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THE ECOSYSTEM APPROACH TO MANAGING FISHERIES: ACHIEVING CONSERVATION OBJECTIVES FOR PREDATORS OF FISHED SPECIES

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Abstract

Managing fisheries to achieve ecosystem objectives is in its infancy. A general approach is proposed for maintaining ecological relationships and providing for the recovery of depleted populations in food webs supporting fisheries. This paper addresses the following general questions for applying the ecosystem approach to managing fisheries: (i) how might fisheries impact incidentally on an ecosystem, (ii) what should be the conservation objectives for predators of fished species, and (iii) what approaches could be considered for achieving the conservation objectives? The approach proposed here takes account of uncertainties in knowledge of the structure of ecosystems. Estimates of predator production arising from the consumption of fished species (encapsulated in proposed indices *P* and *W*) may provide useful indicators for management purposes because they integrate across a range of 'ecosystem' effects and, as formulated here, can also be related directly to the effects of fishing. These features are currently unavailable in ecosystem approaches to managing fisheries, which do not weight input data for assessments, such as per-capita breeding success, according to the relative influence of fished species on those estimates. The paper describes the steps required to establish management procedures based on these indices.

Résumé

La gestion des pêches visant des objectifs écologiques n'en est encore qu'à ses balbutiements. La méthode générale proposée cherche à maintenir les relations écologiques et à permettre la récupération des populations épuisées dans les réseaux trophiques qui soutiennent les pêcheries. Le présent document aborde diverses questions générales applicables à l'approche de la gestion des pêches tenant compte de l'écosystème : i) comment la pêche risque-t-elle d'affecter un écosystème par accident ? ii) quels devraient être les objectifs de conservation des prédateurs d'espèces exploitées ? et iii) quelles approches pourrait-on envisager pour atteindre les objectifs de conservation ? L'approche proposée ici tient compte des incertitudes entourant notre connaissance de la structure des écosystèmes. L'estimation de la production des prédateurs résultant de la consommation d'espèces exploitées (faisant partie des indices *P* et *W* proposés) pourrait fournir des indicateurs utiles pour la gestion du fait qu'ils portent sur tout un intervalle d'effets liés à l'écosystème et, comme cela est mentionné dans le présent document, peuvent être mis en relation directe avec les effets de la pêche. Ces caractéristiques ne font pas encore partie des approches de la gestion des pêches tenant compte de l'écosystème qui n'étalonnent pas les données d'entrée des évaluations, telles que le succès de la reproduction par tête, en fonction de l'influence relative des espèces exploitées sur ces estimations. Le document décrit la marche à suivre pour mettre en place des procédures de gestion reposant sur ces indices.

Резюме

Управление промыслом, направленное на достижение экосистемных целей, находится в самой ранней стадии развития. Предлагается общий подход для поддержания экологических связей и восстановления истощенных популяций в подвергающихся промыслу трофических цепях. В статье рассматриваются следующие вопросы применения экосистемного подхода к управлению промыслом: (i) какое побочное воздействие промысел оказывает на экосистему, (ii) какими должны быть природоохранные цели для питающихся промысловыми видами хищников и (iii) какие подходы позволят достичь этих целей? Предлагаемый подход учитывает неопределенность знаний о структуре экосистемы.

Оценки продукции хищников, связанной с потреблением промысловых видов и описываемой предлагаемыми индексами P и W, могут служить полезными индикаторами при управлении, т.к. они интегрируют диапазон экосистемных эффектов и, как предполагается, могут быть непосредственно связаны с воздействием промысла. В настоящее время это не применяется в экосистемных подходах к управлению промыслом, которые при оценках не взвешивают входные данные (например, репродуктивный успех на особь) в зависимости от относительного влияния промысловых видов на эти оценки. В статье описываются шаги, необходимые для установления основанных на этих индексах процедур управления.

Resumen

La ordenación de pesquerías enfocada la conservación de sistemas ecológicos está en sus albores. Se propone un enfoque general para mantener las relaciones ecológicas y ayudar en la recuperación de las poblaciones mermadas del sistema trófico que sustenta a la pesquería. Este trabajo se refiere a las siguientes cuestiones generales relativas a la aplicación del enfoque ecosistémico en la ordenación de pesquerías: (i) ¿cuáles podrían ser las consecuencias incidentales de las pesquerías en un ecosistema? (ii) ¿cuáles deberían ser los objetivos de conservación para los depredadores de las especies explotadas? y (iii) ¿cuáles enfoques podrían considerarse para alcanzar los objetivos de conservación? El enfoque propuesto toma en cuenta las incertidumbres producidas por la falta de conocimiento sobre la estructura de los ecosistemas. Las estimaciones de la productividad de los depredadores resultante del consumo de especies explotadas comercialmente (incorporada en los índices propuestos P y W) podrían servir como indicadores para la ordenación, ya que estos valores están integrados de una gama de efectos 'ecosistémicos' y, como se explica en este trabajo, también pueden relacionarse directamente con los efectos de la pesca. Los enfoques ecosistémicos utilizados actualmente en la ordenación de pesquerías no incorporan estas características y no ponderan los datos de entrada (tales como el éxito reproductor per cápita) en las evaluaciones de acuerdo a la influencia relativa de las especies explotadas en las estimaciones. El trabajo describe las medidas necesarias para establecer procedimientos de ordenación basados en estos índices.

Keywords: fisheries, ecosystem management, food webs, monitoring, management procedures, productivity, endangered species, management strategy evaluation, CCAMLR

INTRODUCTION

The implementation of ecosystem objectives for managing a variety of aquatic and terrestrial habitats is widely discussed (e.g. Lubchenco et al., 1991; Christensen et al., 1996; Mangel et al., 1996; Dixon et al., 1998; Mooney, 1998). However, there is widespread agreement that managing ecological assemblages remains a mostly data-free activity (Ludwig et al., 1993) and that remedying this situation is an urgent goal (Mangel et al., 1996).

Since its inception, CCAMLR has grappled with the problems of applying an ecosystem approach to the management of fisheries, particularly in relation to the krill fishery. This is encapsulated in the Convention for the Conservation of Antarctic Marine Living Resources (hereafter referred to as 'the Convention') and the obligations contained therein (Article II), which aim to ensure that fisheries do not jeopardise the maintenance of ecological relation-ships, and also to provide for the recovery of depleted populations, notably of great whales (Constable et al., 2000). These two subsidiary objectives of the Convention spawned the CCAMLR Ecosystem Monitoring Program (CEMP), which was initiated to detect significant changes to the ecosystem, particularly in predators of krill, and to signal when such changes were the result of fishing (see Agnew, 1997 for a complete description of the program). In this way, CEMP was intended to provide the necessary advice to the Commission on when fishing may be negatively impacting species dependent on the target species.

The manner in which the data from CEMP will be utilised in the formulation of advice has yet to be decided (Constable et al., 2000), although advances have been made in recent years on how this might be done (de la Mare and Constable, 2000).

In the interim, during the development of a comprehensive procedure for managing the krill fishery (de la Mare, 1996, 1998), CCAMLR has taken a precautionary approach to protecting predators of target species by adopting the krill yield model

(CCAMLR, 1994) and setting precautionary catch limits in the krill and some finfish fisheries (Constable et al., 2000). This approach takes into account the large-scale relationships between krill, its predators and the fishery. However, it has not taken specific account of the potential for localised effects on some land-based krill predators (Everson and de la Mare, 1996) or of the need for recovery of some species, although models have been proposed for monitoring local overlaps between predator foraging areas and fishing activities (see SC-CAMLR, 1997 for review).

The aim of this paper is to examine the mechanisms needed to achieve that part of Article II of the Convention requiring the maintenance of ecological relationships and the recovery of depleted populations. The approach considered here has relevance for managing fisheries generally. An important issue to be considered is whether ecosystem objectives can be met without knowing, in detail, the interrelationships amongst species. The CCAMLR Working Group on Ecosystem Monitoring and Management (WG-EMM) has discussed the need to estimate the relationships between predator survival and krill abundance. It is intended that such information will help build dynamic models of the relationship between target species and predators. However, little work has been undertaken since the early development of such models by Butterworth and his co-workers (e.g. Butterworth and Thomson, 1995; Thomson et al., 2000) and Mangel and Switzer (1998). An important issue to resolve is how to manage the effects of fishing on predators when little information is available on predicting how predators may respond to different levels of harvesting. In other words, how might harvest strategies be adjusted using information on predators in a management procedure?

Prospective Evaluation of Management Procedures

A very important part of developing management procedures is to evaluate them prospectively in order to be confident they will achieve their management objectives (de la Mare, 1996). This provides for testing whether the decision rules for altering harvesting activities will perform well in meeting the objectives for predator production arising from the consumption of fished species. A number of questions can then addressed. First, what combinations of monitoring, assessments and decision rules meet the required performance for different plausible formulations of the food web? Could these parts of the management system be made simpler to work just as effectively? What improvements in performance of the management system could be achieved by altering the rules or other aspects of the management system? Lastly, how much change occurs in aspects of the food web not directly related to the fished species? The advantage of such evaluations is that the initial management system can be built on the simplest of decision rules and then progressively modified to improve performance according to the performance criteria. In some instances, the decision rules may not be based directly on the performance criteria in order to be able to achieve the desired effects. Importantly, management procedures must be robust against uncertainties in the understanding of food web structure and other elements in the assessment process. To undertake these evaluations, simulation models can be constructed to test the performance of proposed management arrangements (e.g. de la Mare, 1986a, 1996, 1998; Smith, 1993; Cooke, 1999; Mangel, 2000).

Aims

This paper addresses the following general questions related to applying the ecosystem approach to managing fisheries:

(i) How might fisheries impact incidentally on an ecosystem?

(ii) What should be the conservation objectives for predators of fished species?

(iii) What approaches could be considered for achieving the conservation objectives?

These questions address a core issue for fisheries in determining what aspects of an ecosystem need to be monitored and how such information might be used to trigger actions to ensure ecosystem objectives are met by fisheries. These points are illustrated using a simple simulation model that could be used as a basis for future testing of a variety of candidate management procedures aimed at managing the effects of fishing on food webs.

HOW MIGHT FISHERIES IMPACT INCIDENTALLY ON AN ECOSYSTEM?

