consumption by seals at Seal Island, False Bay

The most recent estimate of the pup production at Seal Island, False Bay, corresponding to the year 1983 is 9 400 (standard error 1303).[1] Using the estimate of $\theta = 4,77$ from Appendix 1, this corresponds to a total population size of 44 838 seals. This

estimate may be negatively biased as the Seal Island colony is estimated to have decreased over the period 1971 to 1983 ($R = 0,96$), whereas the population as a whole has increased ($R = 1,0365$). From Equations (A1.1) it is clear that θ is a decreasing function of R. However, census data are too sparse to estimate survival rates on a colony-by-colony basis, and these may be correlated with estimates of R. Accordingly, the population 'averaged' estimate of θ has been used here.

Further, using $\bar{w}(SA) = 53,8$ kg (Equation A1.11) and a daily consumption rate range for seals of 5% to 20% of body mass, provides an estimate of the daily consumption by the Seal Island seals of

$$44\,838 \times 53,8 \times (0,05 - 0,20) \simeq 121\,000 \text{ to } 482\,000 \text{ kg.} \quad \text{(A2.1)}$$

Appendix 3
Models of biological seal – fishery interactions

Figure 4 illustrates the interactions between man, seals (N_3), squid (N_2) and anchovy (N_1). It is assumed that anchovy and seals are being harvested (or culled), but squid is unharvested. A Lotka-Volterra characterization of this system is

$$\frac{dN_1}{dt} = r_1 N_1 (1 - N_1/K) - a N_1 N_2 - b N_1 N_3 - F_1' N_1$$

$$\frac{dN_2}{dt} = c N_1 N_2 - d N_2 - e N_2 N_3$$

$$\frac{dN_3}{dt} = f N_2 N_3 + g N_1 N_3 - h N_3 - F_3' N_3 \quad \text{(A3.1)}$$

where harvesting (culling) of anchovy and seals has been assumed for simplicity to be on a constant fishing mortality basis.
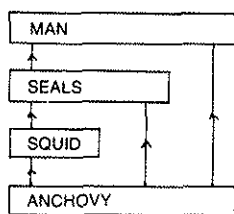

Fig. 4. A diagrammatic illustration of the interactions assumed in the man – seal – squid – anchovy model analysed in Appendix 3.

It is more convenient to consider these equations with renormalized variables ($X_1 = N_1/K$; $X_2 = fN_2/h$; $X_3 = eN_3/cK$) and similarly redefined parameters. Equations (A3.1) can then be rewritten

$$\frac{dX_1}{dt} = r_1 X_1 [1 - X_1 - \alpha X_2 - \beta X_3 - F_1]$$

$$\frac{dX_2}{dt} = r_2 X_2 [X_1 - X_3 - \gamma]$$

$$\frac{dX_3}{dt} = r_3 X_3 [X_2 + \delta X_1 - 1 - F_3] \quad \text{(A3.2)}$$

where $r_2 = cK$; $r_3 = h$; $\alpha = ah/r_1 f$; $\beta = bcK/r_1 e$; $\gamma = d/cK$; $\delta = gK/h$; $F_1 = F_1'/r_1$; and $F_3 = F_3'/h$.

The man – seal – anchovy system

First the situation illustrated in Fig. 5 is considered. In the absence of squid ($X_2 = 0$), Equations (A3.2) reduce to

$$\frac{dX_1}{dt} = r_1 X_1 [1 - X_1 - \beta X_3 - F_1]$$

$$\frac{dX_3}{dt} = r_3 X_3 [\delta X_1 - 1 - F_3]. \quad \text{(A3.3)}$$
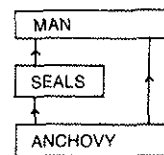

Fig. 5. A diagrammatic illustration of the interactions assumed in the man – seal – anchovy model analysed in Appendix 3.

