

AN ECOSYSTEM FRAMEWORK FOR FISHERIES MANAGEMENT IN THE SOUTHERN BENGUELA UPWELLING SYSTEM

L. J. SHANNON* and C. L. MOLONEY†

A “four-step framework” for applying ecosystem approaches to fisheries management in the southern Benguela is proposed. First, static ecosystem models can be used to highlight important interactions by assessing the net trophic impacts of each species on all the others. Second, using a dynamic simulation approach, indicators quantifying interaction strength and functional impacts can provide information on the size of impacts on ecosystem components when a group is overfished. Third, dynamic simulations can suggest some possible short- and long-term ecosystem effects of altered fishing under strategies developed and selected using standard single-species models. Finally, the net combined ecosystem effects of the revised strategies for all fisheries in the ecosystem need to be considered together. For this to be accomplished, overall objectives for regional fisheries management, objectives for each fishery, and non-consumptive objectives need to be clearly stated and carefully considered in the provision of advice in an ecosystem context. A selected theoretical fishing strategy is examined to explore the possible ecosystem effects of implementing an option such as this in the southern Benguela ecosystem.

Key words: Benguela, ecosystem approach to fisheries, ecosystem models, fisheries management, framework

More than two decades ago, May *et al.* (1979) forecasted the increasing need for fisheries managers to take species interactions into account. It is now widely recognized that ecosystem effects need to be considered in managing fisheries (Pauly 1998, Beamish and Mahnken 1999, Gislason *et al.* 2000). Steele (1996) concluded that a “regime shift in fisheries management” is required if one is to manage fisheries successfully in the context of ecosystem changes. Since 1950, humans have been “fishing down the foodwebs”, in other words there has been a worldwide decline in the mean trophic level of marine and inland fish catches (Pauly *et al.* 1998, 2000b). This has been characterized by an initial increase in catches, followed by levelling or decreases in catches, indicating that current exploitation is unsustainable in many ecosystems (Pauly *et al.* 1998), and that fishing has caused changes in ecosystem structures. It is not known how these changes have affected and will affect ecosystem functioning and future catches.

Until recently, management of fisheries has been from a single-species perspective (Pauly *et al.* 2000a). The Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) is a working example of a programme adopting ecosystem approaches to fisheries management, as opposed to management of single species in isolation (Scully *et al.*

1986). The ecosystem approach to management was defined by Larkin (1996) as “management of marine fisheries with awareness of ecosystem properties”. He considered such approaches to management to consist of holistic approaches to resources, taking into account multispecies interactions and their dependence on underlying ecosystem dynamics, and listed three essential components of ecosystem management:

- (1) sustainable yield of products for consumption by humans and animals;
- (2) maintenance of biodiversity;
- (3) protection from the effects of pollution and habitat degradation.

Larkin (1996) also concluded that scientists are currently a long way from the stage where ecosystem models can predict variations in abundance of individual species, although present ecosystem models describe interdependencies between trophic levels and can at least identify major changes in the ecosystem. Jennings and Kaiser (1998) propose that fisheries management in future should incorporate conventional fisheries management into an ecosystem-based approach, aiming towards achieving a balance between the economic gain from fisheries and the maintenance of diversity, the sustainability of top predators, ecosystem functioning, and conservation of the ecosystem.

* Marine & Coastal Management, Department of Environmental Affairs and Tourism, Private Bag X2, Rogge Bay 8012, South Africa.
E-mail: lshannon@deat.gov.za

† Formerly Marine & Coastal Management; now Marine Biology Research Institute, University of Cape Town, Rondebosch 7701, South Africa

Livingston and Tjelmeland (2000) suggested that it was particularly important that ecosystem considerations be incorporated into fisheries management in systems in which exploited fish stocks interact strongly with one another and are very important for sustaining top predators, i.e. marine mammals and seabirds. The Bering Sea is an example of an ecosystem for which good progress has been made towards ecosystem-based management (Witherell 1999). A precautionary approach to managing the Bering Sea groundfish fishery has been adopted, based on scientific research and advice, extensive monitoring, enforcement, bycatch controls, conservative quotas, conservation of habitat and the seasonal and spatial allocation of fishing. This reduces potential detrimental effects of local prey depletion on marine mammals and seabirds.

In South African fisheries, most of the commercial catch is taken from the productive upwelled waters of the southern Benguela, off the western and south-western coasts of the country. The catch is dominated by a few species that occur in large quantities (Cochrane *et al.* 1997). The most important fisheries in terms of landed catch are the purse-seine fishery, mainly for sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* (formerly *E. capensis*) and the demersal trawl fishery, mainly for the Cape hake *Merluccius capensis* (shallow-water Cape hake) and *Merluccius paradoxus* (deep-water Cape hake). These dominant species interact: large adult hake feed on small pelagic fish (including small hake), and small pelagic fish and small hake take zooplankton prey. Also important are top predators, including many species of seabirds and growing populations of Cape fur seals *Arctocephalus capensis capensis* and southern right whales *Eubalaena glacialis*. These top predators, which are the basis of a developing and lucrative ecotourism industry, can be indirectly affected by fisheries on other species, especially through competition for food.

The southern Benguela is one of many ecosystems experiencing regime shifts (Schwartzlose *et al.* 1999), with alternating periods of dominance by anchovy and sardine. In the southern Benguela, sardine dominated during the 1950s but declined in the 1960s, as anchovy became more abundant. Anchovy dominated the pelagic fish biomass in the 1970s and 1980s, but fluctuated erratically during the 1990s as sardine began to show signs of recovery. During the late 1990s and early 2000s, both anchovy and sardine attained large stock sizes off South Africa.

Fisheries management should consider fish stocks as part of the whole ecosystem, and due consideration should be given to the potential effects harvesting one group has on other groups and on other existing fisheries (Murawski 1991). To achieve this aim, practical

methods are needed to manage fisheries as parts of ecosystems. One such widely applied method has been based on ECOPATH, an ecosystem modelling approach for aquatic ecosystems (Christensen and Pauly 1992). ECOPATH is a mass-balance modelling approach, first described by Polovina (1984), and subsequently developed into a software package (www.ecopath.org). A dynamic simulation routine was incorporated into the ECOPATH modelling package, leading to the release of ECOPATH with ECOSIM (EwE; Walters *et al.* 1997). The primary aim of developing this software was to provide a tool for addressing fisheries policy questions that single-species approaches were not equipped to answer (Christensen and Walters 2000).

Mass-balance trophic models have been developed and used to understand the structure and functioning of the southern and northern Benguela ecosystems (Jarre-Teichmann *et al.* 1998, Shannon and Jarre-Teichmann 1999a, Heymans and Baird 2000, Shannon 2001, Roux and Shannon 2002, Shannon *et al.* 2003, Heymans *et al.* 2004). Mass-balance models serve as the basis for dynamic models in EwE. Dynamic models have been used to examine some of the possible ecosystem implications of altered fishing strategies in the southern Benguela region (Shannon and Jarre-Teichmann 1999b, Shannon *et al.* 2000, 2004). What is now needed is a plan or procedure for using the information derived from these ecosystem models to provide advice for resource management.

In this paper, guidelines are presented for the establishment of a framework of research and other activities to support ecosystem-based management advice for fisheries-related activities in the southern Benguela. Static and dynamic trophic models are used to give ecosystem-based hindsight responses to a hypothetical question concerning the anchovy resource in the southern Benguela during the 1980s, viz. could larger catches of anchovy in the southern Benguela have been supported during the 1980s? The trade-off between allowing substantial pelagic fisheries and the objective of conservation of predators of small pelagic fish, including seabirds and marine mammals, is evaluated. These predator groups are important for their potential to sustain the lucrative ecotourism industry.

THE MODELS AND ALGORITHMS USED

In the example used for illustrative purposes in this paper, ECOPATH and ECOSIM models of the southern Benguela ecosystem during the 1980s are used to explore the possible ecosystem implications had increased

catches of anchovy been taken during the 1980s. Outputs of these mass-balance, dynamic ecosystem models are briefly presented and used to illustrate how such model results could be incorporated into the proposed ecosystem approach to fisheries management.