Fishing can affect marine species directly through mortality or injury. Incidental effects can arise as a result of modifications to the habitat,

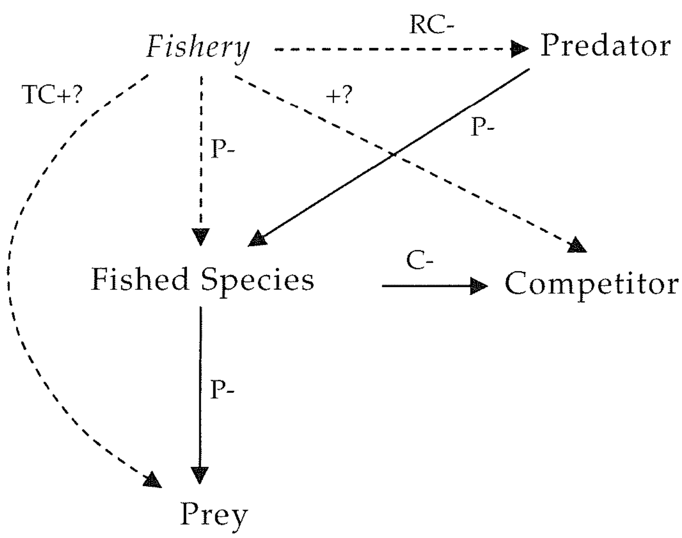

Figure 1: Schematic diagram showing the primary food web relationships between a fished species and other key species in the system (solid lines and plain symbols). The effects of the fishery on this ecosystem are shown with dashed lines and italicised symbols. Arrows indicate the direction of effect. Type of effect is indicated by the letters: C- is a negative competitive effect on the species to which the arrow is pointing, P- is a negative predatory effect, +? is a potential positive effect by the fishery on an inferior competitor of the fished species, TC+? is a potential positive effect arising from an apparent trophic cascade by the fishery and RC- is potential resource competition between a fishery and predators. (Following the schema of Fairweather, 1990 for biological interactions.)

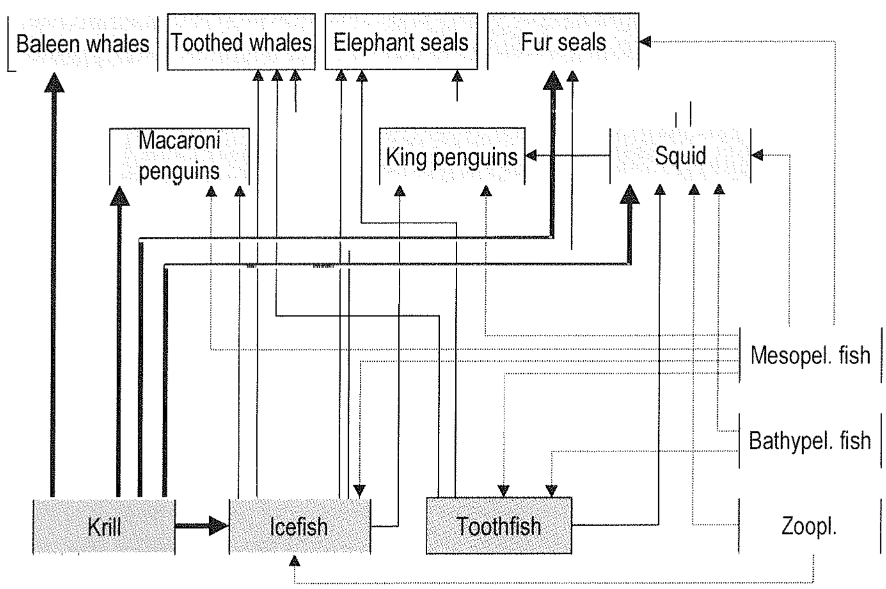

Figure 2: Structure of the food web around South Georgia Island in the Atlantic Ocean, including the fisheries for krill, Patagonian toothfish and mackerel icefish. The dark grey boxes represent fished species, the light grey boxes are predators of fished species and the white boxes are other types of prey, including mesopelagic (mesopel.) and bathypelagic (bathypel.) fish species and zooplankton (zoopl.) (derived from Constable et al., 2000).

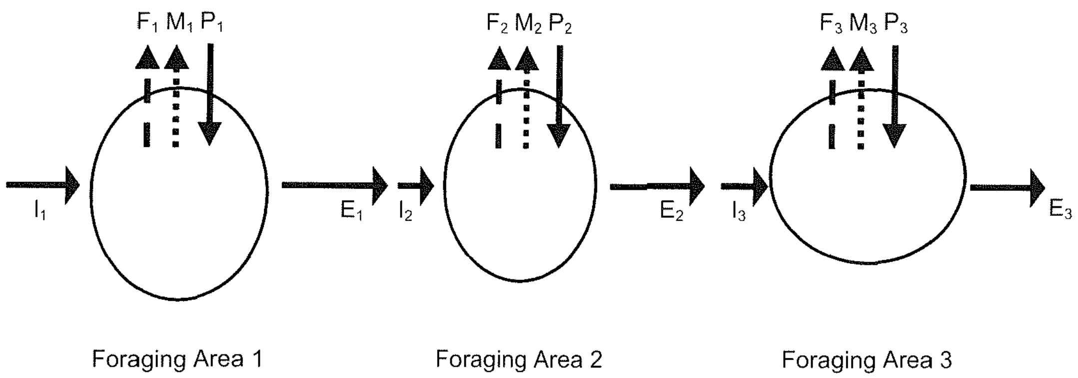

Figure 3: Schematic diagram showing the potential linkages between different predator foraging areas and the dynamics of the fished population, including immigration of the fished species (I), emigration (E), natural mortality (M), fishing mortality (F) and production (P), which includes recruitment and growth of individuals. Subscripts indicate area specific rates.

such as through bottom trawling (Jennings and Kaiser, 1998) or from alterations in the structure of the food web. Habitat issues are not considered further here.

The Scientific Committee of CCAMLR has considered many of these issues, particularly in relation to the krill fishery (SC-CAMLR, 1992, 1995) and its potential effects on krill predators. This section provides a summary of those issues as an example for considering fisheries generally.

The results of discussions in SC-CAMLR can be summarised into three important areas: (i) the importance of krill in the diet of predators and how this may vary over time as a result of changes in productivity as well as changes in availability, (ii) the effects of the fishery on the availability of krill to predators at critical times of the year, and (iii) the potential interannual variation in krill abundance and how it affects predators. The last two points involve understanding the spatial and temporal scales of interaction in the system (Murphy et al., 1988; SC-CAMLR, 1992), while the first involves the strengths of the ecological interactions between species.

Species that directly interact with the target and by-catch species (hereafter collectively termed 'fished species') (Figure 1) are the most likely to exhibit an indirect response to fishing, particularly those with the strongest interactions with the fished species (Paine, 1980; but see Yodzis, 1994, 2000). A simplified food web based on the fished species at South Georgia is shown in Figure 2.

The effects of fishing on dependent or related species are only important if there is the potential for the strengths of interactions to be altered amongst species as illustrated in Figure 1, i.e. the magnitude and/or direction of effects between species are changed. For example, theory tells us that predators of fished species would be competing with the fishery only if they are feeding substantially from the fished population and the fished population is insufficient to meet the needs of predators and support the fishery at the same time. In this case, competition would be evident if the productivity of the predators is reduced as a result of fishing. Reduced net productivity may be evident in a reduction of the biomass of the predator population (reduced growth or weight loss in individuals), reduced recruitment or increased mortality and/or migration from the area. In addition, wider effects on the ecosystem may be experienced if predators switch from the fished species to preying on other species in the system.

To examine the potential for interaction between fisheries, fished species and dependent species, such as predators, a spatially explicit model is required that explores the interactions at scales common to the three different components, i.e. one that examines the interrelationships between productivity of fished species, sources of mortality (predators, fishing, other) and migration of fished species in and out of the local areas (SC-CAMLR, 1995) (Figure 3).

Complexities in the model may arise if there are critical stages in the life cycle of some dependent species (such as breeding time for some land-based krill predators) or if there is a spatial shift in the foraging areas relative to the fished population (e.g. different feeding grounds in summer and winter).

WHAT SHOULD BE THE CONSERVATION OBJECTIVES FOR PREDATORS OF FISHED SPECIES?

The important ecosystem-oriented objective for CCAMLR is contained in Article II of the Convention, paragraph 3(b), which requires 'maintenance of the ecological relationships between harvested, dependent and related populations of Antarctic marine resources and the restoration of depleted populations to the levels defined in sub-paragraph (a) above'. In the latter case, this refers to a population level providing the 'greatest net annual increment' (CCAMLR, Article II; de la Mare and Constable, 1990) Beyond this, CCAMLR has not provided an operational interpretation of this objective or determined the critical status of the ecosystem that can be used as a benchmark for ensuring that the general ecosystem objective is being met.

The term 'management' is used here to indicate the actions taken to control human intervention in ecosystems. For many systems, management has been centred on single-species or 'multi-species' assemblages (as distinct from ecological assemblages) where the multiple species are of economic interest, particularly in fisheries where the species are all exploited or managed in some way (May et al., 1979; Beddington and May, 1982; Punt et al., 1995; Larkin, 1996).

For ecological assemblages, most attention seems now to be focused on the maintenance of biodiversity and the potential consequences of loss of biodiversity to the overall ecological function of those assemblages. In this case, field research is concentrating on identifying what gross changes occur in ecosystems as a result of human activities and theoretical models endeavour to understand the implications of those changes (e.g. Tilman, 1999). Very little research effort seems focused on understanding the important mechanisms that cause the changes observed and what such changes mean in terms of the long-term ecological status of the assemblage (e.g. estuaries – Constable, 1999). More importantly, very little attention has been given to actions that might be required if an assemblage is found to change as a result of human activities, i.e. what sorts of adjustments to the activity could be made to prevent serious undesirable alteration of the assemblages? In most cases, studies focus on the extreme undesirable cases of change and the remedial action required to restore the system, if only in terms of its main structural components, i.e. there is a focus on extreme needs for conservation and restoration rather than prevention.

In contrast to studies on assemblages, much work is available examining the status of species, independent of whether they are being affected by harvesting or other human activities (e.g. Soule, 1986; Ferson and Burgman, 2000). In some cases, these works identify whether species require specific conservation measures because of their status as vulnerable, threatened, or endangered; a number of criteria have been established to assist with such classification (IUCN, 1994). While these may be the last form of protection for individual species, the triggering of such classifications in the ecosystem approach to fishing would signal a failure in the management of those fisheries.

Developing Operational Objectives for Predators of Fished Species

Operational objectives based on reference points for 'ecologically-related' species (assemblages) that are not directly affected by the fishing operation have been much more difficult to enunciate than reference points for target species (e.g. May et al., 1979; Beddington and May, 1982). In CCAMLR, this ecosystem objective has been made operational, in part, as one of the reference points for individual fished species (the predator criterion – see Constable et al., 2000 for review) rather than specifically for the related species or assemblages. The aim of this criterion is for the long-term annual yield of krill not to cause a decline in the long-term median krill abundance to below 0.75 of the pre-exploitation median abundance. This is important because, even though predators are accounted for in part by the natural mortality rate of krill, the total amount consumed (predator food requirements) is contingent on the total abundance of krill. The Scientific Committee of CCAMLR recognises that the predator criterion of 0.75 may need to be altered as more information on the food requirements of predators becomes available (de la Mare, 1996).

