2. Review of current modelling approaches

An overview is given below of some of the current approaches to modelling multi-species/ecosystem effects in the context of their possible application to fisheries management. This review is by no means exhaustive but has attempted to capture broadly the main model types that are either well known and widely available and show potential as a tool in this context. The aim here was thus not to exactly describe every multi-species/ecosystem model developed – models such as that by May *et al.* (1979), Beddington and May (1982), Skeleton bulk biomass ecosystem model (SKEBUB) (Bax, 1985) and Pech *et al.* (2001) were not deemed to meet these criteria but future revisions will take into account approaches that are sufficiently strongly supported. Moreover, the purpose of comparing the models is to assist in greater understanding of the models available and in making informed decisions in instances where resources are limited and hence it is important to select the best possible model upfront. It is acknowledged that the choice of method depends on the question and research objectives and that the ideal (if not always practical) scenario is one in which a suite of models is developed and compared (Fulton, Smith and Johnson, 2003a). Moreover, in ideal circumstances the suite of models will be drawn from a wide range of types, as the model structure (and even its development history) can have significant implications for the potential range of dynamics displayed (Fulton and Smith, 2004).

Plagányi and Butterworth (2004) outline an increasing hierarchy of multi-species model complexity to account for biological interactions that pertain to commercially important species. It is important to appreciate that increasing model complexity to take better account of biological realism which can lead to an associated increase in scientific uncertainty, as a result both of lack of knowledge of functional relationships and of imprecision in estimates of the associated parameter values. The reader is referred to other texts (e.g. Fulton, Smith and Johnson, 2003a; Raick, Soetaert and Grégoire, 2006) for further discussions dealing with the important issue of model complexity. The reader is also referred to the excellent text of Walters and Martell (2004) for an overview of food web modelling, parameterization of ecosystem models and strategies for ecosystem management.

The simplest multi-species models explore the question of how to harvest a target population appropriately, whilst simultaneously accounting for the needs of a predator dependent on that population as prey. If both predator and prey are subject to exploitation, it is necessary to simultaneously model both predator and prey populations as functions of physical variability, catch levels and the strength and nature of the functional relationship between the two populations. If an intermediate trophic level species is targeted (in a "wasp-waist" system, see Cury *et al.*, 2000 in particular), it may be necessary to account for the functional relationships between the targeted species and its key predators, competitors and prey items. In this case appropriate catch levels are likely to be affected by variability in both upper and lower trophic levels. The most complex multi-species models strive to suggest modifications in the catch level of a species based on the direct and indirect predation and competition effects associated with the simultaneous removal of other food web components. In addition, it may be necessary to consider negative feedback loops such as cannibalism. Other factors such as human and fleet dynamics may also play a role at various levels, but consideration of these factors was considered beyond the scope of this report.

Models and their categorization

The different models discussed can broadly be categorized according to the framework presented in Hollowed *et al.* (2000) which has been slightly modified and updated as shown in Figure 1. Models which represent only a subset of the ecosystem are termed Minimally Realistic Models and typically focus on inter-species interactions only and hence may also be termed Dynamic multi-species models. They may however also include some consideration of physical and environmental forcing actors. In contrast, Dynamic system models incorporate the environment and lower trophic levels, although this is often at the expense of not representing the higher trophic levels in sufficient detail (when considered in a fisheries management context). In classifying models further, it is important to differentiate between models that take age structure and spatial aspects into account (Figure 1). Finally, the term Whole ecosystem models is reserved for models that attempt to represent all trophic levels in an ecosystem in a balanced way. Note further that Figure 1 is necessarily simplistic as it does not reflect other important details relevant to the organization and regulation of ecological systems (M. Koen-Alonso, pers. comm.) – for example, modelling predation as size-dependent produces different results to models assuming age-dependent predation (de Roos, Persson and McCauley, 2003; de Roos and Persson, 2005).

This review focuses on the following types of models (Figure 1, Table 1):

- **Whole ecosystem models**: models that attempt to take into account all trophic levels in the ecosystem, including ECOPATH (Polovina, 1984; Christensen and Pauly, 1992), ECOSIM (Walters, Christensen and Pauly, 1997) and ECOSPACE (Walters *et al.*, 2000) and other bioenergetic trophodynamics models (e.g. Yodzis, 1998; Koen-Alonso and Yodzis, 2005);
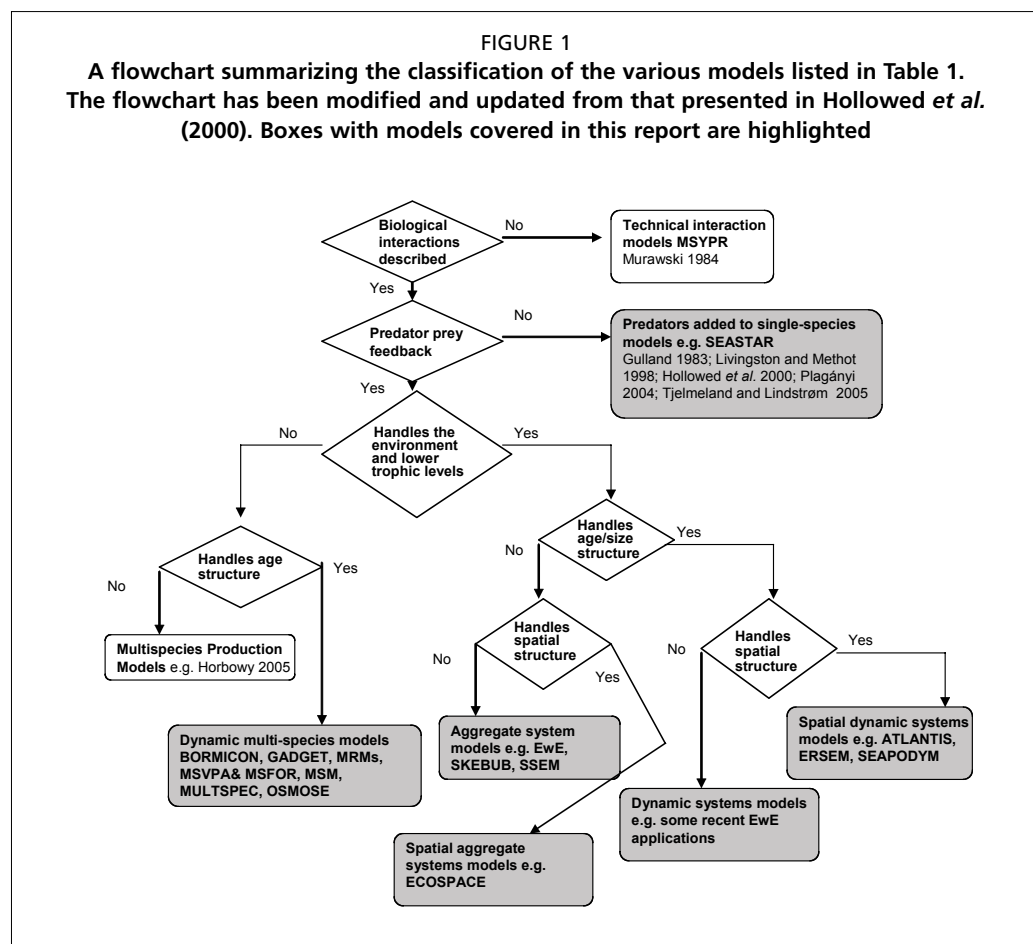

FIGURE 1
A flowchart summarizing the classification of the various models listed in Table 1. The flowchart has been modified and updated from that presented in Hollowed *et al.* (2000). Boxes with models covered in this report are highlighted

TABLE 1
Alphabetical list of model acronyms, full names and references to primary developers/users

