3. Comparison of models

3.1 LEVEL OF COMPLEXITY AND REALISM

There is a wide range in the levels of complexity of the 20 modelling approaches considered here (Tables A1-A4, Figures 1-3). Most of the models may be categorized as of the MRM-type, with only EwE and ATLANTIS representing the full trophic spectrum (Figure 2). There is typically a trade-off between the range in trophic levels considered and the corresponding detail with which each group is represented – for example, in practice EwE models cannot represent the full age-structure of all groups whereas models built using a restricted subset only of the ecosystem may include very detailed length/age structure information (e.g. GADGET).

It was not considered practical or feasible to list model parameters in detail for all 20 modelling approaches. However, entries in Table A2 are intended to give a rough idea of the sorts and numbers of parameters required for each model. By their nature, ecosystem models are parameter- and data-hungry. It is sometimes argued that single-species assessment models contain as many or more parameters. However, these parameters are typically estimated by fitting to data and it is relatively straightforward to test sensitivity to alternative values. The difficulty with considering multi-species effects is that the field is still wide open in terms of understanding of the functional forms of interaction and the availability of data to specify or estimate many of the parameter values is limited. In the synthesis presented here, attention is drawn to selected parameter values to which it is difficult to ascribe values conclusively.

3.2 FUNCTIONAL RESPONSE FORMULATIONS

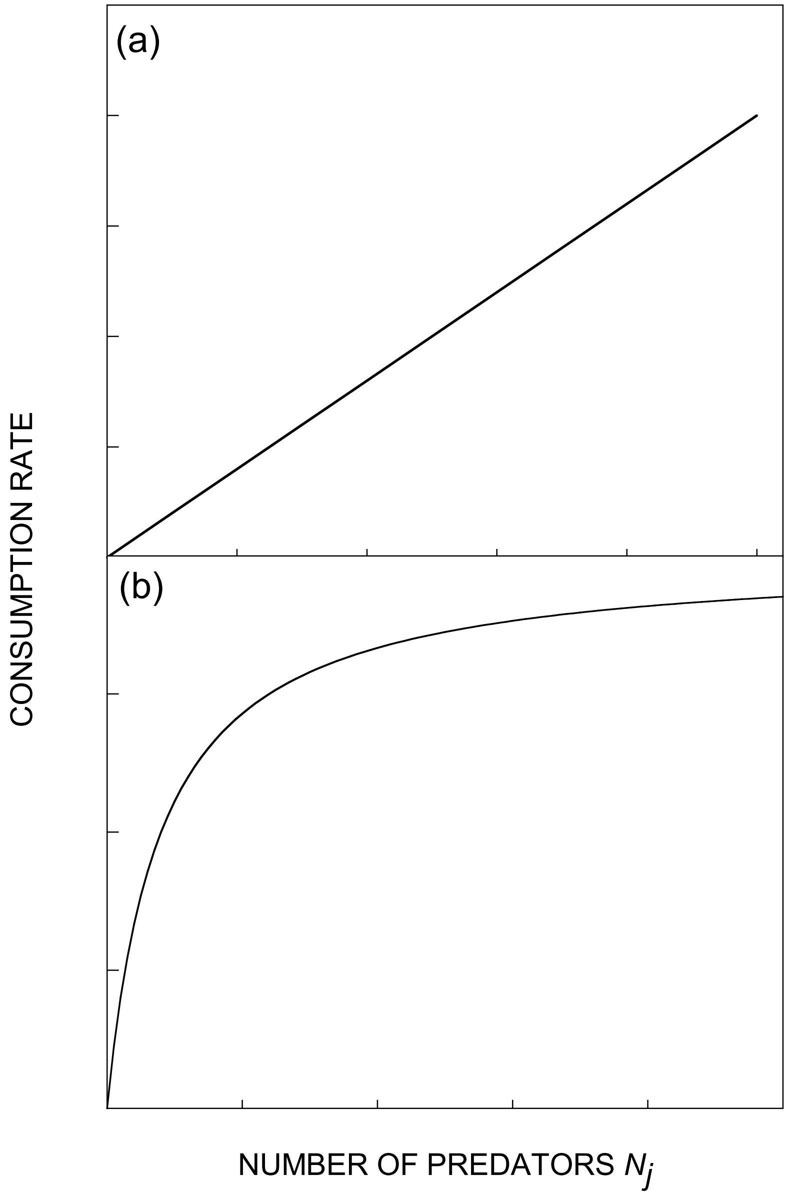
The different functional form of interactions in EwE's foraging arena (per-capita consumption by a predator decreases with the overall abundance of that predator) compared to MSVPA's (and other models') constant ration model (per-capita consumption is set equal to the predator's required daily ration) for predator feeding has important implications for model behaviour and predictions. It tends (desirably) to damp the large amplitude oscillations in population size that are frequently predicted by multi-species models (see, for example, Mori and Butterworth, 2004). However, this has additional consequences as detailed below.

Butterworth and Plagányi (2004) contrast the assumptions of the MSVPA (and its associated derivatives that provide projections) and ECOSIM approaches, which they categorize as "efficient predator models" and "hungry predator models" respectively. MSVPA assumes that a predator is always able to consume its desired daily ration of food. If N_j is the number of predators of species j and the number of their prey species i (N_i) is kept fixed, then Figure 4a shows the implication of the MSVPA assumption for how the total consumption rate Q_{ij} of prey i by predator j grows as the number of predators increases: linear proportionality.

On the other hand, ECOSIM is based upon the foraging arena model (Walters, Christensen and Pauly, 1997) (Equation 5) which leads to the form of relationship between total consumption rate Q_{ij} and the number of predators N_j as shown in Figure 4b. When used in combinations, MSVPA and ECOSIM can possibly make a first attempt at bounding the likely impact on a fishery of, for example, a reduction in seal numbers in that, based on the assumed forms of interaction, the former approach is likely to overestimate the effect and the latter to underestimate it (at least when using default or low vulnerability settings) (Plagányi and Butterworth, 2005). The data

FIGURE 4

Schematic showing how the total consumption rate Q_{ij} of prey species i by predator species j grows as the number of predators increase for the two contrasted cases: a) MSVPA (and its derivatives providing projections) showing a linear proportionality relationship and b) ECOSIM's foraging arena-based model (shape shown typical for default parameters) in which the total rate saturates at a constant level for high numbers of predators (from Plagányi and Butterworth, 2004, 2005a)



hungry nature of MSVPA does not necessarily preclude the use of MSFOR to predict forwards, provided the model is initialized using sensible assumptions based on at least some data (see IWC, 2004a).