Mass-balance model

The mass-balance southern Benguela ecosystem model for the 1980s was prepared using ECOPATH (version 4.0). The EwE package is described in detail by Christensen and Walters (2000), and the model equations are not repeated here. Similarly, the southern Benguela model developed with the EwE software is described in detail elsewhere (Shannon 2001, Shannon *et al.* 2003). In brief, the mass-balance model consists of 32 trophic categories that represent the southern Benguela pelagic ecosystem during the period 1980–1989 (Fig. 1). Phytoplankton, benthic producers and detritus are located at Trophic Level 1, and the trophic levels of consumers are calculated to be 1 plus the average trophic level of their prey, weighted by the proportion in the diet of the predator. For model analyses and simulations, Cape hake were subdivided into four groups, small and large shallow- and deep-water Cape hake, and large pelagic fish were split into two. Commercially important predatory snoek *Thyrsites atun* were modelled separately from the others. Demersal fish and chondrichthyans (sharks, skates and rays) were split according to feeding guilds: benthic-feeding and pelagic-feeding demersal fish, benthic-feeding, pelagic-feeding and apex predatory chondrichthyans. Sources of data for the model and the ways in which the ECOPATH model was balanced are described in full by Shannon (2001) and Shannon *et al.* (2003). As stated above, anchovy were the dominant pelagic fish in the southern Benguela in the 1980s, having a stock size estimated as ten times larger than that of sardine then. Cape hake are key species of the ecosystem, both commercially and trophically. Larger biomass in the juvenile hake model groups was required to balance the model, suggesting that small Cape hake are undersampled and consequently underestimated by the current assessments. Mesopelagic fish and another small pelagic fish, round herring *Etrumeus whiteheadi*, are also abundant in the ecosystem and serve as important prey items for many predators, including predatory pelagic fish, marine mammals and seabirds.

The static model results were used to investigate the direct and indirect impacts of different fisheries on one another. The routine used produces measures called mixed trophic impacts. Mixed trophic impact assess-

ment is based on an input-output method developed for an economic model (Leontief 1951), modified by Ulanowicz and Puccia (1990) for ecological applications. It produces a matrix of relative net impacts (scaled between -1 and +1) of each group on all other groups in the ecosystem. The results can be used to assess how a change in the biomass of one group would affect the biomasses of other groups. The method assumes that trophic structure is constant, so the results cannot be used for predictive purposes, but instead help to identify groups having large trophic impacts on others, and for which it would be useful to refine estimates. The mixed trophic impact assessment was used to suggest likely answers to the question asked above.

Dynamic simulation model

Increased anchovy catches in the 1980s were simulated using the ECOSIM dynamic simulation routines (Christensen and Walters 2000) in EwE (version 4.0). In brief, ECOSIM is a dynamic biomass model that simulates changes in the biomass of groups in an ecosystem on the basis of changes in total mortality, determined by the sum of the quantities consumed by predators, including fisheries. ECOSIM models are based on balanced ECOPATH models. The ecosystem dynamics are implemented by changing the rates of fishing mortality over time, or by using forcing functions to alter biomasses of model groups over time. All trophic interactions are mediated by predator-prey “vulnerability” parameters, which determine the availability of prey to their predators and act as trophic control parameters. Following Cury *et al.* (2000) and Shannon *et al.* (2000), it is assumed here that the southern Benguela ecosystem is “wasp-waisted”, so trophic controls reside in small pelagic fish, which control both their prey (top-down) and their predators (bottom-up).

ECOSIM (version 4.0) allows model groups to be split into linked juvenile and adult groups, using a delay-differential model to simulate the recruitment of juveniles/small fish into the adult/large size pool (Walters *et al.* 1997). Adults and juveniles of three species are linked in this way in the models used here: juvenile and adult horse mackerel *Trachurus trachurus capensis*, small and large shallow-water Cape hake, and small and large deep-water Cape hake. Using this approach, it is possible to keep track of recruitment changes when feeding conditions alter (Christensen and Walters 2000).

Information about fishing gear types is included in the models, so the effects of fishing by the major fisheries can be distinguished. Six gear types are considered:

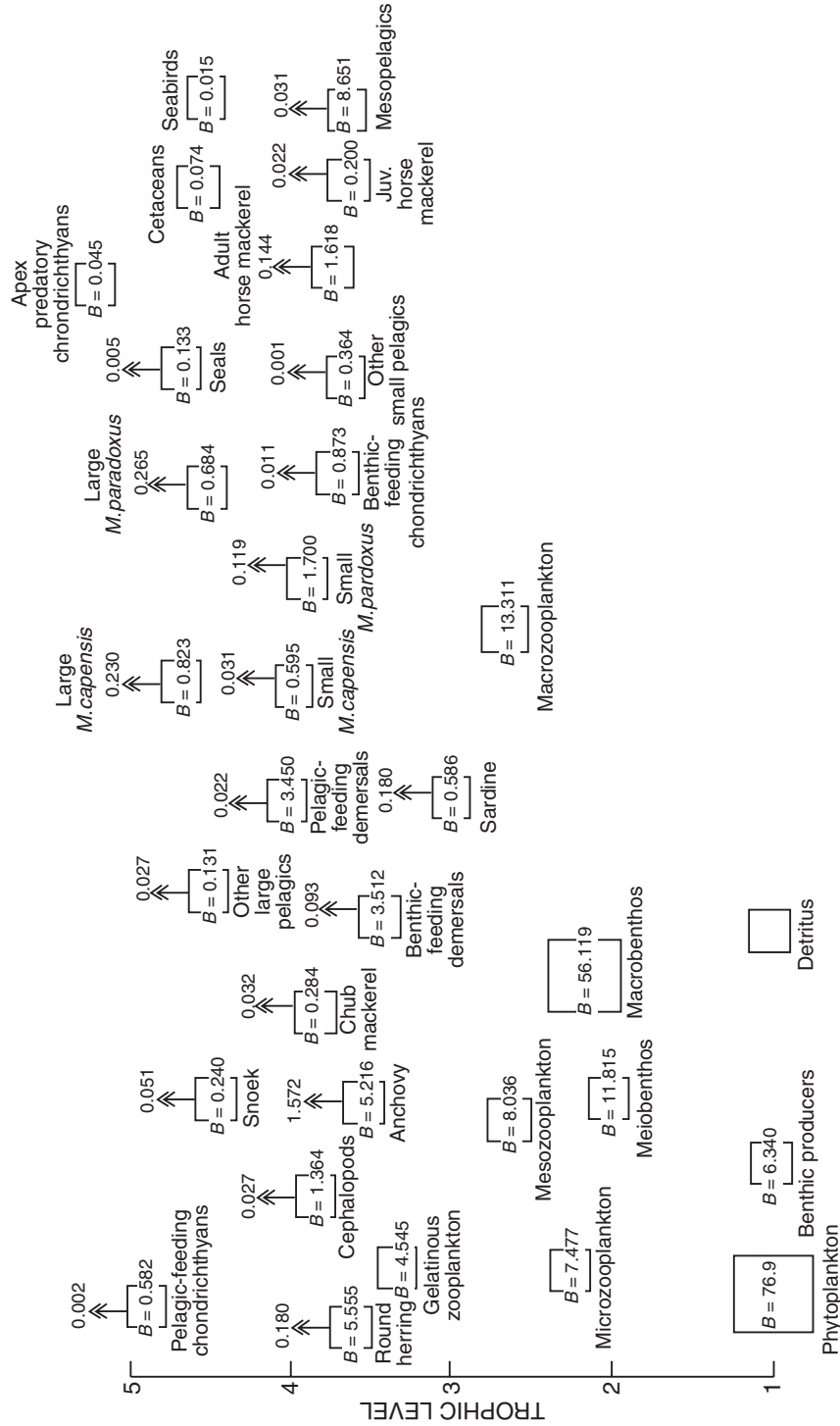


Fig. 1: Structure of the southern Benguela ecosystem model for the 1980s. Model groups are arranged along the vertical axis according to trophic level. Estimates of biomass (B) and catches (indicated by arrows leaving groups) are given in tons km⁻² and tons km⁻² year⁻¹ respectively

purse-seine, midwater trawl (a very small component of the total catch), demersal trawl (including inshore and offshore trawls on the south coast of South Africa, and demersal trawls on the West Coast), handline, longline and “other” (includes beach-seine, gillnet, the jig fishery for squid, recreational, and deaths of seals by culling and from fishery-related causes).

Because anchovy dominated the small pelagic fish assemblage of the southern Benguela during the 1980s, dynamic model simulations were used to explore whether larger catches of anchovy than were really taken could have been supported under this average ecosystem scenario. The ECOSIM simulation was run for 50 years to avoid missing long-term effects and to allow most groups to reach stable equilibria after the onset of the altered modelled fishing strategy. Fishing mortality of anchovy was increased by 10, 25 and 50% from Year 10 to Year 50. The results were summarized by plotting the changes in biomass at the end of the 50-year simulation relative to those at the start.