Model	Name	References
ATLANTIS	ATLANTIS	Fulton, Smith and Johnson, 2004; Fulton, Smith and Punt, 2004; Fulton, Smith and Punt, 2005
Bioenergetic/ allometric model	Multi-species trophodynamic model using bioenergetic and allometric approach	Yodzis and Innes, 1992; Yodzis, 1998; Koen-Alonso and Yodzis 2005
BORMICON	BOReal Migration and CONsumption model	Bogstad, Hauge and Ulltang, 1997; Stefansson and Palsson 1998
CCAMLR models	Commission for the Conservation of Antarctic Marine Living Resources	Butterworth and Thomson 1995; Thomson *et al.*, 2000; Mori and Butterworth 2004, 2005, 2006
EPOC	Ecosystem Productivity Ocean Climate model	Constable 2005, 2006
ERSEM II	European Regional Seas Ecosystem Model	Baretta, Baretta-Bekker and Ruardij, 1996; Baretta-Bekker and Baretta, 1997~; Download from http://www.ifm.uni-hamburg. de/~wwwem/dow/ERSEM/
ESAM	Extended Single-species Assessment Models - Models that are extensions to more conventional single-species stock assessment models	Livingston and Methot, 1998; Hollowed *et al.*, 2000; Plaganyi, 2004; Tjelmeland and Lindstrøm, 2005
EwE	ECOPATH with ECOSIM	Polovina, 1984; Christensen and Pauly, 1992; Walters, Christensen and Pauly, 1997; Walters *et al.*, 2000; Christensen and Walters, 2000, 2004; Christensen, Walters and Pauly, 2000; Website: www.ecopath.org
GADGET	Globally applicable Area Disaggregated General Ecosystem Toolbox (GADGET); old name was BORMICON (BOReal Migration and CONsumption model); Fleksibest is a variant of Gadget.	Trenkel, Pinnegar and Tidd, 2004; Begley and Howell, 2004; Taylor *et al.*, 2004; Taylor and Stefansson, 2004; Begley, 2005. Website: www.hafro.is/gadget,
GEEM	General Equilibrium Ecosystem Model	Tschirhart and Finnoff, 2003; Tschirhart, 2004; Eichner and Tschirhart (in press)
IBM	Individual-Based Models (e.g. OSMOSE)	DeAngelis and Gross, 1992; Shin and Cury, 2001; Ginot, LePage and Souissi, 2002; Ginot *et al.*, 2006; Alonzo, Switzer and Mangel, 2003; Colomb et al., 2004; Kirby et al., 2004
IGBEM	Integrated Generic Bay Ecosystem Model	Fulton, 2001; Fulton, Smith and Johnson, 2004
INVITRO	INVITRO	Gray *et al.*, 2004; Gray *et al.*, 2006
KPFM	Krill-Predator-Fishery Model (KPFM, also KPFM2)	Watters *et al.*, 2005, 2006
MRM	Minimally Realistic Model	E.g. Punt and Butterworth, 1995
MSM	Multi-species Statistical Model	Jurado-Molina, Livingston and Ianelli, 2005; Jurado-Molina, Livingston and Gallucci, 2005
MSVPA and MSFOR	Multi-species Virtual Population Analysis and Multi-species Forecasting Model	Helgason and Gislason, 1979; Pope, 1979, 1991; Sparre, 1991; Magnússon, 1995; Vinther, 2001
MULTSPEC	Multi-species model for the Barents Sea; simplified version is AGGMULT which is also connected to a ECONMULT - a model describing the economies of the fishing fleet	Bogstad, Hauge and Ulltang, 1997; Tjelmeland and Bogstad, 1998
MOOVES	Marine Object-Oriented Virtual Ecosystem Simulator	Colomb *et al.*, 2004
OSMOSE	Object-oriented Simulator of Marine ecOSystem Exploitation	Shin and Cury, 2001, 2004
SEAPODYM	Spatial Ecosystem and Population Dynamics Model (SEAPODYM) - previously Spatial Environmental Population Dynamics Model (SEPODYM)	Bertignac, Lehodey and Hampton, 1998; Lehodey et al. 1998; Lehodey, 2001; Lehodey, Chai and Hampton, 2003; www.seapodym.org
SEASTAR	Stock Estimation with Adjustable Survey observation model and TAg-Return data	Tjelmeland and Lindstrøm, 2005
SKEBUB	SKEleton BUlk Biomass ecosystem model	Bax, 1985
SMOM	Spatial Multi-species Operating Model	Plagányi and Butterworth, 2006 a,b
SSEM	Shallow Seas Ecological Model	Sekine *et al.*, 1991
SystMod	System Model for the Norwegian and Barents Sea	Hamre and Hattlebakk, 1998

- **Dynamic multi-species models or Minimum Realistic Models**: models restricted to represent a limited number of species most likely to have important interactions with a target species of interest, for example, Punt and Butterworth (1995). The term Minimally Realistic Model (MRM) was first coined by Butterworth and Harwood (1991) in response to recommendations to this effect made at a preceding international workshop. Other models that fall into this category include Multi-species Virtual Population Analysis MSVPA and MSFOR (Pope, 1991; Sparre, 1991; Magnússon, 1995; Vinther, 2001); Scenario Barents Sea (Schweder, Hagen and Hatlebakk, 2000); Systmod (System Model) (Hamre and Hattlebakk, 1998); MULTSPEC (Bogstad, Hauge and Ulltang, 1997; Tjelmeland and Bogstad, 1998); BORMICON (A BOReal Migration and CONsumption model) (Stefansson and Palsson, 1998); SEASTAR; GADGET (Globally applicable Area-Disaggregated General Ecosystem Toolbox) (see e.g. webpage http://www.hafro.is/gadget; coordinator G. Stefánsson); CCAMLR predator-prey models (e.g. Butterworth and Thomson, 1995; Thomson *et al.*, 2000), Individual-Based Models (IBM) and MSM (Multi-species Statistical Models) (Jurado-Molina, Livingston and Ianelli, 2005);
- **Dynamic System Models**: models that attempt to represent both bottom-up (physical) and top-down (biological) forces interacting in an ecosystem, including Individual-Based Models (IBM), OSMOSE (Object-oriented Simulator of Marine ecOSystem Exploitation) (Shin and Cury, 2001; Shin, Shannon and Cury, 2004), INVITRO (Gray *et al.*, 2006), biogeochemical models e.g. IGBEM (Integrated Generic Bay Ecosystem Model) (Fulton *et al.*, 2004) ATLANTIS (Fulton and Smith, 2004) and SEPODYM/SEAPODYM (Spatial Environmental POpulation DYnamics Model) (Bertignac, Lehodey and Hampton, 1998; Lehodey *et al.*, 1998; Lehodey, 2001; Lehodey, Chai and Hampton, 2003).
- **Extensions of single-species assessment models**: models that expand on current single-species assessment models taking only a few additional interactions into account (e.g. Livingston and Methot, 1998, Hollowed *et al.*, 2000; Tjelmeland and Lindstrøm, 2005). For convenience, these models are here termed ESAM (Extended Single-species Assessment Models).

Models can be classified as Minimally Realistic Models (MRM) on the one hand and "ecosystem" models on the other. A MRM seeks to include only those species considered likely to have important interactions with the species of primary interest. The MRM group includes MSVPA and its derivatives which project into the future (e.g. Vinther, 2001), MULTSPEC, BORMICON/GADGET, Seastar, Scenario Barents Sea and the original seal-hake MRM of Punt and Butterworth (1995). Shared characteristics of these models include the following (NAMMCO, 2002):

- they are system specific;
- only a small selected component of the ecosystem is modelled, and
- lower trophic levels and primary production are modelled as constant or varying stochastically.

In contrast, the ATLANTIS and ECOPATH/ECOSIM models, for example, are generic and capable of explicitly including most ecosystem components as well as incorporating lower trophic levels and primary production, though naturally they can also be applied in a simplified form closer to the MRM concept.

In discussing these different modelling approaches below, it is useful to further classify models (see Table 2) as either "Efficient predator" models or "Hungry predator" models (Butterworth and Plagányi, 2004). In the former set of models the predator is assumed to always get its daily ration (e.g. MSVPA, MULTSPEC), though the species composition of this ration may change with varying prey abundances over time. In contrast, in the latter set, predators are assumed to compete with others of the same (and possibly other) species for limited vulnerable proportions of prey (e.g. "foraging arena"-based models applied in approaches such as ECOSIM).

TABLE 2

Categorization of models according to feeding relationships assumed as well as whether the primary model focus is on the effects of non-target species on a commercial prey species, the effects of fishing on the population of interest or on effects operating in both directions

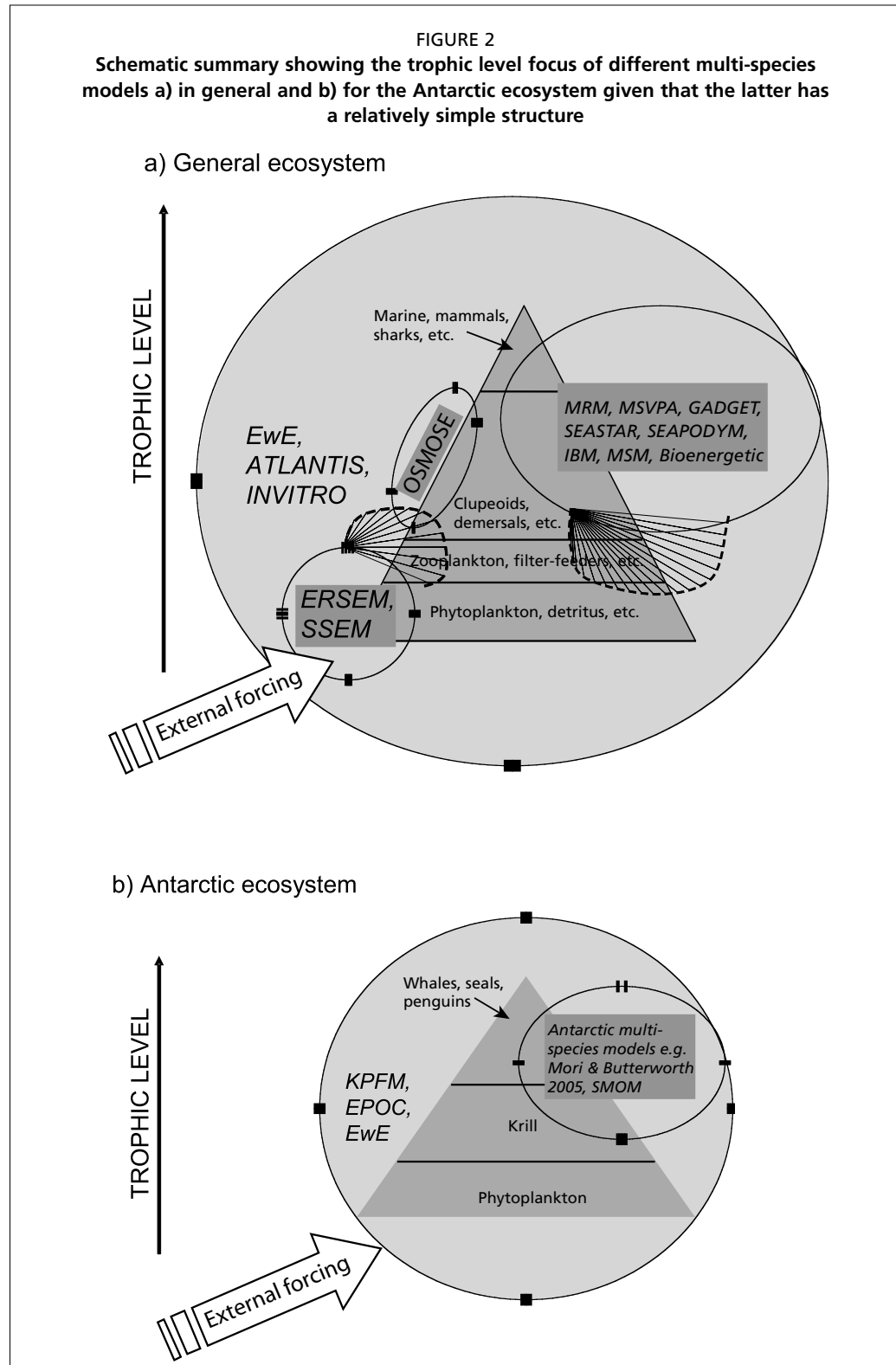| Model	Model units (biomass or nutrient pools)	"Efficient predator" or "Hungry predator" model	Primary model focus
ATLANTIS	Nutrient	Hungry predator	Effects in both directions
Bioenergetic/allometric models	Biomass	Both	Effects in both directions
CCAMLR models	Biomass	Efficient predator	Effects of fisheries on protected or other species
ERSEM II	Nutrient	Hungry predator	Effects in both directions
EwE	Biomass	Hungry predator	Effects in both directions
GADGET	Biomass	Both	Ecosystem effects on target population
IGBEM	Nutrient	Hungry predator	Ecosystem effects on target population
Individual-based Models (IBM)	Biomass	Efficient predator	Ecosystem effects on target population
INVITRO	Biomass	Efficient/Hungry[1] predator	Effects in both directions
KPFM	Biomass	Efficient predator	Effects of fisheries on protected or other species
MRM (Punt and Butterworth 1995)	Biomass	Efficient predator	Ecosystem effects on target population
MSM	Biomass	Mixed	Limited effects in both directions
MSVPA and MSFOR	Biomass	Efficient predator	Ecosystem effects on target population
MULTSPEC	Biomass	Efficient predator	Ecosystem effects on target population
OSMOSE	Biomass at different levels of aggregation	Efficient predator but can starve	Effects in both directions
ESAM	Biomass	Efficient predator	Ecosystem effects on target population
SEAPODYM	Biomass	Efficient predator	Ecosystem effects on target population
SEASTAR	Biomass	Efficient predator	Ecosystem effects on target population
SMOM	Biomass	Efficient predator	Effects of fisheries on protected or other species
SSEM	Nutrient	Efficient predator	Ecosystem effects on target population

