

# Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem

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## Summary

1. A method for finding the consequences of long-term generalized press perturbations in multispecies ecological communities, with relatively modest requirements for data, is explicated. The approach uses energetic and allometric reasoning to set some parameter values for which data are not available. The remaining unknown parameters are treated as random variables, enabling the calculation of probability distributions for the outcomes that are of interest.

2. The method is used to investigate the effect of a cull of fur seals on fisheries in the Benguela ecosystem, using a 29-species foodweb for that system. In the case of Cape fur seals treated here, it is found that a cull of seals is more likely to be detrimental to total yields from all exploited species than it is to be beneficial.

3. The influence of weak links on the effects of a cull is investigated. Using both consumption by each species and consumption of each species to define link strength, a clear threshold in link strength is found, indicating that 44% of all links could be deleted from the foodweb without affecting the predictions significantly. Even using a criterion based on consumption by each species alone (conventional dietary proportion data), about the same number of links can be deleted without seriously affecting the predictions of the model. This is a very helpful (and encouraging) result for the design of an observational protocol for systematic efforts to gather data for multispecies modelling.

*Key-words:* food web, indirect effect, mathematical model, perturbation experiment.

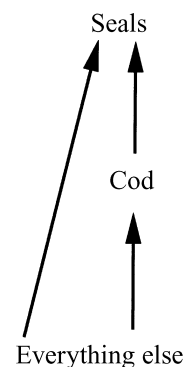
*Journal of Animal Ecology* (1998), **67**, 635–658

## Introduction

Marine mammals are present in the waters utilized by many of the world's major marine fisheries, where they frequently are regarded as pests and their presence is seen as detrimental to the fishery. In part, this is due to operational interactions, in which marine mammals damage or become entangled in fishing gear (Anonymous 1981), but it has been claimed repeatedly that there are significant ecological interactions as well. In the basic argumentation ('surplus yield calculation'), the system is conceived of as in Fig. 1, in which the 'target species' is the particular commercial fish species of interest. The argument runs: we harvest the target species; marine mammals eat the target species; if marine mammal populations are reduced by some amount  $X$ , then we can increase our harvest by the amount those  $X$  marine mammals would have eaten, without any net decrease in target species stock.

Much of the controversy surrounding these claims has revolved around the question of how much fish marine mammals in fact consume (for instance, Bed-

dington, Beverton & Lavigne 1985; Anonymous 1981, 1991, 1992, 1994). Another debate has followed from the recognition that the system sketched in Fig. 1 is actually embedded in a more complex web of interactions, which may affect the outcome (Lavigne 1995); for instance, an international workshop convened in Cape Town (Anonymous 1991) reached the con-



**Fig. 1.** A foodweb for the Benguela ecosystem.

clusion that, at the very least, one needs to take into account the interactions sketched in Fig. 2 (for the particular case of Cape fur seals [*Arctocephalus pusillus pusillus* (Schreber)] and the hake (*Merluccius capensis* Castelnau, and *Merluccius paradoxus* Franca) fishery in the Benguela ecosystem). A subsequent analysis based on this view of the system (Punt & Butterworth 1995) concluded that any benefit to the hake fishery caused by a reduction in fur seal stocks would be small compared to the surplus yield calculation.

However, Fig. 2 oversimplifies as well; for instance, the Benguela ecosystem is at least as complex as the foodweb shown in Fig. 3 (modified from Field *et al.* 1991). There are many paths of influence (at least 28 million) from seals through this foodweb to hake. While most ecologists would assert that all but the most direct of these can safely be ignored (thus legitimizing the use of some simplified foodweb such as Fig. 2), such an assertion is baseless until an analysis is carried out that does not adopt it as an *a priori* assumption.

This study will investigate the effects on fisheries of a cull of fur seals in the Benguela ecosystem, as depicted in Fig. 3. Thus, one way to read this paper is as a further contribution to the ongoing discussion of the interaction between marine mammals and fisheries. Another way to read it is as a demonstration of a novel methodology with a wide range of applicability to problems, both practical and theoretical, involving multispecies interactions. The approach has relatively modest requirements for data, namely: dietary proportions, population biomasses, and typical individual biomasses for all species in the system.

There are numerous situations like that in the Beng-

uela, in which, for practical reasons, one needs to have some notion of the probable outcomes of manipulations that affect many species. Because of limitations imposed by spatial and temporal scales, as well as the inherent indeterminacy of outcomes of multispecies manipulations (Yodzis 1988), in many of these systems an experimental approach is impracticable. In the realm of 'pure' (as opposed to 'applied') ecology as well, experimental ecologists have called for a theory that is capable of predicting the outcomes of experimental manipulations (Paine 1988). These researchers generally are interested in the consequences of complete removals of species from a system, but it is at least a start to be able to cope with relatively small perturbations, as is the case here.

One may explicate this wider context as follows. Consider any system of many interacting entities that can be viewed as state variables in the sense of dynamical systems theory. (Typically the state variables will be population densities, but they could also include nutrient concentrations, toxin concentrations, or other quantities of interest.) Suppose the system has a stable equilibrium. (This assumption is discussed at the end of the Model section.) A *generalized press perturbation* is an experiment of the following form: (i) measure the equilibrium values of one or more state variables of interest; (ii) change the numerical values of one or more parameters in the system to new values, and hold them at those new values long enough for the system to reach a new equilibrium [the *perturbation*]; (iii) measure the new values of the state variables of interest. The difference between measurement (iii) and measurement (i) is the *response* to the perturbation.

The adjustment of quotas in an exploited system

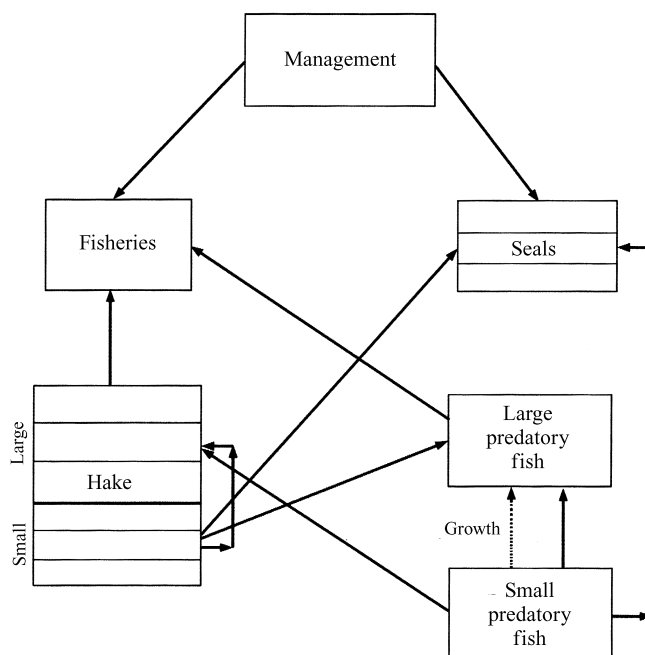


Fig. 2. Another foodweb for the Benguela ecosystem (Anonymous 1991).

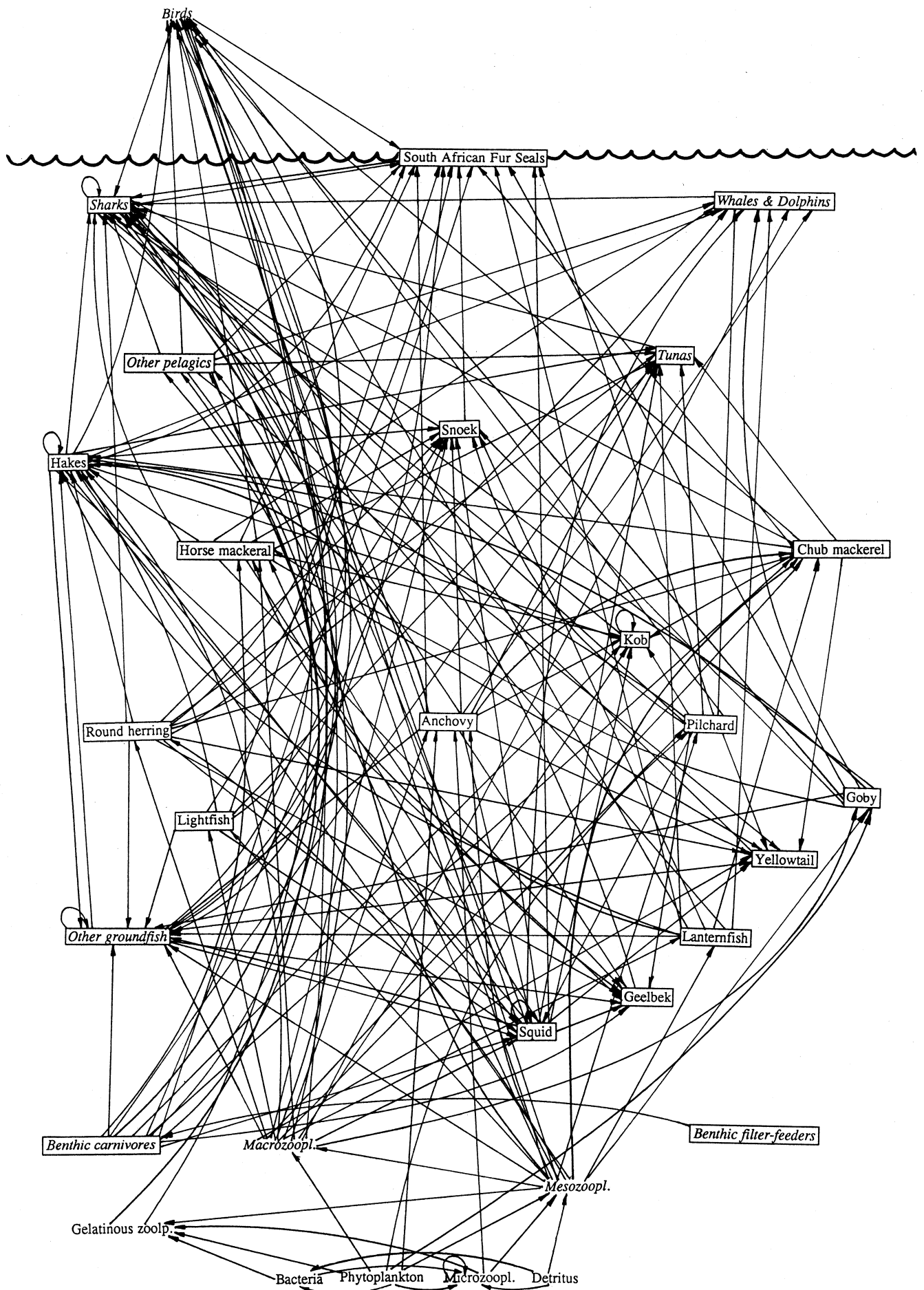


Fig. 3. Another foodweb for the Benguela ecosystem (modified from Field *et al.* 1991).

may be viewed as such an experiment; as may addition/removal experiments in field ecology, changes in the rate of discharge of toxic substances into an ecological community (be it intentionally or unwittingly), and many other manipulations of practical interest. In any such 'experiment', the very same issue arises that has been discussed above in connection with the interaction of marine mammals and fisheries: what is the role of complex multispecies interactions? Thus, the case study presented here may have very wide ramifications in both pure and applied ecology.

The root issue is something one might call *locality* of interactions in the foodweb. Do we really need to take into account all the pathways of influence, even quite long ones, through a foodweb such as that in Fig. 3? In order to understand generalized press perturbations in a system such as Fig. 3, can we manage with some simplified foodweb such as Fig. 2, or even Fig. 1? More or less equivalently, what is the relative role of direct and indirect effects in this context (Abrams *et al.* 1996)? The following case study suggests that, at least in some systems, responses to generalized press perturbations may involve highly *non-local* interactions: many pathways of influence, nonviability of highly simplified foodwebs, important indirect effects.

### The model

There are many kinds of interactions among the species in an ecological community, but by far the most conspicuous, and arguably the most crucial, are the *trophic* interactions among predators and their prey. The viewpoint adopted here, which one may call *trophodynamics*, is to ignore all interspecific interactions other than these. This is a bold simplification, but not an entirely unreasonable one for pelagic systems. Trophic interactions in the Benguela ecosystem are summarized by the foodweb in Fig. 3. While, admittedly, still a vast simplification of the actual Benguela foodweb, this version is moderately well resolved taxonomically, and is relatively consistent in its treatment of the various taxonomic groups, as befits the outcome of a group endeavour to use data from a long-term, intensive project to produce the most reasonable summary of the whole system (Field *et al.* 1991).