The results of dynamic simulation models can provide quantitative indicators of interactions in ecosystems (Shannon 2001, Shannon and Cury 2004). These indicators are estimated for situations when diets and biomasses of all ecosystem components fluctuate over time in response to altered fishing and abundance of affected groups. Therefore, they represent the results of dynamic as opposed to static analyses, and further advance ecosystem understanding. They are derived from theoretical simulations of intense overfishing on one group, causing its stock to collapse. By looking at the extreme situation of species “deletion” from an ecosystem, it is possible to derive indicators that could be applied in a generic fashion across different ecosystems. For the purposes of this paper, three of the indicators proposed by Shannon and Cury (2004) were considered. The indicator of interaction strength (*IS*) measures the relative impact of a reduction in one group on others in the ecosystem:

$$IS = 1 - \frac{\left| \frac{\Delta B_i}{B_i} \right|}{\sum_{j=1}^n \left| \frac{\Delta B_j}{B_j} \right|}, \quad (1)$$

where *B* is biomass in Year 0, ΔB the change in biomass of a group over the simulation period, *i* the group being tested for interaction strength, *j* a species or group in the ecosystem, and *n* is the total number of model groups. *IS* values range between 0 and 1; large values indicate that a species/group *i* has a strong impact on other model groups. *IS* is derived by simulating a change in the biomass of one group at a time;

the model group collapses within the first 10 years of simulation as a consequence of overfishing, and the resulting ecosystem dynamics are modelled for a further 40 years. This indicator can be used to determine which groups could have the strongest effects on others in the ecosystem, so affecting ecosystem structure.

The functional impact (*FI*) indicator, based on the “community importance” indicator of Power *et al.* (1996), measures the relative impacts of one functional group on its own and on other functional groups, and can indicate sensitivities in the functioning of the ecosystem to altered exploitation of species. *FI_{pelagics}* is defined as the relative change in the biomass of small pelagic fish (anchovy, sardine, round herring and other small pelagic fish, excluding the species being tested) as a proportion of the relative change in biomass of the species being tested for its functional impacts. A small *FI* indicates that removal of the target species has a small impact on the overall model biomass of the functional group being considered:

$$FI_{pelagics} = \frac{\sum_{j=1}^m \Delta B_j}{\sum_{j=1}^m B_j} \times \frac{B_T}{|\Delta B_i|}, \quad (2)$$

where *B* is biomass in Year 0, ΔB change in biomass of a group over the simulation period, and group *i* is the target group being investigated for impacts on the functional group under consideration. Species or group *j* belongs to set *m* (the functional group being considered). *T* is all groups (excluding detritus) within the model ecosystem.

The trophic replacement indicator quantifies the extent to which a group that is removed from the system is replaced by others in that system. It quantifies the density compensation when a stock collapses and others increase in size to partly fill the resultant vacant niche, and is calculated for each group *j* belonging to the set of groups *k* that show a change in biomass of the opposite sign to that of target group *i*. For example, if target group *i* collapses, *j* is a model group undergoing an increase following the collapse of group *i*. Collapse is defined as elimination, i.e. reduction of stock size to zero biomass:

$$TR_j = \left| \frac{\Delta B_j}{\sum_{j=1}^k \Delta B_j} \right|,$$

where *B* is biomass in Year 0 and ΔB is the change in biomass of a group between Year 50 and Year 0. *TR*

ranges between 0 (no replacement) and 1 (total replacement).

RESULTS AND DISCUSSION

The example used here is based on a simplified model and datasets that were averaged over 10 years. Clearly, the results should be considered as only illustrative at this stage, the intention being to use this example to help develop pragmatic guidelines for development of an ecosystem approach to fisheries management, by applying available tools and showing how the anchovy-directed fishery could impact other components of the ecosystem. Results of this nature should be considered when management objectives are formulated.

When making use of model results such as those presented later, the question arises whether they are realistic. They depend on the assumptions underlying the models used:

1. Fisheries and biological estimates have been averaged over 10 years for the 1980s scenario, and the ecosystem is assumed to be in steady state. Christensen (1995) found that adopting average parameter values for a reference state when parameters changed over the model period led to overestimation of sustainable rates of fishing. It is possible that the same could apply here, but the situation for the southern Benguela is confounded by the fact that increased stock sizes of many groups were observed for the decade following (the 1990s), and both sardine and anchovy attained very large biomasses in the late 1990s. It is not known to what extent those biomass increases resulted from conservative fisheries management (especially for sardine) or from environmental influences on recruitment (especially for anchovy). However, the net effect was an increase rather than a decrease in biomass, and it is assumed here that this indicates that the impacts of fisheries in the averaged 1980s model are conservative.
2. Trophic models are sensitive to diet compositions of the various groups. As tends to be the case in many such analyses, these diet compositions were derived from poor or scanty data, and in some cases depended on assumptions made during the balancing of the model (Shannon 2001). Although ECOSIM accounts for changes in trophic interactions associated with changes in the diet composition of predators, switching of prey and satiation are not well represented (Walters *et al.* 1997). In particular, prey switching can be a confounding problem where predators of pelagic fish have fairly plastic diets and are able to switch prey species according to their

abundance (Crawford *et al.* 1987). At this stage, there is little that can be done to improve the model, but it is clear that routine diet studies need to be established as part of ongoing monitoring.

3. It was assumed that there was "wasp-waist" flow control in the southern Benguela, with small pelagic fish controlling prey (top-down) and predators (bottom-up). Results would have been different if different "vulnerabilities" had been selected to represent an alternative assumption regarding species interactions (as shown in Shannon *et al.* 2000). However, current understanding of the functioning of the southern Benguela ecosystem supports this assumption (Cury *et al.* 2000), so it is probably the most realistic option at present.
4. Ecosystem effects of fishing are considered from a trophic perspective. Other considerations, such as environmental and/or spatial effects, are not incorporated into these models. Environmental perturbations may well affect different ecosystem components differently, and could change their responses to altered fishing. Therefore, to accommodate the effects of the environment, it may be useful to combine the results of these models with those of environmentally linked models. This is not a trivial exercise, but the problems should be tackled from many different aspects, because no single model is likely to be sufficient. Further, changes in the spatial distributions of fish are often associated with changes in abundances of these species, affecting their availability to predators, particularly those with limited feeding ranges. For example, the population of African penguins *Spheniscus demersus* on the South African south coast declined sharply as a result of shifts in anchovy and sardine distributions and abundances between the 1980s and 1990s, reducing the availability of pelagic fish to penguins (Crawford 1998). Therefore, simply putting into place management approaches that ensure sufficient biomass of small pelagic fish to sustain marine mammal or seabird populations in an ecosystem as a whole may well be inappropriate if availability of the prey species to their predators is not also taken into account. It may be necessary to consider spatial restrictions on fishing in important feeding areas of marine mammals and seabirds, as has been implemented in the management of the Bering Sea ecosystem (Livingston and Tjelmeland 2000).

In addition to realism, the question also arises as to whether results such as these are useful. Despite some of the problems mentioned above, these results are believed to be a synthesis of current best understanding of the southern Benguela pelagic ecosystem. Therefore, they are useful for at least two reasons. First, the results provide plausible hypotheses that can form a

basis for structuring ecosystem management objectives. Such hypotheses are based on a trophic model with important mass-balance constraints, ensuring consistency in the depiction of the ecosystem. Second, the results underscore the poor assumptions and other limitations of the model, providing guidance for research and monitoring programmes that should be able to support ecosystem approaches to fisheries management.

Balancing management objectives

Increasing catches of one group or expanding one fishery could require a corresponding reduction in catches of other groups or fisheries. Although the ecosystem might appear to be stable (often at very different biomass equilibria from original levels after such management actions), socio-economic factors need to be carefully considered and management objectives carefully defined before a new strategy can be implemented as a preferred option.

Incorporating ecosystem considerations into fisheries management is problematic, because management objectives are often only stated broadly (Sainsbury *et al.* 2000). Fisheries management advice should be based on a trade-off between the net benefits of social and economic implications in an ecologically sustainable set of fisheries strategies (Larkin 1996, Jennings and Kaiser 1998, Pauly 1998, Caddy 1999). Moreover, to maximize economic benefit, future fisheries management should aim at rebuilding ecosystems to achieve species compositions and abundance levels closer to those in the ecosystems before heavy anthropological exploitation (Pitcher and Pauly 1998, Pitcher 2000).