At coexistence equilibrium,

$$\bar{X}_1 = (1 + F_3)/\delta$$

$$\bar{X}_3 = [1 - F_1 - (1 + F_3)/\delta]/\beta. \quad \text{(A3.4)}$$

The sustainable anchovy harvest rate, Y_1, is given by

$$\begin{aligned} Y_1 &= r_1 F_1 \bar{X}_1 \\ &= r_1 F_1 (1 + F_3)/\delta \\ &= r_1 F_1 (1 - F_1 - \beta \bar{X}_3) \end{aligned} \quad \text{(A3.5)}$$

and the maximum sustainable rate, MSY_1 (which is a function of the corresponding equilibrium seal population size), is

$$MSY_1 = \tfrac{1}{4} r_1 (1 - \beta \bar{X}_3)^2. \quad \text{(A3.6)}$$

From the last two equations it is clear that Y_1 is a decreasing function of the number of seals ($\bar{X}_3$) (or correspondingly an increasing function of the fishing mortality $r_3 F_3$ on seals). Thus this model of the man – seal – anchovy system indicates that reducing the seal numbers would produce a higher potential sustainable yield of anchovy for man—as might be expected with man and seals being modelled to be in direct competition for the anchovy resource.

The man – seal – squid – anchovy system

First consider a simpler version of this system as illustrated in Fig. 6. This assumes that seals do not eat anchovy directly, but only squid. Accordingly, parameters $b = g = 0$ in Equations (A3.1), or correspondingly $\beta = \delta = 0$ in Equations (A3.2). At coexistence equilibrium then

$$\bar{X}_1 = 1 - F_1 - \alpha(1 + F_3)$$

$$\bar{X}_2 = 1 + F_3$$

$$\bar{X}_3 = 1 - F_1 - \alpha(1 + F_3) - \gamma \quad \text{(A3.7)}$$

and so

$$\begin{aligned} Y_1 &= r_1 F_1 [1 - F_1 - \alpha(1 + F_3)] \\ &= r_1 F_1 (\bar{X}_3 + \gamma). \end{aligned} \quad \text{(A3.8)}$$
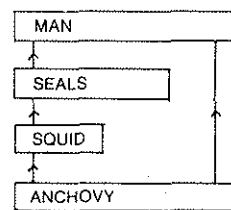

Fig. 6. A simpler version of the man – seal – squid – anchovy system, in which direct consumption of anchovy by seals does not occur.

Equations (A3.8) show that Y_1 is an increasing function of the number of seals ($\bar{X}_3$) (or correspondingly a decreasing function of the fishing mortality $r_3 F_3$ on seals). Hence reducing the seal numbers would *decrease* the potential sustainable yield of anchovy for man. This somewhat counter-intuitive result arises because fewer seals eat less squid; the squid accordingly increase in number and eat more anchovy.

However, return now to the original version of the system depicted in Fig. 4, with seals able also to eat anchovy. *A priori* one might expect two competing effects as regards the sustainable

anchovy harvest possible: direct consumption of anchovy by seals having a negative influence (as in Equation A3.5); and seal consumption of squid making a positive contribution (as in Equation A3.8). Further, one might surmise that the former single-link process would tend to dominate the latter double-link process.

The coexistence equilibrium for Equations (A3.2) is

$$\bar{X}_1 = [1 - F_1 + \beta\gamma - \alpha(1+F_3)] \, [1 + \beta - \alpha\delta]^{-1}$$
$$\bar{X}_2 = [(1+F_3)(1+\beta) - \beta\gamma\delta - \delta(1-F_1)][1 + \beta - \alpha\delta]^{-1}$$
$$\bar{X}_3 = [1 - F_1 - \gamma + \alpha\gamma\delta - \alpha(1+F_3)] \, [1 + \beta - \alpha\delta]^{-1},$$
$$(A3.9)$$

so that as before

$$Y_1 = r_1 F_1(\bar{X}_3 + \gamma), \tag{A3.10}$$

which indicates *again that reducing the seal numbers decreases* the potential sustainable anchovy yield.

This rather surprising conclusion (given the competing effects referenced above) merits further investigation. Equation (A3.10) can be written alternatively as

$$Y_1 = r_1 F_1[1 - F_1 + \beta\gamma - \alpha(1+F_3)] \, [1 + \beta - \alpha\delta]^{-1}. \tag{A3.11}$$

From this it is clear that Y_1 is only a decreasing function of F_3 *(and so of the fishing mortality on seals) provided*

$$1 + \beta - \alpha\delta > 0. \tag{A3.12}$$

What might be typical values for the left-hand side of (A3.12)? If ξ_{ij} measures the conversion efficiency (by mass) when species j eats species i, and if $w_1/w_2/w_3$ are typical average masses of an anchovy/squid/seal, then Equations (A3.1) imply

$$\xi_{12} = \frac{w_2}{w_1} \cdot \frac{c}{a}$$

$$\xi_{23} = \frac{w_3}{w_2} \cdot \frac{f}{e}$$

$$\xi_{13} = \frac{w_3}{w_1} \cdot \frac{g}{b}, \tag{A3.13}$$

so that

$$\frac{\alpha\delta}{\beta} = \frac{a}{c} \cdot \frac{e}{f} \cdot \frac{g}{b} = \frac{\xi_{13}}{\xi_{12}\xi_{23}}. \tag{A3.14}$$