Little or nothing can be concluded about the responses to generalized press perturbations from the foodweb itself. In order to reach such conclusions, a dynamical model must be associated with the foodweb. However, to avoid overcomplication (and the risk of losing touch with attainable requirements for data), something needs to be traded off in return for the increased detail in terms of foodweb complexity relative to other modelling approaches such as those of Figs 1 and 2. Therefore, size or age structure will not be included: each population will be characterized by one number, total biomass. Additionally,

no extrinsic variation of any kind will be included. Another approximation in the model is to neglect the dynamics of detritus and nutrient recycling. Therefore the compartment 'detritus' in the foodweb of Fig. 1 is ignored, and the 'benthic filter feeders' are assigned a carrying capacity.

The model associates with the foodweb of Fig. 3 a system of differential equations of the form:

$$\frac{dW_i}{dt} = r_i W_i \left(1 - \frac{W_i}{K_i}\right) - \sum_k F_{ik} W_k - H_i \equiv g_i \quad \text{eqn 1}$$

for each basal species *i* (those that have no prey), and

$$\frac{dW_i}{dt} = [-T_i + \sum_k (1 - \delta_k) F_{ki} - I_i] W_i - \sum_k F_{ik} W_k - H_i \equiv g_i \quad \text{eqn 2}$$

for each nonbasal species *i*, where  $W_i$  = population biomass of species *i*,  $r_i$  = intrinsic rate of growth of species *i*,  $K_i$  = environmental carrying capacity for species *i*,  $T_i$  = mass specific rate of respiration for species *i*,  $\delta_i$  = fraction of ingested energy lost to excretion by species *i*,  $F_{ki}$  = biomass of species *k* ingested by species *i* per unit time per unit biomass of species *i*,  $I_i$  = per capita influence of intraspecific interference *not* associated with feeding and  $H_i$  = harvest rate of species *i*. The form of these equations, particularly the above interpretation of the symbols, generalizes to the multispecies context a family of energy-based consumer-resource models (Yodzis & Innes 1992).

The quantities  $r_i$ ,  $K_i$ ,  $T_i$ ,  $\delta_i$ , are parameters that take on (at least to a reasonable approximation) fixed numerical values. The population biomasses  $W_i$  are functions of time. The harvest rates  $H_i$  are extrinsically driven functions of time, which will be taken as constant in this modelling exercise (see below). The functions  $I_i$  express the per capita effect of intraspecific interference *not* associated with feeding. (Intraspecific interference associated with feeding is incorporated in the functions  $F_{ki}$ .) It will be assumed that  $I_i$  is a function of  $W_i$  only. The functional response  $F_{ki}$  is a function of the biomass  $W_k$ , possibly of the biomass  $W_i$ , and also, possibly, of the biomasses of all other prey species of species *i*. It need not be linear in any of these arguments: these functions are permitted (and expected) to be highly nonlinear, complicated functions of their many arguments. This is *not* a Lotka–Volterra model!

One reason why the model is based on the consumer-resource models of Yodzis & Innes (1992) is that their framework includes estimates for some of the parameters of the model in terms of allometric relations involving individual body size. This is an important consideration in a model that involves so many parameters as this one does. We can, with Yodzis and Innes, write:

$$r_i = a_i m_i^{-0.25} \quad \text{eqn 3}$$

$$T_i = a_T m_i^{-0.25} \quad \text{eqn 4}$$

$$F_{ki} = p_{ki} f_{ji} a_j m_i^{-0.25} \quad \text{eqn 5}$$

where  $m_i$  = typical adult individual body mass for species  $i$ ,  $a_r$ ,  $a_T$ ,  $a_j$  = allometric coefficients, typifying broad classes of animals,  $p_{ki}$  = proportion of the diet of species  $i$  that comes from species  $k$ ,  $f_{ji}$  = fraction of physiologically maximal ingestion realized by species  $i$ . The meaning of these equations is discussed by Yodzis & Innes (1992).

The above set of 29 coupled, nonlinear differential equations is an immensely complex mathematical system, the analysis of which requires further simplification. In this paper, two further simplifying assumptions are made, which, in the author's view, do not take us overly far from the natural system in the Benguela Current. These assumptions are: *local* perturbations (which will be discussed under Local dynamics and perturbations) and *equilibrium* dynamics.

It is well known that even very simple systems of coupled nonlinear differential equations can have very complex dynamics, including chaos, and some researchers have argued that nonequilibrium dynamics may be common in nature (Wiens 1989; Hastings 1996). On the other hand, many observed systems of interacting species seem to exhibit equilibria. In an example not so very far removed from the system at hand—another rich, exploited marine system, the Barents Sea—Yodzis (1997a) has obtained good fits to observed time series for exploited stocks using a system of differential equations that, when the harvest rates are held constant, show equilibrium behaviour. In that case, the fluctuations in stock sizes can be viewed as being due primarily to variations in harvest rates, modulated through nonlinear population interactions.

Thus, a very great simplification of the system here can be achieved by taking the harvest rates  $H_i$  to be constant in time, at values that typify the variable harvest rates suffered by the actual system. Additionally, all parameters, including the carrying capacities  $K_i$ , will be taken to be constant in time. This means that extrinsically driven variation is neglected, including seasonality—the weakest assumption, for the Benguela system is highly seasonal. But it seems incredibly unlikely that to caricature the system in this way would have a significant effect on the root issue under investigation, namely the relevance of complex multispecies effects. It may well be expected that the responses to perturbations would be of similar magnitude whether the harvests and parameters were constant or fluctuating. Mathematically, the constancy assumption makes the dynamical equations autonomous and opens up a huge body of theory for their analysis. Furthermore, the equations are assumed to possess stable equilibria. Again, one would hardly expect that perturbations around a time-varying solution would differ significantly from those around a

constant solution, particularly with regard to the role of complex multispecies effects, and the equilibrium assumption opens up an even larger body of theory for use.

## Statics

Under the assumption of equilibrium dynamics, constraints on the parameters can be obtained that involve only *point estimates* of those complicated multivariate functions  $F_{ki}$ . Namely, let  $W_i^e$  represent the equilibrium biomasses. Then using eqns 3–5 in the right-hand-sides of eqns 1 and 2, and setting those right-hand-sides equal to zero, we find:

$$a_r m_i^{-0.25} W_i^e \left(1 - \frac{W_i^e}{K_i}\right) - \sum_k p_{ik} f_{jk} a_j m_k^{-0.25} W_k^e - H_i = 0 \quad \text{eqn 6}$$

for each basal species  $i$ , and

$$[-a_T m_i^{-0.25} + \sum_k (1 - \delta_k) p_{ki} f_{ji} a_j m_i^{-0.25} - I_i(W_i^e)] W_i^e - \sum_k p_{ik} f_{jk} a_j m_k^{-0.25} W_k^e - H_i = 0 \quad \text{eqn 7}$$

for each nonbasal species  $i$ .

In order to make the best use of these equations, let us consider what we know about the parameters, and what we might hope to know. The harvests  $H_i$  can be estimated from available data on catches (Field *et al.* 1991). The study by Field *et al.* (1991) includes estimates for the dietary proportions  $p_{ki}$ . The parameters  $a_r$ ,  $a_T$ ,  $a_j$ ,  $\delta_i$  have been estimated from data surveys (Yodzis & Innes 1992). Individual body masses  $m_i$  are relatively easy to measure. The numbers  $I_i(W_i^e)$  and  $f_{ji}$  are incredibly difficult to estimate, as are the carrying capacities  $K_i$ . Population biomass data are difficult but not impossible to obtain.

In short, we can hope, with varying degrees of confidence, to estimate everything in eqns 6, 7 except  $I_i(W_i^e)$ ,  $f_{ji}$ , and  $K_i$ . The next section discusses those estimates.

## Data

### DIETS

Field *et al.* (1991) contains dietary proportion data for all species in the foodweb of Fig. 1 except goby (*Sufflogobius bibarbatus* Smith). Presence/absence trophic data for goby, as predator and as victim, were obtained from the following sources: Crawford (1987); Crawford, Shannon & Pollock (1987); David (1987); Payne, Rose & Leslie (1987); Berruti, Adams & Jackson (1989); Payne, Crawford & van Dalsen (1989); Adams, Seddon & Van Heezik (1992); Sekiguchi, Klages & Best (1992); Smale (1992); Wilson (1992). However, quantitative data on proportions in the diet could not be found in the literature. Since goby are intermediate in size between anchovy (*Engraulis*

*capensis* Gilchrist) and pilchard [*Sardinops ocellatus* (Pappe)], and similar in their ecology (Dr R. Winterbottom, Royal Ontario Museum, personal communication), it was decided to assign them proportions intermediate between those of anchovy and pilchard, where prey or predators were shared. The resulting dietary proportions are listed in Appendix 1, with prey in rows and predators in columns. The parameter  $p_{ki}$  is the number in row  $k$  and column  $i$ , divided by the sum of the numbers in column  $i$ .

#### HARVESTS

Field *et al.* (1991) give harvest data for all exploited species in the system, from 1977 to 1989. For the constant harvest rates  $H_i$  used in the model, the average annual harvest over the years 1987–89 was used. These numbers are listed in Appendix 2.

#### BODY MASSES

Typical adult body masses  $m_i$  were obtained from published sources or from discussions with knowledgeable colleagues. The results are listed in Appendix 3. The length data in Smith (1977) were converted to masses by using weight–length relationships for North American fishes which appeared similar in morphology. For ‘whales and dolphins’, the single most abundant species, the common dolphin (*Delphinus delphis* L.), was used. For ‘birds’, an average was taken over the body masses of the jackass penguin [*Spheniscus demerus* (L.)], the Cape cormorant (*Phalacrocorax capensis* Sparrman), and the Cape gannet [*Morus capensis* (Lichtenstein)].

#### POPULATION BIOMASSES

These were the most difficult data to obtain, and the numbers used must be considered rough approximations. The numbers are listed in Appendix 4 (the numbers in parentheses will be explained in the following section). The sources for these numbers were a combination of articles in the literature, allometry, plausible guesses and wild guesses. For ‘whales and dolphins’, the single most abundant species, the common dolphin, was used. For ‘birds’, the sum of the population biomasses of the jackass penguin, the Cape cormorant, and the Cape gannet was used.

#### INTRINSIC POPULATION GROWTH RATES

Allometric relationships based on body size (Yodzis & Innes 1992) gave  $22.49 \text{ year}^{-1}$  for  $r_{\text{phytoplankton}}$  and  $2.91 \text{ year}^{-1}$  for  $r_{\text{benthic filter feeders}}$ . The value for  $r_{\text{phytoplankton}}$  is not far from the value  $25 \text{ year}^{-1}$  considered typical for upwelling areas by Whittaker & Likens (1975).

#### Remaining parameter estimates

Now we may take up the discussion where we left off at the end of the section on Statics. Using the numbers obtained as above, we know everything in eqns 6 and 7 except  $I_i(W_i^e)$ ,  $f_{ji}$  and  $K_i$ . For given values of  $I_i(W_i^e)$ , eqns 7 are a system of 27 linear equations for the 27  $f_{ji}$ ; then putting those values into eqns 6, the two carrying capacities  $K_{\text{phytoplankton}}$  and  $K_{\text{benthic filter feeders}}$  are determined. There is room for some experimentation here. Since they are fractions,  $f_{ji}$  must lie between 0 and 1. There are no values for  $I_i(W_i^e)$  that produce values for  $f_{ji}$  which obey this constraint.

Of all the parameter estimates above, by far the least reliable are the biomasses  $W_i^e$ . Therefore, the biomasses were adjusted, by a process of trial and error, until  $f_{ji}$  in the interval (0,1), and positive  $K_i$ , were obtained with  $I_i(W_i^e) = 0$  for all  $i$ . A set of ‘adjusted biomasses’ that accomplish this are listed in Appendix 4, in parentheses. The corresponding values for  $f_{ji}$  and  $K_i$  are listed in Appendix 5.

#### Local dynamics and perturbations

We now have a reasonable set of parameter estimates that describes the *static* behaviour of our system—essentially an energy budget. But this in itself does not *imply* anything. In order to investigate *dynamics*, including the results of perturbations such as a fur seal cull, something needs to be known about the functional forms of the functional responses. If we restrict ourselves to *local* dynamics—in a sufficiently small neighbourhood of equilibrium, corresponding to sufficiently small perturbations—then the dynamics are governed by the Jacobian matrix

$$A_{ij} = \left[ \frac{\partial g_i}{\partial W_j} \right]_e \quad \text{eqn 8}$$

where  $g_i$  are the right-hand-sides of eqns 1 and 2, and the derivatives are evaluated at equilibrium. In particular, the Jacobian determines the outcomes of sufficiently small long-term press perturbations through the relationship:

$$\frac{\partial W_i^e}{\partial H_j} = (A^{-1})_{ij} \quad \text{eqn 9}$$

For more details about press perturbations, see Yodzis (1989, Chapter 7, 1996).