One reason advanced for the failure of fisheries management worldwide is the conflict between sustainability of fisheries and economic and social priorities (Cochrane 2000). An example of such conflict from the southern Benguela is the pelagic fishery, in which the overriding factors influencing management decisions in the past were the short-term benefits of maintaining employment and income (Cochrane *et al.* 1998). An additional economic consideration is the large difference between the economic values of anchovy and sardine. Sardine are more valuable because they are directly consumed by humans, whereas anchovy are reduced to oil and meal (Shelton 1992). Expanding the conflicts within a fishery are broader conservation issues, highlighted in this example by the dependence of the African penguin on small pelagic fish, and the importance of penguins to the tourism industry.

Successful fisheries management procedures need constant monitoring and revision (Cochrane 2000). This

has been the case in implementing the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). Its management approach is based on the "precautionary approach" (Garcia 1996) and involves assessment of catch controls on single species, prediction of the effects of fishing and monitoring of the ecosystem (Constable *et al.* 2000). The last authors highlight two important lessons learnt from CCAMLR, that it is necessary to implement management measures even in the absence of extensive datasets, and that it is possible to reach scientific consensus despite uncertainties in parameter estimates and predictions of ecosystem responses. The latter is also emphasized by de la Mare (1998) and Cochrane (1999), who caution against the current belief that quantification of uncertainties and improved implementation through ever-increasing consultation are the panacea to fisheries management problems. Attempting to estimate all the uncertainties is impossible and may lead to further uncertainties, according to de la Mare (1998). Instead, he proposes that the objectives of fisheries management should be carefully formulated, and that an ecosystem should be considered as a whole.

Management of anchovy and sardine in the southern Benguela

The present management of small pelagic fish off South Africa is based on single-species approaches, although elements of multispecies interactions are considered. Total Allowable Catches (TACs) are set for the two most important commercial species, anchovy and sardine. Round herring is non-quota, but it is also caught commercially. Initially (1979–1982), a combined TAC was set for all pelagic species, fluctuating between 360 000 and 450 000 tons. From 1983, single-species TACs were introduced (Butterworth 1983). From 1987, anchovy management comprised three phases (Cochrane *et al.* 1998):

- (i) setting a provisional TAC to enable the fishing industry to plan ahead;
- (ii) setting a TAC in January, when fishing commences, based on spawner biomass estimated from the previous November's hydroacoustic survey;
- (iii) revising the TAC in the middle of the year, once an estimate of recruitment from the May/June hydroacoustic survey is available.

From 1988 to 1990, the South African anchovy TAC was set on the basis of constant escapement, but from 1991 to 1993, a constant proportion strategy was used (Cochrane *et al.* 1998). In 1991, a Management Procedure (MP) was first applied to anchovy and, from 1994, a combined anchovy-sardine MP was imple-

mented (de Oliveira *et al.* 1998a). Adult sardine (1-year-old fish and older) are caught in a directed fishery as well as in a fishery targeting round herring (mixed shoaling of sardine and round herring), whereas juvenile sardine (0-year fish) are caught as bycatch in the anchovy fishery (Cochrane *et al.* 1998). Sardine TACs were kept low between 1984 and 1989 to encourage rebuilding the small sardine stock (Anon. 1986, 1989). Until 1994, a single TAC for sardine was set in January. From 1994, a three-phased MP was adopted (Cochrane *et al.* 1998, de Oliveira *et al.* 1998b):

- (i) a directed-catch sardine TAC is set in January/February (calculated as a proportion of the spawner biomass estimate from the previous November);
- (ii) an initial bycatch TAC for sardine is set in January, based on the assumption of average recruitment in midyear and dependent on the anchovy TAC;
- (iii) a revised bycatch TAC is set mid-year, depending partly on sardine recruitment estimated from the May/June hydroacoustic survey, and partly on the revised anchovy TAC.

The joint anchovy-sardine MP is not free of problems. The procedure was designed to account for a maximum of 12% juvenile sardine bycatch in the anchovy fishery, but in 1994 and 1995, it rose to >20% and in 1996, it reached >50% (Marine & Coastal Management, unpublished data). Industry therefore requested a larger sardine bycatch so that the anchovy fishery was viable, whereas scientists were concerned that this would impact negatively on the fishery for adult sardine, upon which the valuable canning industry is based. Economically, it would probably have been best to concentrate on the sardine-directed fishery at the expense of the anchovy fishery (Cochrane *et al.* 1997), but the social upheavals to those dependent on the anchovy fishery and the ecological consequences for sardine and anchovy predators also had to be considered.

A four-step procedure to manage fisheries in an ecosystem context

Management of fisheries is usually applied within a specific legal and policy framework. Ecosystem approaches to fisheries management should be subject to similar procedures as those applied to single-species fisheries management (Christensen 1996). In a South African fisheries management context, some of the formal procedures that should precede ecosystem-based management have been established. The

Marine Fisheries Policy for South Africa (Anon. 1997) has, as a management objective, clauses that aim to ensure that fisheries exploitation does not jeopardize those features of the ecosystem on which biodiversity and long-term sustainability depend. These stated goals were incorporated into the Marine Living Resources Act No. 18 (Anon. 1998), which is intended "to provide for the conservation of the marine ecosystem [and] the long-term sustainable utilization of marine living resources..." What is currently lacking is a process for implementing these policy objectives, and a plan to inform the implementation process through appropriate research and monitoring activities. Here, a four-step framework for planning research activities to implement ecosystem approaches to management is proposed.

STEP 1

The first step is to construct a trophic ecosystem model and to examine the interactions among species groups implied by that ecosystem structure. In standard fisheries stock assessment models, this would be equivalent to gathering biological data on the species to be modelled. In this example, a mass-balance model of the southern Benguela has been built, one for which there were sufficient data to carry out the exercise. One way of examining interactions is to use the mixed trophic impact results from the balanced model; this assists in establishing the groups that have negligible impacts on others in the ecosystem, and the groups that are likely to have large effects. This step therefore indicates areas for further investigation, and can help in formulating and refining hypotheses about the consequences of management actions (Step 1, Fig. 2). In the example using the mass-balance southern Benguela model for the 1980s, anchovy had negative trophic impacts on pelagic fish such as sardine, round herring, other small pelagic fish, chub mackerel (*Scomber japonicus*) and horse mackerel (Fig. 3). Anchovy also negatively impacted some of the Cape hake groups and other pelagic-feeding demersal fish (such as angelfish *Brama brama*, John Dory *Zeus capensis* and ribbonfish *Lepidopus caudatus*). Predators of anchovy, such as snoek and other large pelagic fish, seals, cetaceans and seabirds, were positively affected by anchovy abundance. All fisheries except demersal trawl and longline were impacted positively by anchovy.

This step, to identify the positive and negative interactions among species groups from static ecosystem models, allows the construction of working hypotheses and highlights effects to be considered when applying a dynamic modelling approach (Steps 2–4). In this example, the fact that anchovy negatively impact

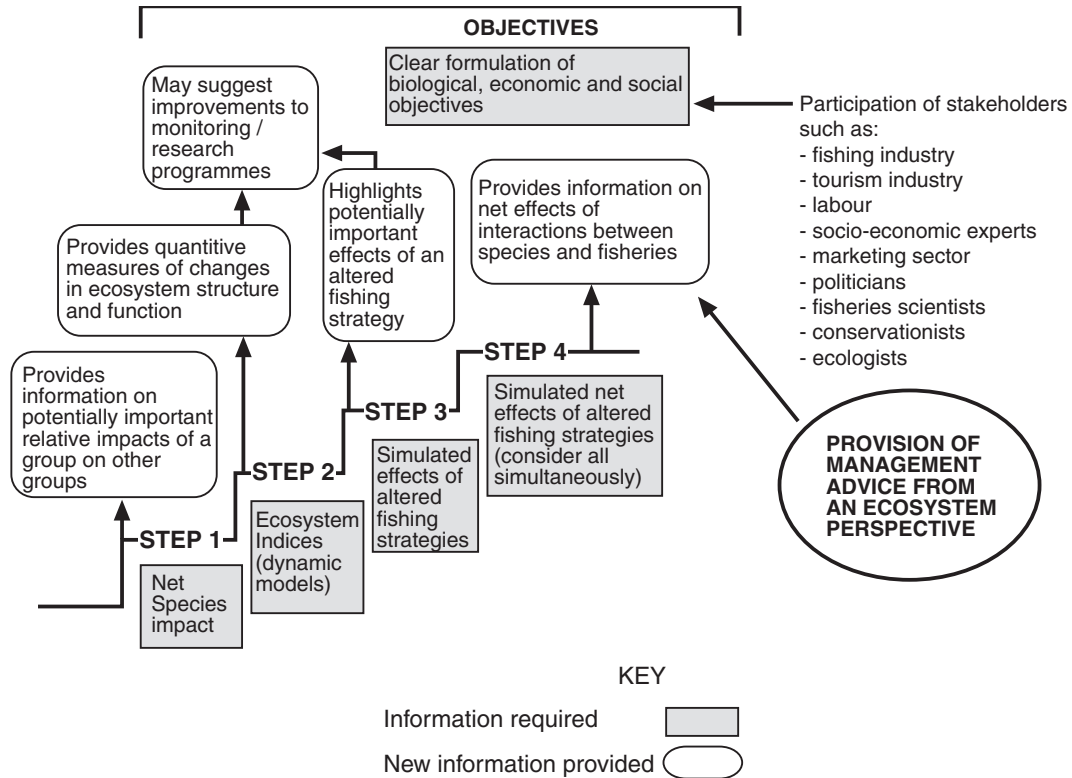


Fig. 2: Diagrammatic representation of proposed four-step framework to manage fisheries in an ecosystem context

horse mackerel in the static model is highlighted (Fig. 3).