Walters *et al.* (2000) advance two arguments to support the foraging arena over the constant ration model, namely that satiation is rare in nature "predators with full stomachs are not a common field observation" (Walters and Kitchell, 2001) and that handling time effects are trivial in the field because if animals increased their rate of effective search to the extent where handling time became an issue, they would be exposed to additional risk of predation hence they avoid doing this. Walters and Martell (2004) explain further that the basic idea of EwE's foraging arena theory is that marine species have limited access to prey resources because of spatial habitat-choice behaviours aimed at moderating their predation risk. The IWC (2004a) describes the biological underpinnings of the foraging arena model as "controversial and uncertain" because there appears to be little observational evidence to distinguish the two models.

One of the key issues in moving the development of multi-species models forward is thus the appropriate form of the functional response formulations to be considered in the models. At opposite extremes, formulations such as that used by ECOSIM depict per-capita consumption by a predator as decreasing with the overall abundance of that predator, whereas constant ration formulations (such as that used in MSVPA approaches) set per-capita consumption as equal to the predator's required daily ration. It is strongly recommended that effort be focused on appropriate data collection and/ or experiments to assist in shedding light as to the most appropriate choice of model form to represent feeding behaviour. Fenlon and Faddy (2006) argue that rather than using mechanistic models to interpret data from predator-prey systems, simple logistic regression analyses are more consistent with the data and take stochastic variation into account. They present some models for dealing with over-dispersion, including one based on the beta-binomial distribution which is shown to provide a better fit to experimental data.

However, extrapolations from the microscale to the macroscale require integrating the form of a functional response over the area concerned and independent estimates of parameters at the microscale will not necessarily remain appropriate if the same functional form is assumed to govern macroscale behaviour. Experimental estimates of suitability often refer only to the microscale, but multi-species models require parameter values that reflect effective responses at the macroscale level (Lindstrøm and Haug, 2001). Reliable integration of microscale estimates of suitabilities over the spatio-temporal distributions for both predators and prey to provide macroscale parameter values, is likely a realistic objective for the longer term only; in the shorter term, regression approaches will probably be needed to attempt to relate macroscale changes in diet to variations in prey abundance. Studies comparing the performance or predictions of models representing processes at different scales and/or with different levels of spatial aggregation can also be informative (Fulton, Smith and Johnson, 2003a).

Most multi-species models utilize a hyperbolic (Type II) functional relationship (Jeschke, Kopp and Tollrian, 2002; Mackinson *et al.*, 2003). Although difficult to implement because additional parameters need to be estimated, a sigmoidal (Type III) functional response is likely more appropriate when modelling generalist predators, such as whales (Mackinson *et al.*, 2003). This is because these predators are generalists and hence exert less of a strong effect on depleted prey stocks, as can be depicted using a sigmoidal relationship. Given model structural uncertainty due to a paucity of knowledge on functional responses, definitive conclusions cannot be drawn from models based on a single structure (Koen-Alonso and Yodzis, 2005). However, the biomass of available food is often such that it spans a limited section of the functional response curves where they are all very similar so that it is hard to differentiate between alternative representations, unless there exists some form of extreme or transient conditions either temporally or spatially (Walters 1986, Fulton, Smith and Johnson, 2003b). Ideally, evaluations to provide advice on the impact of, say, the effects of fishing a predator on fisheries for prey species should not be based on a single representation of species interactions; but rather the robustness of results across a range of plausible functional forms needs to be considered. Bayesian methods are a useful tool for taking account of variability in and uncertainty about feeding relationships.

3.3 WHOLE ECOSYSTEM MODELS VS MRMS

As highlighted by an international review panel at the 2004 BENEFIT Stock Assessment Workshop (BENEFIT, 2004), the choice of which multi-species models to use needs to be linked to scientific goals and/or management objectives. For objectives related to broad-scale questions regarding the structure of the ecosystem, ECOPATH/ ECOSIM models might be used; other models may be more appropriate for more specific questions. Unlike EwE, individually tailored approaches such as MRMs have more flexibility in modelling the dynamics of marine predators, but usually ignore any potential effects that changing prey populations may have on the predators themselves. Fulton and Smith (2004) strongly recommend that ideally a suite of different "minimum-realistic" ecosystem models should be constructed and their results compared. However, given limited person-power and pressure to produce results, it is important first to engage in discussions regarding which are the preferred modelling approach/es to be pursued in each context. Thus, for example, as a first attempt to address hake multi-species interactions, the 2004 BENEFIT Workshop recommended that existing models should be adapted to provide estimates of the predation mortality on hake that is generated by the two hake species. Similarly, CCAMLR has tended to consider simpler predator-prey type models for the Southern Ocean (e.g. Thomson *et al*., 2000).

Nevertheless, whole ecosystem models clearly have an important role to play, given that few of the other models discussed are suitable for exploring broader ecosystem questions (Figure 3, Table A4). While predictive multi-species population models may have limited impact on management decisions in the short-term, if only because of considerations of lack of data, model complexity and uncertainty and research costs, there are some initiatives that are being pursued with the information that is at hand at present. It may be instructive to investigate possibilities of closer links between ECOPATH data inputs and single-species stock assessment models. In considering ECOPATH's potential to contribute to single-species models, there is a need to pursue the question of whether the constraints provided by the ECOPATH mass-balance equation appreciably reduce uncertainties associated with single species models. The mass-balance relationships of the ECOPATH approach (Christensen and Pauly, 1992) provide some information beyond that conventionally incorporated in single-species assessments and do so essentially independent of concerns about how best to model the functional forms of species interactions. Preliminary computations (Somhlaba *et al*., 2004; Somhlaba, 2006) suggest that for the Benguela system, the precision of single-species assessment estimates is unlikely to be improved through taking account of mass-balance constraints. On the other hand, outputs from single-species stock assessment models may have some utility for improving biomass and productivity estimates (and their associated variance estimates) used as inputs to ECOPATH and hence ECOSIM. Recent additions to the EwE software (Christensen and Walters, 2004) mean that it is possible to include more life history stages in ECOSIM models.