Taking conversion efficiencies ξ_{ij} to be typically of order 10%, this suggests that

$$\alpha\delta/\beta \simeq 10$$
$$1 + \beta - \alpha\delta \simeq 1 - 9\beta, \tag{A3.15}$$

so that the inequality of (A3.12) is satisfied only for $\beta \leqslant 0{,}11$; this indicates that Y_1 is a decreasing function of F_3 only for fairly weak anchovy–seal interactions. (The large value of $\alpha\delta/\beta$ is a manifestation of the earlier supposition that a single-link process will dominate a double-link one.)

Linearizing Equations (A3.2) about the coexistence equilibrium provides the eigenvalue equation

$$\lambda^3 + r_1\bar{X}_1\lambda^2 + (r_2r_3\bar{X}_2\bar{X}_3 + \alpha r_1r_2\bar{X}_1\bar{X}_2 + \beta\delta r_1r_3\bar{X}_1\bar{X}_3)\lambda$$
$$+ r_1r_2r_3\bar{X}_1\bar{X}_2\bar{X}_3 (1 + \beta - \alpha\delta) = 0. \tag{A3.16}$$

Since this equation has a positive real root if and only if

$$1 + \beta - \alpha\delta < 0, \tag{A3.17}$$

it is clear that the conditions under which Y_1 is an increasing function of F_3 correspond to an unstable coexistence equilibrium. Further, given condition (A3.17), a physical (positive) solution for $\bar{X}_2$ from (A3.9) requires

$$(1 + F_3)(1 + \beta) - \beta\gamma\delta - \delta(1 - F_1) < 0. \tag{A3.18}$$

This happens to be just the condition required for the equilibrium solution to (A3.2) with $X_2 = 0$ to be stable. A similar argument shows that the equilibrium solution with $X_3 = 0$ is also stable in these circumstances, so that either squid or seals (depending on the initial conditions) will go to extinction if condition (A3.17) holds. (Essentially this is a form of competitive exclusion between the two predators. Note that this result is independent of the values of F_1 and F_3; accordingly, it holds also for the unexploited system.)

Since the model specified by Equations (A3.1) is attempting to represent a real situation in which anchovy, squid and seals can coexist, the region of parameter space defined by inequality (A3.17) must be regarded as unfeasible, in order that the continued existence of both squid and seals may be maintained. In other words, a realistic value of β must be fairly small, corresponding to seals being relatively inefficient at catching anchovy directly. Hence the man–seal–squid–anchovy system of Fig. 4 as modelled by Equations (A3.1) is such that *decreasing* the seal numbers will *reduce* the potential sustainable harvest rate for anchovy.

It should be noted that the above argument is an equilibrium argument, relating to *eventual* outcomes. In the short term, reducing seal numbers may (depending on the parameter values) allow anchovy harvest rates to increase *until* the squid population has had time to respond to decreased predation pressure—a time scale perhaps in the neighbourhood of 3 years. Further, Equations (A3.1) assume the predator populations to be limited by food; if space limitation is locally the dominant control mechanism (as might be argued for seals), different conclusions may result.

Appendix 4
Feasibility analysis of an experiment to determine empirically the effect on anchovy of reducing the seal population

Consider the following idealised experiment to take place over a period of n years. For the first $n/2$ years, the seal population is held fixed at its present level, and the biomass of spawning anchovy is measured by survey each year. After that time the seal population is halved, and maintained at this new level for the remaining $n/2$ years, while the biomass of spawning anchovy continues to be monitored. The combination of direct (e.g. seals eat anchovy) and indirect (e.g. seals eat squid which eat anchovy) effects of seals on the anchovy population is to be assessed by comparing the estimates of mean anchovy spawning biomass over the two experimental periods.