The requirement for CCAMLR to maintain the ecological relationships in the Antarctic ecosystem implies that the ecosystem should, by and large, be able to absorb the consequences of fishing without major changes in the strengths of natural interactions discussed in Figure 1. There are a number of points pertinent to determining a target status of the ecosystem. First, removal of fished species results in the removal of production in the system and, therefore, reduces the potential for production amongst higher-order predators. If the system was in equilibrium then the carrying capacity of the environment for the higher order predators would be reduced. Second, the objectives imply that reductions of the magnitude considered appropriate in managing single-species fisheries, say to 50% of pre-exploitation levels, is likely to be inappropriate for such predators, although CCAMLR may decide that some predators may be subject to such criteria. Third, some predators of the fished species may be in need of explicit conservation efforts to enable recovery, e.g. the great whales. The trajectories of these populations should be upwards towards some target levels while the other predators remain at the same level or would be expected to decrease over time toward a lower acceptable target level given the overall reduced abundance of the fished species.

Given the predator criterion for determining catch limits of krill described above, a simple expectation would be that abundances of predators solely dependent on krill would eventually be reduced by approximately 25%, provided that per-capita productivity of krill and maximum per-capita productivity of the predators remained unaltered at these new equilibria (but see Mangel and Hofman (1999) for further discussion). However, it is the productivity of predators attributed to krill consumption that would be reduced by 25%, and most predators do not rely solely on krill.

The consequences for the current abundance and overall productivity of predators and the structure of the food web generally are contingent on a number of factors, including: (i) the degree to which predators are obligate foragers on krill (i.e. abundance may not decline if the predator switches diet), (ii) the availability of other prey to replace the lost production of krill (i.e. if the predator switches diet and the new prey species has used the surplus production available from removal of the fished species then no other alterations in the food web might arise), (iii) the degree to which a predator population can absorb a reduced food supply (i.e. a reduction in fished species might not cause a consequent reduction in reproductive success or increase in mortality because, prior to fishing, consumption exceeds the amount of food required to maintain critical population processes), (iv) whether there is an exploitable surplus of the fished species in the system, (v) the ability of a predator to compete for food with other predators and the fishery, and (vi) the relationship between prey availability and predator production may be non-linear. In addition, the consequences for the food web generally will depend on the overall abundance of individual predators and their individual roles as consumers of and competitors with other species, which could lead to unexpected indirect feedbacks (positive and negative) to species of interest (Yodzis, 2000). The situation is made more complex when a number of prey species are being harvested. Combined, these factors potentially make the abundance and overall production (in number or biomass) of species relatively insensitive indicators of the effects of fishing on the ecosystem.

Operational objectives for dependent species (not directly affected by the fishery) will need to encompass the general effect of lost production and ensure that the lost production does not have an unacceptable disproportionately large effect on any one dependent species, including the potential for flow-on effects in the food web.

Thus, what would be an operational objective for the ecosystem to encompass the need to maintain ecological relationships and to allow for the recovery of some species? Also, are there target levels of abundance or some other measure that might be appropriate for dependent species that help protect these predators from being classified as needing special recovery measures?

In the general case, the assumption is that the catch limits are derived with sufficient confidence that the median annual predator production arising from the consumption of fished species will not be reduced by more than the expected reduction in median biomass of the target species, although this may be modified according to the expected increased production of recovering species. In terms of maintaining ecological relationships, is there a minimum level of predator production arising from the consumption of fished species necessary to provide relative stability in or maintenance of the food web?

Both of these elements can be combined into an operational objective that aims to maintain the predator production arising from the consumption of fished species at or above some limit reference point. A subsidiary objective would be to ensure that the productivity of individual predator species is not disproportionately affected even though the overall objective is satisfied. The expected outcome of these objectives is that the contributions of different species to the food web structure would remain largely unaltered through fishing, thereby maintaining ecological relationships in the system. This will result in attention being given to the primary interaction between fished species and their predators rather than examining the consequences of secondary and other indirect interactions distant in the food web from the fished species.

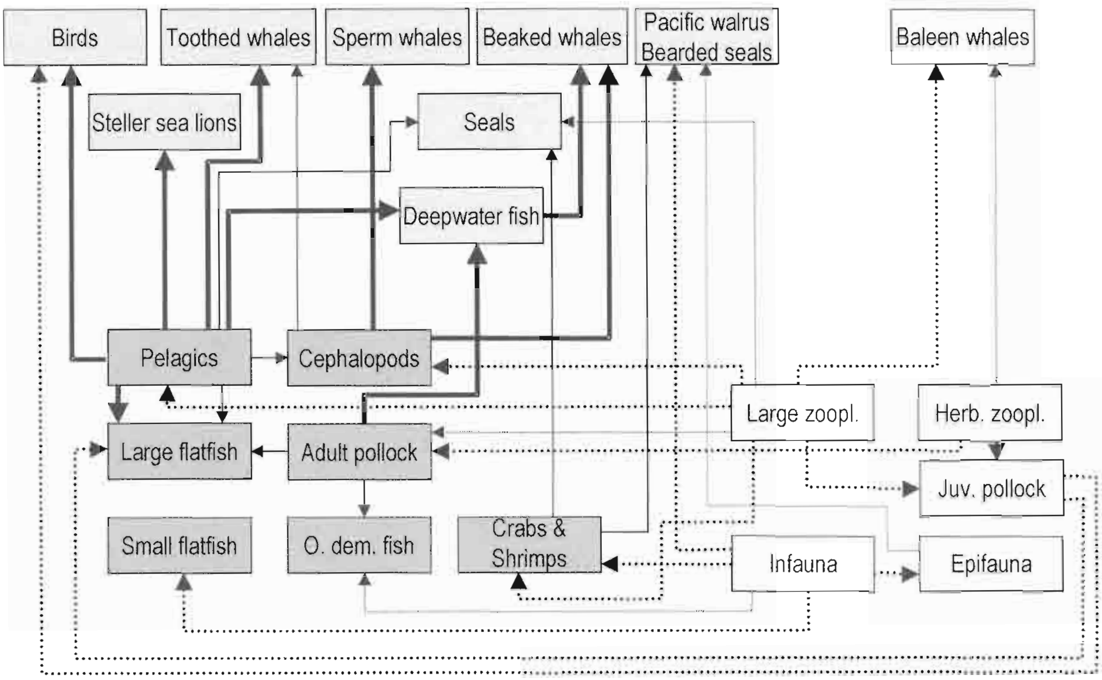

Figure 4: Food web of the Eastern Bering Sea showing primary interactions with fished species along with other marine mammals and birds (based on data and taxonomic groups from Trites et al., 1999). Fished taxa are indicated by dark grey boxes (O. dem. = other demersal). Predators of fished taxa are in light grey boxes. Other taxa are in white boxes (herb. = herbivorous, zoopl. = zooplankton, juv. = juvenile). Arrows indicate direction of prey to predators. Solid lines indicate predation on fished species, dotted lines indicate predation on non-fished species. The heavier weighted lines indicate where prey make up at least 50% of the diet, lighter lines are where prey make up at least 20% but less than 50% of the diet. Interactions where prey make up less than 20% of the diet are not shown.

This approach recognises the hierarchy of objectives relating to the effects of fishing on the productivity of a system and the potential for changes to the food web. It can easily be made general for systems much more complex than the Antarctic and for which fisheries are already present. For example, the Eastern Bering Sea ecosystem has been examined for its food web dynamics (Trites et al., 1999). This is a system in which many species are exploited and for which there are complex dynamics between fished species as well as between predators of these species and other types of prey species (see Figure 4). This system provides a useful illustration of how the general objectives discussed for the Antarctic system may be applied elsewhere.

The Eastern Bering Sea ecosystem illustrates how an ecosystem can be subdivided into a number of groups. The first group is the taxa comprising fished species. This group is a managed system, where all species presumably have target levels or threshold reference points applicable to them. In that context, it is a contrived system in which the abundance of each species could be manipulated in a variety of ways by varying the harvest strategies on each of the taxa. The second group comprises the dependent predators of fished species. The effect of fishing on this group can be considered as a whole, i.e. the effect of lost production in the system, or could be subdivided to explore the effects on individual species or groups of species. The third group is the prey of fished species and/or alternative prey of those predators. These taxa might assume greater importance in the diet of predators and/or might increase their productivity as a result of reductions in abundance of their predators and competitors. The fourth group is the predators of the non-fished prey species in the third group. The response of these predators would be difficult to foreshadow without good knowledge of the function of the food web.

The strengths of interactions between species in this system indicate that the system could be divided into a number of management units. For example, the primary effect of fishing for crabs and shrimps could be isolated relatively easily, as could the effect of fishing for cephalopods. Similarly, flatfish and other demersal fished species seem to be prey mostly for other fished species.

The fishery with the widest implications for the food web would be for pelagic species. In this coarse overview of the system, monitoring for the primary effects of fishing on the food web would involve five different higher order taxa. So what types of information would be required to evaluate the effects of lost production on predators of fished species and how could this information be combined taking into account the uncertainties on the dynamics of the food web?

Background to a Production Model

Production of a species in a given year is related to the accumulation of biomass through growth of individuals and reproduction. Production $P_{p,y}$ (in mass) of a predator, p, in a given year, y, can be represented by the following equation, which includes variation in some parameters with age, a,

$$P_{p,y} = R_{p,y}\hat{B}_{p,0,y} + \sum_{a>0}\int_0^1 N_{p,a,y}(t)\hat{B}_{p,a,y}(t)G_{p,a,y}(t)dt \tag{1}$$

where $N_{p,a,y}$ is the number at age in that year, $\hat{B}_{p,a,y}$ is the individual mass of the predator at age in that year, $G_{p,a,y}$ is the age-specific growth rate of individuals, $R_{p,y}$ is the number of offspring (age 0) in that year (for simplicity below, recruitment is assumed to occur at end of the year, although growth during the year can be accommodated within the summation term as required), and t is the proportion of the year passed.

The rate of change of $N_{p,a,y}$ during the year is given by

$$\frac{dN_{p,a,y}}{dt} = -M(p,a+t)N_{p,a,y} \tag{2}$$

where $M(p,a+t)$ is an age-specific function of natural mortality.