STEP 2

Dynamic ecosystem models should be used to explore and quantify the interactions among species groups and to develop further understanding of how food-webs function (Step 2, Fig. 2). This step is equivalent to applying a single-species population model (preferably a suite of models) to better understand the dynamics of the population. Ecosystem indicators should be developed that quantify species interactions, and that can be used to compare ecosystem dynamics in different situations. This would be analogous to producing reference points and thresholds (e.g. Maximum Sustainable Yield) in single-species models (Garcia and Staples 2000). In this example, we used ECOSIM models to develop indicators derived from theoretical simulations of intense overfishing on anchovy, causing its stock to collapse. Such ecosystem

indicators can indicate how strongly the ecosystem might respond to altered fishing on different fish stocks. They can also give added support to existing hypotheses, or indicate caution where results are contradictory.

Of the three main small pelagic fish in the southern Benguela in the 1980s, anchovy had the largest interaction strength and functional impact on the small pelagic fish functional group (Table I, Shannon 2001, Shannon and Cury 2004), suggesting that a reduction in anchovy biomass would be likely to be followed by an increase in abundance of other small pelagic fish, such as sardine, round herring and horse mackerel. This is further supported by the trophic replacement indicators for anchovy by other species of zooplanktivorous fish, in particular round herring and horse mackerel (Table II). Groups such as these become more abundant when anchovy biomass decreases. Biomass of mesopelagic and large pelagic fish decreased when a collapse of the anchovy stock was modelled.

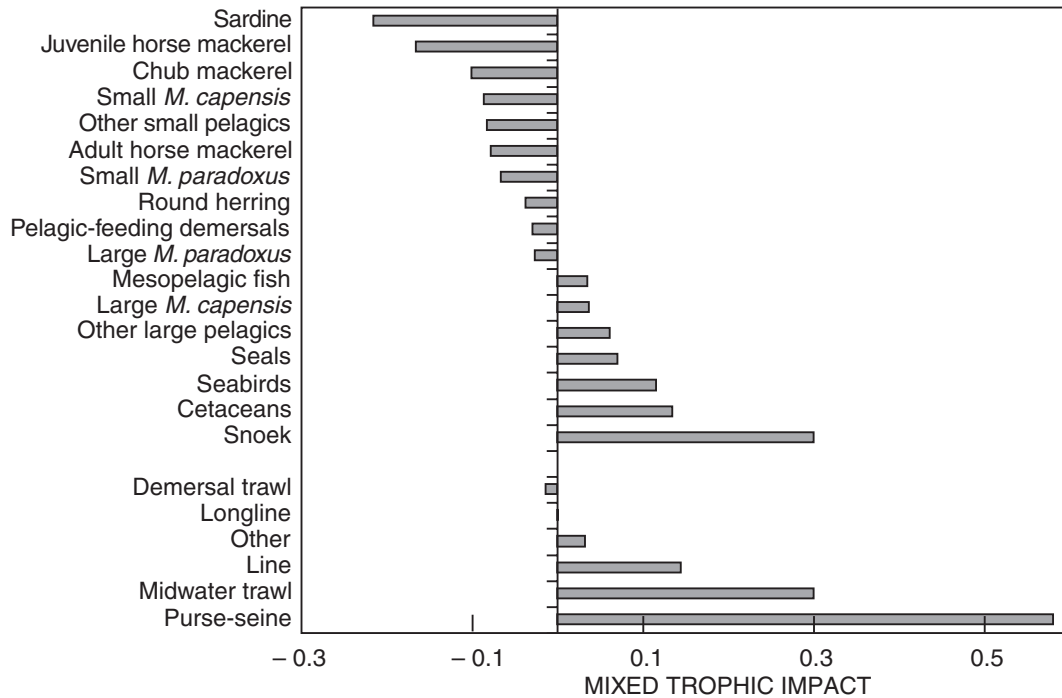


Fig. 3: Static model – mixed trophic impacts of anchovy on main fish and predator groups (upper section), and on the six fisheries (lower section), estimated using the model of the southern Benguela ecosystem for the 1980s. Bars indicate negative or positive relative net impacts (scaled between -1 and 1)

The indicators presented here are just a few examples that were developed from the model application used in this study as a test case for the proposed four-step procedure. As examples they support the result highlighted in Step 1: horse mackerel should increase

Table I: Dynamic model simulations; ecosystem indicators for anchovy, sardine and round herring, calculated from simulations using a model of the southern Benguela ecosystem for the 1980s. Interaction strength represents how much a change in one group or species will affect other components in the ecosystem. Functional impact represents how much other small pelagic fish will change when the abundance of one group changes. See text for details

Small pelagic fish	Interaction strength (<i>IS</i>); ranges from 0 to 1	Functional Impact (<i>FI_{pelagics}</i>); ranges from 0 to 100%
Anchovy	0.845	38.1
Sardine	0.366	24.1
Round herring	0.818	20.2

when anchovy decreases. There is a whole suite of more general and widely applied indicators available, arising from various ecosystem syntheses and modelling approaches. Much effort is being directed at exploring, developing and evaluating quantitative ecosystem indicators for fisheries management (SCOR/IOC Working Group 119 [<http://www.ecosystemindicators.org>]).

Table II: Dynamic model simulations; trophic replacement indicator of groups relative to anchovy in the southern Benguela ecosystem during the 1980s. See text for details

Group modelled	Trophic similarity indicator (<i>TS</i>)
Sardine	0.022
Round herring	0.413
Cape hakes	0.050
Other small pelagic fish	0.045
Horse mackerel	0.186
Mesopelagic fish, large pelagic fish (including snoek)	Biomass does not increase when anchovy biomass decreases

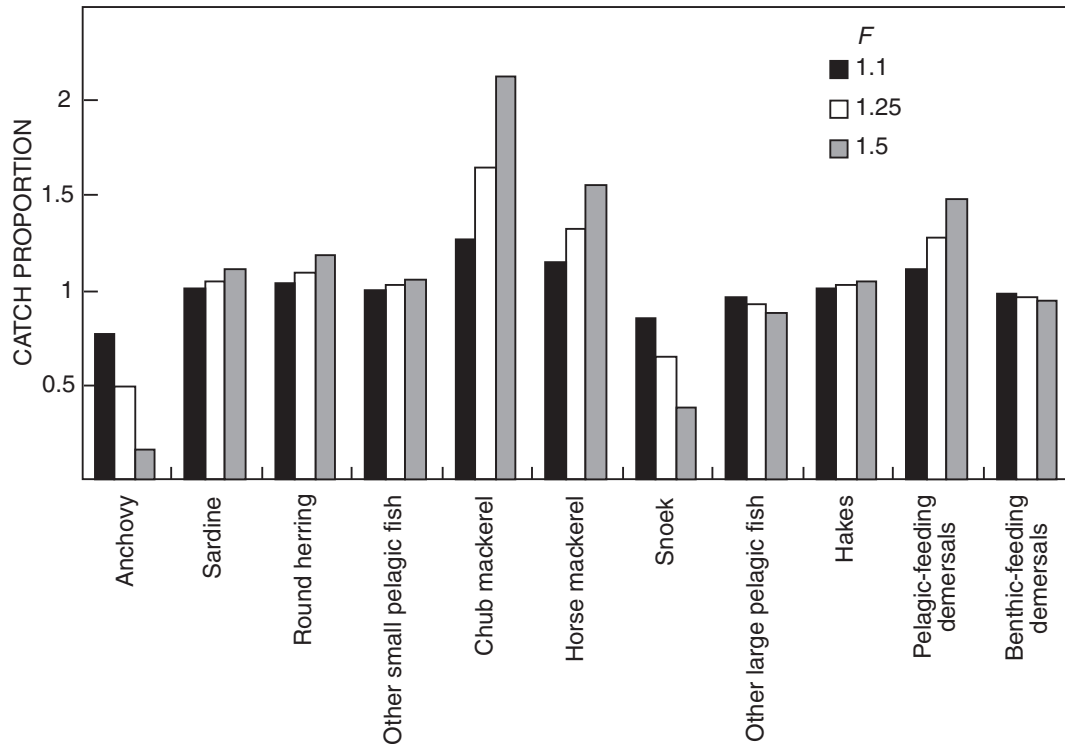


Fig. 4: Dynamic model simulations – impacts of increased anchovy fishing mortality on species-based fisheries: catches at the end of the 50-year simulation period as a proportion of the catch under the actual anchovy fishing mortality. Fishing mortality rate (F) for anchovy was increased by three different factors (1.1, 1.25 and 1.5) from Year 10 onwards, and expressed as proportions of means estimated for the 1980s