The results found here apply, then, to culls that are sufficiently small. It is very difficult to know how small is sufficiently small in any given instance. If we think of plotting the size of the response vs. the size of the cull, then the number we are calculating is the slope of that relationship at the origin. If the relationship is linear or nearly so, then our results can be extrapolated to quite ‘large’ culls. Even if the results apply only to very ‘small’ culls, they can still serve as a

testing ground for one's preconceptions as to possible effects of a cull.

In order to work out the Jacobian matrix, we need to know the *first derivatives* of those complicated multivariate functions  $F_{ki}$ , and of the functions  $I_i$ . It was felt that we do not know enough about these functions to assume some concrete functional form, so instead, the derivatives were treated as random variables, forming a basis for probabilistic prediction. There are three families of derivatives.

#### RESPONSE OF CONSUMPTION TO RESOURCE ABUNDANCE

The derivatives  $\partial F_{ki}/\partial W_k$  correspond to the familiar univariate functional responses of elementary predator-prey theory. They may be scaled quite naturally as follows:

$$\frac{\partial F_{ki}}{\partial W_k} = q_{3i} \frac{F_{ki}}{W_i} \quad \text{eqn 10}$$

where  $q_{3i}$  are random variables. The point of writing it this way is that  $q_{3i} = 1$  corresponds to a linear functional response,  $q_{3i} < 1$  corresponds to a Holling type II functional response, and  $q_{3i} > 1$  corresponds to a Holling type III functional response.

#### RESPONSE OF CONSUMPTION AND OF NONCONSUMPTIVE INTERFERENCE TO CONSUMER ABUNDANCE

The derivatives  $\partial F_{ki}/\partial W_i$  measure the strength of intraspecific interference, associated with feeding, among members of species  $i$ . The derivatives  $dI_i/dW_i$  measure the change in nonconsumptive (not having to do with feeding) intraspecific interference with respect to population abundance. Two families of assumptions were made. In the first, intraspecific interference is associated entirely with feeding, in the second, it is associated entirely with activities other than feeding.

For intraspecific interference that is associated with feeding, it was felt sensible to scale the derivatives in comparison to the derivatives with respect to  $W_k$ , but rather than risk being tied to any one functional form, four classes of assumption were used, containing various combinations of quantities available:

Class 1:

$$I_i = 0; \quad \frac{\partial F_{ki}}{\partial W_i} = q_{1i} F_{ki} \frac{\partial F_{ki}}{\partial W_k} \quad \text{eqn 11}$$

Class 2:

$$I_i = 0; \quad \frac{\partial F_{ki}}{\partial W_i} = q_{1i} \frac{\partial F_{ki}}{\partial W_k} \quad \text{eqn 12}$$

Class 3:

$$I_i = 0; \quad \frac{\partial F_{ki}}{\partial W_i} = q_{1i} p_{ki} \frac{\partial F_{ki}}{\partial W_k} \quad \text{eqn 13}$$

Class 4:

$$I_i = 0; \quad \frac{\partial F_{ki}}{\partial W_i} = q_1 \frac{\partial F_{ki}}{\partial W_k} \quad \text{eqn 14}$$

where  $q_{1i}$  and  $q_1$  are random variables.

When consumer interference is associated entirely with activities other than feeding, the derivatives were treated in the spirit of eqn 10:

Class 5:

$$\frac{dI_i}{dW_i} = q_{4i} \frac{I_i}{W_i}; \quad \frac{\partial F_{ki}}{\partial W_i} = 0 \quad \text{eqn 15}$$

Class 6:

$$\frac{dI_i}{dW_i} = q_{4i} \frac{I_i}{W_i} \quad \text{if } i \text{ has no predators}$$

$$I_i = 0 \quad \text{for all other species}$$

$$\frac{\partial F_{ki}}{\partial W_i} = 0 \quad \text{eqn 16}$$

where  $q_{4i}$  are random variables. In Class 6, only top predators have consumer interference. Startlingly little is actually known about the distribution of consumer interference in nature, but one viewpoint sometimes expressed (for instance, T. Schoener, personal communication) is that top predators are more likely than other consumers to have strong intraspecific interference, because they are often territorial. The variables  $q_{4i}$  have to do with the *shape* of the function  $I_i$  at equilibrium: if  $I_i$  is a linear function of  $W_i$ , then  $q_{4i} = 1$ ; deviations of  $q_{4i}$  from 1 measure deviations of  $I_i$  from linearity. Of course, a linear per capita effect  $I_i$  corresponds to the conventional assumption of a quadratic effect of interference on the population growth rate itself.

#### RESPONSE OF CONSUMPTION TO ABUNDANCE OF OTHER RESOURCES

Depending upon how the animals forage, the consumption by species  $i$  of species  $k$  may depend upon the abundance of other prey species of  $i$ ; for instance, if other prey are more abundant, then species  $i$  may spend more time on those other species and less on  $k$ . This sort of effect is expressed in the derivatives  $\partial F_{ki}/\partial W_m$ , where  $m \neq k$  is another prey of  $i$ . The following form for the derivatives is scaled in such a way that  $q_{2i} < 1$  ensures a positive response of *total consumption* to an increase in abundance of any one resource species:

$$\frac{\partial F_{ki}}{\partial W_m} = -\frac{q_{2i}}{n-1} \frac{\partial F_{mi}}{\partial W_m} \quad \text{eqn 17}$$

where  $n$  is the number of resource species of consumer  $i$ .

For classes 5 and 6 we also need to specify random variables for the equilibrium values  $I_i(W_i^e)$  of per capita nonconsumptive interference. We expect these functions to increase as  $W_i$  increases. Additionally, there is more scope for interference in the dynamics if the intrinsic rate of population growth is larger. An upper bound on the intrinsic growth rate is given by  $(a_J - a_T)m_i^{-0.25}$ , where  $a_J$ ,  $a_T$  are the allometric coefficients in eqns 4 and 5 (Yodzis & Innes 1992). Therefore, in classes 5 and 6 we define the random variables:

$$I_i(W_i^e) = q_{1i}W_i(a_J - a_T)m_i^{-0.25} \quad \text{eqn 18}$$

There is insufficient information about the system to make definite predictions, but for any of the above six classes, we may define a *statistical universe of Benguela models* by specifying probability distributions for the random variables  $q$ . Within such a statistical universe we can calculate a *probability distribution*, conditional upon current knowledge of the system (with remaining ignorance expressed in the distributions for the random variables  $q$ ) for any result in which we might be interested, by means of Monte Carlo simulation: generate a random sample of models, do the calculation within each model, and look at the probability distribution of the results.

In the work reported here, the variables  $q$  were drawn from uniform distributions as follows:

$$q_{1i} \in (0, s_1)$$

$$q_{2i} \in (0, s_2)$$

$$q_{3i} \in (s_3, 1)$$

$$q_{4i} = 1.$$

Additionally, in classes 5 and 6 we need to impose the following two constraints on derived quantities, in order that a model be admitted to our statistical universe:

$$f_{ji} < 1, (A^{-1})_{ii} < 0 \quad \text{for all } i \quad \text{eqn 19}$$

The first of these is required because the quantities  $f_{ji}$  are fractions (eqn 5). This condition prevents the random variables  $q_{1i}$  from being generally too large. The matrix element  $(A^{-1})_{ii}$  is the response of the abundance of stock  $i$  to a continual removal of stock  $i$  (eqn 8). In order to ensure that no single  $q_{1i}$  is too big, we require that all of these responses be negative.

So, we have six classes of three-parameter families of statistical universes of Benguela models. Classes 1–4 have been discussed elsewhere (Yodzis 1994). It was found that in order to obtain stable Jacobian matrices, the self-damping parameter  $s_1$  had to be taken as implausibly large, so large that many of the consumer populations in the system would have absurdly large intrinsic growth rates at low abundance. A precisely analogous situation was found with a different mod-

elling approach (a global system of differential equations) to a different system (the Barents Sea). In that case, in order to obtain good fits to observed time series for population abundance, self-damping within the functional response had to be so large that population growth at low densities was ridiculously rapid, while self-damping in the manner of class 5 permitted good fits to observed time series together with reasonable growth rates at low abundance (Yodzis 1997a).

For classes 5 and 6, the constraints (19) keep  $s_1$  within biologically realistic bounds. Thus, reasonable values for  $s_1$  emerge from the model itself: if  $s_1$  is too small, stable Jacobian matrices will be highly unlikely; if  $s_1$  is too big, (19) will probably not be satisfied. It turns out that for class 6, it is not possible to satisfy simultaneously the two requirements of stable Jacobian matrices and the constraints (19), so, henceforth, we will discuss class 5 only.

### Signs of the responses to a cull of fur seals

If we cull seals at a fixed annual rate  $dH_{\text{seals}}$ , without any other changes in harvests, and wait for the stocks to re-equilibrate, then the change in stock  $i$  (difference between the new equilibrium value and the old) is:

$$dW_i^e = (A^{-1})_{i,\text{seals}} dH_{\text{seals}} \quad \text{eqn 20}$$

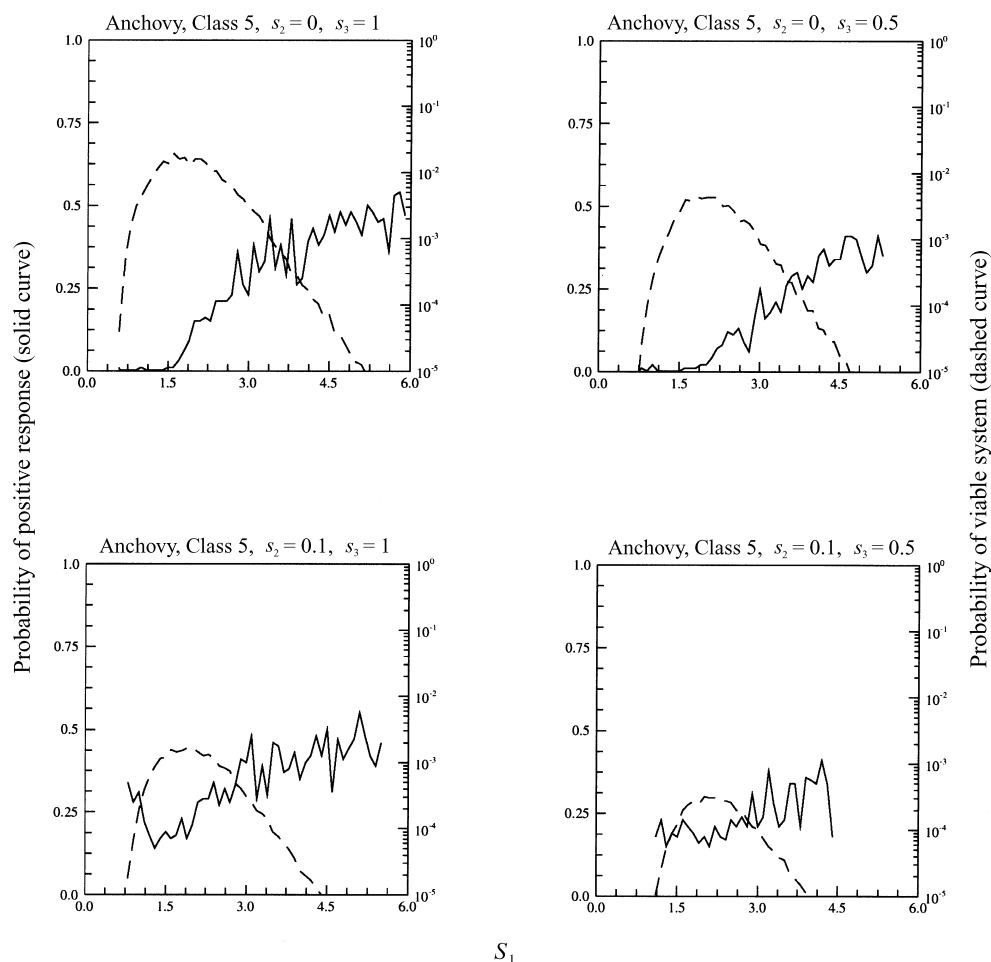
where  $A$  is the Jacobian matrix (8) at the original equilibrium (for instance, Yodzis 1989). If the species  $i$  of interest is eaten by seals, then one might expect an increase of the stock in response to a seal cull (that is the idea of the surplus yield calculation). However, it is well known (Levine 1976; Yodzis 1988; Stone & Roberts 1991) that counterintuitive responses to perturbations can occur in a system of interacting populations as complex as, or even far less than, our representation of the Benguela ecosystem (Fig. 3). This is because effects propagate over many pathways through the foodweb, with the cumulative effect being impossible to divine intuitively.

So, the first question we need to pose is whether commercial stocks in the Benguela system will increase or decrease in response to a cull of fur seals. Figures 4–6 summarize the outcomes for anchovy, horse mackerel (*Trachurus trachurus capensis* Castelnau), and hake, respectively. These species were chosen because they are prey of fur seals that span a wide range of trophic positions in the foodweb.