Butterworth and Plagányi (2004) suggest that until "Whole Ecosystem" approaches have been shown to demonstrate adequate robustness in their predictions to uncertainties in input data and alternative plausible choices for the functional forms of interactions between species, they should have lower priority than the development of Minimum Realistic Models, given an aim of providing inputs on say catch levels of a target species. They argue that in the context of providing fisheries management advice, MRMs would seem the obvious first step to take in the process of moving from single-species models to the extremely ambitious and demanding aim of a reliable predictive model for all major ecosystem components. On the other hand, depending on the nature of the question, whole ecosystem models may be the only suitable tool to use, particularly when management strategies other than simple TAC application are being considered. Ecosystem-based management is still in its infancy and hence there is as yet no consensus on what are the most appropriate management tools. In many areas there is the realisation that TACs spatial or temporal are unlikely to be appropriate (or feasible) for all species and that other tools such as closures and gear mitigation devices may need to be called upon (E. Fulton, pers. comm.). In this context, multi-species and ecosystem models have a large role to play in assessing the utility of these tools and even the effectiveness of proposed monitoring schemes or indicators (e.g. Fulton, Smith and Punt, 2005).

3.4 ADVANTAGES, DISADVANTAGES AND LIMITATIONS

Selected advantages, disadvantages and limitations of the 20 modelling approaches considered are listed in Table A3. This is by no means a comprehensive list and it would be instructive for future studies to expand this list. In its current form, it provides a rough overview of some of the strengths and weaknesses of the different approaches.

4. Potential of tools to address multi-species research questions

In reviewing the methods available for assessing the impacts of ecological interactions between species and fisheries, it is important not to lose sight of the aims of the various approaches. In the current (fisheries management) context, most of the questions to be addressed by multi-species/ecosystem models fall under one of the following headings.

1. Understanding ecosystem structure and functioning, e.g. relative roles of top-down and bottom-up processes.
2. What is the impact of a target fish species on other species in the ecosystem? For example, does the removal of the target species negatively impact other species which depend on it as prey (e.g. Gislason, 2003)? Bycatch issues are dealt with separately under 13 below.
3. What is the effect on top predators of removing their prey? This question is listed separately given that it is the focus of many multi-species studies. The classic example is CCAMLR's focus on the possible impacts on Southern Ocean predators of an expanding krill fishery.
4. What is the extent of competition between marine mammals and fisheries (see e.g. Trites, Christensen and Pauly, 1997; Harwood and McLaren, 2002; Kaschner, 2004; Plagányi and Butterworth, 2002; 2005a)? This includes consideration of both "direct competition", which involves reduction (by consumption or utilisation) of a limited resource, but with no direct interactions between the competing species (Clapham and Brownell, 1996), as when a marine mammal eats a fish that could otherwise have been caught by a fisherman and "indirect competition" (e.g. Pauly and Christensen, 1995) in which the competitors may target different resources but these are linked because of a foodweb effect (e.g. when a marine mammal consumes a fish that is an important prey species of a commercially desirable fish species).
5. What ecosystem considerations need to be taken into account to rebuild depleted fish stocks?
6. Is the single-species-based assessment of the status and productivity of a target species severely biased because of a failure to consider multi-species interactions (e.g. Pope, 1991; Walters and Kitchell, 2001; Walters *et al.*, 2005)?
7. Is there an ecologically or economically better way to distribute fishing effort in an ecosystem? The focus here is, for example, on the extent to which different species should be targeted so as to optimise use of the ecosystem both ecologically and economically.
8. Are there relatively unexploited species in an ecosystem which could be targeted without having a detrimental effect on other components of the ecosystem?
9. Is fishing on particular stocks driving the ecosystem to a less productive/less desirable state (e.g. a new stable state or an adverse shift in marine communities (Trites *et al.*, 1999, Scheffer, Carpenter and de Young, 2005)?
10. Is the spatial and temporal concentration of fishing negatively impacting the longterm viability of species such as land-breeding marine mammal predators and seabirds? Should the spatial distribution of fishing effort be altered to account for the needs of e.g. land-breeding predators. This includes consideration of, for example, fishing exclusion zones and MPAs (see e.g. Dalton, 2004; Hilborn *et al.*, 2004).

11. Effects of physical/environmental factors on the resources on which fisheries depend.
12. Effects of habitat modification. This includes consideration of effects such as trawling damaging benthic habitats and hence having an indirect negative effect on fish stocks.
13. What are the impacts of bycatch?
14. Effects of the introduction of non-native species.

Naturally there is a large number of very specific questions that models have been constructed to address and every (good) model is useful in the context for which it has been designed. The list above is far from complete, but encompasses most of the commonly phrased questions.

In terms of a broad overview of the usefulness of the different modelling approaches discussed here, some preliminary suggestions are presented in Table A4 which highlights those models considered by the report's author to show the most potential to address each of the questions above. This is not intended as the final word on the subject, but rather as a starting point to compare the models with slightly more specific aims in mind. Given that it can be argued that any ecosystem model contributes to one's understanding of the system, the models have been categorized as either showing the potential to contribute to an understanding of the functioning of the ecosystem as a whole or to a subset only, recognizing that both these aims are important in different contexts. Glancing across the 20 modelling approaches considered in Table A4, it is evident that collectively they cover all the research questions posed here, but that there are fairly large gaps in the suitability of specific approaches to address subsets of the questions posed above. Although the finer details of Table A4 can and indeed should be further debated, the schematic presented here may be useful as a first step to assist in choosing between models given specific EBFM research questions. Note that although EwE, ATLANTIS and INVITRO emerge as the clear "winners" in terms of the range of questions they are capable of addressing, a word of caution is necessary here because that feature alone does not guarantee that they necessarily provide the best approaches to address a specific issue.

The research question that emerged as most poorly addressed across all models was that of the effects of habitat modification, with only ATLANTIS rating highly as a tool in this regard (Table A4). ECOSPACE can also be used to evaluate the effects of habitat modification and EwE has some potential for indirectly exploring aspects of this issue, through trophic mediation. Although there are fairly straightforward examples of this issue, less direct cases can be rather intractable (see e.g. Sainsbury *et al.*, 1997, Auster and Langton 1998). On the other hand, the deleterious effects of trawling have long rung alarm bells (e.g. McConnaughey, Mier and Dew, 2000) and this may point to a need for more focussed attention to address this issue – naturally in combination with empirical studies. In contrast, Table A4 suggests that there has been a definite increasing trend towards constructing models capable of being driven by physical and other environmental variables. This may be in response to the indication that trophic interactions are limited in the extent to which they can explain observed trends and changes in the ecosystem.