[1]Dependent on agent types used

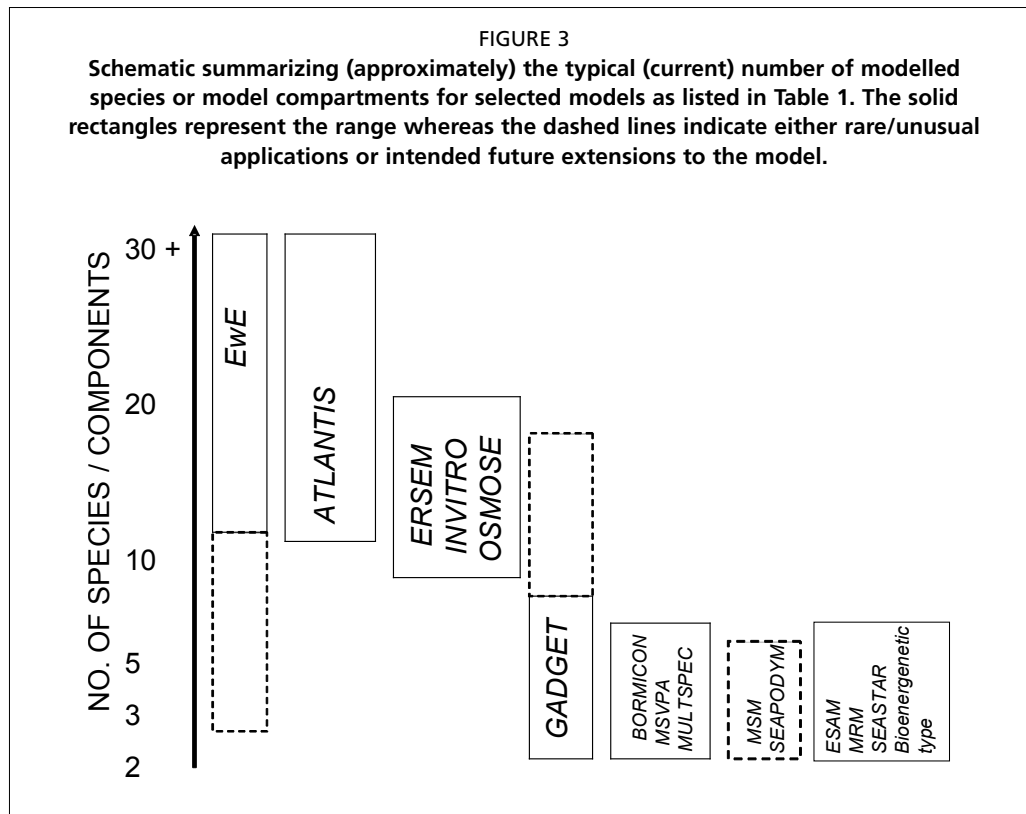In general, the models presented also differ substantially (Table 2) in terms of whether they represent:

i. only the effects of non-target species on a commercial prey species (e.g. MSVPA, BORMICON and other models were originally constructed with the primary aim of assessing fish stocks);

ii. only the effects of fishing (e.g. resulting in prey depletion) on the population of interest (e.g. CCAMLR models constructed with this aim in mind); or

iii. effects operating in both directions (e.g. ECOSIM).

Criteria used to compare models

The tables in the Appendixes can be consulted to further examine the above models. The models are compared (Tables A1 a-d) based on the following criteria:

  1. The level of complexity and realism, e.g. the number of modelled species (Figures 2, 3), the representation of size/age structure of the species and the types

FIGURE 2
Schematic summary showing the trophic level focus of different multi-species models a) in general and b) for the Antarctic ecosystem given that the latter has a relatively simple structure

FIGURE 3

Schematic summarizing (approximately) the typical (current) number of modelled species or model compartments for selected models as listed in Table 1. The solid rectangles represent the range whereas the dashed lines indicate either rare/unusual applications or intended future extensions to the model.

of represented processes (physical and biological). Although it is not the subject of the report, brief commentary is provided regarding the representation of technical interactions or the direct ecosystem effects of fisheries (e.g. bycatch);

2. The types of functional responses of predators to changes in abundance of prey species and their consequences and limitations;
3. How uncertainties in model structure, parameters and data are treated;
4. How environmental effects and interactions with non-target species (e.g. marine mammals; sea turtles; sea birds) are incorporated;
5. The spatial representation of species interactions and habitat related processes;
6. Model suitability for dealing with migratory species, i.e. species that cross ecosystem boundaries;
7. Where possible, model adequacy to allow the analysis of the different types of management controls in use, such as effort control, minimum size, total allowable catch, protected areas and seasons;
8. Model adequacy to allow the assessment of the effects of short, medium and long-term ecosystem changes;
9. Model suitability to conduct assessments and policy exploration, considering its potential use to conduct historical reconstruction of resources to describe the current status of the ecosystem and to evaluate the potential effects of various kinds of decisions (short and long term);
10. Model transparency of operation and ease of use;
11. Data requirements and model suitability for data poor areas.

A second set of tables (Tables A2 a-d) summarizes for each of the 20 models compared, a description of model parameters, some important assumptions, data requirements, technical information such as the computing platform, a list of examples where used, notes on the model history as well as any additional useful features of an approach. Finally, a summary is presented in a third set of tables (Tables A3 a-d) of some advantages, disadvantages and limitations of each method, as well as notes

on the ease of presentation of model outputs and the user-level of programming and mathematical skills required.

A preliminary comparison is attempted of the potential of the different modelling approaches to address a range of Ecosystem-Based Fisheries Management (EBFM) research questions outlined in the text (Tables A4).

Discussion is also provided regarding the incorporation of ecosystem considerations into current Operational Management Procedures (OMPs) and other management strategies for marine resources. An OMP is the combination of a prescribed set of data to be collected and the analysis procedure to be applied to these data, to provide a scientific recommendation for a management measure, such as a Total Allowable Catch (TAC), for a resource (Butterworth, Cochrane and Oliveira, 1997; Butterworth and Punt, 1999; Cooke, 1999). A key aspect of the OMP approach is that the analysis procedure has been tested across a wide range of scenarios for the underlying dynamics of the resource using computer simulation. This is to ensure that the likely performance of the OMP in terms of attributes such as (high) expected catch and (low) risk of unintended depletion is reasonably robust to the primary uncertainties about such dynamics. By way of example, this approach is used at present to manage South Africa's three most valuable fisheries: for hake, for pilchard and anchovy and for west coast rock lobster (De Oliveira *et al.,* 1998; Butterworth and Punt, 1999; Geromont *et al.*, 1999) and initial progress has been made in including ecosystem considerations into these OMPs (Plagányi *et al.*, 2007).

In what follows, a relatively brief description of the various modelling approaches is presented with much of the supplementary information given in the Tables. The author's discretion has been used in drawing the reader's attention to aspects of the various modelling approaches that may be of interest and hence, unlike in the Tables, model descriptions given in the text hereunder are presented at different levels of details.