Each figure contains four graphs, which bracket extreme values of the parameters  $s_2$  and  $s_3$ . In the left column,  $s_3 = 1$  (linear responses to prey abundance), and in the right column  $s_3 = 0.5$  (type II functional responses). In the top row,  $s_2 = 0$  (no effect of other prey abundance on the functional response), while in the bottom row  $s_2 = 0.1$  (strong effect of other prey abundance).

Within each figure, each graph plots two probabilities against the parameter  $s_1$ , which measures the strength of intraspecific interference. The solid curve





**Fig. 4.** Probability of a viable system (dashed curve) and probability of a positive response of anchovy to a cull of fur seals, plotted against the self-damping parameter  $s_1$ . The two plots on the left are for type I functional responses, while the two plots on the right are for type II functional responses. The two upper plots have no 'other prey' effect in the functional response, while the two lower plots do have the 'other prey' effect.

is the probability of a positive response of the stock (that is, an increase in abundance) to a cull of fur seals. The dashed curve is the probability of a viable system—the probability of a stable equilibrium times the probability of satisfying the constraints (19)—given the specified random choices for the variables  $q$ .

Although all three species considered are prey of fur seals, so that 'low-dimensional', surplus yield thinking would lead one to expect a positive response to a cull, for two of the three species there is a significant probability of a negative response.

### Quantitative response to a cull

In this section not only the sign but also the magnitude of the response to a cull is calculated; specifically, (the probability distribution of) the gain to each fishery that can be achieved because of a cull, while maintaining stock levels, which is the response of practical interest. This gain will depend not only upon biological interactions, but also upon the fisheries management strategy employed. Two idealized strategies

will be considered. These strategies are not easy to accomplish in practice, but that is a separate issue from how the fishery would respond if it were possible and in fact if it were managed in this way.

**Management Strategy 1.** In response to a cull of fur seals, adjust the harvest of stock  $i$  so as to maintain the same biomass of that stock as before the cull. We require:

$$0 = dW_i^e = \frac{\partial W_i^e}{\partial H_i} dH_i + \frac{\partial W_i^e}{\partial H_s} dH_s$$

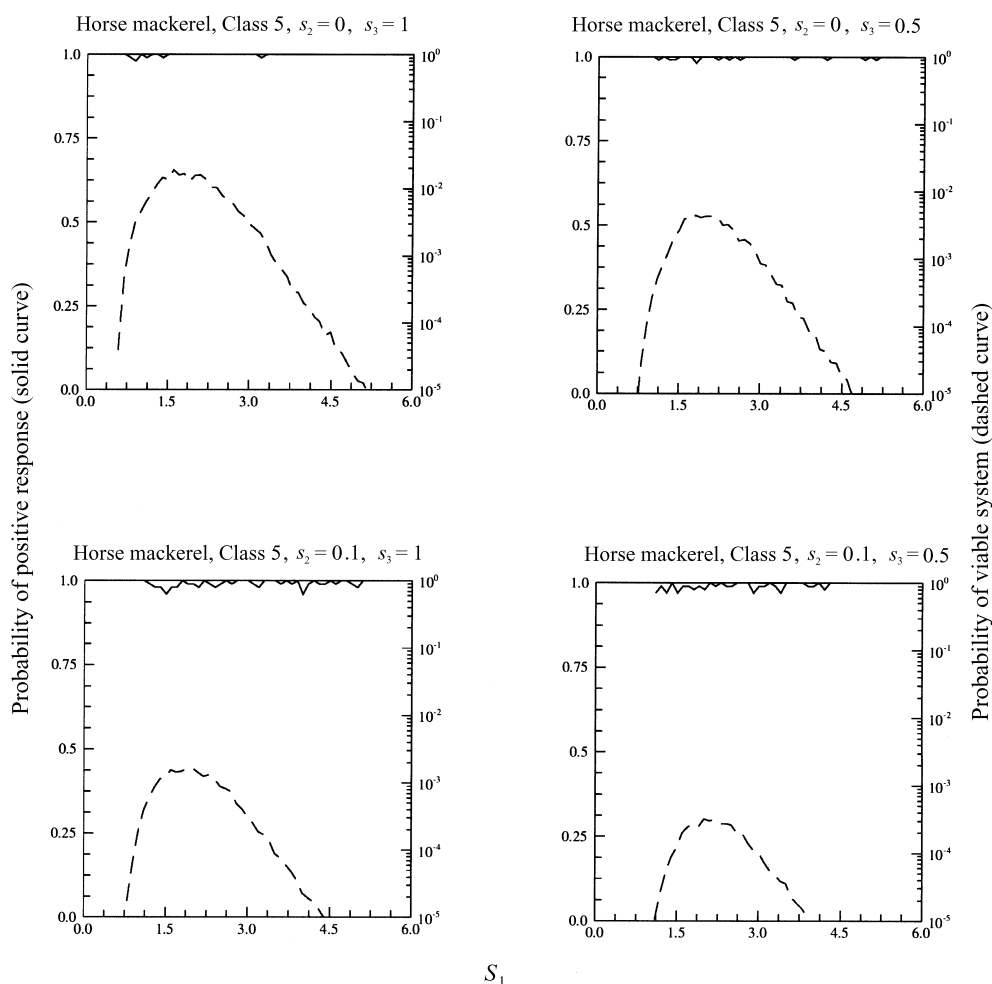
where the subscript  $s$  refers to seals. Furthermore:

$$dW_s^e = \frac{\partial W_s^e}{\partial H_i} dH_i + \frac{\partial W_s^e}{\partial H_s} dH_s$$

and these two equations imply, together with eqn 9:

$$dH_i = \frac{(A^{-1})_{is}}{(A^{-1})_{si}(A^{-1})_{is} - (A^{-1})_{ss}(A^{-1})_{ii}} dW_s^e \quad \text{eqn (21)}$$

**Management Strategy 2.** In response to a cull of seals, adjust the harvests of all exploited stocks so as to



**Fig. 5.** Probability of a viable system (dashed curve) and probability of a positive response of horse mackerel to a cull of fur seals, plotted against the self-damping parameter  $s_1$ . The two plots on the left are for type I functional responses, while the two plots on the right are for type II functional responses. The two upper plots have no 'other prey' effect in the functional response, while the two lower plots do have the 'other prey' effect.

maintain the same biomass of all exploited stocks as before the cull. In this case we need to solve the system of equations:

$$\sum_i \frac{(A^{-1})_{is}(A^{-1})_{sj} - (A^{-1})_{ss}(A^{-1})_{ij}}{(A^{-1})_{is}} dH_j = dW_s^e \quad \text{eqn 22}$$

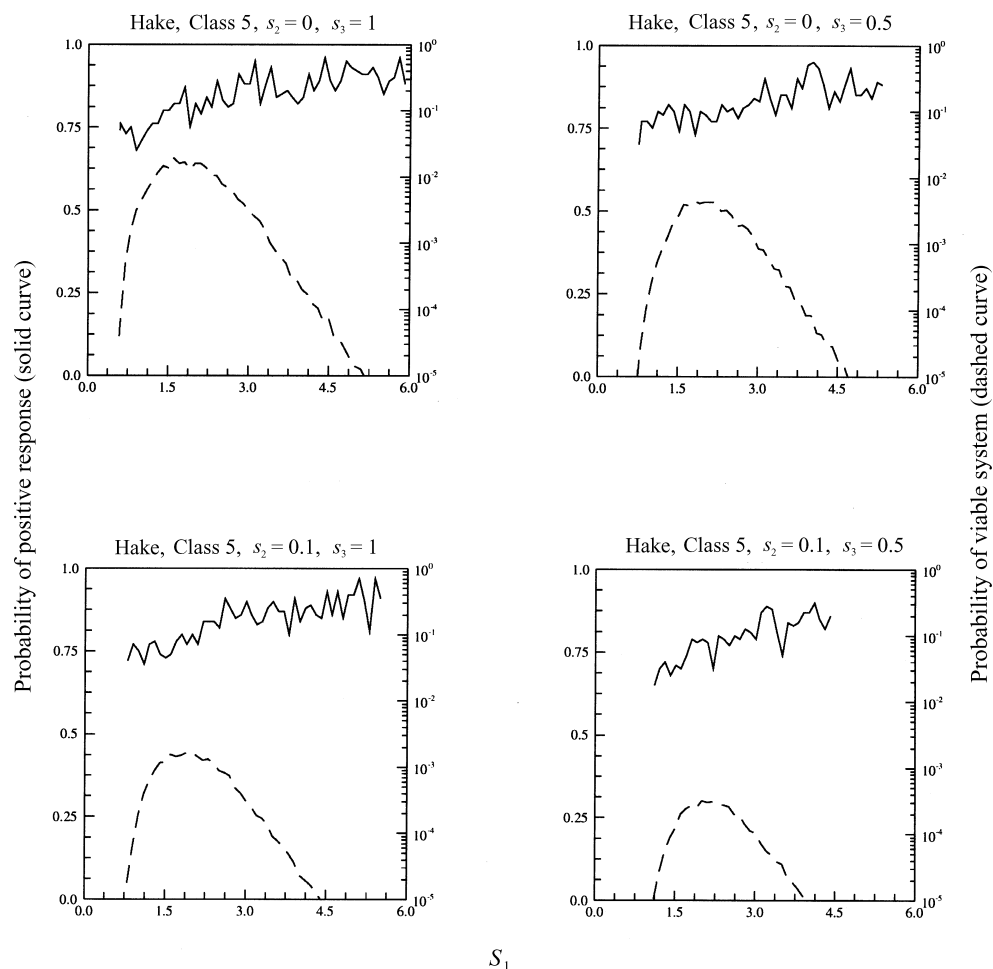
for the gains  $dH_j$  to all exploited stocks  $j$ . Here  $i$  ranges over the set of all exploited stocks, and the sum is over all exploited stocks  $j$ .

Using these relationships, it is possible to calculate probability distributions for the responses of interest within each statistical universe of Benguela models. These probability distributions are plotted, for Management Strategy 2, in Figs 7–10, which are for anchovy, horse mackerel, hake, and total biomass of all exploited species, respectively. Again there are four plots per figure, arranged as in Figs 4–6 so as to bracket extreme values of  $s_2$  and  $s_3$ , while  $s_1$  is fixed at the value 1.8, which is near the peaks in the viability curves in Figs 4–6. In each plot, the vertical dashed line is the surplus yield value, obtained simply as the annual consumption by seals of each fish species per

kilogram of seal biomass. Table 1 summarizes the results for both management strategies, listing the median gain to each fishery, the probability of a gain less than the surplus yield value, and the probability of a negative gain.

Several points are noteworthy. The distributions in Figs 7–10 contain some quite extreme values, but most of the answers are confined to a relatively small range of values. The choice of management strategy for *other* stocks can have quite a large influence on the gain to a given stock (compare 'single species' with 'all species' management in Table 1). Thus, management decisions made for one stock may affect management of another stock (see also May *et al.* 1979; Yodzis 1996).

Returning to the practical problem that motivated this study, we may note from Table 1 that, on the whole, it is difficult to make a case for culling fur seals on the basis of benefits to the Benguela fishery. Similar results were obtained for classes 1–4 (equations 11–14), although, as noted above, self-damping had to be implausibly large to obtain stability (Yodzis 1994). A cull is quite likely to be detrimental to anchovy yields.



**Fig. 6.** Probability of a viable system (dashed curve) and probability of a positive response of hake to a cull of fur seals, plotted against the self-damping parameter  $s_1$ . The two plots on the left are for type I functional responses, while the two plots on the right are for type II functional responses. The two upper plots have no 'other prey' effect in the functional response, while the two lower plots do have the 'other prey' effect.