A separate category altogether pertains to ecosystem models constructed with the primary purpose of being used for model testing (e.g. Yodzis, 1998), comparison purposes (e.g. Fulton *et al.*, 2004) or in a simulation testing framework. An example of the latter is the use of ATLANTIS as an operating model (see next section) to evaluate the performance of ecological indicators (Fulton, Smith and Punt, 2004). These are critical issues to be addressed and it is hoped that in future as much effort will be focused on these questions as on the further development of new or existing models. It is particularly useful to test ecosystem models such as EwE by generating simulated data with known parameters using an operating model such as ATLANTIS. In testing

ECOPATH in this way, it was found that while useful for capturing snapshots and giving great insight into ecosystem structure and potentially counter-intuitive system responses in a "what-if" context, it was ill suited in the role of an assessment model (Fulton, Smith and Punt, 2005; E. Fulton, *pers. comm.*). This was due to changing error structures through time, the potential problems with data compatibility (particularly when diet data was collected at a point in time that is distant from the time the biomass estimates are made) and the potential to miss once rare links that can become important if conditions change substantially (E. Fulton, pers. comm.). These are the same sorts of problems likely to afflict most ecosystem models, highlighting the importance of seeking the same thorough understanding of the limitations of ecosystem models as is the case for single-species assessment models.

5. Roles for models in operational management procedure development

Operational Management Procedure (OMP) (Butterworth, Cochrane and De Oliveira, 1997; de Oliveira *et al.,* 1998, Butterworth and Punt, 1999), or Management Strategy Evaluation (MSE) approaches (Smith, Sainsbury and Stevens, 1999), provide scientific recommendations for management measures such as TACs, closures, gear modifications and monitoring schemes. The OMP approach has the potential to complement multi-species approaches through its focus on the identification and modelling of uncertainties, as well as through balancing different resource dynamics representations and associated trophic dependencies and interactions (Sainsbury, Punt and Smith, 2000). It has already been used in this role in Australia (Little *et al*., 2006; Smith *et al*., 2004) and a spatial and multi-species MP is being developed for the Antarctic Peninsula krill-predator-fishery system (Plagányi and Butterworth, 2006, a&b). Elsewhere in the world attempts are increasingly been documented to incorporate bycatch, stock structure and spatial aspects into MPs (e.g. Punt, Smith and Cui, 2002; Dichmont *et al*., 2005).

OMPs typically involve both "*Decision Models*" and "*Operating Models*" (also termed "*Testing Models*"). The former essentially integrate resource-monitoring information (e.g. *CPUE*, survey indices of abundance) together with a control rule to provide a scientific recommendation for management such as a TAC and thus do not necessarily provide an accurate representation of the possible underlying resource dynamics (Butterworth and Plagányi, 2004). In contrast *Operating Models* should accurately reflect alternative possibilities for the true underlying dynamics of the resource or resources under consideration. They may seek a high degree of realism and hence may be quite complex (e.g. IWC, 2003; Fulton, Smith and Punt, 2004). Operating models provide the basis for simulation testing to assess how well alternative candidate *Decision Models* achieve the objectives sought by the management authority.

Butterworth and Plagányi (2004) speculate that there is clearly an immediate role for ecosystem models as *Operating Models,* but that the development of tactical ecosystem models as the basis for computing harvest limits within the OMPs themselves still seems some time off. This is primarily because of the uncertainty surrounding appropriate choices for the numerous parameter values and the functional forms to describe species interactions. Cochrane (1998, 2002) and Sainsbury, Punt and Smith (2000) note that it remains to be seen whether or not the associated levels of uncertainty can be adequately constrained to yield scientifically defensible and practically useful conclusions. Prior to the work of Fulton, Smith and Punt (2004), the inclusion of ecosystem effects in OMP evaluation exercises was generally implicit only. For example, rather than using a full multi-species operating model in simulation testing of its Revised Management Procedure, the Scientific Committee of the International Whaling Commission (IWC) used a simpler approach that allowed for time-dependence in the intrinsic growth rate and carrying capacity parameters to mimic the typical impacts on that population of changing levels of other predator and prey species (IWC, 1989). OMP testing procedures for some key South African resources have similarly used changes in single species parameters (such as *K*) as a surrogate for ecosystem effects (Rademeyer, Plagányi and Butterworth, 2005) and attempts are underway to incorporate functional relationships between seabirds and their prey into the operating models for sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*), with these in turn augmented by population dynamic model/s for the predator/s of concern (Plagányi *et al*., 2007).

6. Moving models forward – future developments

This report has focused on describing many of the multi-species and ecosystem models in their current form. However, in several cases, these are constantly evolving and there is currently a global increase in the effort directed at developing ecosystem models. This ranges from increasing attempts to extend single-species assessment models to include additional important prey or predator species, to extending ecosystem models to evaluate policy options for management.

The MSVPA/MSFOR class of models, initially applied to the ICES areas, were some of the first multi-species approaches to be developed but are still being applied and adapted (e.g. Livingston and Jurado-Molina, 2000). Hybrid versions (e.g. Mohn and Bowen, 1996) have been developed and more recently MSFOR is bring rewritten as MSM (Multi-species Statistical Model) (Jurado-Molina, Livingston and Ianelli, 2005; Jurado-Molina, Livingston and Gallucci, 2005). Lewy and Vinther (2004) (see also Lewy and Nielsen, 2003) are similarly developing a stochastic multi-species model that takes account of uncertainties in catch-at-age, stomach content and other data.

Regarding other MRMs, there are plans to revise the original Punt and Butterworth (1995) MRM of hake-seal interactions in the southern Benguela. The BORMICON model has evolved into GADGET and the latter is currently still being developed with case-studies having commenced only recently. A Mediterranean Sea model is being developed and is the first attempt at including a very large number of species in a GADGET model (see e.g. http://www1.uni-hamburg.de/BECAUSE/content/case_study_5.html).

The pelagic ecosystem model SEAPODYM has evolved from the earlier SEPODYM. Recent work has focused on running simulations at a global scale (with a resolution of one month x 1° latitude x 2° longitude) and preliminary predictions have been produced for the mid-trophic (forage) components, with a run covering 1860-2100, using a Intergovermental Panel on Climate Change (IPCC) climate change scenario for the coming century. New modules are on the table to be developed, first for marine turtles and then for sharks, marine mammals or even small pelagics such as anchovies and sardines. Similar advances are being made in other biological models tied to global ocean models, such as NEMURO (Nishikawa and Yasuda, 2005; Kishi, Nakajima and Kamezawa, 2005).

EwE has evolved considerably over the past few years and a large project is currently underway to develop a new generation of EwE (see www.lenfestoceanfutures.org) that will be fully modularized. A building-block version is to be created that will facilitate construction of individually tailored versions (V. Christensen, University of British Columbia, Canada, pers. comm.). The new version is scheduled for release by September, 2007 and may substantially advance ecosystem-based fisheries management by providing a readily accessible and easy to use tool capable of producing predictions based on user inputs by managers and others.