STEP 3

Dynamic ecosystem models should be used to conduct simulated fishing trials to test the ecosystem effects of fishing under various fishing scenarios (Step 3, Fig. 2). This step is equivalent to projecting a single-species population model into the future, under different catch scenarios. The dynamic simulation example shows that, if anchovy fishing mortality had increased, even by as little as 10%, there may have been a long-term reduction in the anchovy fishery of >20% and a 15% decrease in snoek catches (Fig. 4). These results suggest that “optimal” anchovy catches were made in the 1980s. Biomass and catches of most groups show signs of stabilizing by Year 50 when the anchovy fishing mortality rate was increased by 25%. At the end of the simulation, anchovy biomass and yield were half the mean of the 1980s, and snoek biomass and catches were about 65% of their previous levels (Fig. 4). Chub mackerel biomass and yield were still

increasing in Year 50, when they were larger by a factor of 1.64 than the 1980s mean. Pelagic-feeding demersal fish (excluding Cape hake) and horse mackerel were sustained at biomasses 30% larger than those of the 1980s. Overall, total catches were 16% smaller when fishing on anchovy was increased by 25%.

Biomass and catches of many groups were still changing at the end of the simulation period when fishing mortality of anchovy was increased to $1.5 \times$ the 1980s rate; the anchovy fishery collapsed, with catches in Year 50 only 16% of the previous mean levels. The demersal trawl fishery expanded (Table III) as catches of chub mackerel, horse mackerel and pelagic-feeding demersal fish increased. At the end of the simulation, catches of other groups were similar to those at the start of simulations, or had declined (Fig. 4), with a one-third overall reduction in total catches (Table III).

Altered fishing scenarios do not necessarily involve

overexploitation. However, the persistence of any changes in the ecosystem and the resilience of the model ecosystem to perturbations caused by fishing should be investigated. Possible undesirable short- and long-term effects can be identified using dynamic simulation models, and scientists, managers and decision-makers should be alerted to such risks. In the current example, horse mackerel increased in response to the decrease in anchovy biomass, as expected from Steps 1 and 2. In addition, the economically valuable snoek stock was greatly reduced (to 38% of its original biomass) when fishing on anchovy was increased by a factor of 1.5, and biomasses of other anchovy predators such as seabirds, seals and cetaceans decreased, to 77, 83 and 96% respectively of original levels estimated for the 1980s.

One of the advantages of ecosystem models is that they can assist in directing research by identifying data and information gaps (Christensen and Walters 2000). Based on such insights, it might be necessary to suggest changes to sampling programmes in order to monitor changes in ecosystem structure and functioning. For example, in the southern Benguela, round herring and mesopelagic fish are not heavily exploited and therefore their stocks are not regularly assessed or monitored. However, both groups are highly utilized in the ecosystem, because they are important prey for many forage fish that are commercially important (Shannon 2001). Their heavier exploitation is therefore likely to have consequences for species currently supporting large fisheries. For example, increased exploitation of round herring is likely to cause a reduction in size of the valuable horse mackerel stock (Shannon 2001). Foresight would suggest that a programme to monitor such stocks and their interactions with others should be initiated.

STEP 4

Finally, it is proposed that a synthesis should be conducted, whereby the ecosystem effects of an altered fishing strategy are considered for all fisheries in an ecosystem, so that the net effect can be quantified (Step 4, Fig. 2). In this example, increasing fishing mortality on anchovy by a factor of 1.5 caused the anchovy stock and its fishery to collapse, resulting in reduced catches of snoek, an important predator, and increased catches of horse mackerel (Fig. 4).

There is no real analog to Step 4 in single-species management. At present in the southern Benguela, fisheries management is based mostly on single-species assessments. In some instances, a few species are managed together. For example, sardine are managed as a directed fishery on adults and as a bycatch of juveniles and adults in directed fisheries on an-

Table III: Dynamic model; model catches, expressed as the deviation from unity after 50 years of simulation (i.e. as the proportion of the estimated mean 1980's catch), made in fisheries in the southern Benguela when fishing on anchovy was increased by a factor of 1.5 in simulations

Fishery	Catch proportion
Purse-seine	0.44
Midwater trawl	0.39
Demersal trawl	1.13
Line	0.69
Longline	0.98
Other	0.93
Total	0.67

chovy and round herring (de Oliveira *et al.* 1998b). In other cases, the ecosystem effects of fishing have been taken into account by considering the effects of an exploited species on non-exploited species, including species of conservation concern. The interactions between seals and Cape hake off the west coast of South Africa were modelled to examine the possible effects of seal culling on catches of Cape hake in demersal trawls (Punt and Butterworth 1995). Further, a model linking anchovy and Cape cormorants *Phalacrocorax capensis* suggested that the purse-seine fishery for anchovy may have reduced the bird population off South Africa (Crawford *et al.* 1992). Increased competition between fishers, seals and seabirds for pelagic fish may have reduced the reproductive success or juvenile survival rate of African penguins *Spheniscus demersus* (Crawford 1998). The African penguin is a species "vulnerable" to extinction and of considerable importance to South Africa's ecotourism industry (Crawford *et al.* 2001).

The above examples, although using multispecies considerations, are not ecosystem approaches to management in the strict sense of the definition (see Larkin's 1996 three essential principles of ecosystem management in the introduction). They do not make provision for the full impact of fisheries on all ecosystem components, nor do they quantify the net effects of the various fisheries on one another. A new approach to ecosystem management is required, whereby all fishing strategies under consideration are tested simultaneously, and their net potential long-term effects are taken into account.

Future development of a management procedure for ecosystems

To carry out Steps 3 and 4 effectively, the underlying

fisheries management objectives need to be known and clearly formulated (Fig. 2). One example from the southern Benguela would be how to weight the objective of maximizing catches of anchovy and sardine against conservation and ecotourism objectives for African penguins. It is likely that developing explicit ecosystem-based management objectives will be an iterative process that involves refinement using Steps 3 and 4.

The proposed four-step framework (Fig. 2) could be extended further to put into place a formal MP for ecosystems. An MP is a set of rules, pre-agreed by scientists, industry, managers and decision-makers and their advisers, to use fishery data to regulate fisheries, e.g. by setting annual TACs (Butterworth *et al.* 1997, de Oliveira *et al.* 1998a). Selection of a suitable MP for the South African anchovy and sardine fisheries has been based on Monte Carlo simulations to assess trade-offs in the medium term between catches or profits, risks (e.g. of collapse of a stock) and inter-annual variability in catches (Butterworth *et al.* 1997). The idea is that, once an MP is adopted for a resource, it should be allowed to run its course for a period of 3–5 years before being extensively reviewed and modified (Butterworth *et al.* 1997, Cochrane *et al.* 1998). This differs from conventional fishery management procedures requiring review and incorporation of updated data on an annual basis. In South Africa, MPs are in place for three fisheries: the demersal trawl fishery for Cape hake, the purse-seine fishery targeting anchovy and sardine, and the West Coast rock lobster *Jasus lalandii* fishery (Cochrane *et al.* 1998, de Oliveira *et al.* 1998a). It is suggested that the four-step framework proposed here be used as part of an MP in which all the important components of the southern Benguela ecosystem (all fisheries, as well as resources that are important for non-consumptive exploitation) are considered simultaneously. Once an ecosystem MP is agreed, it should be allowed ideally to function for a period of 5–10 years before being reviewed and modified according to revised management objectives. Ecosystem models and analyses should be updated continuously.

Cochrane (2000) suggested that, if eight principles were to be followed, fisheries management worldwide would be improved. Of particular relevance here is his fourth principle stating that it is not possible to optimize or maximize catches of all fisheries simultaneously. This principle gives rise to the likelihood of conflicting objectives, and responsible fisheries management requires that unambiguous objectives are agreed upon and that all users participate and cooperate (Cochrane 2000).