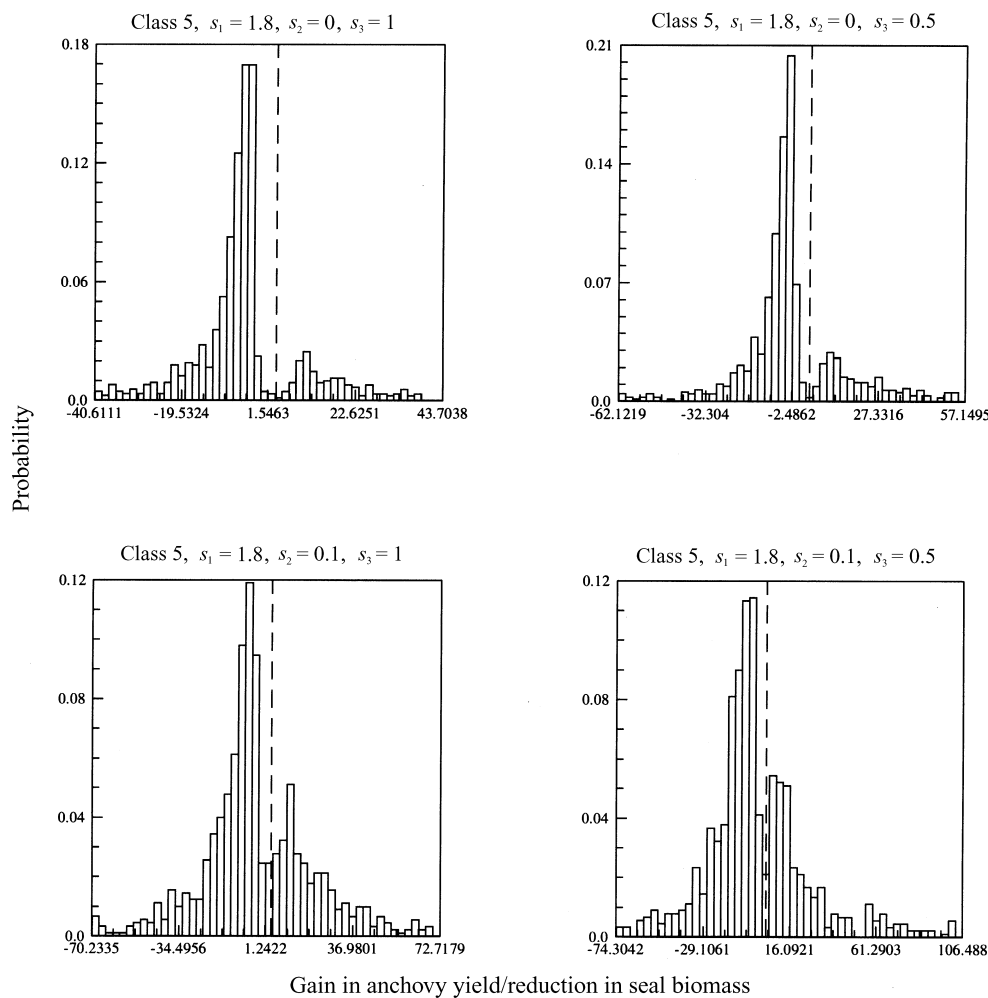
One could almost certainly maintain horse mackerel stocks in such a way as to realize a gain from a cull, although almost certainly less than the surplus yield gain. However, this would have to be at the cost of other exploited stocks, for the expected gain to the horse mackerel fishery that is achieved from managing only horse mackerel turns into an expected loss if all exploited stocks are managed. One could probably realize a gain of the order of the surplus yield gain from the hake fishery, although with considerable risk (at least 20%) of a loss instead. Perhaps the best overall index of the utility of a cull is to ask what would happen to total yield from all exploited stocks if all those stocks were maintained. As we see from Table 1, this is somewhat more likely to be a loss than it is to be a gain.

#### Influence of weak links on the response to a cull

The data used for this study required many person-years of research effort. For future studies, it is important to know in what ways and to what extent data

requirements can be simplified without seriously affecting the predictions of the model. Indeed, this is a core issue motivating the present work: having tried to minimize *a priori* simplifying assumptions, we now have a laboratory—the model presented above—in which the effects of simplifications can be investigated.

Given a foodweb for some whole system, for instance, the foodweb of Fig. 3 for the Benguela ecosystem, there are two ways that one might go about simplifying it. One way is to ignore some interactions. An extreme form of this approach is to ignore *all* the interactions involving one or more species, which is equivalent to removing those species from the foodweb. Another way is to lump some species together into aggregated categories (some of which has already been done in Fig. 3, for instance 'sharks', 'other groundfish'). Whatever one does, it ought to be done in a rational, objective, and sensible manner. Yodzis (1997b) has investigated to what extent an objective algorithm for the aggregation of species can simplify the foodweb. The results are not encouraging if one wants to study the interaction between fur seals



**Fig. 7.** Probability distribution for the gain in anchovy yield per reduction in seal biomass, in response to a cull of fur seals, under the assumption that the biomass of all exploited stocks is maintained at constant levels. The two plots on the left are for type I functional responses, while the two plots on the right are for type II functional responses. The two upper plots have no 'other prey' effect in the functional response, while the two lower plots do have the 'other prey' effect.

and hake: if species are gradually aggregated according to trophic similarity, fur seals and hake quickly lose their identities, each becoming part of an aggregate of several species, so that one has to stop aggregating before much simplification has been achieved.

Here we consider the other form of simplification mentioned above: ignoring some interactions. Specifically, we investigate the influence of weak trophic links on the response to a cull by progressively removing links in order of their strength.

For each predator  $j$ , let  $p_{ij}$  be the fraction of  $j$ 's intake (measured as biomass per unit time) that comes from species  $i$ . For each prey  $i$ , let  $q_{ij}$  be the fraction of consumption of  $i$  that goes to  $j$ , measured as biomass per unit time. For a given cutoff level, remove any foodweb link from  $i$  to  $j$  for which both  $p_{ij}$  and  $q_{ij}$  are less than or equal to the chosen cutoff level. Figure 11 shows, for all cutoffs from 0 to 1, the number of links in the foodweb (solid curve), the number of disjoint pieces in the foodweb (dashed curve), and the

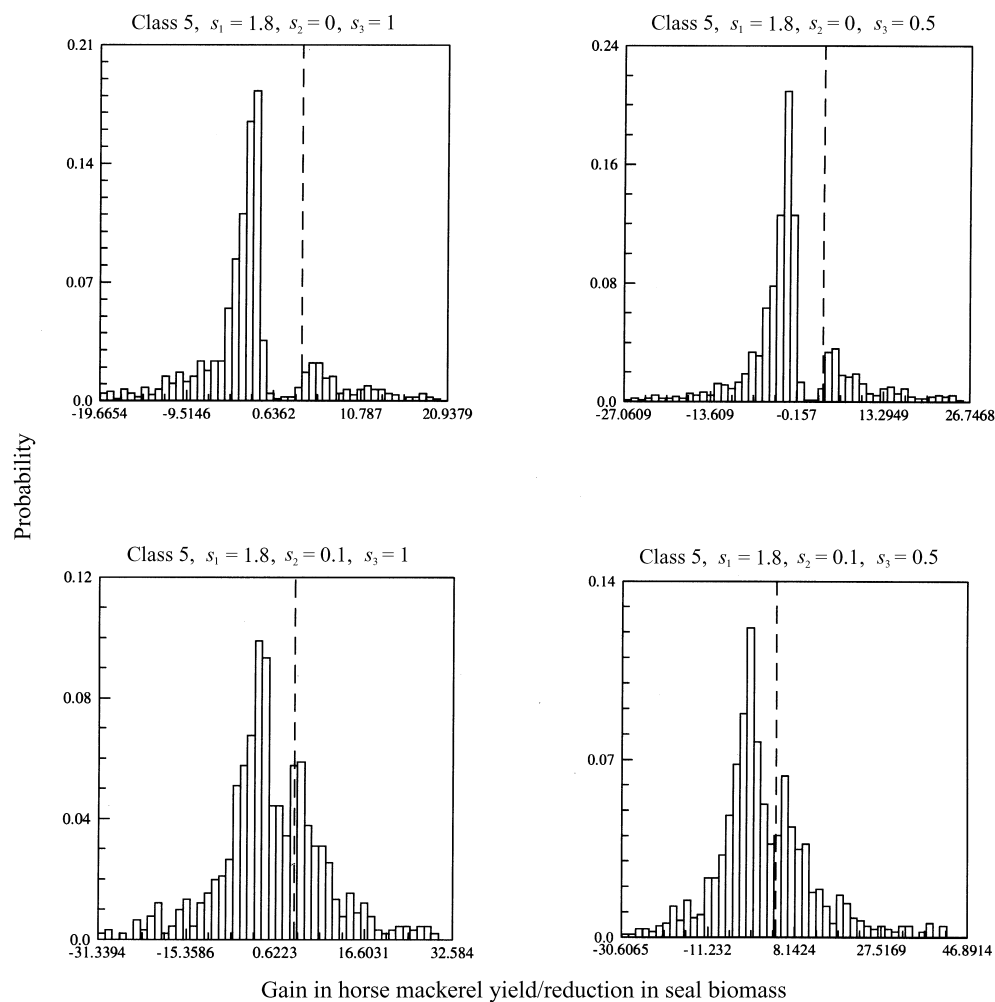
size of the connected foodweb piece that contains fur seals (dotted curve).

We note that the link from anchovy to fur seals is lost at the cutoff 0.29, and fur seals become completely disconnected from anchovy at a cutoff of 0.56; horse mackerel at 0.78 and 0.78; and hake at 0.10 and 0.58.

Figure 12 shows the effect of a cull on the total yield to all fisheries—expressed by median gain to the fishery (solid curve), probability of a result less than the surplus yield result (dashed curve), and probability of a result less than zero (dotted curve)—plotted against the cutoff level for removing weak links. Again, each figure contains four plots, which span extremes of  $s_2$  and  $s_3$  as in Figs 4–6.

It can be seen that, as the cutoff increases above 0.1, the calculations quickly become unreliable (relative to the results with no cutoff), eventually wildly so. The results, not plotted here, are quite similar for the individual species anchovy, horse mackerel and hake.

However, there is a bright side. Cutoffs less than



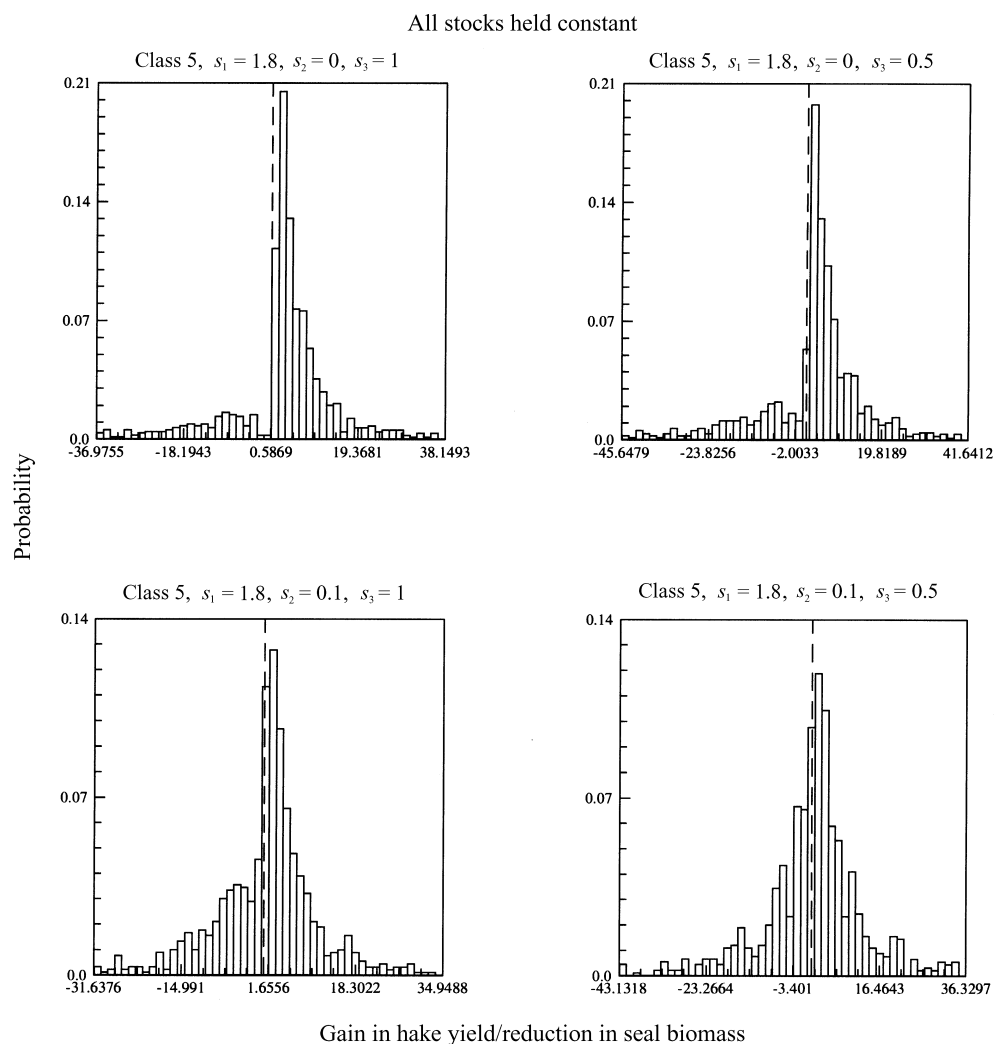
**Fig. 8.** Probability distribution for the gain in horse mackerel yield per reduction in seal biomass, in response to a cull of fur seals, under the assumption that the biomasses of all exploited stocks are maintained at constant levels. The two plots on the left are for type I functional responses, while the two plots on the right are for type II functional responses. The two upper plots have no 'other prey' effect in the functional response, while the two lower plots do have the 'other prey' effect.