Production can be related back to total consumption of prey, $C_{p,y}$, by accounting for the metabolic and other energetic costs of producing measurable biomass, $E_{p,y}$, and the proportion of food assimilated, $A_{p,y}$, such that

$$C_{p,y} = \frac{P_{p,y} + E_{p,y}}{A_{p,y}} \tag{3}$$

Combining equations (1) and (3), consumption can be defined using energetic models in terms of the size of the population, the mass of an individual, the overall reproductive output and growth rate of the individual:

$$C_{p,y,Total} = \frac{\hat{R}_{p,y} + \hat{G}_{p,y}}{A_{p,y}}$$

and

$$\begin{aligned}
\hat{R}_{p,y} &= r_{p,y}R_y\hat{B}_{0,y} \\
\hat{G}_{p,y} &= \sum_{a>0}\int_0^1 N_{a,y}(t)\hat{B}_{a,y}(t)\left(m_{p,a,y}(t) + g_{p,y}(t)G_{a,y}(t)\right)dt \\
A_{p,y} &= \sum_{i=1}^{D} d_{p,y,i}A_{p,i}
\end{aligned} \tag{4}$$

where $g_{p,y}$ is the predator-specific cost of producing one unit of mass, $r_{p,y}$ is the predator-specific cost of producing one offspring in that year, and $m_{p,a,y}$ is the predator-specific metabolic cost of maintaining one unit of mass in animals of that age including the basic metabolism, costs of foraging and other factors. For an individual prey species, i, the contribution to predator production is governed by its proportion (mass) in the diet, $d_{p,y,i}$, as well as its food value with respect to other prey, which is the value of $A_{p,i}$, the assimilated proportion of an ingested species. The products of these are summed for all species in the diet, D. For many species, the denominator is equal to 1 because of an assumption of equal food value of all prey.

General Considerations in the Application of a Production Model

Marine ecosystems are not static; they are extremely variable from year to year. Consequently, the productivity of predators is expected to vary from one year to the next and the consequences for the populations of predators of a changing food supply will depend on how predator production relates to the various autecological (life-history, metabolic and foraging) processes of the predator over the course of a number of years of varying prey production coupled with potential variations in the dependence of the predator on the prey. Understanding this variability has been problematic and construction of suitable autecological models may take many years. Given this naturally varying and complex system and the potential for the system to undergo long-term changes in its average production as a result of climate change (e.g. the Antarctic marine ecosystem – de la Mare, 1997; Constable et al., in press), an approach is needed that takes account of a number of issues.

First, the average production of a prey species and its consumption would be expected to remain relatively constant in a relatively stable system even though production may vary from one year to the next. If the environment is changing, then the prey species may assume greater or lesser importance in the system depending on the changes in secondary production as well as changes in the interactions of predators with prey species. Second, conservation objectives must be met for some species, e.g. great whales, whose recovery requires an allocation of production to them. In both cases, there is a need to identify target levels for the system that take account of these potential future states, or at least provide the tools for monitoring them. Last and most importantly, the approach must be robust against the lack of knowledge about the role of some species in the food web. For example, squid, mesopelagic and bathypelagic fish are mostly unknown quantities in the Antarctic food web. The amount of krill production that they consume combined with the potential secondary feedbacks that may arise through their role as alternative prey species are unknown. Consequently, the effect of krill fishing on the abundance of some land-based predators that feed on a combination of krill, squid, and mesopelagic and bathypelagic fish may be difficult to predict.

Reference Points and Indicators Based on Production

The effects of fishing on food webs will be most easily observed for species most directly interacting with the fished species, i.e. the predators or competitors of fished species. In the following discussion, the terms 'predators' and 'dependent species' will be used interchangeably to refer to those species that are the predators of species caught in the fisheries. Understanding and monitoring of second-order effects, such as higher-order predators, is not discussed in this paper.

Reference points based on production will naturally be derived in some way from production and/or consumption equations. The needs of predators are often considered in terms of the consumption of prey (e.g. Everson and de la Mare, 1996). However, while the relationship between consumption and production given in equation (4) may be relatively unaffected by $r_{p,y}$ and $g_{p,y}$, because these parameters may be relatively constant from one year to the next, interannual variation in $m_{p,y}$ could significantly influence the relationship. This is because the amount of energy expended obtaining food may be dependent on food abundance and patchiness, and on foraging tactics employed in a given year by each age class such that the relationship between consumption and production may be non-linear, i.e. increased foraging may conceivably yield the same consumption but with increased metabolic cost when the food is reduced to low abundance and/or it becomes patchily distributed. As a result, objectives and reference points based on consumption (or overall prey abundance) may not be helpful in practice because predator production may decline even though consumption may appear stable.

In most systems, the initial reference points for dependent species include the current status combined with recovery of some species. For example, species dependent on krill in the Antarctic include largely unaffected species of seabirds as well as species of whales and seals that are in the process of recovery. If a system was largely unaffected by exploitation or some other disruption to the food web (such as pollution), then the current average status of predator production could be considered the baseline and a limit reference point could be derived as some proportion of this. In systems already affected by exploitation, that proportion for a limit reference point would vary depending on the degree to which recovery of species was required. It is conceivable that in some systems requiring recovery of most species, the limit reference point may be greater than the current average production.

An Illustrative Model

A simple food web model has been constructed to illustrate the development of the operational objectives. It is based on the approach presented by MRAG Americas (2000). The mathematical formulation of the model is presented in the appendix.

The model comprises two trophic levels consisting of two prey species and three predators. The values of the parameters used in the model are

Table 1: Parameter values used in the illustrative food web model described in the text and for which the formulation is given in the appendix.

Prey Characteristics		**Prey 1**	**Prey 2**	
Annual carrying capacity of primary production	Mean	10000	10000	
	CV	0.45	0.3	
Natural mortality (year^{-1})		0.3	0.3	
Maximum per-biomass recruitment		0.4	0.5	
Competition with the other prey species		0.3	0.3	
Predator Characteristics		**Predator 1**	**Predator 2**	**Predator 3**
Maximum per-capita recruitment (Age 0)		0.1	0.1	0.1
Degree of density dependence in recruitment (typical for marine mammals – MRAG Americas, 2000)		2.4	2.4	2.4
Age at maturity (years)		8	8	8
Plus class		10	10	10
Natural mortality (year^{-1})	Recruits	0.07	0.07	0.07
	Adults	0.03	0.03	0.03
Body growth [Length = L_∞(1-exp(-K.age))]	L_∞	1	1	1
	K	0.8	0.8	0.8
Length to weight conversion (a.Length^b)	a	0.1	0.1	0.1
	b	3	3	3
Competition coefficients	with Predator 1	1	0.5	0.1
	with Predator 2	0.5	1	0.1
	with Predator 3	0.1	0.1	1
Selectivity of prey (Diet 1 given here)	Prey 1	1.0	0.5	0.2
	Prey 2	0.2	0.5	1.0
Food value of prey species	Prey 1	1	1	1
	Prey 2	1	1	1

given in Table 1. One of the prey species, Prey 1, is targeted by a fishery. The two prey species vary in abundance as a result of natural mortality and recruitment which varies according to stochastic changes in the environment. The two prey species are in competition. The model is constructed in a way that the predators do not directly affect the abundance of prey. It is assumed that the predators satisfy their requirements as part, not all, of the removal of prey which corresponds to the rates of natural mortality.

The three predators have different degrees of reliance on the target prey species. Predator 1 is the predator that is the focus of the model here, and it primarily relies on the target prey species. Predator 2 has equal prey selectivity between the two prey species, while Predator 3 depends mostly on the non-target prey species. Although the model can be used to simulate different demographic, body growth and reproductive parameters, these model parameters are the same for all three predator species. The only differences between species are diet selectivity and the degree of competition between them. Predator 1 and Predator 2 are in greater competition between each other (0.5) compared to either of the competitive interactions between these species and Predator 3, which are equal (0.1), indicating the greater degree of overlap between those two species and the respective isolation of Predator 3 in the food web.

The simulation is seeded with initial values for each of the five species and run for 500 years before a trial begins. The trial is run for 100 years with fishing beginning in year 50. Fishing is characterised by a constant catch of 50 biomass units of Prey 1 each year. This approach is used because the Antarctic krill fishery is currently managed by determining a long-term constant annual yield (Constable et al., 2000). The amount was selected to deplete the stock in 20–30 years, which is the critical period over which the system should not be irreversibly changed by fishing (Constable et al., 2000) and enables different estimated parameters to be examined for their utility in helping avoid such an outcome.

Three trials were undertaken to examine the effects of differences in the diet of Predator 1. The parameters altered were the degree of selectivity by Predator 1 of Prey 1 and of Prey 2; Diet 1 had selectivities of 1.0 and 0.2 respectively; Diet 2 had 0.7 and 0.3; Diet 3 had 0.5 and 0.5. The same random number sequence is retained in each trial to facilitate direct comparisons of results.

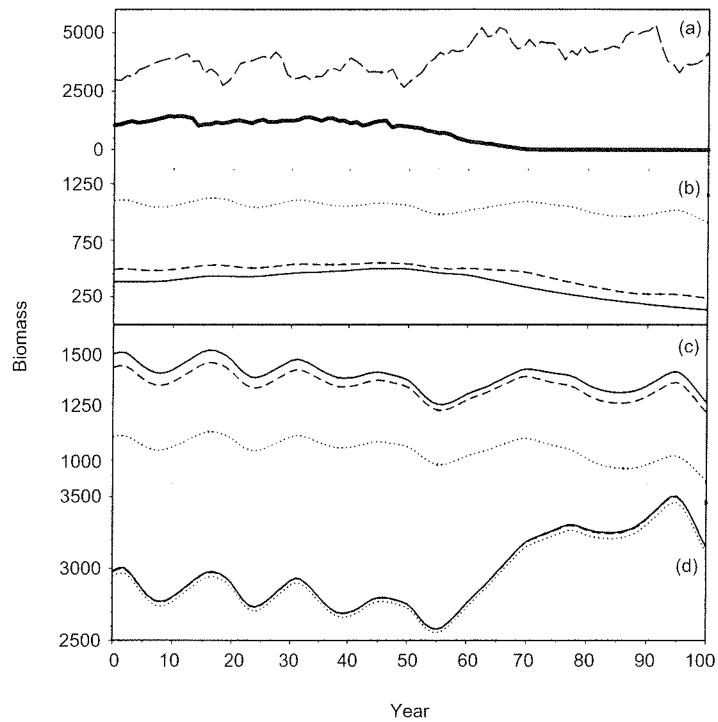

Figure 5: Biomass trajectories of predators and prey over 100 years in a simulated food web under three different scenarios of diet in Predator 1. Predator trajectories for three diets of Predator 1 with respective selectivity of prey species 1 and prey species 2 being 1.0 and 0.2 for Diet 1 (solid line), 0.7 and 0.3 for Diet 2 (dashed line), and 0.5 and 0.5 for Diet 3 (dotted line). (a) Biomass of prey species 1 (solid line) and 2 (dashed line). Prey 1 is the target species, 50 biomass units of which are removed each year, if possible. (b) Predator 1, (c) Predator 2 with selection values of prey species 1 and 2 being 0.5 and 0.5 respectively, and (d) Predator 3 with selection values of prey species 1 and 2 being 0.2 and 1.0 respectively (see text for details).