It is not too soon to implement practical ecosystem management measures in the southern Benguela.

Information from ecosystem models can be used to follow the proposed four-step procedure given carefully defined objectives, and in this way can contribute towards a first attempt at incorporating ecosystem considerations into fisheries management. Other studies in which different modelling approaches are taken, or in which ecosystem data are collected and analysed, will feed into the process at some or all of the steps, so the advice provided is continuously improved and updated. For example, other measured or model-derived indicators could provide helpful input at Step 2. Garcia and Staples (2000) discuss the value of sustainability indicators based on measured parameters or calculated from models, and which track changes in resources, socio-economic aspects, environmental conditions, technological limitations or developments, management policies, fishing rights and enforcement measures.

Reiterating the importance of trying to achieve a balance between economic benefits and ecosystem sustainability (Jennings and Kaiser 1998, see Introduction), it is imperative that objectives are carefully defined for each fishery and for each non-consumptively exploited group when undertaking Step 3. Further, it is essential that the overall objectives for fisheries and non-consumptive exploitation of the southern Benguela ecosystem are negotiated before undertaking Step 4. It is suggested that all stakeholders be involved in formulating and refining these management objectives (Fig. 4). This would involve public participation through an integrated approach, as suggested by Penzhorn (1999) for the South African demersal fishery, and their inputs to high-level policy-making. A formal procedure by which these inputs should be considered and by which consensus would be reached in setting management objectives should be established, aimed ultimately at advising the final decision-making body. Once there is agreement on the objectives, it is a matter of following the four steps proposed to provide fisheries management advice that accounts for ecosystem considerations based on sound objectives. This gives rise to optimism that it will be possible to provide advice on fisheries management strategies from a true ecosystem perspective, and that this may not be as far into the future as has been predicted by many thus far, at least in South Africa and other countries where resource status is not too depressed.

ACKNOWLEDGEMENTS

We thank Dr Villy Christensen, Prof. John Field and Dr Astrid Jarre for their helpful comments and suggestions on an earlier version of the manuscript.

LITERATURE CITED

- ANON. 1986 — Recommendations to the Fisheries Advisory Council for pelagic fish stock management in 1987. Unpublished Report, Sea Fisheries Research Institute, South Africa: 7 pp.
- ANON. 1989 — Pilchard TAC recommendations for 1990. Unpublished Report, Sea Fisheries Research Institute, South Africa: 8 pp.
- ANON. 1997 — *White Paper. A Marine Fisheries Policy for South Africa*. [Cape Town; Department of Environmental Affairs & Tourism]: 46 pp.
- ANON. 1998 — Marine Living Resources Act 1998 (Act No. 18 of 1998). *Government Gazette, S. Afr.* **395**(18930): 66 pp.
- BEAMISH, R. J. and C. MAHNKEN 1999 — Taking the next step in fisheries management. In *Ecosystem Approaches for Fisheries Management*. University of Alaska Sea Grant **AK-SG-99-01**: 1–21.
- BUTTERWORTH, D. S. 1983 — Assessment and management of pelagic stocks in the southern Benguela region. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *FAO Fish. Rep.* **291**(2): 329–405.
- BUTTERWORTH, D. S., DE OLIVEIRA, J. A. A. and K. L. COCHRANE 1997 — Management procedures: a better way to manage fisheries? The South African experience. In *Global Trends: Fisheries Management*. Pikitch, E. K., Huppert, D. D. and M. P. Sissenwine (Eds). *Am. Fish. Soc. Symp.* **20**: 83–90.
- CADDY, J. F. 1999 — Fisheries management in the twenty-first century: will new paradigms apply? *Revs Fish Biol. Fish.* **9**: 1–43.
- CHRISTENSEN, V. 1995 — A model of trophic interactions in the North Sea in 1981, the year of the stomach. *Dana* **11**: 1–28.
- CHRISTENSEN, V. 1996 — Managing fisheries involving predator and prey species. *Revs Fish Biol. Fish.* **6**: 417–442.
- CHRISTENSEN, V. and D. PAULY 1992 — ECOPATH II — a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol. Model.* **61**: 169–185.
- CHRISTENSEN, V. and C. J. WALTERS 2000 — ECOPATH with ECOSIM: methods, capabilities and limitations. In *Methods for Assessing the Impact of Fisheries on Marine Ecosystems of the North Atlantic*. Pauly, D. and T. J. Pitcher (Eds). Fisheries Centre Research Reports **8**: 79–105.
- COCHRANE, K. L. 1999 — Complexity in fisheries and limitations in the increasing complexity of fisheries management. *ICES J. mar. Sci.* **56**: 917–926.
- COCHRANE, K. L. 2000 — Reconciling sustainability, economic efficiency and equity in fisheries: the one that got away? *Fish and Fish.* **1**: 3–21.
- COCHRANE, K. L., BUTTERWORTH, D. S. and A. I. L. PAYNE 1997 — South Africa's offshore living marine resources: the scientific basis for management of the fisheries. *Trans. R. Soc. S. Afr.* **52**: 149–176.
- COCHRANE, K. L., BUTTERWORTH, D. S., DE OLIVEIRA, J. A. A. and B. A. ROEL 1998 — Management procedures in a fishery based on highly variable stocks and with conflicting objectives: experiences in the South African pelagic fishery. *Revs Fish Biol. Fish.* **8**: 177–214.
- CONSTABLE, A. J., DE LA MARE, W. K., AGNEW, D. J., EVERSON, I. and D. MILLER 2000 — Managing fisheries to conserve the Antarctic marine ecosystem: practical implementation of the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR). *ICES J. mar. Sci.* **57**: 778–791.
- CRAWFORD, R. J. M. 1998 — Responses of African penguins to regime changes of sardine and anchovy in the Benguela system. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci.* **19**: 355–364.
- CRAWFORD, R. J. M., DAVID, J. H. M., SHANNON, L. J., KEMPER, J., KLAGES, N. T. W., ROUX, J.-P., UNDERHILL, L. G., WARD, V. L., WILLIAMS, A. J. and A. C. WOLFAARDT 2001 — African penguins as predators and prey — coping (or not) with change. In *A Decade of Namibian Fisheries Science*. Payne, A. I. L., Pillar, S. C. and R. J. M. Crawford (Eds). *S. Afr. J. mar. Sci.* **23**: 435–447.
- CRAWFORD, R. J. M., SHANNON, L. V. and D. E. POLLOCK 1987 — The Benguela ecosystem. 4. The major fish and invertebrate resources. In *Oceanography and Marine Biology. An Annual Review* **25**. Barnes, M. (Ed.). Aberdeen; University Press: 353–505.
- CRAWFORD, R. J. M., UNDERHILL, L. G., RAUBENHEIMER, C. M., DYER, B. M. and J. MÁRTIN 1992 — Top predators in the Benguela ecosystem — implications of their trophic position. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 675–687.
- CURY, P., BAKUN, A., CRAWFORD, R. J. M., JARRE-TEICHMANN, A., QUINOÑES, R., SHANNON, L. J. and H. M. VERHEYE 2000 — Small pelagics in upwelling systems: patterns of interaction and structural changes in “wasp-waist” ecosystems. *ICES J. mar. Sci.* **57**: 603–618.
- DE LA MARE, W. K. 1998 — Ttidier fisheries management requires a new MOP (management-oriented-paradigm). *Revs Fish Biol. Fish.* **8**: 349–356.
- DE OLIVEIRA, J. A. A., BUTTERWORTH, D. S. and S. J. JOHNSON 1998a — Progress and problems in the application of management procedures to South Africa's major fisheries. In *Fishery Stock Assessment Models*. Alaska Sea Grant College Program **AK-SG-98-01**: 513–530.
- DE OLIVEIRA, J. A. A., BUTTERWORTH, D. S., ROEL, B. A., COCHRANE, K. L. and J. P. BROWN 1998b — The application of a management procedure to regulate the directed and bycatch fishery of South African sardine *Sardinops sagax*. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci.* **19**: 449–469.
- GARCIA, S. M. 1996 — The precautionary approach to fisheries and its implications for fisheries research, technology and management: an updated review. In *Precautionary Approach to Fisheries*. **2. Scientific papers**. *FAO Fish. tech. Pap.* **350/2**: 76 pp.
- GARCIA, S. M. and D. J. STAPLES 2000 — Sustainability reference systems and indicators for responsible marine capture fisheries: a review of concepts and elements for a set of guidelines. *Mar. Freshwat. Res.* **51**: 385–426.
- GISLASON, H., SINCLAIR, M., SAINSBURY, K. and R. O'BOYLE 2000 — Symposium overview: incorporating ecosystem objectives within fisheries management. *ICES J. mar. Sci.* **57**: 468–475.
- HEYMANS, J. J. and D. BAIRD 2000 — A carbon flow model and network analysis of the northern Benguela upwelling system, Namibia. *Ecol. Model.* **126**: 9–32.
- HEYMANS, J. J., SHANNON, L. J. and A. JARRE 2004 — Changes in the northern Benguela ecosystem over three decades: 1970s, 1980s, and 1990s. *Ecol. Model.* **172**: 175–195.
- JARRE-TEICHMANN, A., SHANNON, L. J., MOLONEY, C. L. and P. A. WICKENS 1998 — Comparing trophic flows in the southern Benguela to those in other upwelling ecosystems. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds).