In the present model for the South African anchovy resource,[18] annual recruitment (R_i) is assumed to be log-normally distributed about a modal value $\tilde{R}$:

$$R_i = \tilde{R} \, e^{\epsilon_i} \qquad \epsilon_i \text{ from } N(0,\sigma^2) \text{ with } \sigma = 0{,}4. \tag{A4.1}$$

Ageing studies and length distribution data indicate that the spawning stock consists of 3 year-classes. Assuming for simplicity that annual harvests (this is essentially a recruit fishery, with catches dominated by 0-year-old anchovy) are proportional to R_i, it follows that

$$B_i \propto e^{\epsilon_i} w_1 e^{-M} + e^{\epsilon_{i-1}} w_2 e^{-2M} + e^{\epsilon_{i-2}} w_3 e^{-3M} \tag{A4.2}$$

where B_i = end-of-year spawning biomass; M = natural mortality rate for anchovy; and $w_1/w_2/w_3$ = mass of 1/2/3-year-old anchovy.

These parameters are estimated[18] to have values $w_1 = 13{,}3$ g, $w_2 = 17{,}9$ g, $w_3 = 21{,}6$ g and $M = 1{,}12$ yr^{-1}, from which the coefficient of variation of year-to-year anchovy spawning biomasses may be calculated to be

$$\text{c.v. } (B) = 0{,}286. \tag{A4.3}$$

The present shipboard hydroacoustic surveys of the biomass of spawning anchovy are providing relative estimates with a coef-

ficient of variation (from sampling and inter-annual calibration effects) approaching 18% (from data in Hampton[28]). Assuming a similar survey effort during the idealised experiment, the observed coefficient of variation of spawning biomass would then be

$$\text{c.v. } (B_{\text{obs}}) = \sqrt{(0{,}286^2 + 0{,}18^2)} = 0{,}338. \tag{A4.4}$$

Thus the precision of the estimate of mean spawning biomass over the first $n/2$ years of the experiment would be

$$\text{c.v. } (\bar{B}'_{\text{obs}}) = 0{,}338 \sqrt{(2/n)}. \tag{A4.5}$$

Seals are estimated to account for 6% of the natural mortality of anchovy, so that assuming the simplest form of interaction means that halving the seal population would reduce M by 3%:

$$M' = 0{,}97\, M = 1{,}086 \text{ yr}^{-1}. \tag{A4.6}$$

From Equation (A4.2), this would correspond to a 5,2% increase in mean spawning biomass. How long would the experiment need to run for a change of this magnitude to be detectable at a 5% significance level?

For the second $n/2$ year period, similar calculations to those above yield

$$\text{c.v. } (\bar{B}'_{\text{obs}}) = 0{,}335 \sqrt{(2/n)}, \tag{A4.7}$$

so that

$$\text{s.e. } (\bar{B}'_{\text{obs}} - \bar{B}_{\text{obs}}) \simeq 0{,}337 \sqrt{(4/n)}\, \bar{B}_{\text{obs}}. \tag{A4.8}$$

Detecting a change at the requisite significance level thus requires

$$1{,}96 \times 0{,}337 \sqrt{(4/n)} \leqslant 0{,}052$$
$$\text{i.e. } n \geqslant 645. \tag{A4.9}$$

Thus this analysis indicates that an experimental period of about 650 years would be required for an empirical determination of the effect of changing seal numbers on the anchovy resource. Further, it should be stressed that this estimate is based on idealised and over-optimistic assumptions; in practice neither could the seal numbers be held exactly fixed, nor would other ecosystem influences on the seals and anchovy remain constant. Such effects would tend to increase variation in B_{obs} and hence lengthen the experimental period required.

[With tongues slightly in cheek, two of the authors have suggested Marine Ecosystem analogies of Heisenberg's uncertainty principle from physics and Gödel's incompleteness theorem from mathematics:

'Bergh's Uncertainty Principle': Certain hypotheses about marine ecosystems are untestable because the level of sampling required for the precision necessary for the test would greatly perturb the system.

'Butterworth's Incompleteness Principle': Certain hypotheses about marine ecosystems are untestable because the length of the data time-series required for the precision necessary for the test is unrealistically great ($\geqslant 50$ years).

The result of the feasibility analysis above is a ready demonstration of the second of these two 'principles'. The authors question whether sufficient attention is being given to consistency with these two 'principles' in the design and review of research projects on marine ecosystems in South Africa.]