The time series of biomass of all species in these trials are given in Figure 5. The time series for prey species do not vary between trials. The fishery depletes Prey 1 to zero after 20 years. Prey 2 is more abundant (~3x) than Prey 1 in the absence of fishing and then increases its mean abundance over 10 years after the fishery begins as a result of the reduction in its competitor. As expected, the trajectory of Predator 3 is relatively insensitive to the changes in the diet of Predator 1 and alters directly in response to the changes in Prey 2. The time series of abundances for Predator 2 appear mostly influenced by the time series of Prey 2 with some noticeable affects of the decline of Prey 1 when compared to the trajectory of Predator 3. However, in the absence of knowledge on Predator 3 it could be construed that Predator 2 was unaffected by fishing. The magnitude of abundance of Predator 2 is directly influenced by the diet of Predator 1, reflecting the relationship between the degree of competition occurring between the species and the diet composition of Predator 1. When Predator 1 has the same diet as Predator 2 the time series of these two species are the same, with Predator 1 increasing in abundance compared to other trials and Predator 2 decreasing in abundance. For both Predators 1 and 2, there is little difference between Diets 1 and 2.

In this simple model, recruitment is the only population parameter to vary each year as a result of changes in prey abundance due to all other parameters being equal. Thus, recruitment is used as an index of annual production in this simulation. Per-capita recruitment for each trial is shown in Figure 6, and productivity for each predator (number of new recruits) in the trial with Diet 1 for Predator 1 is shown in Figure 7. Notably, per-capita recruitment differs little between Predators 2 and 3 and between each trial, indicating the relative insensitivity of this parameter in species for which diet is mixed. The results for Predator 1 show that Diet 2 is sufficient to sustain per-capita recruitment until the target prey species has all but disappeared.

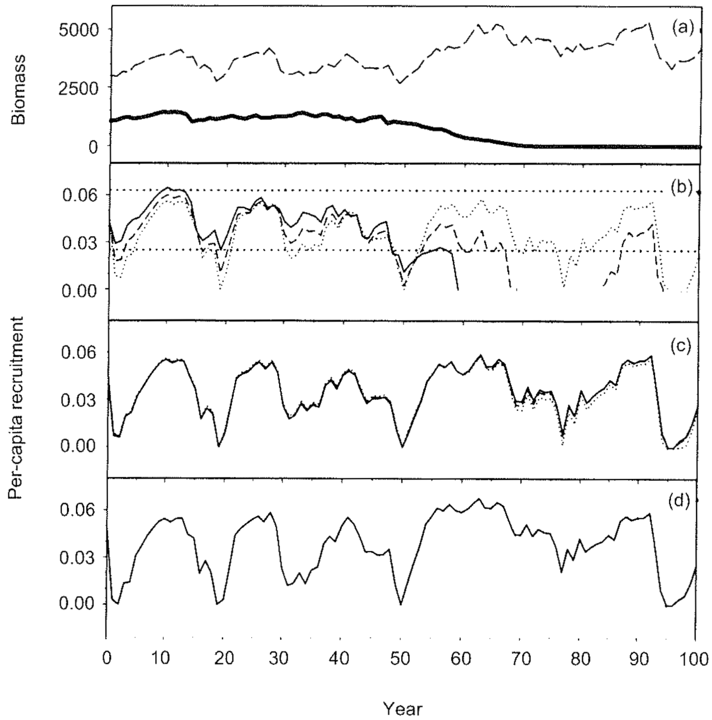

Figure 6: Per-capita recruitment for each predator in the food web model. Lines and panels are as for Figure 5. Panel (a) is shown for reference. The horizontal dotted lines in (b) reflect the critical range of values for Diet 1 for Predator 1; values outside the range are considered by CCAMLR to be anomalous years (see text for details).

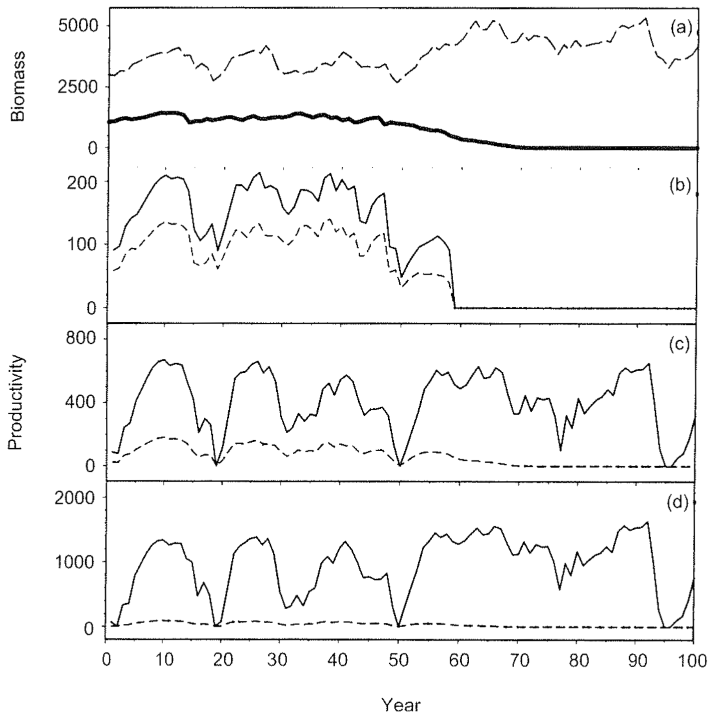

Figure 7: Individual productivity for each predator in the trial with Diet 1 for Predator 1, in which the target species is the primary prey species. Panels are as for Figure 5. Panel (a) is shown for reference. Solid lines indicate total productivity; dashed lines indicate predator productivity arising from the consumption of fished species, P.

Developing Operational Objectives for Predator Production

As discussed previously, the operational objectives need to focus on limit reference points for predator production arising from the consumption of fished species rather than overall production of predators of fished species. An index of such production can be developed in the following way. For a predator, p, in a given year, y, the production arising from the consumption of fished species, $\tilde{P}_{p,y}$, can be specified as a fraction of the overall production of the predator, such that

$$\tilde{P}_{p,y} = \frac{\sum_{j=1}^{F} d_{p,y,j} A_{p,j}}{\sum_{i=1}^{D} d_{p,y,i} A_{p,i}} P_{p,y} \tag{5}$$

where F is the number of species that are caught in fisheries, i.e. fished species. Clearly, $\tilde{P}_{p,y}$ would equal zero if no species in a predator's diet were being caught in a fishery because all $d_{p,y,j}$ would be zero. In practice, the assimilation efficiency, $A_{p,i}$, would be assumed to equal 1. This would make the denominator equal to 1 and the equation is simply the fraction of the diet comprising fished species, such that

$$\tilde{P}_{p,y} \approx \sum_{j=1}^{F} d_{p,y,j} P_{p,y} \tag{6}$$

The overall sensitivity of the approach to this assumption could easily be tested in the simulation framework, however this is not discussed here.

Figure 7 uses the results of the illustrative model to show what part of the total production (annual recruitment) can be attributed to fished species, i.e. Prey 1. It can be seen for each predator that the amount of production arising from the consumption of fished species is proportional to the dietary composition.

The production in the whole food web arising from the consumption of fished species in year, y, would be

$$W_y = \sum_{p} \tilde{P}_{p,y} \tag{7}$$

The summation applies to all potential predators of fished species in the system because the number of predators of fished species may vary from one year to the next, such that there may be more predators of fished species in years when those prey are abundant.

For the illustrative model, the production arising from the consumption of fished species for all predators is compared to the total production in Figure 8. In both cases, the results are relatively insensitive to the different diets of Predator 1, unlike the time series of the biomass of individual predators and per-capita recruitment.

The use of productivity as an indicator of food web status relative to the status of the fished species was further explored by applying the CCAMLR approach for detecting anomalies in time series (SC-CAMLR, 1996) but updated according to the method of de la Mare and Constable (2000). This method uses a randomisation procedure to determine critical values of the estimated parameter, which in this case are, respectively, production and per-capita recruitment. Once determined, the critical values prescribe a range outside of which values have only a 5% chance of occurring and are called anomalies if they arise. It is considered that a series of anomolies would require the harvesting strategy to be altered. The critical ranges for per-capita recruitment for Predator 1 (Figure 6b) and W (productivity arising from the consumption of fished species – Figure 8c) were determined based on a 20-year observation period just prior to fishing (a length of time consistent with existing monitoring programs – Constable et al., 2000). These were only estimated for Diet 1 when Predator 1 was most dependent on the target species.

This analysis indicates equivalent results for management procedures based on either the per-capita recruitment of Predator 1 or W when Predator 1 is mostly dependent on the target species. In this case, the time series of these parameters moves below the critical range and becomes permanently anomalous after 10 years and prior to the elimination of the target species. However, a small change in the diet of Predator 1, i.e. to Diet 2, could lead to per-capita recruitment of Predator 1 being relatively insensitive to the effects of fishing on Prey 1 until after the disappearance of the target species. Most predators in the Antarctic are not obligate feeders on krill. Consequently, the scenario of Diet 2 may be a realistic one and raises concerns about the utility of per-capita recruitment as an index of food web status.

So, how might a set of reference points be developed without simply relying on when the state of the system may appear to be anomalous?