0.1 have little effect on the outcome. At least for the system considered here, it is a reasonable approximation to neglect all individual feeding links that represent less than 10% of consumption both by and of any species. In the present case these amount to 91 out of 203 links, about 44% (Fig. 11). However, at the 10% level of cutoff the foodweb still consists of one piece (Fig. 11): we are not yet able to ignore any species.

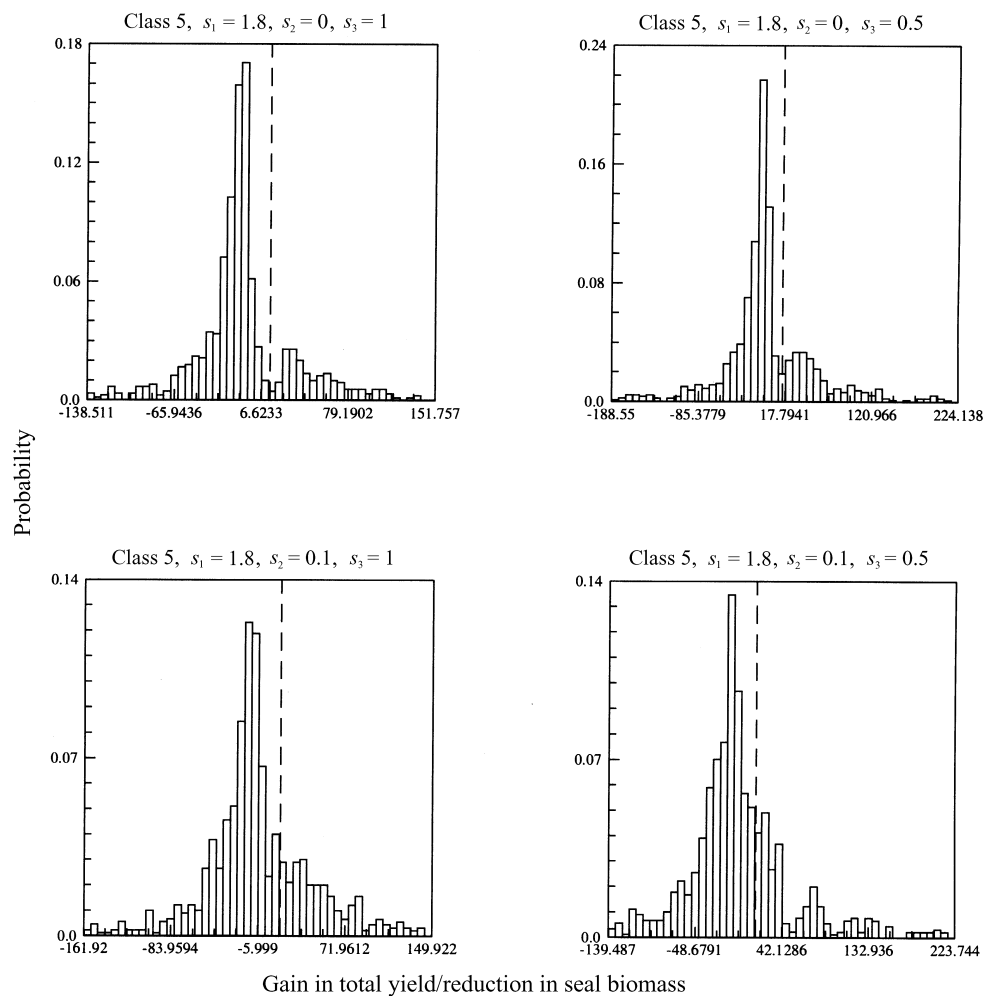
One is tempted to see here an observational protocol that potentially could help simplify a future systematic effort to gather appropriate data for multispecies modelling. Unfortunately, we have based our cutoff both on the proportions  $p_{ij}$  of consumption by each species and on the proportions  $q_{ij}$  of consumption of each species. While this makes sense from a theoretical perspective, it does not produce a useable observational protocol, for it is the proportions  $p_{ij}$  that are actually measured. We cannot know the  $q_{ij}$  until we have measured *all* the  $p_{ij}$ , even small ones. We need a protocol based only on  $p_{ij}$ .

Figure 13 shows the same effects of a cull as Fig. 12, this time removing, at each level of cutoff, any foodweb link from  $i$  to  $j$  for which  $p_{ij}$  is less than or equal to the chosen cutoff level. While Fig. 12 shows a fairly clear threshold at cutoff = 0.1, with little variation for smaller cutoffs, in Fig. 13 there is a gradual and rather rapid change in each plotted measure, starting from cutoff = 0. Unsurprisingly, judging weak links on the basis of dietary proportions  $p_{ij}$  alone is far riskier than the earlier procedure.

However, at least in the system treated here, it would not be a bad approximation to neglect all links such that  $p_{ij} < 0.05$ , say, with no allowance made for  $q_{ij}$  (Fig. 13). This is a considerable simplification, as we see from Fig. 14, which shows, for the cutoff based on  $p_{ij}$  alone, the number of links in the foodweb (solid curve), the number of disjoint pieces in the foodweb (dashed curve), and the size of the connected foodweb piece that contains fur seals (dotted curve). There are 97 links in the foodweb with  $p_{ij} < 0.5$ , about 48% of all links.



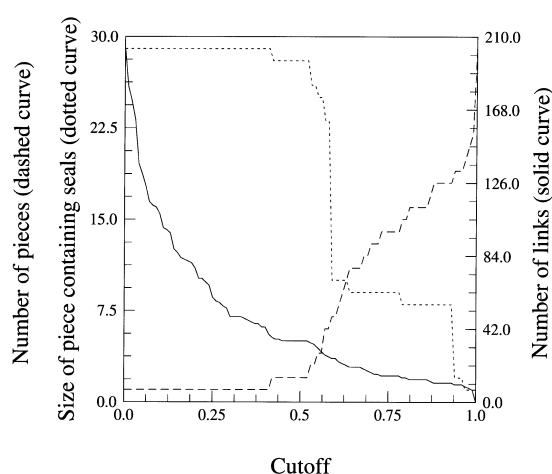
**Fig. 9.** Probability distribution for the gain in hake yield per reduction in seal biomass, in response to a cull of fur seals, under the assumption that the biomasses of all exploited stocks are maintained at constant levels. The two plots on the left are for type I functional responses, while the two plots on the right are for type II functional responses. The two upper plots have no 'other prey' effect in the functional response, while the two lower plots do have the 'other prey' effect.



**Fig. 10.** Probability distribution for the gain in total yield from all exploited stocks per reduction in seal biomass, in response to a cull of fur seals, under the assumption that the biomass of all exploited stocks is maintained at constant levels. The two plots on the left are for type I functional responses, while the two plots on the right are for type II functional responses. The two upper plots have no 'other prey' effect in the functional response, while the two lower plots do have the 'other prey' effect.

**Table 1.** Quantitative gains to the fisheries under Management Strategy 1 (single species management) and under Management Strategy 2 (all species managed)

Stock	Management	$s_2$	$s_3$	Median gain	$P$ (gain < seal consumption, %)	$P$ (gain < 0, %)
Anchovy	Single species	0.0	1.0	-1.82	94.0	87.0
		0.0	0.5	-3.14	95.0	93.0
		0.1	1.0	-1.70	96.0	74.0
		0.1	0.5	-2.97	96.0	83.0
	All species	0.0	1.0	-4.87	80.0	79.0
		0.0	0.5	-4.86	75.0	74.0
		0.1	1.0	-5.17	66.0	63.0
		0.1	0.5	-5.45	64.0	62.0
Horse mackerel	Single species	0.0	1.0	3.72	99.9	0.2
		0.0	0.5	3.69	99.9	0.4
		0.1	1.0	3.76	99.5	1.0
		0.1	0.5	3.71	98.6	1.0
	All species	0.0	1.0	-2.31	81.0	79.0
		0.0	0.5	-1.93	76.0	75.0
		0.1	1.0	-1.21	67.0	56.0
		0.1	0.5	-0.64	63.0	53.0
Hake	Single species	0.0	1.0	2.28	97.0	20.0
		0.0	0.5	1.98	95.0	22.0
		0.1	1.0	1.94	97.0	21.0
		0.1	0.5	1.46	97.0	30.0
	All species	0.0	1.0	3.70	20.0	20.0
		0.0	0.5	3.63	25.0	24.0
		0.1	1.0	2.03	39.0	35.0
		0.1	0.5	1.80	44.0	40.0
All	All species	0.0	1.0	-12.04	78.0	74.0
		0.0	0.5	-9.92	73.0	68.0
		0.1	1.0	-11.80	72.0	65.0
		0.1	0.5	-10.31	70.0	61.0



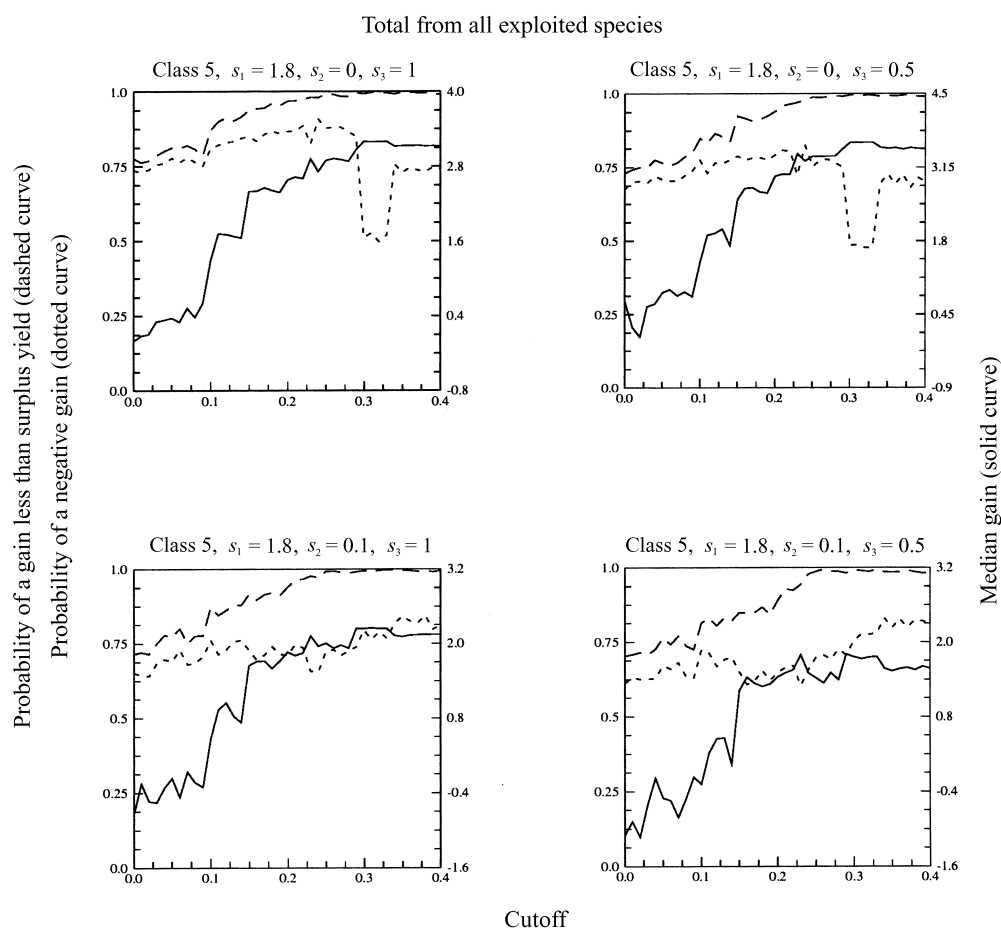
**Fig. 11.** Effect on foodweb structure of excluding links weaker than a cutoff, on the basis both of consumption by and consumption of each species. The solid curve is the number of links in the foodweb, the dashed curve is the number of disjoint pieces in the foodweb, and the dotted curve is the number of species in the connected piece that includes fur seals.