- S. Afr. J. mar. Sci.* **19**: 391–414.
- JENNINGS, S. and M. J. KAISER 1998 — The effects of fishing on marine ecosystems. *Adv. mar. Biol.* **34**: 201–352.
- LARKIN, P. A. 1996 — Concepts and issues in marine ecosystem management. *Revs Fish Biol. Fish.* **6**: 139–164.
- LEONTIEF, W. W. 1951 — *The Structure of the American Economy, 1919–1939*, 2nd ed. New York; Oxford University Press: 264 pp.
- LIVINGSTON, P. A. and S. TJELMELAND 2000 — Fisheries in boreal ecosystems. *ICES J. mar. Sci.* **57**: 619–627.
- MAY, R. M., BEDDINGTON, J. R., CLARK, C. W., HOLT, S. J. and R. M. LAWS 1979 — Management of multispecies fisheries. *Science, N.Y.* **205**(4403): 267–277.
- MURAWSKI, S. A. 1991 — Can we manage our multispecies fisheries? *Fisheries* **16**(5): 5–13.
- PAULY, D. 1998 — Large marine ecosystems: analysis and management. In *Benguela Dynamics: Impacts of Variability on Shelf-Sea Environments and their Living Resources*. Pillar, S. C., Moloney, C. L., Payne, A. I. L. and F. A. Shillington (Eds). *S. Afr. J. mar. Sci.* **19**: 487–499.
- PAULY, D., CHRISTENSEN, V., DALSGAARD, J., FROESE, R. and F. TORRES 1998 — Fishing down marine food webs. *Science, N.Y.* **279**(5352): 860–863.
- PAULY, D., CHRISTENSEN, V., FROESE, R. and M. PALOMARES 2000b — Fishing down aquatic food webs. *Am. Scient.* **88**: 46–51.
- PAULY, D., CHRISTENSEN, V. and C. WALTERS 2000a — ECOPATH, ECOSIM and ECOSPACE as tools for evaluating ecosystem impact of fisheries. *ICES J. mar. Sci.* **57**: 697–706.
- PENZHORN, L. J. 1999 — Viewpoint: a demersal fishing industry management perspective of risk. *ICES J. mar. Sci.* **56**: 1070–1072.
- PITCHER, T. J. 2000 — Ecosystem goals can reinvigorate fisheries management, help dispute resolution and encourage public support. *Fish and Fish.* **1**: 99–103.
- PITCHER, T. J. and D. PAULY 1998 — Rebuilding ecosystems, not sustainability, as the proper goal of fishery management. In *Reinventing Fisheries Management*. Pitcher, T. J., Hart, P. and D. Pauly (Eds). London; Kluwer.: 311–329 (*Fish and Fisheries Series 23*).
- POLOVINA, J. J. 1984 — Model of a coral reef ecosystem. 1. The ECOPATH model and its application to French Frigate Shoals. *Coral Reefs* **3**: 1–11.
- POWER, M. E., TILMAN, D., ESTES, J. A., MENGE, B. A., BOND, W. A., MILLS, L. S., DAILY, G., CASTILLA, J. C., LUBCHENCO, J. and R. T. PAINE 1996 — Challenges in the quest for keystones. *Bioscience* **46**: 609–620.
- PUNT, A. E. and D. S. BUTTERWORTH 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 hakes *Merluccius capensis* and *M. paradoxus*. *S. Afr. J. mar. Sci.* **16**: 255–285.
- ROUX, J-P. and L. J. SHANNON 2002 — Some considerations for ecosystem management of the northern Benguela ecosystem. *Workshop Report, Swakopmund, Namibia, May 2001. BENEFIT/FAO/Government of Japan Cooperative Programme GCP/INT/643/JPN, Report 2.5*: 42 pp.
- SAINSBURY, K. J., PUNT, A. E. and A. D. M. SMITH 2000 — Design of operational management strategies for achieving fishery ecosystem objectives. *ICES J. mar. Sci.* **57**: 731–741.
- SCHWARTZLOSE, R. A., ALHEIT, J., BAKEN, A., BAUMGARTNER, T. R., CLOETE, R., CRAWFORD, R. J. M., FLETCHER, W. J., GREEN-RUIZ, Y., HAGEN, E., KAWASAKI, T., LLUCH-BELDA, D., LLUCH-COTA, S. E., MacCALL, A. D., MATSUURA, Y., NEVÁREZ-MARTÍNEZ, M. O., PARRISH, R. H., ROY, C., SERRA, R., SHUST, K. V., WARD, M. N. and J. Z. ZUZUNAGA 1999 — Worldwide large-scale fluctuations of sardine and anchovy populations. *S. Afr. J. mar. Sci.* **21**: 289–347.
- SCULLY, R. T., BROWN, W. Y. and B. S. MANHEIM 1986 — The Convention for the Conservation of Antarctic Marine Living Resources: a model for large marine ecosystem management. In *Variability and Management of Large Marine Ecosystems*. Sherman, K. and M. Alexander (Eds). Colorado, USA; Westview Press: 281–286 (*AAAS Selected Symposia Series 99*).
- SHANNON, L. J. 2001 — Trophic models of the Benguela upwelling system: towards an ecosystem approach to fisheries management. Ph.D. thesis, University of Cape Town. xxxv + 319 pp.
- SHANNON, L. J., CHRISTENSEN, V. and C. J. WALTERS 2004 — Modelling stock dynamics in the southern Benguela ecosystem for the period 1978–2002. In *Ecosystem Approaches to Fisheries in the Southern Benguela*. Shannon, L. J., Cochrane, K. L. and S. C. Pillar (Eds). *Afr. J. mar. Sci.* **26**: 179–196.
- SHANNON, L. J. and P. M. CURY 2004 — Indicators quantifying small pelagic fish interactions in the southern Benguela ecosystem. *Ecol. Indicators* **3**(4):305–321.
- SHANNON, L. J., CURY, P. M. and A. JARRE 2000 — Modelling effects of fishing in the southern Benguela ecosystem. *ICES J. mar. Sci.* **57**: 720–722.
- SHANNON, L. J. and A. JARRE-TEICHMANN 1999a — A model of the trophic flows in the northern Benguela upwelling system during the 1980s. *S. Afr. J. mar. Sci.* **21**: 349–366.
- SHANNON, L. J. and A. JARRE-TEICHMANN 1999b — Comparing models of trophic flows in the northern and southern Benguela upwelling systems during the 1980s. In *Ecosystem Approaches for Fisheries Management*. University of Alaska Sea Grant **AK-SG-99-01**: 55–68.
- SHANNON, L. J., MOLONEY, C. L., JARRE, A. and J. G. FIELD 2003 — Comparing trophic flows in the southern Benguela during the 1980s and 1990s. *J. mar. Syst.* **39**: 83–116.
- SHELTON, P. A. 1992 — Detecting and incorporating multispecies effects into fisheries management in the North-West and South-East Atlantic. In *Benguela Trophic Functioning*. Payne, A. I. L., Brink, K. H., Mann, K. H. and R. Hilborn (Eds). *S. Afr. J. mar. Sci.* **12**: 723–737.
- STEELE, J. H. 1996 — Regime shifts in fisheries management. *Fish. Res.* **25**: 19–23.
- ULANOWICZ, R. E. and C. J. PUCCIA 1990 — Mixed trophic impacts in ecosystems. *Coenoses* **5**: 7–16.
- WALTERS, C., CHRISTENSEN, V. and D. PAULY 1997 — Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Revs Fish Biol. Fish.* **7**: 139–172.
- WITHERELL, D. 1999 — Incorporating ecosystem considerations into management of Bering Sea groundfish fisheries. In *Ecosystem Approaches for Fisheries Management*. University of Alaska Sea Grant **AK-SG-99-01**: 315–327.