Several hybrid EwE versions have already been constructed to date (e.g. Aydin *et al.*, 2002) and are being used as sensitivity analyses in stock assessments, for example to address questions such as the potential impacts of a single-species TAC on other species (K. Aydin, pers comm.). Given a growing appreciation of the need to consider economic factors, one encouraging development is that of the GEEM (General Equilibrium Ecosystem Model) (Tschirhart and Finnoff, 2003; Tschirhart, 2004, Eichner and Tschirhart *in press*) which combines multi-species and economic sector modelling. The starting base is the same as ECOPATH, but GEEM incorporates a novel approach to predict functional responses by allowing predators to make "rational economic choices" based on the expected energetic gain from different prey types (K. Aydin, pers. comm.).

The bioenergetic-allometric modelling approach of Koen-Alonso and Yodzis (2005) is being extended to permit investigation of some of the potential effects of temperature, with a longer term goal being the integration of economic considerations into ecosystem-based management (Koen-Alonso, Northwest Atlantic Fisheries Centre, Fisheries and Oceans Canada, pers comm.). Temperature-dependence is being introduced into the dynamics based on the framework developed by Vasseur and McCann (2005). This will permit initial investigations of the potential effects of global warming through an analysis of, *inter alia*, the effects of temperature on basic metabolic pathways.

Substantial progress has been made in coupling physical models to biological models. Taking this one step further, others have argued for the importance of considering the coupling between ecosystems – the meta-ecosystem approach (Loreau, Mouquet and Holt, 2003; Varpe, Fiksen and Slotte, 2005). This is particularly important when considering species such as salmon which migrate from oceanic feeding grounds to rivers and lakes and species such as herring which migrate between feeding, overwintering and spawning areas (Varpe, Fiksen and Slotte, 2005). In a similar vein, Vidal and Pauly (2004) recently demonstrated how a number of local ECOPATH models can be combined into a single integrated, spatially explicit large marine ecosystem (LME) – scale model.

This idea of linking across systems is also helping to drive the current development path of the Australian models ATLANTIS and INVITRO. While both are benefiting from collaborative work that is expanding the ecological potential of the model, there has been a growing focus on developing the socio-economic components and the links to other ecosystem types (such as river catchments) so that broad flow-on and multiple use management questions can be considered (E. Fulton, pers. comm.).

Nevertheless the development of moderately easy to use full meta-ecosystem approaches that are useful to management seems some way off. Rather, it is likely that there will be an increase in the trend to incorporate greater spatial detail into models, as has been done in ECOSPACE and is being achieved with GADGET and ATLANTIS for example. Considerable efforts need to be devoted to compile spatially-explicit or GIS-based data to meet this aim. Parallel increases in computing power and efficiency of numerical and optimisation methods seem a necessary prerequisite for further developments on this front. GADGET appears to be a forerunner in terms of the use of multiple computers to speed runtime as well as attempts to base multi-species models on a robust statistical framework comparable to that used in single-species assessment models.

There is an increasing interest in the use of ecosystem models as Operating Models used to test OMPs. This is an excellent approach to providing a strategic and practical framework for developing an operational ecosystem approach to management. However, data limitations are likely to restrict the number of multi-species models that reach the stage of being considered viable operating models to assist in the management of target species. At the current level of development, most multi-species models cannot provide quantitatively reliable predictions. However, if a variety of alternative plausible models yield qualitatively similar predictions, this could provide a basis for management response.

7. Prudent use of the precautionary principle

Given the difficulties of providing definitive scientific advice on stock status and ecosystem "quality" and interactions, managers are increasingly called upon to apply the precautionary principle or approach (FAO, 1995). The "Precautionary Principle" (Principle 15 of the UNCED Rio Declaration (Agenda 21) of 1992) requires that "where there are threats of serious or irreversible damage, lack of full scientific certainty shall not be used as a reason for postponing cost-effective measures to prevent environmental degradation" (FAO 1995) (see also Hilborn *et al.*, 2001). However, Plagányi and Butterworth (2005) argue that naive application must be avoided because unsubstantiated claims and overstatements can damage scientific credibility. Acknowledging the difficulties of providing definitive scientific advice on ecosystem effects, arguments based on best scientific evaluations, rather than upon unsubstantiated impressions of the state of a resource, may better safeguard the interests of scientific credibility (and hence resource conservation) in the long run. Notwithstanding, it is increasingly being recognized that at least some ecosystem-based management may need to be based on qualitative considerations only.

8. Pointers from previous studies and workshops

Several factors have contributed to the current worldwide boom in developing multi-species and ecosystem models to advise fisheries management decisions, with interest in this topic evinced by a number of recent conferences on ecosystem considerations, including the ICES-SCOR, 1999 ecosystem effects of fishing symposium in Montpelier, France (ICES, 2000), the 2001 FAO expert consultation on ecosystem-based fisheries management held in Reykjavik, Iceland (FAO, 2003b, see also Sinclair and Valdimarsson, 2003), the Workshop on the Use of Ecosystem Models to Investigate Multi-species Management Strategies for Capture Fisheries (Fisheries Centre Research Reports Vol. 10, no. 2, 2002), the IWC Modelling Workshop on Cetacean-Fishery Competition (IWC, 2004a) and the 2002 Workshop on an Ecosystem Approach to Fisheries Management in the Southern Benguela, held in Cape Town, South Africa (*African Journal of Marine Science* 26, 2004). A number of policy documents have attempted to set targets, establish universal definitions of terms such as an "ecosystem approach to fisheries" or EAF (Garcia *et al*., 2003) and formulate guidelines to operationalise EAF by suggesting ways of implementing it at a practical level (FAO, 2003a, b). These initiatives date roughly from the 1982 UN Convention on the Law of the Sea, to the influential 1995 FAO Code of Conduct for Responsible Fisheries and finally to the somewhat ambitious 2002 World Summit on Sustainable Development which "*encourage (d) the application by 2010 of the ecosystem approach*." and set as a target to "*Maintain or restore stocks to levels that can produce the maximum sustainable yield with the aim of achieving these goals for depleted stocks on an urgent basis and where possible not later than 2015*" (WSSD, 2002). Unfortunately the socio-economic reality in most cases of resources well below their *MSY* level is that the large short-term catch reductions needed to achieve anything other than a relatively slow rate of recovery are very unlikely to be politically acceptable in many countries.