## Discussion

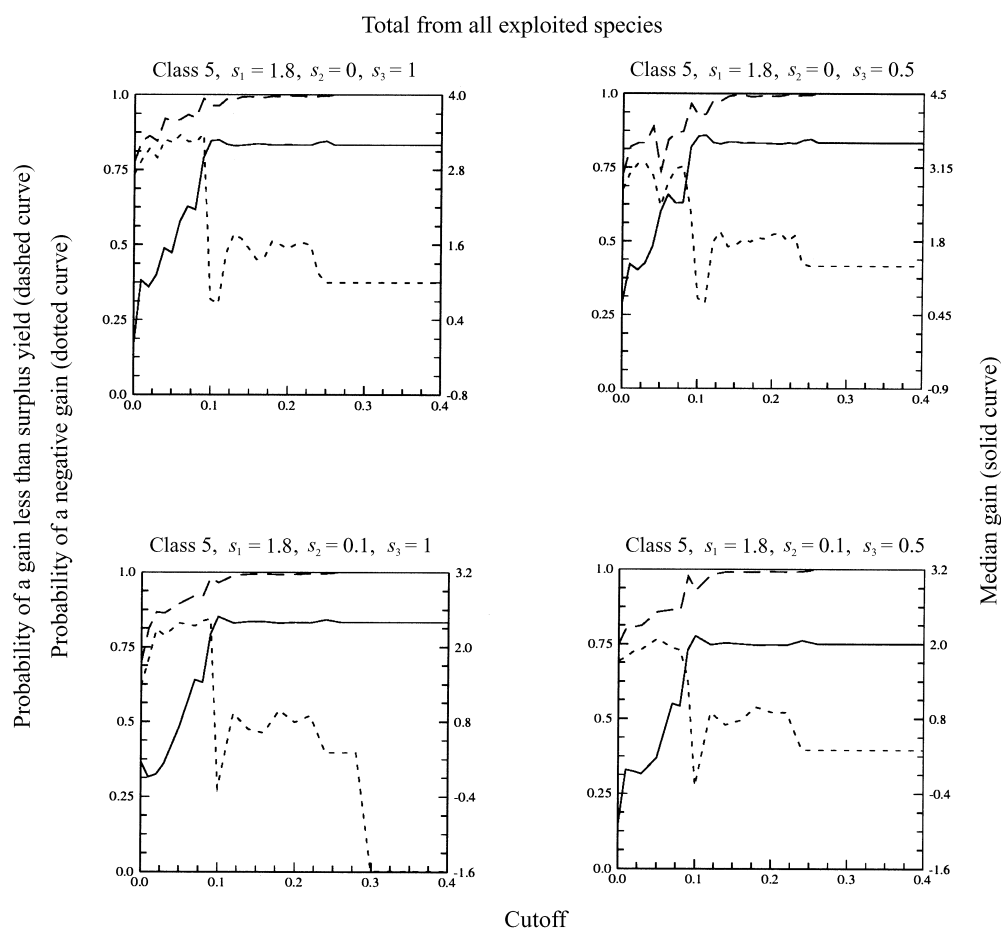
The approach taken here enables us to quantify both our knowledge of the system and our ignorance of it: we cannot in this way calculate exact predictions for the response to a cull, but we can calculate probability distributions for the response. Even though these probability distributions acknowledge our ignorance, they do, as outlined above, have practical implications that could be of use in managing the system.

There are two possible interpretations for the variation that exists within our statistical universes of Benguela models and, therefore, in our final results. This random variation could reflect our own ignorance of the system, due to limitations of our measurements; or it could reflect random influences that are actually experienced by the system and cannot be eliminated no matter how many measurements we might carry out. Quite likely it is a mixture of the two, so that replicated experiments on the system (if such a thing were possible) would exhibit variable results, but less variable than predicted by the model in its present form. In a far simpler setting—experimental systems consisting of grasshoppers and four perennial plant species—Schmitz (1997) measured the direct

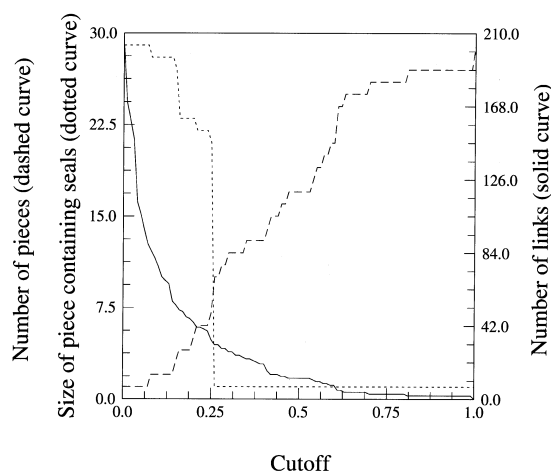




**Fig. 12.** Effect of a cull on the total yield to all fisheries, vs. the cutoff used to remove weak links, based on both consumption by and consumption of each species. The solid curve is the median gain to the fisheries, the dashed curve is the probability of a result less than the surplus yield result, and the dotted curve is the probability of a result less than zero.



**Fig. 13.** Effect of a cull on the total yield to all fisheries, vs. the cutoff used to remove weak links, based only on consumption by each species. The solid curve is the median gain to the fisheries, the dashed curve is the probability of a result less than the surplus yield result, and the dotted curve is the probability of a result less than zero.



**Fig. 14.** Effect on foodweb structure of excluding links weaker than a cutoff, on the basis only of consumption by each species. The solid curve is the number of links in the foodweb, the dashed curve is the number of disjoint pieces in the foodweb, and the dotted curve is the number of species in the connected piece that includes fur seals.

effects that form the elements of the Jacobian matrix, and found that variation in the outcomes of press perturbation experiments was well predicted from the observed variation in those direct effects, using eqn 9. In this case, variation is reduced to something close to that actually experienced by the system.

The model presented here lacks age structure, spatial structure, and seasonal and other extrinsic variation. As well, the data used to parameterize it, while admirable by comparison with our knowledge of many other complex systems, are surely questionable in many regards. However, all other dynamical Benguela models of which the author is aware lack taxonomic completeness and resolution. The present model and its parameterization cannot be considered grossly unrealistic, and they provide a plausible arena in which to explore the ramifications of multispecies effects. This study shows that taxonomic completeness and resolution, detailed foodweb structure, does make an enormous difference in predicting the outcomes of generalized press perturbations, such as culling fur seals in the Benguela ecosystem. This can be seen particularly in the previous section. Possibly we do need to take into account other details such as age structure, spatial structure, and extrinsic variation. But models that take these things into account cannot be trusted unless they also contain sufficiently complete foodweb structure.

### Acknowledgements

Discussions with Dave Lavigne and Mike Earle are gratefully acknowledged. Dean Huyck and (especially) Jan Hannah worked tirelessly and effectively at the frustrating but crucial task of getting numbers for me. Comments on the work, in various stages of development, by Justin Cooke, Don DeAn-

gelis, John Harwood, Bob Holt, Sidney Holt, Mike Kaspari, Tom Nudds, Bob Paine, and Kirk Wine-miller were helpful and much appreciated. The final stages of writing were undertaken at the School of Mathematics, Trinity College, Dublin, and I thank Petros Florides and the department for their kind hospitality.

### References

- Abrams, P., Menge, B.A., Mittelbach, G.G., Spiller, D. & Yodzis, P. (1996) The role of indirect effects in food webs. *Food Webs: Integration of Patterns and Dynamics* (eds G. A. Polis & K. O. Winemiller), pp. 371–395. Chapman & Hall, New York.
- Adams, N.J., Seddon, P.J. & Van Heezik, Y.M. (1992) Monitoring of seabirds in the Benguela upwelling system: can seabirds be used as indicators and predictors of change in the marine environment? *South African Journal of Marine Science*, **12**, 959–974.
- Anonymous (1981) *Report of IUCN workshop on marine mammal/fishery interactions*. 30 March–2 April 1981, La Jolla, California. International Union for the Conservation of Nature and Natural Resources, Gland, Switzerland.
- Anonymous (1991) Report on the Benguela Ecology Programme workshop on seal-fishery biological interactions. *Reports Of The Benguela Ecology Programme of South Africa*, No. 22.
- Anonymous (1992) *Marine mammal/fisheries interactions: analysis of cull proposals*. Report of the second meeting of the Scientific Advisory Committee of the Marine Mammals Action Plan. Liège, Belgium, 27 November–1 December 1992.
- Anonymous (1994) *Marine mammal/fisheries interactions: analysis of cull proposals*. Report of the third meeting of the Scientific Advisory Committee of the Marine Mammals Action Plan. Crowborough, UK, 24–27 August 1994.
- Augustyn, C.J. (1991) Estimated prey consumption by chokka squid *Loligo vulgaris reynaudii*. *Benguela Ecology Programme, Workshop on Seal-Fishery Biological Interactions*. University of Cape Town, 16–20 September, 1991. BEP/SW91/F10.
- Beddington, J.R., Beverton, R.J.H. & Lavigne, D.M. (eds) (1985) *Marine Mammals and Fisheries*. George Allen and Unwin, London.
- Berruti, A., Adams, N.J. & Jackson, S. (1989) The Benguela ecosystem. Part VI. Seabirds. *Oceanography and Marine Biology Annual Reviews*, **27**, 273–335.
- Cockcroft, V.G. & Peddemors, V.M. (1990) Seasonal distribution and density of common dolphins *Delphinus delphis* off the southeast coast of southern Africa. *South African Journal of Marine Science*, **9**, 371–377.
- Crawford, R.J.M. (1987) Food and population variability in five regions supporting large stocks of anchovy, sardine and horse mackerel. *South African Journal of Marine Science*, **5**, 735–757.
- Crawford, R.J.M., Shannon, L.V. & Pollock, D.E. (1987) The Benguela ecosystem. Part IV. The major fish and invertebrate resources. *Oceanography and Marine Biology Annual Reviews*, **25**, 353–505.
- David, J.H.M. (1987) Diet of the South African fur seal (1974–85) and an assessment of competition with fisheries in southern Africa. *South African Journal of Marine Science*, **5**, 693–713.
- D'Or, R.K. (1992) Big squid in big currents. *South African Journal of Marine Science*, **12**, 225–235.
- Duffy, D.C., Siegrid, W.R. & Jackson, S. (1987) Seabirds as

- consumers in the southern Benguela region. *South African Journal of Marine Science*, **5**, 771–790.
- Field, J.G., Crawford, R.J.M., Wickens, P.A., Moloney, C.L., Cochrane, K.L. & Villacastin-Herrero, C.A. (1991) Network analysis of Benguela pelagic food webs. *Benguela Ecology Programme, Workshop on Seal-Fishery Biological Interactions*. University of Cape Town, 16–20 September, 1991. BEP/SW91/M5a.
- Furness, R.W. & Cooper, J. (1982) Interactions between breeding seabird and pelagic fish populations in the southern Benguela region. *Marine Ecology Progress Series*, **8**, 243–250.
- Gordoa, A. & Duarte, C.M. (1992) Size dependent density of the demersal fish off Namibia: patterns within and among species. *Canadian Journal of Fisheries and Aquatic Science*, **49**, 1190–1193.
- Hampton, I. (1992) The role of acoustic surveys in the assessment of pelagic fish resources on the South African continental shelf. *South African Journal of Marine Science*, **12**, 1031–1050.
- Hastings, A. (1996) What equilibrium behavior of Lotka–Volterra models does not tell us about food webs. *Food Webs: Integration of Patterns and Dynamics* (eds G. Polis & K. O. Winemiller), pp. 211–217. Chapman and Hall, New York.
- Lavigne, D.M. (1995) Interactions between marine mammals and their prey: unravelling the tangled web. *Studies of High-Latitude Homeotherms in Cold Ocean Systems* (ed. W. A. Montevecchi). Canadian Wildlife Service Occasional Paper. [Also available as Technical Report 95–02, International Marine Mammal Association, Guelph, Ontario.]
- Levine, S. (1976) Competitive interactions in ecosystems. *American Naturalist*, **110**, 903–910.
- Macpherson, E. & Gordoa, A. (1992) Trends in the demersal fish community off Namibia from 1983–90. *South African Journal of Marine Science*, **12**, 635–649.
- May, R.M., Beddington, J.R., Clark, C.W., Holt, S.J. & Laws, R.M. (1979) Management of multispecies fisheries. *Science*, **205**, 267–277.
- Moloney, C.L., Field, J.G. & Lucas, M.I. (1991) The size-based dynamics of plankton food webs. II. Simulations of three contrasting southern Benguela food webs. *Journal of Plankton Research*, **13**, 1039–1092.
- Paine, R.T. (1988) Food webs: road maps of interactions or grist for theoretical development. *Ecology*, **69**, 1648–1654.
- Payne, A.I.L., Rose, B. & Leslie, R.W. (1987) Feeding of hake and a first attempt at determining their trophic role in the South African west coast marine environment. *South African Journal of Marine Science*, **5**, 471–501.
- Payne, A.I.L., Crawford, R.J.M. & van Dalsen, A.P. (eds) (1989) *Oceans of life*. Vlaeberg Publishers, Cape Town.
- Penny, A.J., Krohn, R.J. & Smale, M.J. (1991) Assessment precis for predatory fish and elasmobranchs in the Benguela and Agulhas ecosystems. *Benguela Ecology Programme, Workshop on Seal-Fishery Biological Interactions*. University of Cape Town, 16–20 September, 1991. BEP/SW91/A19.
- Punt, A.E. & Butterworth, D.S. (1995) The effects of future consumption by the cape fur seal on catches and catch rates of the cape hakes. 4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the Cape hake *Merluccius capensis* and *Merluccius paradoxus*. *South African Journal of Marine Science*, **16**, 255–285.
- Schmitz, O.J. (1997) Press perturbations and the predictability of ecological interactions in a food web. *Ecology*, **78**, 55–69.
- Sekiguchi, K., Klages, N.T.W. & Best, P.B. (1992) Comparative analysis of the diets of smaller Odontocete cetaceans along the coast of southern Africa. *South African Journal of Marine Science*, **12**, 843–861.
- Smale, M.J. (1992) Predatory fish and their prey—an overview of trophic interactions in the fish communities of the west and south coasts of South Africa. *South African Journal of Marine Science*, **12**, 803–821.
- Smith, J.L.B. (1977) *Smith's Sea Fishes*. Valiant Publishers, South Africa.
- Stone, L. & Roberts, A. (1991) Conditions for a species to gain advantage from the presence of competitors. *Ecology*, **72**, 1964–1972.
- Valdés Szeinfeld, E.S. & Cochrane, K.L. (1992) The potential effects of cannibalism and intraguild predation on anchovy recruitment and clupeoid fluctuations. *South African Journal of Marine Science*, **12**, 695–702.
- Watson, L. (1988) *Whales of the World*. Hutchinson, London.
- Whittaker, R.H. & Likens, G.E. (1975) The biosphere and man. *Primary Productivity of the Biosphere* (eds H. Lieth & R. H. Whittaker), pp. 305–328. Springer-Verlag, Berlin.
- Wiens, J.A. (1989) *The Ecology of Bird Communities*. Cambridge University Press, Cambridge.
- Wilson, R.P. (1992) Environmental monitoring with seabirds: do we need additional technology? *South African Journal of Marine Science*, **12**, 919–926.
- Yodzis, P. (1988) The indeterminacy of ecological interactions, as perceived through perturbation experiments. *Ecology*, **69**, 508–515.
- Yodzis, P. (1989) *Introduction to Theoretical Ecology*. Harper & Row, New York.
- Yodzis, P. (1994) *Local trophodynamics in the Benguela ecosystem: effect of a fur seal cull on the fisheries*. Third meeting of the Scientific Advisory Committee of the Marine Mammal Action Plan, United Nations Environmental Programme, Crowborough, UK. Working paper SAC94/WP14.
- Yodzis, P. (1996) Food webs and perturbation experiments: theory and practice. *Food Webs: Integration of Patterns and Dynamics* (eds G. Polis & K. O. Winemiller), pp. 192–200. Chapman and Hall, New York.
- Yodzis, P. (1997a) Five scholia on unstructured trophodynamics. *Food Web Structure and Dynamics in Marine, Terrestrial and Freshwater Environments* (eds H. Caswell & A. Solow). Chapman and Hall, London (in press).
- Yodzis, P. (1997b) Simplifying the interaction between fur seals and fisheries in the Benguela ecosystem. I. Aggregation. *Harp seal-fisheries interactions in the northwest Atlantic*. Workshop held at St. John's, Newfoundland, 24–27 February 1997, Canadian Centre for Fisheries Innovation. Document HW39.
- Yodzis, P. & Innes, S. (1992) Body size and consumer-resource dynamics. *American Naturalist*, **139**, 1151–1175.