2.1 WHOLE ECOSYSTEM AND DYNAMIC SYSTEM MODELS

Such approaches attempt to take all trophic levels in the ecosystem into account, from primary producers to top predators. Quite sweeping simplifications and assumptions may need to be made in this process. Examples are the ECOPATH with ECOSIM (EwE) framework, which is usually applied in this manner and biogeochemical models such as IGBEM and ATLANTIS (Fulton, 2001; Fulton, Smith and Johnson, 2004; Fulton, Smith and Punt, 2004).

2.1.1 ECOPATH with ECOSIM (EwE)

Given that the ECOPATH (Polovina 1984; Christensen and Pauly, 1992), ECOSIM (Walters, Christensen and Pauly, 1997) and ECOSPACE (Walters, Pauly and Christensen, 1999) suite is currently dominating attempts worldwide to provide information on how ecosystems are likely to respond to changes in fishery management practices, it is important that the applicability of these approaches to answering questions in this context be carefully reviewed (Aydin and Friday, 2001; Aydin, 2004; Aydin and Gaichas 2006; Plagányi and Butterworth, 2004). A description of the ECOPATH with ECOSIM approach is given below (see also www.ecopath.org):

Briefly, the fundamental ECOPATH mass balance equation is based on that originally proposed by Polovina (1984). This balance for each functional group *i* in an ecosystem (detritus excepted) is described by (Walters and Martell, 2004):

$$B_i \cdot \left(P/B \right)_i \cdot EE_i = \sum_j \left(Q/B \right)_j \cdot DC_{ij} \cdot B_j + C_i + BA_i + NM_i \qquad (1)$$

where B_i and B_j are the biomasses of *i* and the consumers (*j*) of *i* respectively;

$(P/B)i$	is the production/biomass ratio for i;
EE_i	is the fraction of production of i that is consumed within, or caught from the system (the balance being assumed to contribute to detritus);
C_i	is the fishing mortality (landings + discards) on i;
$(Q/B)_j$	is the total food consumption per unit biomass of j;
DC_{ij}	is the fractional contribution by mass of i to the diet of j;
BA_i	is a biomass accumulation term that describes a change in biomass over the ECOPATH base-reference-unit time step (usually one year), and
NM_i	is the net biomass migration (immigration-emigration) for i.

Methods to achieve mass balance in an ECOPATH model include both *ad hoc* trial and error adjustments and the use of inverse models to minimize the imbalances between inputs and outputs (e.g. Savenkoff, Vézina and Bundy, 2001). Inverse methods attempt to provide an internally consistent description of trophic interactions between all functional groups by finding a solution subject to the constraints posed by the available data on prior knowledge of the system (Savenkoff *et al.,* 2004). There are several studies based on an inverse modelling approach (e.g. Vézina *et al.*, 2000, Vézina and Pahlow, 2003; Savenkoff *et al.,* 2004). Although they have limited practical applicability because of their static-flow nature, they are useful in addressing issues of parameter uncertainty and the weighting of evidence from different sources in a statistically defensible manner.

The ECOSIM models convert the above "steady-state"[1] trophic flows into dynamic, time-dependent predictions. At basis, for prey i and predator j, Walters, Christensen and Pauly (1997) model the dynamics of the vulnerable (V_{ij}) and non-vulnerable (N_i-V_{ij}) components of the prey abundance (by number) of i as:

$$\frac{d\left(N_i - V_{ij}\right)}{dt} = -v_{ij}\left(N_i - V_{ij}\right) + v'_{ij} V_{ij} \tag{2}$$

$$\frac{dV_{ij}}{dt} = +v_{ij}\left(N_i - V_{ij}\right) - v'_{ij} V_{ij} - a_{ij}V_{ij}N_j \tag{3}$$

where the total consumption rate Q_{ij} of prey i by predator j is $a_{ij}V_{ij}N_j$ and N_j represents the number of predator group j.

Under the assumption that the dynamics of the V_{ij} are much faster than those of the N_i, dV_{ij}/dt is set to zero, yielding:

$$V_{ij} = v_{ij}N_i \Big/ \left(v_{ij} + v'_{ij} + a_{ij}N_j\right) \tag{4}$$

and hence (taking biomass to be proportional to numbers) the standard ECOSIM interaction term for describing trophic flows Q_{ij} between prey group i and predator group j:

$$Q_{ij} = a_{ij}v_{ij}B_iB_j \Big/ \left(v_{ij} + v'_{ij} + a_{ij}B_j\right) \tag{5}$$

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[1] Strictly in applications where some BA term is non-zero, the ECOPATH approach does not reflect "steady-state"/"equilibrium". However, the spirit of the approach, even with this adjustment, is to represent balances in a "steady" (possibly steadily changing) situation, in contrast to modelling the dynamics fully.

where a_{ij} is the rate of effective search for prey i by predator j and v_{ij}, v'_{ij} are prey vulnerability parameters.

This consumption equation has been amended in subsequent versions of ECOSIM to the form (Christensen and Walters, 2004):

$$Q_{ij} = \frac{a_{ij}v_{ij}B_i B_j T_i T_j S_{ij}M_{ij} / D_j}{v_{ij} + v_{ij}T_i M_{ij} + a_{ij}M_{ij}B_j S_{ij}T_j / D_j} \tag{6}$$

where T_i is the prey (i) relative feeding time;

T_j is the predator (j) relative feeding time;

S_{ij} are the user-defined seasonal or long-term forcing effects;

M_{ij} represents mediation forcing effects; and

D_j accounts for handling time limitations on consumption rate by predator j as follows:

$$D_j = \frac{h_j T_j}{1 + \sum_k a_{kj} B_k T_k M_{kj}} \tag{7}$$

where h_j is the predator handling time.

As in the classic Lotka-Volterra formulation ($Q_{ij} = a_{ij}B_i B_j$), flows are determined by both prey and predator biomasses, but Equation (5) (and its extended form shown in Equation (6)) incorporates an important modification in that it encompasses a framework for limiting the vulnerability of a prey species to a predator, thereby including the concept of prey refugia and also tending to dampen the unrealistically large population fluctuations usually predicted by the Lotka-Volterra formulation.

Earlier, to overcome the limitations of a biomass dynamics framework, where relevant, juvenile and adult pools in ECOSIM II were linked using a delay-differential equation system that kept track of flows in terms of numbers as well as biomass. However, more recent versions of EwE include a facility to model fully age-structured population dynamics with multiple life history stanzas and recommend the use of this approach in favour of the adult/juvenile splitting implemented earlier (see Walters and Martell, 2004). The multiple-stanza version of ECOSIM is a major advancement and permits testing of, *inter alia*, the effects of biomass pool composition on aggregated consumption estimates, the introduction of greater resolution on size-dependent interaction rates and evaluation of problems such as growth overfishing (Walters and Martell, 2004).

In many respects, EwE achieves a good balance in model structure between simplicity and the level of complexity that often accompanies other ecosystem model representations. Although users have tended to include a large number of components in their EwE models, it can also be used in more of a Minimum Realistic Model (MRM) sense (Butterworth and Plagányi, 2004).

Plagányi and Butterworth (2004) review the basic equations and assumptions, strengths and weaknesses, some past and possible future applications and hence the potential of this approach to contribute to practical fisheries management advice. Strengths include the structured parameterisation framework, the inclusion of a well-balanced level of conceptual realism, a novel representation of predator-prey interaction terms, the use of a common framework for making comparisons between systems studied by different researchers, the rigorous analytical framework provided by ECOPATH (in contrast to an *ad hoc* type model) and the inclusion of a Bayes-like approach (ECORANGER) to take account of the uncertainty associated with values for model inputs. Somhlaba (2006) suggests that ECORANGER is likely computationally inefficient and could be improved. Aspects of the actual EwE model structure that

may merit further attention or are potentially problematic include the need to initiate projections from "steady state" ECOPATH solutions[2] (in standard applications), the questionable handling of life history responses such as compensatory changes in the natural mortality rates of marine mammals, possible problems in extrapolating from the microscale to the macroscale[3], as well as some (though not too far-reaching in practice) mathematical inconsistencies in the underlying equations.

Many of the shortcomings of EwE applications are attributable to user misuse (or insufficient use) rather than to the actual model structure. Uncritical use of default parameter settings or setting of vulnerability values to the same constant for all species is unsatisfactory, because *inter alia* it assumes the same prior exploitation history for all species and may result in overcompensatory stock–recruitment relationships. There is a paucity of systematic and stepwise investigations into model behaviour and properties. As with all multi-species approaches, the major limitation in applying the EwE approach lies in the quality and quantity of available data. Plagányi and Butterworth (2004) argue that current EwE applications generally do not adequately address uncertainty in data inputs and model structure. Recent improvements to the software that use a computer-automated iterative technique for mass-balancing Ecopath models are a step in the right direction in the sense that it incorporates a facility for Monte Carlo–based explorations of sensitivity to different starting conditions (Kavanagh *et al.,* 2004). Nevertheless such developments must be used with care as dependence solely on such methods can see the modeler lose their sense of the model's driving forces and many useful insights into system dynamics can be lost (E. Fulton, pers. comm.).

Implications of the ECOSIM interaction representation

Plagányi and Butterworth (2004) argue that models need to be closely scrutinized to understand the extent to which underlying model assumptions predetermine or have implications for the results obtained. By virtue of EwE being packaged in a form that is readily digested by as many people as possible, undiscerning users can more readily use it as a "black-box", neglecting to test the appropriateness of default parameter settings and conferring inadequate consideration to alternative functional relationships. The modular version currently under development is likely to improve issues of transparency and accessibility as well as forcing less discerning users to better explore the robustness of their model predictions.