8.1 MODELLING INTERACTIONS BETWEEN MARINE MAMMALS AND FISHERIES

Butterworth and Punt (2003) argue that consideration of the indirect interactions between marine mammals and fisheries is an appropriate starting point for developing and testing multi-species models because of the lesser number of foodweb linkages for apex predators. It is thus instructive to begin discussion with a fairly narrow focus, namely that of bodies interested predominantly in a small subset of ecosystem interactions, as it should in theory be easier to reproduce these than the full spectrum of ecosystem interactions. The North Atlantic Marine Mammal Commission (NAMMCO) has focused for a number of years on marine mammal-fisheries interactions. For example, workshops have been convened to investigate the role of minke whales, harp seals and hooded seals in the North Atlantic (NAMMCO, 1998), the economic aspects of marine mammal–fisheries interactions (NAMMCO, 2001), the main uncertainties in extrapolating from feeding behaviour or stomach contents to annual consumption (NAMMCO, 2002) and to model marine mammal-fisheries interactions in the North Atlantic (NAMMCO, 2003). Given the conclusion of the first of these workshops, namely that marine mammals have substantial direct and indirect effects on commercial fisheries in the North Atlantic (NAMMCO, 1998), attention was focused on studies related to competition and the economic aspects of marine mammal-fisheries interactions (e.g. NAMMCO, 2001).

In light of uncertainties in calculations of consumption by marine mammals, concrete recommendations were sought with regard to estimating this consumption in the North Atlantic (NAMMCO, 2002). The next step was to review how available ecosystem models could be adapted to quantify marine mammal-fisheries interactions in the North Atlantic. The lessons learnt in this exercise provide a useful framework in terms of assessing different multi-species models. NAMMCO (2003) listed the following requirements as being particularly relevant in identifying the desirable features of a multi-species modelling framework:

1) flexibility of functions for prey selection;
2) flexibility of age structuring (from fully age-structured to fully aggregated);
3) accessible code and transparent operation (not "black-box");
4) able to be tailored to area and species of concern;
5) includes interactions accounting for most of the natural mortality, *M,* for species of concern;
6) spatial and temporal resolution able to be tailored for target species; and
7) uncertainty in data and model structure reflected in results.

One of the conclusions arising from the most recent in this series of workshops (NAMMCO, 2003) was that while the output from a model such as GADGET was not expected to be able to predict all aspects of future states of the ecosystem, the model was seen to have potential utility for management through testing scenarios where abundances of target species are manipulated. In addition, the workshop recommended the development of a generic (or "template") North Atlantic model, based on GADGET and including major fish and marine mammal species. The main use of such a model was seen to be to identify the inputs which had the greatest effect on model predictions and hence to guide research priorities in different regions each subject to different deficiencies in data.

Plagányi and Butterworth (2005) assessed a number of models in terms of these seven requirements, as well as the additional requirement that marine mammals be explicitly included, rather than treated as exogenous components. They concluded that GADGET and Minimally Realistic Models (MRM), such as the approach of Punt and Butterworth (1995), show the most promise as tools to assess indirect interactions between marine mammals and fisheries. Bioenergetic/allometric modelling approaches such as that of Koen-Alonso and Yodzis (2005) have a role to play too in attempting to characterize the finer details of these interactions. Given that the Antarctic marine ecosystem could be viewed as a case on its own, further development of the suite of CCAMLR predator-prey models (essentially also MRM-type models) is considered the most appropriate approach for this region. The importance of applying different modelling approaches to the same system is stressed (provided that appropriate resources, in terms of both person power and data, are available). This is particularly useful for qualitative cross-checking to determine whether different approaches give similar results and therefore gauging how much confidence can be placed in their reliability. Furthermore, given the importance of comparing the outputs of different modelling approaches as well as the need to test model predictions both against simulations and against reality, the suggestion has been made that there needs to be an internationally-coordinated effort to provide a structure within which model testing can take place (I. Boyd, University of St Andrews, pers. comm.).

An appreciation for the need to understand the assumptions underlying each model considered emerged from both the NAMMCO workshop on modelling marine mammal–fisheries interactions (NAMMCO, 2003) and the IWC workshop on cetacean-fishery competition (IWC, 2004a). Both meetings stressed the need for:

- careful consideration as to whether or not underlying model assumptions are appropriate for the case under investigation;

- tests of the sensitivity of predictions to alternative assumptions, particularly regarding interaction terms (e.g. Vasconcellos and Gasalla, 2001, Mackinson *et al.*, 2003); and
- addressing uncertainty, in particular by focusing research on the discrimination of alternative assumptions that yield appreciably different predictions.

8.2 AREAS OF FOCUS

A further pragmatic recommendation from the IWC workshop (IWC, 2004a) was that modelling efforts should focus on specific areas/systems where there is the greatest chance of success. Given a choice of systems to model, it does seem sensible to start with the "easier" cases, but naturally practical realities may mean that analyses are needed for more "difficult" areas/systems. Key characteristics of systems proposed for initial focus included reasonable data availability, relatively simple foodwebs, strong species interactions, relatively closed system boundaries and low (or obvious) environmental forcing (IWC, 2004a). One ideal ecosystem for such investigations is the Barents Sea, where there is evidence of relatively tight predator-prey coupling with only a few fish species (herring, cod and capelin) playing key roles. Systems characterized by strong physical forcing (bottom-up control) are likely to show little or no response to the removal of predators because even strong trophic interactions may be insufficient to increase the spatial and temporal variability in the abundance of a species in systems characterized by high residual variabilities as a result of such physical forcing (Benedetti-Cecchi, 2000). Navarrete *et al.* (2005) demonstrated that in benthic communities, the strength of species interactions depends to some extent on regional discontinuities in oceanographic conditions. The Antarctic ecosystem has often been proposed as a suitable starting point for developing ecosystem models because it is a relatively simple ecosystem that has suffered large impacts from overfishing (e.g. Mori and Butterworth, 2004). However, as with other high-latitude regions with short links to high trophic levels, it is subject to large physical variability that may need to be better understood before reliable conclusions can be drawn regarding trophic interactions.

The agreed conclusion of the IWC's Scientific Committee following discussion of the report of its workshop (IWC, 2004b) provides some useful insights and reads:

> *"for no system at present are we in the position, in terms of data availability and model development, to provide quantitative management advice on the impact of cetaceans on fisheries, or of fisheries on cetaceans. However, this does not rule out the possibility of providing qualitative advice if a number of different approaches yield qualitatively similar results."*

8.3 GENERAL GUIDELINES

General guidelines stressed by most of the previous studies and workshops include:

- the overriding importance of further investigations regarding the appropriate form for functional responses (the prey-predator interaction terms) and feeding selectivities/suitabilities;
- the need to consider operational (i.e. management) issues;
- the need for further systematic investigations (presumably through simulation studies) of the numbers of links that have to be included in a non-trivial ecosystem model for reliable predictive ability.