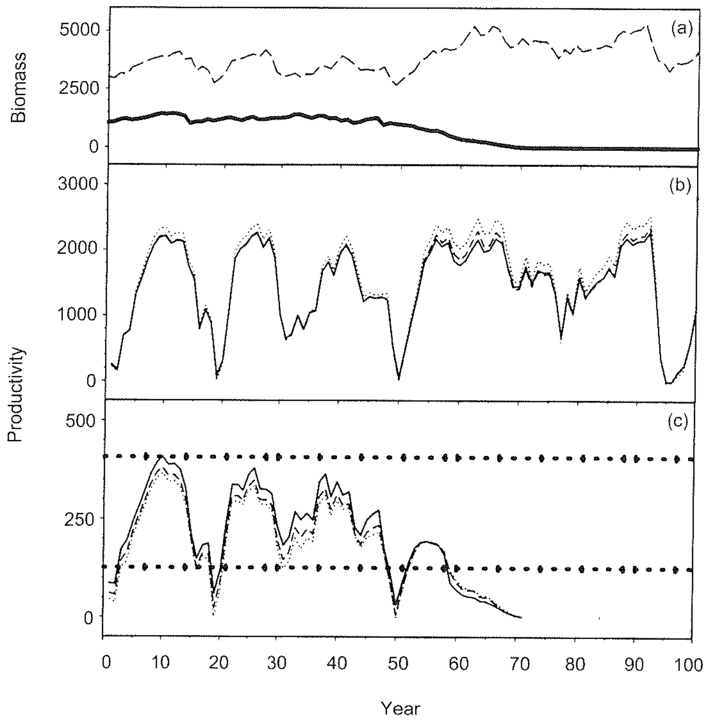

Figure 8: Productivity integrated for all predators for each of the diet scenarios shown in Figure 5 (the same line types are used). (a) Prey biomass for reference, (b) total production for each scenario, (c) production arising from the consumption of fished species, W. As in Figure 6, the horizontal dotted lines are the critical bounds for Scenario 1; values outside this range are considered by CCAMLR to be anomalous.

Prior to exploitation or for a recognised initial baseline period in an exploited system, the average production in the food web arising from the consumption of fished species would be

$$W_0 = \frac{\sum_{y=1}^{Y} W_y}{Y} \tag{8}$$

where Y is the number of years in the time series to estimate the mean production with reasonable precision.

After fishing begins, the acceptable degree of change (limit reference point/threshold) in production arising from the consumption of fished species, designated as a proportion, a_W, of W_0, would depend on the objectives for individual species. For a given predator, the average production arising from the consumption of fished species during the baseline period would be the reference level. The limit reference points for individual predators would be a proportion of this a_p. In most systems, production arising from the consumption of fished species may be expected to be reduced by the same amount in each predator, such that the proportion for an individual predator, a_p, would be equal to a_W, and be less than one. For predators that require recovery, the proportion, a_p, will need to be greater than 1. The actual value for each predator will depend on the conservation requirements and target level of recovery for that species as well as its dependency on the fished species.

Thus, rearranging equations (7) and (8), the limit reference point for average production arising from the consumption of fished species and combined for all predators during the fishing period would be

$$W_{ref} = \sum_{p} \left[a_p \frac{\sum_{y=1}^{Y} \tilde{P}_{p,y}}{Y} \right] = a_W W_0 \tag{9}$$

From this, the subsidiary objective for individual predators would be to maintain average production arising from the consumption of fished species during the period of fishing above a threshold level prescribed by

$$\tilde{P}_{ref,p} = a_p \frac{\sum_{y} \tilde{P}_{p,y}}{Y} \qquad (10)$$

This formulation of a threshold status of the food web relative to the fished species explicitly provides for both dependent species as well as for the recovery of other species, which has only been considered by CCAMLR in a general sense (de la Mare and Constable, 1990). Importantly, it provides an approach for monitoring changes in an ecosystem that are directly consistent with the effect of fishing – reduced production in predators of fished species. Variation in the overall index, W_y, would be expected to be much less than variation that might arise in production of individual species, $\tilde{P}_{p,y}$. This is because the importance of fished species in the diet will vary among predators and this will vary between years with little positive correlation between the diets of predators. Thus, the overall consequences of lost production from the system will be more easily highlighted by using W_y. Of interest to managers would be whether the production in an individual predator arising from its consumption of fished species is undergoing a long-term change, either through changes in the abundance of the predator or through switching of the diet. Both types of changes will potentially have consequences for the food web. Thus, evaluation of trends in $\tilde{P}_{p,y}$ will be an important part of the assessment process.

WHAT APPROACHES COULD BE CONSIDERED FOR ACHIEVING THE CONSERVATION OBJECTIVES?

The current approaches in CCAMLR for achieving conservation objectives are described in Constable et al. (2000) and include:

(i) assessments of precautionary yield using the predator criterion (discussed above);

(ii) monitoring the ecosystem; and

(iii) undertaking ecosystem assessments.

To date, CCAMLR is still to develop methods that incorporate ecosystem assessments into a management procedure (Constable et al., 2000).

The development of any approach requires: (i) specification of clear operational objectives, (ii) designation of performance criteria for evaluating management procedures and actions, (iii) specification of alternative management procedures, each of which includes fishing controls, monitoring, as well as decision rules for altering fishing controls or monitoring, and (iv) prospective evaluation of management procedures to determine which satisfy the performance criteria (de la Mare, 1986b, 1996; see also Cooke, 1999; Smith et al., 1999).

This section provides an initial framework for developing parts of a management procedure for fisheries based on predator information. It is designed to be complimentary to the developments in the precautionary approach to managing target species discussed above. The decision rules applied to krill in CCAMLR are similar to the types of rules needed for predators, i.e. to establish target levels for the central tendency of the productivity of the food web (e.g. median at the end of a specified management period) combined with threshold levels indicating extreme undesirable states.

Operational Objectives

The section above articulates how an objective (target level) can be formulated for average production arising from the consumption of fished species. Such an operational definition helps discern which parameters are centrally important to assessments of the status of the system in relation to the fished species and how various kinds of parameters and different predators may be given appropriate statistical weights in the assessment process. This overcomes the difficulty of trying to formulate ecosystem objectives in terms of abundance of species or other parameters, knowing that many factors other than lost production of fished species might influence these parameters.

Performance Criteria

Performance criteria are used to evaluate management procedures (see de la Mare, 1996 for detailed discussion of performance criteria). An operational objective based on production provides a framework for determining ecologically important events (years) in a time series (de la Mare and Constable, 2000) that relate directly to the impact of fishing on the food web. W_{ref} provides a theoretical foundation for testing the status of the system each year and over a series of years. Thus, W_y can be used as a performance measure when prospectively evaluating a management procedure (see below) by determining how far W_y might deviate from the target level of W_{ref} given various harvest and other management strategies.

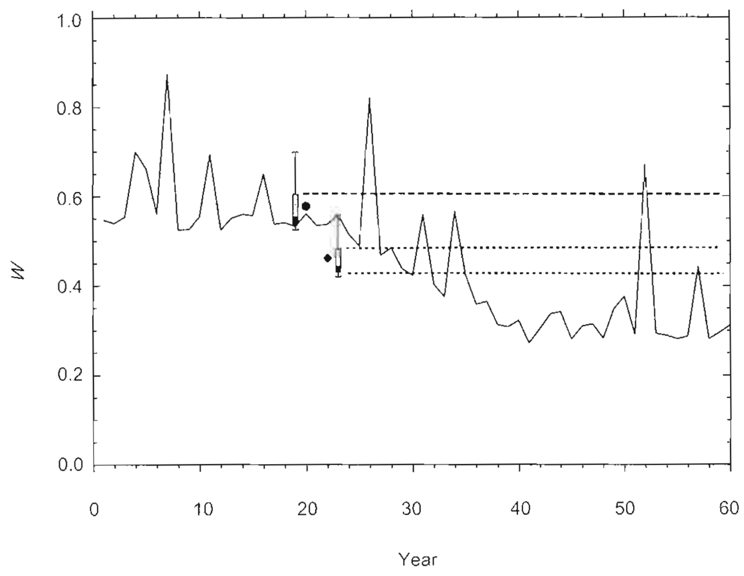

Figure 9: Hypothetical time series in W over 60 years. No fishing occurred in the first 20 years, over which time a baseline W series was used to estimate W_0 (solid circle). $W_{ref} = 0.8\ W_0$; ($a = 0.8$ for all species) (solid diamond). The box and whisker plots show the frequency distribution of W during that baseline period. The box and whiskers adjacent to W_0 show the relationship between the mean and the distribution of values. This relative distribution is applied as the expected distribution around W_{ref} during the management period. The upper and lower dotted lines show the critical upper and lower range limits, W_H and W_L, discussed in the text for a case when the critical acceptable frequency outside the limit is $\phi = 0.25$. The dashed line refers to the interim upper range limit, W_{iH}, during the period when the system is adjusting to the fishing activity. In this example, the trend for W to remain below the lower range limit after 16 years of fishing would signal that a reduction in fishing was required.

Figure 9 provides a hypothetical time series of W_y and how it might change after a baseline period. In this case, the baseline period is for a period of no fishing. Over many years of fishing, the average state of predator production arising from the consumption of fished species would be expected to approach W_{ref}. Performance criteria usually relate to the central tendency of the characteristics of the management system, including the median status as well as the variation. Critical levels are also of interest. Such levels for ecosystems may relate to characteristics that would be precursors to shifts towards new stable states from which the original system is unlikely to be restored through the cessation of fishing alone.

A number of performance measures may be developed in relation to these aims. The first measure would be the deviation of the average W during the management period following the baseline period, W_m, from W_0. A second performance measure could be the deviation of the coefficient of variation (CV) for W_m from the CV for W_0. Given these two performance measures, a successful management procedure could be one that results in maintaining W_y with a central tendency around W_{ref} and a CV similar to that for W_0 (Figure 9).

Other performance measures may be developed to determine whether the range of W_y exceeds critical limits during the management period. Such measures could be specified in two parts, indicating upper and lower range limits according to the frequency distribution of values of W_y relative to the average value. The range limit could be set according to the critical maximum acceptable frequency, ϕ, of exceeding the limit such that a lower range limit W_L could be set as

$$W_L = W_{crit} - \left(\bar{W}_0 - W_{l\phi}\right) \tag{11}$$

where $W_{l\phi}$ is the value of W corresponding to the lower percentile, $l\phi$, of the distribution of W during the baseline period.

The upper range limit could be determined in the same way such that

$$W_H = W_{crit} + \left(W_{h\phi} - W_0\right) \tag{12}$$

where $W_{h\phi}$ is the value of W corresponding to the upper percentile, $h\phi$, of the distribution of W during the baseline period. In the early years of fishing during the management period, the upper range limit may be more appropriately set in reference to W_0 rather than W_{ref} in order to detect if the production arising from the consumption of fished species was increasing, indicating that the system was changing in ways not accounted for in the baseline monitoring period prior to fishing. Thus, an interim upper limit during the early years could be

$$W_{iH} = W_{h\phi} \tag{13}$$

The performance of a prospective management procedure can be judged by comparing the frequency at which W_y exceeds the range limits during the fished period with the expected frequencies of $l\phi$ and $h\phi$. As for the decision rules underpinning the precautionary approach to determining krill yield described above, a second performance criterion would be concerned with the expected median of W at the end of the management period.

Decision Rules

Decision rules need to identify how assessments will signal when action may be required to alter harvest strategies in order to restore production to predators or to avoid unacceptable consequences to the food web. Similarly, the decision rules can be structured to increase harvesting if predator production appears able to accommodate it.