The ECOSIM "foraging arena" concept (see Walters, Christensen and Pauly, 1997; Walters and Kitchell, 2001; Walters and Martell, 2004) (see Equations 5 and 6), is a novel functional response representation that is supported to some extent by studies of fish populations. However, complications to be borne in mind include the fact that EwE cannot straightforwardly depict instances where the foraging arena V's (vulnerability pools) are used simultaneously by multiple predators. This may be important in instances such as when a fish predator targets similar prey to those targeted by a marine mammal, or in which there are overlaps in the vulnerability pools available to marine mammals and to fisheries. EwE as presently configured implicitly assumes that direct interference between predator species (which it ignores) is inherently different from within-species interference (explicitly modelled by Equation (5)).

Caution is advised regarding earlier published results from ECOSIM in which users adopted earlier default settings. As explained in Plagányi and Butterworth (2004, 2005),

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[2] As with most modelling approaches, it is problematic to extrapolate to situations far from the initial/ equilibrium state.

[3] The point here is that if one has a particular functional form at the microscale and the parameters of that form vary from place to place, this does not mean that when you integrate that form over space the resultant functional form will necessarily lie within the set of forms covered by varying the parameters of the original form. This is a problem that persists with almost all models.

these early versions of ECOSIM could not yield pure-replacement results when predicting the effects of a "predator" (a fishing fleet, say, that acts identically in terms of prey selection) in supplanting marine mammals. Expressed another way, this argument is that default parameter value selections for the model effectively hard-wired it to such an extent that they effectively swamped other signals pertinent to predicting the effects of a marine mammal reduction. Cooke (2002) similarly demonstrated through the use of a simple model that whether or not the reduction in cetaceans results in higher fishery yields than would otherwise, other things being equal, be obtained, depends critically on the assumed vulnerability of the fish to the whales. It is only under scenarios assuming a high vulnerability of fish to whales that fishery yields are predicted to be sensitive to the abundance of whales. These results highlight the importance of exploring robustness to assumptions related to consumption because *a priori* assumptions in this regard strongly influence model outcomes in terms of whether or not they yield pure-replacement results. Values other than default could of course be selected, for example, Mackinson *et al.* (2003) showed that particular combinations of ECOSIM settings can be used to produce alternative "emergent" forms of functional responses, specifically Type I and II, but not Type III, behaviours. In recent years Type II and Type III functional responses have been built into the ECOSIM general functional response, which even permits combinations of these variants and hence is now extremely flexible.

The current and future EwE

A number of modifications and improvements have recently been added to EwE. Given fairly recent improvements in terms of age-structure handling, many of the older models have or are in the process of being modified and this is likely to result in valuable new insights. EwE has in the past been criticized for inadequate handling of issues of uncertainty (e.g. Plagányi and Butterworth, 2004) but the more recent versions include improved capabilities to balance models based on uncertainty, examine the impact of uncertainty as part of the management process and to quantify input parameter uncertainty to run ECOSIM using a Monte Carlo approach to fit to time series (V. Christensen, University of British Columbia, Canada, pers comm., Kavanagh *et al.*, 2004). (see also Future Developments section).

2.1.2 Biogeochemical models

This category of models differs from the other models discussed in being nutrient-pool based rather than biomass-based (Table 2).

2.1.3 ERSEM and SSEM

The European Regional Seas Ecosystem Model (ERSEM) was developed to simulate the annual cycles of carbon, nitrogen, phosphorus and silicon in the pelagic and benthic components of the North Sea (Baretta, Baretta-Bekker and Ruardij, 1996). ERSEM model version II (VII) is described in the special issue of the Journal of Sea Research Vol. 38 (Baretta-Bekker and Baretta, 1997). The model requires detailed data inputs and focuses on the phytoplankton and zooplankton groups, with detailed representation of microbial, detrital and nutrient regeneration dynamics. The model is driven by a wide range of forcing factors including irradiance and temperature data, atmospheric inputs of nitrogen, suspended matter concentration, hydrodynamical information to describe advective and diffusive transport processes and inorganic and organic river load data (Lenhart, Radach and Ruardij, 1997). The spatial scope of the model encompasses the entire North Sea. More recently, Blackford, Allen and Gilbert (2004) provide a mathematical description of ERSEM-2004 (developed from ERSEM II) together with a description of its application to six contrasting sites within the North, Catalan, Cretan and Arabian Seas. They conclude that when coupled to high resolution hydrodynamic

models, ERSEM can be applied over large geographical and temporal scales and is thus a useful tool for studies focusing on lower trophic levels.

The consumers module of ERSEM includes mesozooplankton, microzooplankton and heterotrophic flagellates. Consumer uptake is of a Michaelis-Menton form and depends on both food availability and water temperature. A "food matrix" is used as an input to describe the relative prey availability or preference of the different food sources for each consumer (Solé, Estrada and Garcia-Ladona, 2006). A useful feature described in Blackford, Allen and Gilbert (2004) is the introduction of a Michaelis-Menton term to prevent excessive grazing of scarce prey based on a lower threshold feeding parameter.

In the current context, one of the most useful applications pertains to attempts to link ERSEM to individual growth models for fish (Bryant *et al.*, 1995; Heath, Scott and Bryant, 1997). The entire North Sea herring population was modelled using an age-structured cohort model that was linked by adjusting the biomass of groups in ERSEM to reflect prey uptake by herring and conserving carbon and nutrient balances by accounting for defecation, excretion and mortality products from the fish (Heath, Scott and Bryant, 1997). The detailed representation of transport processes within ERSEM allowed simulation of important juvenile growth processes such as year-specific dispersal and timing of larval recruitment. The model was useful in demonstrating the extent to which hydrographic and planktonic conditions are responsible for short-term year-to-year variability in growth but the model failed to explain longer-term underlying trends thought to be due primarily to density-dependence.

ERSEM could be adapted for other regions as it is essentially a generic model which is then coupled to an appropriate physical model for a region, such as the General Ocean Turbulence Model (GOTM). ERSEM has been shown to be equally applicable in tropical and warm temperate systems such as the Arabian Sea, Mediterranean and Irish Seas (Allen, Blackford and Radford, 1998; Allen, Sommerfield and Siddorn, 2002; Crise *et al.*, 1999). Adapting it to other systems requires a fair amount of data. Given that the focus of ERSEM is on the lower trophic levels, it is unlikely to be able to contribute to practical fisheries management but is nonetheless a good tool for understanding environmental drivers and bottom-up processes impacting fish populations.

The Shallow Sea Ecological Model (SSEM) (Sekine *et al.*, 1991) also includes detailed representation of processes such as swimming, advection and diffusion and requires inputs in the form of water temperature, currents and nutrient loads from surrounding land masses. It has specifically been developed to predict the impact on fisheries of coastal development activities. It is thus adequately tailored for this use but would not be suitable for broader questions related to the ecosystem impacts of fisheries.

2.1.4 IGBEM, BM2 and ATLANTIS

IGBEM (Integrated Generic Bay Ecosystem Model) (Fulton *et al.*, 2004) is a coupled physical transport-biogeochemical process model constructed through amalgamation of ERSEM II and the Port Phillip Bay Integrated Model (PPBIM) (Murray and Parslow, 1999). Some of its main features are summarized in Tables A1a to A4, but it is not further discussed here given that this model is essentially superseded by ATLANTIS. ATLANTIS (Fulton, Smith and Punt, 2004) was developed from the "Bay Model 2" (BM2) ecosystem model of Fulton *et al.* (2004), first applied to Port Philip Bay, Australia. Its development has been tightly coupled to efforts to evaluate potential methods and tools (such as ecological indicators) for use in ecosystem-based fisheries management using a Management Strategy Evaluation (MSE) approach. This approach requires not only models of how the management decisions are made (including associated monitoring activities), but at its core it must have an operating model to represent the "real world" including the impact of fishing and other anthropogenic effects. ATLANTIS is arguably currently the best model worldwide to play this role for some of the following reasons:

1. It includes the full trophic spectrum;
2. It has a more simplified representation of physiological processes than most other biogeochemical models, following a detailed sensitivity analysis to determine the importance of including various processes (Fulton, 2001). On the other hand, some processes not considered in other models, such as mixotrophy, are included as they are considered important;
3. Vertebrates such as fish are modelled using age-structured formulations;
4. Lower trophic level groups are represented better than in most whole ecosystem models (in that it allows some age structuring at the juvenile-adult level for potentially important invertebrates such as cephalopods and large crustaceans), whereas the upper trophic level groups are represented better than in other biogeochemical models;
5. The model is spatially resolved;
6. Multiple vertical layers can be considered;
7. The modular structure allows the substitution of a wide range of different sub-models for various components;
8. The nutrient-pool formulation allows testing of effects such as nutrient inputs from point sources;
9. There is detailed coupling between physical and biological processes
10. Multiple representations of some of the processes are included, thereby allowing the user to choose the preferred option for their modelled system.

Given the above, it is perhaps of interest to briefly describe the equations used to model fish populations in particular. The rates of change for a vertebrate group (FX) are given by (Fulton, Smith and Punt, 2004):

$$\frac{d(FX_{i,s})}{dt} = G_{FX_{i,s}} \tag{8}$$

$$\frac{d(FX_{i,r})}{dt} = G_{FX_{i,r}} \tag{9}$$

$$\frac{d(FX_{i,d})}{dt} = T_{IMM,FX_i} - T_{EM,FX_i} - M_{FX_i} - \sum_{\substack{j=predator \\ groups}} P_{FX,j} - F_{FX_i} \tag{10}$$

where *s* represents structural weight (skeletal and other non-reabsorbable material), *r* reserve weight (fats and other tissues that are broken down when food is limiting), *d* density and *i* age class (either a single year class or a proportion of the total life span of the animal). The rate of change includes consideration of the difference between movement into (T_{IMM,FX_i}) and out of (T_{EM,FX_i}) a cell and removals due to natural mortality *M*, predation mortality *P* (see below) and fishing mortality *F*.