Appendix 5
Calculation of the amount of anchovy production lost annually to natural mortality

An estimate of the median unexploited anchovy spawning biomass, $\tilde{K}$, is 1 706 000 tons.[18] Using the model of anchovy dynamics described in Appendix 4, the corresponding recruitment level, $\tilde{R}$, is given by

$$\tilde{R} = \frac{\tilde{K}}{(w_1 e^{-M} + w_2 e^{-2M} + w_3 e^{-3M})} \tag{A5.1}$$

where the parameters are as defined in Appendix 4.

The instantaneous loss of individuals from age class j to natural mortality in the absence of fishing, $dN_j(t)/dt$, is (by definition of M) proportional to cohort size:

$$\frac{dN_j(t)}{dt} = -MN_j(t). \tag{A5.2}$$

In this notation t runs from 0 to 1 only, so that $N_j(t)$ is the size of a cohort t years after it was j years old. At $t = 1$, j is increased by one. The annual harvest is taken essentially from the $j = 0$ age class, and without serious loss of accuracy the annual harvest is assumed to occur in the middle of the year ($t = 0{,}5$). Losses to natural mortality in the first year are calculated from two integrations, before and after the annual harvest. Let $P_j(t_1 \to t_2)$ represent the number of individuals lost from the j-th age class between the times t_1 and t_2 in any year. Then

$$P_j(t_1 \to t_2) = \int_{t_1}^{t_2} MN_j(t)\, dt. \tag{A5.3}$$

Since $N_j(t) = N_j(0)e^{-Mt}$ in the absence of fishing,

$$P_j(t_1 \to t_2) = N_j(0)(e^{-Mt_1} - e^{-Mt_2}). \tag{A5.4}$$

Before the annual harvest, losses by number are (setting $N_0(0) = \tilde{R}$)

$$P_0(0 \to 0{,}5) = \tilde{R}(1 - e^{-M/2}). \tag{A5.5}$$

Let the annual harvest (by mass) be C. Then $N_0(0{,}5)$ is equal to $Re^{-M/2} - C/w_c$, where w_c is the mean mass of an anchovy in the catch. Losses to natural mortality in the six months after the harvest are therefore

$$P_0(0{,}5 \to 1) = (\tilde{R}e^{-M/2} - [C/w_c])(1 - e^{-M/2}). \tag{A5.6}$$

Total numbers lost to natural mortality are converted to mass by multiplying by w_c (roughly equal to the mid-year mass) for the recruiting age class. Thus

$$
\begin{aligned}
P_0^m(0 \to 1) &= w_c\tilde{R}(1 - e^{-M/2}) + \\
&\quad w_c(\tilde{R}e^{-M/2} - [C/w_c])(1 - e^{-M/2}) \\
&= w_c R(1 - e^{-M}) - C(1 - e^{-M/2}),
\end{aligned} \tag{A5.7}
$$

where $P_j^m(t_1 \to t_2)$ is the mass of anchovy from age class j which is lost to natural mortality between times t_1 and t_2 in the year. Similarly,

$$P_1^m(0 \to 1) = \tfrac{1}{2}(w_1 + w_2)(\tilde{R}e^{-M/2} - C/w_c)e^{-M/2}(1 - e^{-M}) \tag{A5.8}$$

$$P_2^m(0 \to 1) = \tfrac{1}{2}(w_2 + w_3)(\tilde{R}e^{-M/2} - C/w_c)e^{-3M/2}(1 - e^{-M}) \tag{A5.9}$$

$$P_3^m(0 \to 1) = w_3(\tilde{R}e^{-M/2} - C/w_c)e^{-5M/2} \tag{A5.10}$$

(assuming that anchovy growth in mass after age 3 years is minimal, and that anchovy do not attain 4 years of age). The parameter estimates are[18]: $w_c = 6{,}82$ g; $w_1 = 13{,}3$ g; $w_2 = 17{,}9$ g; $w_3 = 21{,}6$ g; $M = 1{,}12$ yr^{-1}.

Using a typical annual catch (C) of 300 000 tons, the total average annual loss to natural mortality is estimated by Equations A5.7 – 10 to be 1,93 million tons.

[Note: The estimate for K above was made before data from the November 1986 survey of anchovy spawning biomass became available. This survey provided a biomass estimate substantially higher than those for the previous two years. Taking these additional data into account would lead to an increased estimate of $\tilde{K}$, and also of the average annual loss of anchovy to natural predation.]