Given the approach using productivity, decision rules could be formulated in a similar way to the performance measures described above, however they would take into account the limitations of and errors arising from a field monitoring program and the assessment process. The success of using the formulation of W is dependent on the robustness of the estimates of production, which is governed by the ability to estimate some of the key parameters in the formulae. If W is found to be robust, then this may be the avenue for providing a feedback management procedure for predators without depending on complex predictive models. Such feedbacks might facilitate updating models used in assessments and/or the characterisation of the ecosystem.

An important task is to determine if overall production can be approximated using basic parameters such as predator density over a relatively large scale, interannual variation in the average biomass of individuals and recruitment density. For example, it may be possible to monitor a few colonies for only a limited time during the year and estimate production coarsely by summarising equation (2) to the form

$$P_{p,y} = R_y \hat{B}_{0,y} + \sum_{a>0} N_{a,y}\left(\hat{B}_{a,y} - \hat{B}_{a,y-1}\right) \tag{14}$$

and inserting this into the system of equations to determine W. Also, it may be necessary to monitor the average mass of individuals at key times.

In addition, some predators may not be able to be sampled for logistic, ethical or other reasons. Thus, the utility of decision rules based on W for use in a management procedure will need to be evaluated to determine whether they are robust against uncertainties arising from errors in the estimates of parameters or W and for the likely case of sampling being limited to a subset of predators of fished species.

CONCLUDING REMARKS

Some approaches to ecosystem management require detailed and complex information. A simpler approach may be one that is based on predators that are eating primarily fished species. Once the relative importance of predators is known, the accumulation of recruiting biomass, the change in average mass of an individual adult and the proportion of fished species in the diet may be all that is required from year to year. The approach proposed here takes account of uncertainties in knowledge of the structure of ecosystems. P and W potentially provide useful indicators for management purposes because they integrate across a range of 'ecosystem' effects and, as formulated here, can also be related directly to the effects of fishing. These features are currently unavailable in ecosystem approaches to managing fisheries, which do not weight input data for assessments, such as per-capita breeding success, according to the relative influence of fished species on those estimates.

An important issue to be examined in developing this approach is whether a management procedure can be developed that is sufficiently robust to the sampling errors and limitations of a field monitoring program required to estimate the parameters. Some predators will not be able to be monitored for logistic, ethical or other reasons and some parameters may not be easy to estimate. These aspects of the monitoring program will need to be evaluated prior to the implementation of a management procedure based on this approach. Simulation modelling to prospectively evaluate the utility of different management approaches need not be complex, at least in the first instance, such as the model presented here and models developed elsewhere to address marine fisheries issues (e.g. Mangel, 2000; MRAG Americas, 2000).

The management approach presented here can be generalised for existing fisheries as well as new fisheries because it simply requires a baseline monitoring period and the establishment of limit reference points relative to the baseline, which can take account of the need for the recovery of species as well as for reduction in production of some species. A satisfactory length of baseline period will need to be determined as part of the evaluation of the robustness of the management procedure.

An important feature of this approach is that it could help determine if the removal of fished species causes predicted changes in productivity of the predators of those species and how such changes translate to changes in the nature of the food web, both for the abundance of individual predators as well as changes in the diet of those predators. Consideration will need to be given as to how such changes may be unambiguously interpreted. For example, an experimental design with open and closed fishing areas may be useful in this context (Constable, 1991).

Lastly, a key goal of managing fisheries is to maintain ecological relationships. In that context, the elaboration of the approach proposed here will help focus attention on determining the minimum level of production that needs to arise from the consumption of fished species in order to provide relative stability in or maintenance of the food web.

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b) production totale pour chaque cas, c) production due à la consommation de l'espèce exploitée *W*. Comme sur la figure 6, les lignes horizontales en pointillés sont les limites critiques du cas 1. Les valeurs situées en dehors de cet intervalle sont considérées par la CCAMLR comme anormales.

Figure 9: Série chronologique hypothétique en *W* sur 60 ans. Aucune pêche n'a eu lieu les 20 premières années, sur lesquelles une série de base *W* a servi à estimer W_0 (cercle plein). $W_{ref} = 0,8\ W_0$; ($a = 0,8$ pour toutes les espèces) (losange plein). La boîte à moustaches indique la distribution des fréquences de *W* pendant cette période de base. La boîte à moustaches adjacente à W_0 indique la relation entre la moyenne et la distribution de valeurs. Cette distribution relative est appliquée en tant que distribution prévue autour de W_{ref} pendant la période gérée. La ligne supérieure et la ligne inférieure en pointillés indiquent les limites critiques supérieure et inférieure, W_H et W_L, discutées dans le texte au sujet d'un cas dans lequel la fréquence critique acceptable en dehors de la limite est $\phi = 0,25$. La ligne en tirets se réfère à la limite supérieure provisoire de l'intervalle, W_{iH}, lors de la période où le système est en cours d'ajustement à l'activité de pêche. Dans cet exemple, la tendance de *W* à rester en dessous de la limite inférieure de l'intervalle après 16 ans de pêche indiquerait la nécessité de réduire la pêche.

Список таблиц

Табл. 1: Значения параметров, используемые в описываемой в тексте иллюстративной модели трофической цепи, формулировка которой дана в приложении.

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Рис. 1: Схематическая диаграмма, показывающая основные трофические связи между промысловым видом и другими ключевыми видами в системе (сплошные линии и буквы). Пунктирными линиями и курсивом обозначено влияние промысла на экосистему. Стрелками обозначено направление влияния. Тип воздействия: C- – отрицательное воздействие конкуренции на вид, на который направлена стрелка, P- – отрицательное воздействие «хищника», +? – потенциально положительное воздействие промысла на конкурирующий вид, второстепенный по отношению к промысловому виду, TC+? – потенциально положительное воздействие, связанное с трофическим каскадом промысла и RC- – потенциальная конкуренция между промыслом и хищниками за ресурсы. (В соответствии со схемами биологического взаимодействия в Fairweather, 1990).

Рис. 2: Структура трофической цепи в районе Южной Георгии (Атлантический океан), включающая промыслы криля, патагонского клыкача и ледяной рыбы. Темно-серые квадратики – промысловые виды; светло-серые квадратики – питающиеся промысловыми видами хищники; белые квадратики – другие потребляемые виды, включая мезопелагические (mesopel.) и батипелагические (bathypel.) виды рыб и зоопланктона (zoopl.) (Из Constable et al., 2000).

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Рис. 4: Трофическая цепь восточной части Берингова моря, показывающая основные взаимодействия с промысловыми видами, морскими млекопитающими и птицами (на основе данных и таксономических групп из Trites et al., 1999). Темно-серыми квадратиками обозначены промысловые таксоны (O. dem. = другие демерсальные виды). Светло-серыми квадратиками обозначены питающиеся промысловыми таксонами хищники. Белыми квадратиками обозначены другие таксоны (herb. = растительноядные, zoopl. = зоопланктон, juv. = молодь). Стрелками обозначено потребление видов хищниками. Сплошные линии показывают потребление промысловых видов, а пунктирные линии – потребление непромысловых видов. Более жирными линиями обозначены случаи, когда потребляемые виды составляют минимум 50% рациона, более тонкими – когда потребляемые виды составляют от 20% до 50% рациона. Не указаны случаи, когда потребляемые виды составляют менее 20% рациона.

Рис. 5: Траектории биомассы хищников и потребляемых видов на протяжении 100 лет в соответствии с моделью трофической цепи, описывающей 3 варианта рациона Хищника 1. Траектории для трех рационов Хищника 1; селективность в отношении потребляемых видов 1 и 2 составляет соответственно 1.0 и 0.2 для Рациона 1 (сплошная линия), 0.7 и 0.3 для Рациона 2 (длинный пунктир), и 0.5 и 0.5 для Рациона 3 (пунктирная линия). (a) Биомасса потребляемых видов 1 (сплошная линия) и 2 (длинный пунктир). Потребляемый вид 1 – объект лова, 50 единиц биомассы которого изымается каждый год (по возможности). (b) Хищник 1, (c) Хищник 2, с селективностью в отношении потребляемых видов 1 и 2 соответственно 0.5 и 0.5, и (d) Хищник 3, с селективностью в отношении потребляемых видов 1 и 2 соответственно 0.2 и 1.0 (более подробно см. текст).

Рис. 6: Пополнение на особь для каждого хищника в модели трофической цепи. Линии и секции как на рис. 5. Секция (a) показана для сравнения. Горизонтальные пунктирные линии в (b) отражают критический диапазон значений для Рациона 1 Хищника 1; значения вне диапазона считаются АНТКОМом аномальными годами (более подробно см. текст).

Рис. 7: Продуктивность каждого хищника в варианте (Рацион 1 Хищника 1), где объект лова – основной потребляемый вид. Секции как на рис. 5. Секция (a) показана для сравнения. Сплошными линиями обозначена общая продуктивность, длинным пунктиром – продуктивность хищников, связанная с потреблением промысловых видов, P.

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Рис. 9: Гипотетический временной ряд W на протяжении 60 лет. В первые 20 лет промысла не велось; для оценки W_0 за этот период (закрашенный кружок) использовался базисный ряд W. W_{ref} = 0.8 W_0; (a = 0.8 для всех видов) (закрашенный ромб). «Ящик с усами» показывает частотное распределение W в течение этого базисного периода. «Ящик с усами» примыкающий к W_0, показывает зависимость между средним и распределением значений. Это относительное распределение применяется в качестве ожидаемого распределения W_{ref} во время периода управления. Верхние и нижние пунктирные линии показывают критические верхние и нижние границы диапазона, W_H и W_L, обсуждавшиеся в тексте для случая, когда критическая приемлемая частота вне границ составляет ϕ = 0.25. Длинный пинктир – промежуточная верхняя граница диапазона, W_{iH}, в течение периода, когда система адаптируется к промысловой деятельности. В данном примере, если W остается ниже нижней границы диапазона после 16 лет промысла, то это означает, что необходимо сократить промысел.

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Figura 2: Estructura del sistema trófico alrededor de Georgia del Sur en el océano Atlántico, incluidas las pesquerías de kril, bacalao de profundidad y draco rayado. Los recuadros con sombreado oscuro representan las especies explotadas, los con sombreado ligero a los depredadores de las especies explotadas y los sin sombreado alguno a otro tipo de especies presa, incluidos los peces mesopelágicos (mesopel) y batipelágicos (bathypel.) y el zooplancton (zoopl.) (de Constable et al., 2000).

Figura 3: Diagrama esquemático de la posible relación entre las distintas zonas de alimentación para los depredadores y la dinámica de la población explotada, incluida la inmigración de la especie explotada (I), su emigración (E), mortalidad natural (M), mortalidad por pesca (F) y productividad (P), que incluye el reclutamiento y crecimiento de los ejemplares. Los subíndices indican las tasas específicas de cada zona.