Received 4 April 1997; revision received 4 November 1997

## Appendix 1

## DIETARY MATRIX

Rows are prey; columns are predators. Key to species identities at end.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	0.0	0.0	98.8	0.0	30.6	45.0	60.0	25.0	5.0	67.0	0.0	0.0	0.0	36.0	0.0	0.0	0.0
2	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	0.0	0.0	0.0	0.0	29.7	0.0	0.0	25.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.5	2.2
5	0.0	0.0	0.0	0.0	29.7	45.0	0.0	25.0	4.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.0
6	0.0	0.0	0.0	0.0	0.0	0.0	40.0	25.0	57.0	30.0	60.0	40.0	40.0	43.5	81.0	58.0	9.0
7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34.0	3.0	40.0	60.0	60.0	18.5	14.0	41.3	54.6
8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0	0.0	0.0
9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.0
10	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
11	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.7
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	29.5
14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
16	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
17	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
18	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
19	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
20	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
21	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
22	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
23	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
24	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
25	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
26	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
27	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
29	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Key: 1 phytoplankton; 2 benthic filter-feeders; 3 bacteria; 4 benthic carnivores; 5 microzooplankton; 6 mesozooplankton; 7 macrozooplankton; 8 gelatinous zooplankton; 9 anchovy; 10 pilchard; 11 round herring; 12 lightfish; 13 lanternfish; 14 goby; 15 other pelagics; 16 horse mackerel; 17 chub mackerel; 18 other groundfish; 19 hakes; 20 squid; 21 tunas; 22 snoek; 23 kob; 24 yellowtail; 25 geelbek; 26 whales & dolphins; 27 birds; 28 seals; 29 sharks

Appendix 1 (Continued)

	18	19	20	21	22	23	24	25	26	27	28	29
1	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
2	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
3	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
4	34·3	0·0	2·2	22·0	1·2	8·8	0·0	1·2	0·0	0·6	9·6	8·0
5	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0
6	15·8	11·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·9	0·0	4·0
7	9·9	11·0	8·1	0·0	3·0	6·8	0·2	0·0	6·6	9·6	0·0	4·0
8	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	4·0
9	0·1	11·0	30·0	15·0	58·6	51·0	1·9	25·0	30·1	36·4	30·1	4·0
10	0·0	6·0	12·0	15·0	4·5	0·6	29·1	25·2	7·4	8·4	3·2	4·0
11	2·5	6·0	10·7	7·0	12·6	0·0	4·1	7·9	1·0	1·9	0·1	4·0
12	2·1	9·0	13·9	4·0	2·5	0·0	0·0	0·0	0·0	4·7	0·3	4·0
13	2·0	12·0	0·0	3·0	2·6	0·0	0·0	0·0	4·3	5·6	0·3	4·0
14	0·1	8·5	21·0	15·0	31·5	25·8	15·5	25·1	18·8	22·4	16·6	4·0
15	2·4	0·0	0·0	4·0	0·0	0·0	12·1	1·9	3·2	5·5	0·4	4·0
16	0·0	1·0	1·0	5·0	1·4	3·3	4·1	20·9	26·8	0·8	18·0	4·0
17	0·0	1·0	0·0	5·0	0·0	1·1	5·9	0·0	0·0	0·4	0·6	4·0
18	17·2	7·0	15·6	0·0	0·0	13·7	13·9	16·6	0·0	0·7	4·4	4·0
19	5·8	15·0	5·3	5·0	13·2	8·2	0·0	0·1	4·4	17·2	6·0	4·0
20	7·9	10·0	1·2	15·0	0·4	6·1	28·7	1·2	16·2	6·5	15·4	4·0
21	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	4·0
22	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·2	10·2	4·0
23	0·0	0·0	0·0	0·0	0·0	0·4	0·0	0·0	0·0	0·0	0·0	4·0
24	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	4·0
25	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	4·0
26	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	4·0
27	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·2	0·6	4·0
28	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·4	0·0	4·0
29	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·0	0·8	4·0

Key: 1 phytoplankton; 2 benthic filter-feeders; 3 bacteria; 4 benthic carnivores; 5 microzooplankton; 6 mesozooplankton; 7 macrozooplankton; 8 gelatinous zooplankton; 9 anchovy; 10 pilchard; 11 round herring; 12 lightfish; 13 lanternfish; 14 goby; 15 other pelagics; 16 horse mackerel; 17 chub mackerel; 18 other groundfish; 19 hakes; 20 squid; 21 tunas; 22 snoek; 23 kob; 24 yellowtail; 25 geelbek; 26 whales & dolphins; 27 birds; 28 seals; 29 sharks

Appendix 2

Annual harvests, averaged over 1987–89 (kg)

Stock	Harvest
Anchovy	470132000
Pilchard	107785667
Round herring	47063000
Lanternfish	1623333
Goby	72333
Horse mackerel	114838333
Chub mackerel	10499333
Hakes	161119000
Squid	493333
Tunas	3903000
Snoek	17405000
Kob	1376333
Yellowtail	809000
Geelbek	527667
Seals	2203336
Sharks	469000

## Appendix 3

Typical adult individual body masses (kg)

Stock	Body mass (kg)	Source
Phytoplankton	$10^{-7}$	Moloney <i>et al.</i> 1991
Benthic filter-feeders	0.01	J. C. Roff, personal communication
Bacteria	$10^{-11}$	Moloney <i>et al.</i> 1991
Benthic carnivores	0.01	J. C. Roff, personal communication
Microzooplankton	$10^{-7}$	Moloney <i>et al.</i> 1991
Mesozooplankton	$10^{-5}$	Moloney <i>et al.</i> 1991
Macrozooplankton	$10^{-3}$	Moloney <i>et al.</i> 1991
Gelatinous zooplankton	0.1	J. C. Roff, personal communication
Anchovy	0.0115	Dr R. Winterbottom, personal communication
Pilchard	0.28	Smith 1977
Round herring	0.2152	Smith 1977
Lightfish	0.0048	Smith 1977
Lanternfish	0.0069	Smith 1977
Goby	0.0186	Dr R. Winterbottom, personal communication
Other pelagics	2.55485	Ave. of horse mackerel and lightfish
Horse mackerel	5.1049	Smith 1977
Chub mackerel	3.2595	Smith 1977
Other groundfish	13.127	ave. of chub mackerel and hakes
Hakes	22.9945	Smith 1977
Squid	0.04	D'Or (1992)
Tunas	909	Smith 1977
Snoek	13.0121	Smith 1977
Kob	68	Smith 1977
Yellowtail	82.0403	Smith 1977
Geelbek	26.12738	Smith 1977
Whales & dolphins	82	Watson (1988)
Birds	2.287	Furness & Cooper (1982)
Seals	136	Lavigne <i>et al.</i> (unpublished information)
Sharks	1.5	Dr R. Winterbottom, personal communication

## Appendix 4

Population biomass (thousand metric tons)

(Adjusted biomass; Stock	Biomass thousand tonnes	Source
Phytoplankton	44900 (44900)	Moloney <i>et al.</i> 1991
Benthic filter-feeders	5055	
Bacteria	3120	Moloney <i>et al.</i> 1991
Benthic carnivores	5055	
Microzooplankton	4690	Moloney <i>et al.</i> 1991
Mesozooplankton	1560 (15600)	Moloney <i>et al.</i> 1991
Macrozooplankton	100 (10000)	Moloney <i>et al.</i> 1991
Gelatinous zooplankton	100	taken equal to macrozooplankton
Anchovy	400	Valdés Szeinfeld & Cochrane (1992)
Pilchard	300	Valdés Szeinfeld & Cochrane (1992)
Round herring	1215·136364	Hampton (1992)
Lightfish	750	Smale 1992
Lanternfish	10000	Smale 1992
Goby	20·507 (205·07)	Macpherson and Gordoia (1992)
Other pelagics	1267·872	
Horse mackerel	13·566(135·66)	Gordoia & Duarte 1992
Chub mackerel	13·566	taken equal to horse mackerel
Other groundfish	143·64	
Hakes	1422·834	
Squid	66·295664	Augustyn (1991)
Tunas	9·65	Penny <i>et al.</i> (1991)
Snoek	180·5	Gordoia & Duarte 1992
Kob	11·4	Gordoia & Duarte 1992
Yellowtail	0·816136(8·16136)	Penny <i>et al.</i> (1991)
Geelbek	0·018136(1·8136)	Gordoia & Duarte 1992
Whales & dolphins	1·435	Cockcroft & Peddemors (1990)
Birds	1·945306	Duffy <i>et al.</i> (1987)
Seals	84·311058	Lavigne <i>et al.</i> (unpublished information)
Sharks	19·95	Gordoia & Duarte 1992

## Appendix 5

Ingestion factors  $f_{ji}$  and carrying capacities  $K_i$ .

Stock $i$	$f_{ji}$	$K_i$ (million tonnes)
Phytoplankton		548·725
Benthic filter feeders		15·942
Bacteria	0·062	
Benthic carnivores	0·055	
Microzooplankton	0·173	
Mesozooplankton	0·087	
Macrozooplankton	0·174	
Gelatinous zooplankton	0·101	
Anchovy	0·405	
Pilchard	0·321	
Round herring	0·280	
Lightfish	0·272	
Lanternfish	0·260	
Goby	0·402	
Other pelagics	0·263	
Horse mackerel	0·769	
Chub mackerel	0·785	
Other groundfish	0·675	
Hakes	0·391	
Squid	0·440	
Tunas	0·668	
Snoek	0·447	
Kob	0·370	
Yellowtail	0·396	
Geelbek	0·683	
Whales and dolphins	0·674	
Birds	0·693	
Seals	0·617	
Sharks	0·345	