Six alternative functional response representations are currently included, with a common feature being the use of prey availability terms (discussed below). An example of one of the most commonly chosen grazing term formulations which describes the consumption of a particular prey group by CX is given by:

$$P_{prey,CX} = \frac{CX \cdot k_{CX} \cdot p_{prey,CX} \cdot \delta_{refuge} \cdot prey}{1 + k_{CX} \cdot \frac{\varepsilon_{CX} \cdot \left(\sum_{j=prey} p_{j,CX} \cdot j\right) + \varepsilon_{CX,DL} \cdot p_{DL,CX} + \varepsilon_{CX,DR} \cdot p_{DR,CX}}{\mu_{CX}}} \tag{11}$$

where k_{CX} is the clearance rate of CX;

$p_{prey,CX}$ is preference (or availability) of that prey for the predator CX;

δ_{refuge} is a term used if the group is dependent on biogenic habitat refuges;

ε_{CX} is the growth efficiency of CX when feeding on live prey;

DL and DR are respectively the labile and refractory detrital pools; and

μ_{CX} represents the maximum temperature-dependent daily growth rate for the group CX.

Fulton, Smith and Punt (2004) note that the prey availability parameter (P_{prey},CX) is similar to the "vulnerability" parameters in ECOSIM (see Equation (5)) as not all prey are simultaneously available for consumption by a predator. Both habitat and size refuges are handled in ATLANTIS. Moreover, it includes the most sophisticated equations (of which this author is aware) to handle the concept of prey refuges given that the habitat refuge variable can take account of, for example, degradation of the physical environment due to coastal developments (see Fulton, Smith and Punt, 2004 for further details).

Short-term spawning and recruitment events are modelled as affecting the various vertebrate pools. Reproduction is modelled as a pulse each year with the materials required to do this being removed from a group's reserve weight and a proportion of the age class simultaneously ageing into the next age class. The amount of reserve weight (mg N per individual) used during spawning is given by:

$$
s_{FX_i} = \begin{cases} U_{FX_i} \cdot \boldsymbol{max}\big(0, \big(Z_{FX} \cdot (1+X_{RS}) \cdot FX_{i,s} - Y_{FX}\big)\big) & , \; FX_{i,s} + FX_{i,r} > (1+X_{RS}) \cdot FX_{i,s} \\[2em] U_{FX_i} \cdot \boldsymbol{max}\left(0, \begin{pmatrix} Z_{FX} \cdot (1+X_{RS}) \cdot FX_{i,s} + (FX_{i,s} + FX_{i,r}) \\ -Y_{FX} - (1+X_{RS}) \cdot FX_{i,s} \end{pmatrix} \right) & , \; FX_{i,s} + FX_{i,r} < (1+X_{RS}) \cdot FX_{i,s} \end{cases}
$$

$$(12)$$

where U_{FX_i} is the proportion of age class *i* that is reproductively mature, Z_{FX} is the fraction of a group's weight used in spawning, Y_{FX} is a spawning function constant and X_{RS} is the ratio of structural to reserve weight in well fed vertebrates.

In the current model, recruitment can be represented using one of 15 alternative stock-recruitment relationships (ranging from standard forms such Beverton-Holt and Ricker, through to more speculative functions conditioned on plankton biomass or other environmental drivers). As an example, the recruitment b_{tj} in cell j at time t when using the well known Beverton-Holt recruitment relationship is given in ATLANTIS by:

$$
b_{tj} = \frac{\left(\dfrac{\alpha \cdot L_{tj}}{\beta + L_{tj}} \right)}{t_x}
$$

$$(13)$$

where α, β are the conventional Beverton-Holt constants, t_x is total length of recruit period; and L_{tj} represents the offspring biomass in cell *j* at time *t*, with:

$$
L_{tj} = \sum_{i=\text{age class}} s_{FX_i} \cdot FX_{i,d} \cdot (1 + \omega_{recruit} \cdot \delta[t])
$$

$$(14)$$

The term s_{FX_i} represents the spawn from age class *i*, $\omega_{recruit}$ is an episodic recruitment scalar and δ is an impulse function, which controls the pulsed nature of recruitment.

An added feature worth mentioning is that ATLANTIS includes a detailed exploitation model that deals with the impacts of multiple anthropogenic pressures

(pollution, coastal development and broad-scale environmental change), with a focus on the dynamics of fishing fleets. Multiple fleets can be simulated, each with their own characteristics (in the form of gear selectivity, habitat association, targeting, effort allocation and management structures). Multiple alternative formulations are available, with the more complicated capable of explicitly handling economics (including quota trading), compliance decisions, exploratory fishing and other complicated real world concerns.

The exploitation model interacts with the biological model and also supplies 'simulated data' to the sampling and assessment sub-model. The 'simulated data', which may be sector dependent or independent data (via a user defined monitoring scheme), include realistic levels of measurement uncertainty in the form of bias and variance. The simulated data are then input to actual assessment models (to date, these have included surplus production, ADAPT-VPA and fully integrated assessments) and the output of these acts as input to the management sub-model that applies a set of decision rules and management actions (currently only detailed for the fisheries sector). The management sub-model includes a broad range of possible management instruments such as gear restrictions, spatial and temporal zoning, discarding restrictions, bycatch mitigation and biomass reference points.

A negative surrounding the breadth and flexibility of the various sub-models (and their modular form) is that it can seem a daunting and parameter-intensive tool that may be associated with large uncertainties (E. Fulton, pers comm.). Supporting software and methods to make this task easier are under parallel development. In a data rich situation, ATLANTIS may be well suited to a user's needs, whereas it may be argued that in a data poor situation the framework is still quite useful for asking "what-if" questions. As with all modelling approaches, ATLANTIS is not appropriate in all circumstances and must be used sensibly.

2.1.5 SEPODYM/SEAPODYM

Tuna fisheries are typically high value multi-species and multi-gear fisheries in which interactions can occur and hence it is not surprising that considerable effort has been focused on developing a Spatial Environmental POpulation DYnamics Model (SEAPODYM, previously SEPODYM) (Bertignac, Lehodey and Hampton, 1998; Lehodey, 2001; Lehodey, Chai and Hampton, 2003). SEAPODYM is a two-dimensional coupled physical-biological interaction model at the ocean basin scale, developed for tropical tunas in the Pacific Ocean (Lehodey, Chai and Hampton, 2003; Lehodey, 2005). The model includes an age-structured population model of tuna species, together with a movement model which is based on a diffusion-advection equation such that swimming behaviour is modelled as a function of habitat quality. The inclusion of spatial structure was essential given the need to account for fishing effort distribution, the widely ranging swimming behaviour of tuna and environmental variations (Bertignac, Lehodey and Hampton, 1998). The latter are simulated using input data in the form of sea surface temperature (SST), oceanic currents and primary production, predicted either from coupled physical-biogeochemical models such as OGCM (Ocean General Circulation Model, Li *et al.*, 2001) or satellite-derived data (Lehodey, Chai and Hampton, 2003).

SEAPODYM has thus far only been run in the Pacific Ocean and the first multi-species simulation including three tuna species (skipjack *Katsuwonus pelamis*, yellowfin *Thunnus albacares* and bigeye *T. obesus*) has only recently been completed. However, there are plans to develop additional modules for other oceanic predators (P. Lehodey, CLS, Toulouse, France, pers. comm.). Moreover, the model executable, associated software and documentation, including a manual (Lehodey, 2005) are available on the website www.seapodym.org. The model structure differs from the other models in the Dynamic systems model category (Figure 1) in terms of representing only a small

subset of the species in the ecosystem but it is linked to a physical model and hence allows investigation of, for example, the relationship between climate variability and recruitment and biomass fluctuations (Lehodey, Chai and Hampton, 2003).

Habitat index and model equations

SEAPODYM incorporates a number of features which render it useful in a broader context, particularly to explore the dynamics of upper trophic level predators which are highly mobile. Several fish and top predator species are likely to distribute themselves spatially based on the availability of prey and the physical characteristics of the environment as is the case for tuna (Lehodey *et al*., 1998). The habitat index H_a included as part of SEAPODYM is thus designed to preferentially distribute tuna in regions with large food availability and temperature in a range deemed favourable for the species in question. Tuna larvae are assumed to be passively transported by surface currents whereas young and adult tuna movements are constrained by the adult habitat index. The rate of movement into and out of favourable and unfavourable habitats is modelled by including a function to increase the diffusion (D) and advection (χ) at low values of habitat index. Movement is also proportional to the size of the fish such that:

$$D_a = D \times L_a \times \left[1 - \left(H_a / (g_2 + H_a)\right)\right]$$
$$\chi_a = \chi_0 \times L_a \times \left[1 - \left(H_a / (g_1 + H_a)\right)\right]$$

(15)

where D_a and χ_a are respectively the diffusion and advection at age a, L_a the length of fish at age a and g_1 and g_2 two coefficients constraining the shape of the function. Parameterisation is achieved by comparing with the results of tagging studies (Lehodey, Chai and Hampton, 2003). The above approach is fairly straightforward and could usefully be applied in other systems/models too provided physical information is available on sea surface temperature, currents and primary production. Tagging information is also required to estimate the parameters of the movement model.