There is a growing realisation that substantial progress towards implementing reliable ecosystem models is still some way off given the need in most regions for considerable data collection and complex analysis. On the other hand, progress in this field has likely developed faster than anticipated given the encouraging number of researchers drawn to the field, the necessary legislation having been put in place, the availability of funding for ecosystem research and the development of tools that are widely accessible as a first step to explore the issues. Given the resource-hungry nature of ecosystem investigations, it is nonetheless important that research priorities in this area be carefully and realistically chosen and weighed against other research needs (Butterworth and Plagányi, 2004).

8.4 ECOSYSTEM-BASED MANAGEMENT STRATEGIES

The objective of the 2000 UBC Workshop on the Use of Ecosystem Models to Investigate Multi-species Management Strategies for Capture Fisheries (Pitcher and Cochrane, 2002) was to explore the impact of different multi-species harvesting strategies, with a view to searching for fishing rates and patterns that would maximize ecological, social or economic goals (Cochrane, 2002). A wide range of EwE models were used by participants to identify the management strategies which would come closest to achieving the objectives for each of the ecosystems considered, as well as estimating the consequences of the various management strategies. This was made possible following the development of routines within EwE to assist the user in exploration of fisheries strategies or policies (Walters, Christensen and Pauly, 2002), effectively using the EwE models in a similar manner to operating models (Cochrane, 2002).

The workshop also stressed the importance of investigating the sensitivity of these policies to uncertainties in trophic dynamics (e.g. by considering a range of vulnerability settings). The workshop stressed the dangers of not using the software cautiously and thoughtfully (Cochrane, 2002). Model results obtained at the workshop were useful in highlighting the types of tradeoffs encountered in trying to simultaneously maximize economic, social and ecological goals, and identifying the need for better economic and other data (e.g. on prices per species and fleet operational costs) before trade-offs can be computed with any confidence (e.g. Bundy, 2002; Vasconcellos, Heymans and Bundy, 2002).

8.5 PRACTICAL STEPS TO IMPLEMENTING AN EAF

The 2002 Cape Town workshop "An ecosystem approach to fisheries management in the southern Benguela: introducing the concept and looking at our options" had two objectives, stated as:

(i) to introduce the concept of ecosystem-based fisheries management to South African fisheries scientists and to present modelling tools to achieve this, in particular the ECOPATH/ECOSIM approach; and
(ii) to propose a framework of practical ways in which the incorporation of ecosystem considerations (potentially using information from ECOPATH/ECOSIM and other types of multi-species modelling approaches) into current Operational Management Procedures (OMPs) and other management strategies for South Africa's marine resources could be attempted.

Consensus was reached that an EAF would be highly desirable and should be implemented immediately using an incremental approach (Shannon *et al.*, 2004). As a step in this direction, a project being implemented by the Benguela Current Large Marine Ecosystem project and the FAO held "Risk Assessment for Sustainable Fisheries" Workshops for a range of stakeholders in each of Angola, Namibia and South Africa. These used the method of Ecological Risk Assessment developed under the National Ecologically Sustainable Development (ESD) framework for prioritizing issues across valuable Western Australian fisheries (Fletcher *et al.*, 2002; Fletcher, 2005). Initial work identified issues surrounding fisheries and the management thereof and ranked these according to the likelihood that an issue occurs and the severity of its consequence (Nel, 2005). This has at least made a first attempt at highlighting important areas to focus modelling efforts. In South Africa, as presumably in many other areas of the world, many of the major ecosystem issues identified are non-trophic (Shannon *et al.*, 2004), emphasizing that biological models may often have a relatively small role to play in an EAF. Alternatively, this may be a consequence of a lack of information and knowledge about the way trophic (indirect) interactions affects fisheries (M. Vasconcellos, FAO, pers. comm.).

The conclusions of the Cape Town workshop overlapped considerably with those discussed elsewhere in this document, namely that the following are important shortcomings of ecosystem modelling studies to be borne in mind (Shannon *et al*., 2004):

- It may be important to consider the effects of short-term variability;
- Models need to improve their representation of regime shifts and other longer term ecosystem dynamics;
- Predator-prey functional responses are in need of further investigation;
- Increased attention should be focused on assessing the robustness of a model to a range of major uncertainties, acknowledging that full sensitivity testing is not always possible.

The workshop stressed that the long term benefits of an EAF need to be strongly emphasized and clearly explained. This follows particularly given that in the short-term at least, it may result in less fish being made available to fishers (D.S. Butterworth, University of Cape Town, South Africa, pers. comm.) and is likely to result in increased political and social pressures as well as stretching limited capacity and resources (Cochrane *et al.*, 2004). An important consideration is that efforts towards this end are impeded by the fact that there is a current paucity of examples of successful case studies to show that an EAF is successful and beneficial (Cochrane *et al*., 2004).

9. Summary of model comparisons and recommendations

Attention worldwide is increasingly being concentrated on establishing frameworks for fisheries management that are ecosystem-oriented, notwithstanding that the operational aspects of this goal are fraught with difficulty (Hall and Mainprize, 2004). This field is still very new and major gaps still exist between single-species and multi-species or ecosystem approaches to practical fishery management.

Three particularly important areas requiring attention are the following:

1. Review of underlying shortcomings and assumptions of available multi-species/ecosystem approaches
   This aspect is seen as critical to advancing attempts to incorporate ecosystem considerations in practical fisheries management. Unfortunately endeavours in this regard appear to be lagging considerably behind the ever-growing number of documented applications of ecosystem models. Critical reviews of methods assist in highlighting weaknesses and hence ultimately in strengthening applications of an ecosystem approach. Where applied most effectively, conventional single-species modelling approaches used to inform the management of commercially important stocks are typically subject to intense scrutiny. Ecosystem models are likely to be subject to a similar level of scrutiny when they reach the state of being used as the basis for management recommendations or decisions (with implications for economically valuable and socially important fisheries in particular). There is therefore a need for parallel processes of model development, application and scrutiny – otherwise the danger exists that considerable time and effort will have been wasted in developing ecosystem models that are later rejected out of hand when they attempt to enter the management arena or that bad management decisions, with potentially serious consequences, will be made on the basis of poor scientific advice.
2. Systematic analyses of alternative functional response formulations to be considered in models
   Although progress in this field is primarily impeded by a lack of suitable data and experimental studies (noting that the focus here is on recommended modelling endeavours), simulation and modelling studies can nevertheless contribute. This issue is critical and hence attention should be focused both on the need to carefully check model robustness to alternative interaction representation hypotheses and on simulation exercises to systematically and thoroughly explore this issue.
3. Consideration of uncertainty in model structure, parameter estimates and data.
   Models need to account for key levels of uncertainty, preferably within a strategic and practical framework. This aspect of multi-species/ecosystem models has lagged unsatisfactorily behind other aspects of model development, given (understandable) arguments to the effect that detailed sensitivity analyses are a major undertaking for these models and there are typically inadequate data available for fitting purposes. While many studies are currently underway (E. Fulton and F. Pantus, CSIRO, *pers. comm.*), the most prominent published example is that of Ginot *et al.* (2006), which demonstrates the usefulness of ANOVA-based global sensitivity analyses for exploring which parameters (in models with only a moderate number of parameters) have an impact on model output and the interactions between the parameters.

It is also important to remember that an assessment method (however rigorously applied) and associated recommendations are unable to successfully achieve conservation when management fails. As stressed by Parma *et al.* (2003), sustainability of a fishery is likely to be achieved only when the right incentives are provided, such as in the form of secure long-term access rights. The correct incentives and management structures need to be firmly in place if success is to be achieved. To reach this goal it is insufficient simply to perfect existing models. Stakeholder participation and dialogue need to be seen as integral components of multi-species fisheries management and scientists need to avoid the temptation to use loosely constructed ecosystem models to justify a preferred point of view. Moreover, although the discussion throughout has focused on specific modelling perspectives, it is important to bear in mind that in some cases the best approach would likely depend on experimental studies and an adaptive management approach (e.g. Walters 1986; Hilborn and Walters 1992; Sainsbury, Punt and Smith, 2000). For example, an actively adaptive management strategy applied to the Australian multi-species fishery was successful in resolving key uncertainties about resource dynamics and sustainable resource use (Sainsbury *et al.*, 1997). The approach involved identifying four different plausible hypotheses and adopting an experimental process involving the sequential closure of areas to trawl fishing. After a period of a few years, the experiment was successful in discriminating among the competing hypotheses (Sainsbury *et al.*, 1997; Sainsbury, Punt and Smith, 2000). The success of this earlier work has lead to its extension into the multiple use realm (Little *et al.*, 2006).

In summary, this report has aimed to document all of the well-known, as well as several of the less well-known multi-species and ecosystem modelling approaches used in Ecosystem-Based Fisheries Management (EBFM). Some 20 approaches have been described (Tables A1-A3), ranging from ESAM (which entails no more than the addition of one or two species to current single-species assessment models) to ATLANTIS (covering the full trophic spectrum) at the opposite extreme. The most widely used approach is undoubtedly EwE, which is likely to remain a forerunner given the user-friendly interface and on-going improvements to the software. Faced with incomplete knowledge of ecosystem functioning, there has been increasing recognition that definitive conclusions cannot be drawn from a single model structure. There has thus been a parallel increase in efforts to modularize models so that different components can be easily substituted. Spatial considerations are similarly playing an increasingly important role in the development of ecosystem modelling approaches. Nonetheless, even some of the earliest approaches such as MSVPA are still being used and improved. To give an idea of directions being taken in on-going model development, a summary has been presented of some other recent advances being planned for the different modelling approaches.

This preliminary analysis of the potential of the various modelling approaches to address specific EBFM research questions suggests that a range of different model constructions are needed; no one model is superior to all others in all respects. This review has stressed several times that ideally a range of models should be applied, but this is not always possible because of limitations on resources available to undertake such analyses. Nonetheless, it may be argued that the model with the greatest potential to contribute to *practical* fisheries management advice in regions with reasonable data availability is GADGET, although as stated throughout, the preferred approach is parallel development of different models. Although still under development, GADGET is currently the model with the most rigorous statistical framework for developing multi-species based management advice. It is also the modelling approach most capable of detailed sensitivity investigations to alternative growth, consumption and recruitment formulations. Additionally, it operates within a spatial framework and overcomes many of the associated computing constraints by running on multiple computers in parallel using PVM. Nonetheless, it too has its limitations in that it is capable of representing only a relatively small subset of the ecosystem and may be less useful in tropical regions with much higher species diversity. Models such as EwE and ATLANTIS are more appropriate for considering broader questions. In particular, EwE is capable of addressing the widest range of topical EBFM research questions. The multiple-stanza version of ECOSIM is a major advancement and greatly expands the potential of this approach to investigate important questions such as the effects of biomass pool composition on aggregated consumption estimates as well as being able to represent cannibalism through size-dependent interaction rates (Walters and Martell, 2004). ATLANTIS is ranked here as the best operating model within a simulation testing framework. Although it seems unlikely that sufficient data will be available to achieve such testing in most marine systems, some argue that "what-if" approaches are becoming more acceptable such that progress could be made on this front. Approaches that have more recently followed in the footsteps of the Punt and Butterworth (1995) MRM approach also deserve a closer look in that such Management Procedure approaches take explicit account of uncertainty and management issues through the use of a simulation framework incorporating feedback control rules used in actual management.

As discussed, simple extensions to current single-species assessment models, termed ESAM approaches here, are often a good first step. Similarly, equations such as those presented in Mori and Butterworth (2005) are a useful starting template for multi-species modelling approaches being built up slowly and in synchrony with data availability. Some of the less well-known (in a global context) approaches have been shown to include some additional useful features, for example, SEAPODYM's habitat index, OSMOSE's explorations with simple individual predation rules and Koen-Alonso and Yodzis's (2005) approach for substituting different functional response variants.

This report is a first step towards initiating more detailed discussions of these models, their uses and their limitations. This process will be critical in moving forward the development of methods for assessing indirect ecosystem impacts of fisheries. Whereas the modelling tool-box is reasonably well developed and diverse, high levels of uncertainty around the nature and consequences of most ecosystem interactions will hinder the efficient application of an EAF. Greater focus is needed on reducing these uncertainties and conducting the necessary data collection and experimentation to strengthen confidence in these approaches. Indeed, before embarking on the construction of a new ecosystem-type model, would-be model developers should assess whether they would be adding anything to the current suite of models, given that approaches such as EwE and GADGET have benefited from an extensive network of collaborators over a number of years. Hopefully, a review such as this will assist in selecting the most appropriate general form of model to match the question of interest.

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