Figura 4: Sistema trófico en el sector este del mar de Bering que muestra las interacciones primarias con las especies explotadas y otras aves y mamíferos marinos (basados en los datos y grupos taxonómicos de Trites et al., 1999). Los grupos taxonómicos de las especies explotadas están representados por recuadros con sombreado oscuro (O. dem. = otras especies demersales). Los depredadores de los grupos taxonómicos explotados están representados por los recuadros con sombreado ligero. Otros grupos taxonómicos están representados por los recuadros sin sombreado alguno (herb. = herbívoros, zoopl. = zooplancton, juv. = juvenil). La dirección de las flechas va desde la presa hacia el depredador. Las líneas continuas indican la depredación sufrida por las especies explotadas, las líneas discontinuas indican la depredación sufrida por las especies que no son objeto de explotación comercial. Las líneas más gruesas muestran cuando la presa representa por lo menos el 50% de los componentes de la dieta, las líneas más finas muestran cuando la presa representa por lo menos un 20% pero menos del 50% de la dieta total. No se muestran las interacciones cuando la presa forma menos del 20% de la dieta.

Figura 5: Trayectorias de la biomasa de los depredadores y de las presas en un período superior a 100 años en un sistema trófico simulado bajo tres hipótesis distintas sobre la dieta del depredador 1. Trayectorias para el depredador 1 para tres tipos de dieta distintos con su correspondiente selectividad de especies presa 1 y 2, siendo igual a 1,0 y 0,2 para la dieta 1 (línea continua), 0,7 y 0,3 para la dieta 2 (línea discontinua), y 0,5 y 0,5 para la dieta 3 (línea punteada). (a) Biomasa de las especies presa 1 (línea continua) y 2 (línea discontinua). La presa 1 es la especie objetivo, de las cuales se extraen 50 unidades de biomasa cada año, de ser posible. (b) Depredador 1, (c) Depredador 2 con valores seleccionados de las especies presa 1 y 2 en el orden de 0,5 y 0,5 respectivamente y (d) Depredador 3 con valores seleccionados de las especies presa 1 y 2 en el orden de 0,2 y 1,0 respectivamente (ver texto).

Figura 6: Reclutamiento per cápita para cada depredador del modelo de la cadena trófica. Los cuadros y las líneas corresponden a los de la figura 5. El cuadro (a) figura como referencia. Las líneas punteadas horizontales en (b) muestran el margen de valores críticos de la dieta 1 para el depredador 1; los valores fuera del intervalo han sido considerados como años anómalos por la CCRVMA (ver texto).

Figura 7: La productividad individual de cada depredador 1 en el experimento con una dieta 1, en que la especie objetivo es la especie presa principal. Los cuadros corresponden a los de la figura 5. El cuadro (a) figura como referencia. Las líneas continuas muestran la productividad total; las líneas discontinuas muestran la productividad del depredador a raíz del consumo de las especies explotadas, *P*.

Figura 8: Productividad integrada de todos los depredadores para cada una de las dietas supuestas mostradas en la figura 5 (se utilizan los mismos tipos de líneas). El cuadro (a) muestra la biomasa de la presa como referencia, (b) producción total para cada caso, (c) producción originada por el consumo de las especies explotadas, *W*. Igual que para la figura 6, las líneas punteadas horizontales representan los límites críticos para el caso 1; los valores fuera del intervalo han sido considerados como años anómalos por la CCRVMA.

Figura 9: Serie cronológica de *W* supuesta para un período de 60 años. No hubo pesca en los primeros 20 años, período donde se utilizó una serie cronológica de *W* como línea base para estimar W_0 (●). $W_{ref} = 0{,}8\ W_0$; (a = 0,8 para todas las especies) (◆). El diagrama cajas y bigotes muestra la distribución de la frecuencia de *W* durante el período de la línea base. Las cajas y bigotes adyacentes a W_0 muestran la relación entre el promedio y la dispersión de los valores. Esta distribución de frecuencia relativa se aplica como la distribución prevista en torno a W_{ref} durante el período de ordenación. La línea punteada superior e inferior muestran el límite superior e inferior críticos del rango para W_H y W_L, considerado en el texto para un caso cuando la frecuencia crítica aceptable fuera del límite es $\phi = 0{,}25$. La línea discontinua se refiere al límite superior provisional del rango, W_{iH}, durante el período cuando el sistema se está ajustando a la actividad de la pesquería. En este ejemplo la tendencia de *W* de permanecer por debajo del límite inferior del intervalo después de 16 años de pesca es indicativa de la necesidad de disminuir el nivel de pesca.

APPENDIX

A FOOD WEB MODEL

The model presented here is a predator–prey–fisheries model where the system is driven by the biomass of prey species. It is based on the approach described in MRAG Americas (2000). Each prey species is governed by a simple model of primary production with variations in the biomass of prey species caused by a mortality rate (natural and fishing mortality) and stochastic variation in available primary production. Each of these parameters can be varied over time but are not influenced by the abundance of predators.

The fishery is modelled using a constant annual catch, similar to the approach used by CCAMLR.

Each of the predators is modelled as an age-structured population with a constant rate of natural mortality. Variation in the abundance of predators is predominantly governed by variation in recruitment. Per-capita recruitment is influenced by the annual carrying capacity determined by the abundance of prey and moderated by the degree of competition with other predators. Competition is determined by the abundance of other predators weighted by the reliance on the same prey. The relationship between predators and prey is determined by relative effects rather than absolute values of parameters defining the interaction, i.e. consumption and conversion into predator biomass. Biomass of predators is monitored by using weight-at-age models.

Prey Dynamics

The change in biomass is given by a density-dependent model, in which the biomass of the subject prey species and other competing prey species will influence the per-biomass recruitment to the population. The biomass, $Bs_{s,y}$, of a prey species, s, at the beginning of a given year, y, is given by

$$Bs_{s,y} = Bs_{s,y-1}e^{-M_s - F_{s,y-1}} + R'_{s,y} \qquad \text{(A1)}$$

where M_s is the natural mortality rate, $F_{s,y-1}$ is the fishing mortality rate of the previous year required to yield the prescribed catch, and $R'_{s,y}$ is the recruitment biomass of the species in that year. Recruitment is determined by

$$R'_{s,y} = \begin{vmatrix} R_s Bs_{s,y-1}E_{s,y-1} & ; & E_{s,y-1} > 0 \\ 0 & ; & E_{s,y-1} \leq 0 \end{vmatrix} \qquad \text{(A2)}$$

where R_s is the maximum per-biomass recruitment rate, and $E_{s,y-1}$ is the density-dependent adjustment of the recruitment rate according to the status of the production environment and the magnitude of the prey populations relative to that status. This is estimated by

$$E_{s,y-1} = 1 - \frac{\sum_{s'=1}^{nS} c_{s,s'} Bs_{s',y-1}}{Ks_{s,y-1}} \qquad \text{(A3)}$$

where $c_{s,s'}$ is the competition coefficients for each prey species and $Ks_{s,y-1}$ is equivalent to the carrying capacity for the prey species in the given year.

The competition coefficients are used to weight the biomass of all prey species to determine the density-dependent adjustment to the per-biomass recruitment, e.g. the subject prey species, $s = s'$, would have $c_{s'} = 1$. Other species will vary from 0 to 1.

The state of the environment (carrying capacity) for the prey species, $Ks_{s,y-1}$, varies each year. Its state is drawn at random from a lognormal distribution based on a specified mean, $\overline{Ks}_s$ and variance, σ^2_{Ks}, such that

$$Ks_{s,y-1} = \overline{K}s_s.\exp\left(\eta - \frac{\sigma^2_{Ks_s}}{2}\right) \tag{A4}$$

where η is drawn randomly from $N\left(0;\sigma^2_{Ks_s}\right)$, which is a normal distribution with zero mean and variance $\sigma^2_{Ks_s}$.

In this case, the carrying capacity of the different prey species varies independently of one another.

The Fishery

The fishing mortality of a target species in a given year, $F_{s,y-1}$, depends on the population size of the target species and the magnitude of the constant annual yield, Y_s. This is solved using Newton's method and the following function

$$\hat{Y}_s = \frac{F_{s,y-1}}{M_s + F_{s,y-1}} B_{s,y-1}\left(1 - e^{-\left(M_s + F_{s,y-1}\right)}\right) \tag{A5}$$

If the stock is too small to support the catch level, then the value of F is constrained to 5 year^{-1}.

Predator Model

Each predator, p, is characterised by fully age-structured models with a plus class. In each year, the numbers, $N_{p,a}$, at age, a, are advanced one year and discounted by natural mortality, $M_{p,a}$, which is unrelated to the abundance of prey, such that

$$N_{p,a} = \begin{cases} N_{p,a\text{-}1}e^{M_{p,a}} & ; \quad a < a_{plus} \\ \left(N_{p,a\text{-}1} + N_{p,a}\right)e^{M_{p,a}} & ; \quad a = a_{plus} \end{cases} \tag{A6}$$

Recruitment of age 0 individuals to the predator population is density dependent, such that the maximum per-capita reproduction of individuals, r_p, is moderated by the biomass of each of the predators, Bp_p, (number at age by weight at age, $w_{p,a}$), statistically weighted by the competition coefficients, $C_{p,p'}$, for each predator as described above for prey, and related to the abundance of prey available to the predator. The latter term is governed by the abundance of prey weighted by the selectivity, $ps_{p,s}$, of that prey by the predator. This can also be adjusted by food value, $pv_{p,s}$, if required. The degree of density dependence can be adjusted using the term, A_p. For example, a value typically used for marine mammals is 2.4 (MRAG Americas, 2000).

The final recruitment is influenced by the natural mortality of new recruits in that first year, $M_{p,0}$ and the number of mature adults in the population.

Thus,

$$N_{p,0} = \begin{cases} r_p e^{-M_{p,0}} \sum_{a=a_{mature}}^{a_{plus}} N_{p,a}Ep_p & ; \quad Ep_p > 0 \\ 0 & ; \quad Ep_p \le 0 \end{cases} \tag{A7}$$

where

$$E_p = 1 - \left(\frac{\sum_{p'=1}^{nP} C_{p,p'}Bp_{p'}}{Kp_p}\right)^{A_p} \tag{A8}$$

$$Bp_{p'} = \sum_{a=1}^{a_{plus}} N_{p',a} w_{p',a} \tag{A9}$$

and

$$Kp_{p,y} = \sum_{s=1}^{nS} ps_{p,s} pv_{p,s} Bs_{s,y} \tag{A10}$$