The natural mortality rate in the model depends also on an index of habitat quality. As in more traditional single-species models, the fishing mortality is computed as proportional to the fishing effort $E_{i,j,t}$, the catchability coefficient of the fishery q and the gear-and age-specific selectivity coefficients s_a, i.e.

$$F_{i,j,t,a} = s_a q E_{i,j,t}$$

(16)

where $F_{i,j,t,a}$, is the fishing mortality rate of age class a fish in spatial cell i, j during time period t. A knife-edge selectivity function is assumed.

Recruitment is modelled as independent of the adult population density. Instead spawning occurs in all cells in which mature tuna are present and SST is above a limit value. Thereafter the larvae are distributed passively by sea currents. The model has also been extended to permit investigations of the effect of other environmental factors, such as food availability and predation, on larval survival and pelagic fish recruitment (Lehodey, Chai and Hampton, 2003). This aspect of the model is thus suitable for extending to other pelagic species such as sailfish, swordfish and sharks.

SEAPODYM has several features which suggest that it could be a useful tool if applied to model marine mammals such as whales, but the recruitment formulations would need to be modified for this purpose. Another limitation relates to the lumping of all the tuna forage items into a single model compartment (as was indeed necessary given the original aims of the model) (Lehodey *et al*., 1998, Lehodey, 2001). This means that the model is not suitable for exploring hypotheses in which it is important to differentiate between the quality and quantity of different types of prey items or to represent unavailable fractions of this component. The model does not explicitly

model inter-species and inter-trophic level interactions and hence is not suitable as a tool to address questions related, for example, to impacts mediated through trophic interactions.

The population dynamics equations underlying SEPODYM are relatively straightforward and as such are generally applicable to a wide range of species. Population size (*P*) is determined as follows:

$$\frac{\partial P}{\partial t} = \frac{\partial}{\partial x}\left(D \frac{\partial P}{\partial x} \right) - \frac{\partial}{\partial x}\left(\chi_0 P \frac{\partial H}{\partial x} \right) - ZP + R \qquad (17)$$

where *R* is recruitment and *Z* is the total mortality rate. The equation above is generalized to two dimensions and solved using the finite difference method using discrete time steps of one month and 1°-square spatial cells (Bertignac, Lehodey and Hampton, 1998). Other methods are used to solve the other partial differential equations and advection terms. In general it appears the numerical solution methods are slow because computing power is currently the major impediment to adding more species groups to the model (P. Lehodey, pers comm.).

SEAPODYM is an improved version of SEPODYM in that it incorporates an improved description of intermediate trophic levels in three vertical layers, as well as improved handling of multiple predators (Lehodey, 2005). Moreover, an improved numerical scheme allows the use of spatial stretched grids so that resolution can be changed (reducing computation time), depending on the level of interest of a region. The six components of the mid-trophic level included in SEAPODYM are epipelagic, migrant mesopelagic, non-migrant mesopelagic, migrant bathy-pelagic, highly migrant bathy-pelagic and non-migrant bathy-pelagic. Given that the most recent version includes several forage components, revisions were necessary to simulate the coupling of forage mortality to the density of predators. This has essentially been done by adding a single mean daily food ration parameter for each predator species, which is used to compute the total forage required by each predator from the various forage components (Lehodey, 2005). Potential problems with this simple approach include the possibility of the combined predator forage requirements exceeding the available forage biomass.

SEAPODYM thus fits under the "fixed ration" model category defined earlier. Most of the models in this category do not include any feedback from predators to prey. SEAPODYM similarly does not explicitly include such feedbacks, but has a number of potential indirect feedback loops in that changes in foraging mortality can change both spawning habitat and feeding habitat, with changes in the latter in turn resulting in changes in natural mortality and fish spatial distribution (Lehodey, 2005).

SEAPODYM is a valuable tool for integrating data from the environment, fisheries and biology of target species to explore bottom-up forces that affect fish populations. An example is the use of SEPODYM to explore the biological consequences of an ENSO (El Niño Southern Oscillation) event in the pelagic ecosystem for the equatorial western and central Pacific ocean (Lehodey, 2001) as well as to explore global warming scenarios (Loukos *et al.*, 2003).

2.2 MINIMUM REALISTIC MODELS

Punt and Butterworth (1995) developed the first so-called MRM in response to a need to quantify the potential effect of seals on hake, the most valuable fishery for both South Africa and Namibia. The Punt and Butterworth (1995) approach was founded in the recommendations of a workshop held in Cape Town in 1991 to develop a basis to evaluate fur seal-fishery interactions off the west coast of South Africa (Butterworth and Harwood, 1991). This led to the coining of the term Minimum Realistic Model (MRM) to describe the concept of restricting a model to those species most likely to

have important interactions with the species of interest.

A critical issue raised in this context relates to the optimal level of complexity for multi-species models (see e.g. Pinnegar *et al.*, 2005; Quince, Higgs and McKane, 2005). Reducing the number of species considered, or aggregating similar species into groups, reduces the number of inter-species links which need to be modelled, but consequently also reduces the number of weak links included in the model. Yodzis (1998) used a food web model of the Benguela ecosystem to show that the exclusion of feeding links representing less than 10 percent of consumption both by and of any species had minimal effect on model predictions, but that above this threshold for linkage strength the model predictions started to become unreliable. The reasons why simplified model outcomes varied drastically from outcomes based on detailed foodweb structure is likely due to the presence of potentially strong diffuse effects in complex food webs (Yodzis, 2000).

2.2.1 The original MRM

Off the South African west coast, the fur seal population (*Arctocephalus pusillus pusillus*) is estimated to consume about as much hake as is landed by fishers (Butterworth *et al.*, 1995), begging the question of whether the hake fishery would benefit in response to a seal cull. The commercially valuable hake consists of two species, a shallow-water (*Merluccius capensis)* and a deep-water species (*M. paradoxus)*, with the larger of the shallow-water species eating the smaller individuals of the deep-water species.

The Punt and Butterworth (1995) model was restricted to the two species comprising the hake resource, seals, a grouped category of large predatory fish and the hake fishery. Together these were estimated to account for more than 90 percent of all mortality of hake. The level of detail taken into account for each component depends on that considered necessary to capture the key aspects of its dynamics. Thus fully age-structured models were used for the two hake species (to capture cannibalism and interspecies predation effects), but the "other" predatory fish components were simply lumped into either a small or large fish category.

One advantage of the Punt and Butterworth (1995) model is that a realistic population dynamics model (Butterworth *et al.*, 1995) was used to simulate the seal population, in contrast to the more usual practice of trying to adapt models originally constructed to simulate fish dynamics. A summary of the major features and assumptions of this approach is listed below:

- the model is discrete (with half-year time-steps);
- the dynamics of the two hake species are modelled separately using a (modified) age-structured production model. The two species are treated as one in a sensitivity test;
- the model includes both cannibalism and interspecific predation;
- equations (18) and (19) below include noise terms which were ignored for all the deterministic calculations and handled in a rather *ad hoc* way for the stochastic runs. This aspect could be improved, for example, through the use of Bayesian methods (A.E. Punt, School of Aquatic and Fishery Sciences, University of Washington, pers. comm.); and
- natural mortality for hake has four sources:

1. **Predation/cannibalism by hake**: this is affected by three factors: the number of predators, the number of prey and the "desirability" of different species/age-classes to a particular predator. The daily hake ration of a predator of species *j* (either seals, *M. capensis* or *M. paradoxus*) is assumed to be given by a Holling Type II feeding function relationship, as recommended by Butterworth and Harwood (1991), on the grounds of simplicity and availability of sufficient data to allow parameter estimation. The daily hake ration of a predator of species *j* and age *a* during the first half of the year *y* is thus given by:

$$R_{y,a}^{j} = \widetilde{R}_{a}^{j}\left(1 - \exp(-\kappa_{a}^{j}V_{y,a}^{j}e^{\eta_{y,a}^{j}-\sigma_{\eta}^{2}/2})\right) \tag{18}$$

$$\eta_{y,a}^{j} \text{ from } N(0;\sigma_{\eta}^{2})$$

where $R_{y,a}^{j}$ is the mass of hake consumed each day by predators of species *j* and age *a* during year *y*;

$\widetilde{R}_{a}^{j}$ is the maximum daily ration for a predator of species *j* and age *a*;

κ_{a}^{j} determines the extent of saturation in the feeding function relationship,

$V_{y,a}^{j}$ is the total biomass of hake which is available for consumption by predators of species *j* and age *a* during the first half of year *y*; and

σ_{η} reflects the extent of the annual variation in the diet.

2.   **Predation by seals** – the same form as above.

3.   **Predation by "other predatory fish"** (e.g. snoek *Thyrsites atun*, kingklip *Genypterus capensis* and sharks): assumed that the number of hake of species *i* and age *a* which are eaten by these fish is related to the abundance of such hake by a Holling Type II feeding relationship. The number, *D*, of hake of species *i* and age *a* which are eaten during the first half of the year is given by:

$$D_{y,a}^{i,predfish} = u_{a}^{i}B_{y}^{opf}\left[1 - \exp\left(-v_{a}^{i}w_{a+\frac{1}{4}}^{i}N_{y,a}^{i} \times e^{\eta_{y,a}^{i,predfish}-\sigma_{\eta}^{2}/2}\right)\right] \tag{19}$$

$$\eta_{y,a}^{i,predfish} \text{ from } N\left(0;\sigma_{\eta}^{2}\right)$$

where u_{a}^{i} is the maximum number of hake of species *i* and age *a* per unit biomass of other predatory fish which could plausibly be eaten (pre-exploitation level);

B_{y}^{opf} is the biomass of "other predatory fish", as a fraction of the pre-exploitation level;

$w_{a+\frac{1}{4}}^{i}$ is the individual mass of hake of age $a+\frac{1}{4}$;

$N_{y,a}^{i}$ is the number of hake of species *i* and age *a* in year *y*;

v_{a}^{i} determines the extent of saturation in the feeding function relationship; and

σ_{η} reflects the extent of the annual variation in the diet.

Note that u_{a}^{i} and v_{a}^{i} were pre-specified inputs (sensitivity to their values was examined).

4.   **Basal natural mortality rate (M_{b})** – mortality attributed to "other causes" not included in the model. This was somewhat arbitrarily set to 0.1 yr^{-1}.

Of the many factors considered in the sensitivity tests by Punt and Butterworth (1995), notable changes to the base-case trial were obtained only by increasing the extent of predation by seals on *M. paradoxus*. There thus exists a need to examine more recent data to check the validity of the assumption in the original model that seals feed mainly in shallow waters and hence that their hake consumption is presumably nearly all constituted by *M. capensis*. A second aspect of the Butterworth *et al.* (1995) seal model which may need to be revised concerns the model structure lacking any feedback

between a paucity of hake and a population-dynamic response in (for example) weight-at-age, survival and/or reproduction of seals, i.e. it was assumed that there was always sufficient "other" food for such predators.

The hake model used a Holling Type II feeding function relationship. The way in which the daily ration of a predator is comprised of different hake species and age-classes depends in part on the "desirability" ($\gamma_{a',a}^{j,i}$ - see eqn. App.II.12 in Punt and Butterworth, 1995) that predators of species *j* and age *a'* exhibit for hake of *i* and age *a,* as estimated from available feeding data.

Punt and Leslie (1995) computed estimates of diet composition and daily ration for the Cape hakes using information on stomach contents collected during demersal trawl surveys by the SFRI (Sea Fisheries Research Institute – now MCM) between 1988 and 1994. Estimates of evacuation rates for Cape hake were obtained using a model of the stomach evacuation process and data for juvenile Cape hake and other gadoids. Of interest is that their estimates of evacuation time were notably larger than those used in earlier analyses, suggesting that the time to evacuate 90 percent of a prey item ranges from 2 to 10 days depending on the meal size and the size of the predator. A key feature of this study was the conclusion that hake meal frequency decreased rapidly with hake size, so that the largest hake were feeding about once every 10 days only. Without this low feeding rate, the model produced a perpetual-fishing-machine - large hake would be so effective at eating small ones, that the harder one fished and removed larger hake, the more smaller hake escaped such predation and became available to make for even larger sustainable fishery catches (D.S. Butterworth, UCT, pers. comm.).

The notion that digestion time constraints likely put a cap on the consumption rates of hakes is important in discussing the appropriate form of the functional response because, for example, it runs counter to one of the assumptions underlying ECOSIM's functional response formulation, namely that "predators with full stomachs are not a common field observation" (Walters and Kitchell, 2001). Walters and Martell (2004) note further that studies such as that by Schindler and Eby (1997) (based on 18 freshwater fish species in lakes) suggest that realized growth rates are typically only 26 percent of the maximum possible rate predicted from bioenergetics. Other data such as that in Table I of Punt and Leslie (1995) suggests predators such as hake regularly show full stomachs, but there is evidence in the literature in support of both views. For example, Arrington *et al. (2002)* showed that across 254 fish species the mean percentage of empty stomachs was some 16 percent, but this varied from 0 percent to 79.4 percent among individual species. Arrington *et al. (2002)* suggest that piscivorous fish in particular regularly experience long periods of empty stomachs.

A potential problem with the "desirability" parameters concerns the fact that these are assumed to be independent of density. This could be addressed to some extent by a more intensive stomach sampling exercise, for example by using techniques to smooth spatial and temporal variability in food composition and predator abundance, such as the geostatistical approach of kriging (Bulgakova, Vasilyev and Daan, 2001). A further example of methods used to separate prey size preference from prey availability is given in Floeter and Temming (2003) (who consider North Sea cod).

Management procedure considerations
A noteworthy feature incorporated in the Punt and Butterworth (1995) approach involved taking explicit account of uncertainty and management issues through the use of a simulation framework that incorporated the feedback control rules actually in place for setting TACs for the hake fishery. The purpose of this approach was to check whether, even if a seal reduction did increase hake sustainable yields, the management system applied to compute TACs was such as to be able to take advantage of this. In a similar context, Cooke (2002) stresses the importance of considering management

constraints and issues of uncertainty as integral components of attempts to assess the effects of changing cetacean abundance on fishery yields. The approach of Punt and Butterworth (1995) provided a useful framework for further work in this field and it is encouraging that there are currently a steadily increasing number of multi-species Management Procedure/MSE studies taking this approach beyond single and limited multi-species applications to consider much broader aspects of ecosystems or assemblages.

2.2.2 ESAM (Extended Single-species Assessment Models)

Livingston and Methot (1998) and Hollowed, Ianelli and Livingston (2000) explicitly modelled predation mortality in a catch-at-age stock assessment model applied to the Gulf of Alaska walleye Pollock (*Theragra chalcogramma*). They incorporated the effect of three predators: arrowtooth flounder (*Atheresthes stomias*), Pacific halibut (*Hippoglossus stenolepis*) and Steller sea lion (*Eumetopias jubatus*) by defining predation mortality as a type of fishery. Two important features of this approach were the use of a flexible functional response form capable of reflecting varying levels of predator satiation and of statistical methods to fit the model to the data. Tjelmeland and Lindstrøm (2005) provide a further example of the incorporation of predators into standard fish stock assessment models. They incorporated predation by northeast Atlantic minke whales in the SeaStar herring stock assessment model and estimated the parameters of the consumption formula by directly including the consumption term in the likelihood function maximized.

A first step to constructing a multi-species model based on a rigorous assessment model is to include the various predators simply as alternative "fishing fleets", rather than estimating their effects as part of a "natural mortality" term. Gulland (1983) outlined methodology for extending single-species models to take account of multi-species considerations. Plagányi (2004) similarly applied the "predators as a fishing fleet" approach to a simple representation that incorporated the two Cape hake species as two separate species with *M. capensis* preying on *M. paradoxus* and both of the hake species acting as a predator on juveniles of their own species to emulate the cannibalism known to occur. Seals were included as a separate "fishing fleet" that preyed on *M. capensis*. Each predator was ascribed a selectivity function (based on stomach content data). The two hake species were modelled simultaneously using an age-structured production model (ASPM) (e.g. Hilborn, 1990; Butterworth and Rademeyer, 2005) approach and by fitting to GLM-standardized CPUE data.

As in a typical ASPM, the predator-specific catch by mass in year y is given by:

$$C_y^{pred} = \sum_{a=0}^{m} w_a N_{y,a} S_a^{pred} F_y^{pred} \qquad (20)$$

where

w_a is the mass of an animal of age *a;*

$N_{y,a}$ is the number of animals of age *a* at the start of year *y*;

S_a^{pred} is the fishing selectivity-at-age for a predator *pred*; and

F_y^{pred} is the fishing "mortality" (strictly here that proportion of the fully selected numbers present which are caught by predator *pred*).

The proportion of the selected component of the resource harvested each year (F_y^{pred}) by predator *pred* is therefore given by:

$$F_y^{pred} = C_y^{pred} / \hat{B}_y^{pred} \qquad (21)$$

with the number of animals of age *a* taken by predators in year *y* ($C_{y,a}^{pred}$) given by:

$$C_{y,a}^{pred} = S_a^{pred} F_y^{pred} N_{y,a} \qquad (22)$$

The major challenge in constructing such a model obviously lies in the choice of a suitable interaction term. The simplest way to estimate the predator-specific catch by mass in year *y* is to use a Lotka-Volterra-type interaction of the form:

$$C_y^{pred} = a^{pred} B_y^{pred} B_y^{prey} \qquad (23)$$

where a^{pred} is an "availability" constant (i.e. the interaction constant). However, this is a particularly strong interaction form and alternative forms should be explored, such as:

$$C_y^{pred} = a^{pred} B_y^{pred} B_y^{prey} / \left(1 + b^{pred} B_y^{prey}\right) \qquad (24)$$

which allow for predator satiation. More complicated functional response formulations (such as the various Holling functional response formulations or ECOSIM's foraging arena formulation) can readily be incorporated in a simple model of this form.

Plagányi (2004) simultaneously estimated biomasses of the two hake species in the model fitting process and initial attempts were made to fit the extra parameters, namely the interaction constants corresponding to each interaction (e.g. estimate a^{pred} describing predation by *M. capensis* on *M. paradoxus*). Initial investigations suggested that the data were not sufficient to support estimation of (all of) these additional parameters. However, given appropriate data, it may be possible to input estimates of the predator-specific catch by mass in year *y* directly, e.g. seal predation on *M. capensis* could be fixed in a base-case.

The development of a simple "fishing fleet" type model as described above is a good starting point to address multi-species issues, particularly because it could be based upon existing single-species models (preferably length-based). The approach could be improved by building on length-structured models given that most feeding interactions are strongly size-based (see discussion under OSMOSE). By building these models in a stepwise fashion, they could be extended to achieve greater realism, or moulded to provide greater insight into predation-mediated changes (BENEFIT, 2004).

A further example relating to modifying conventional age-structured assessment models to investigate multi-species effects is presented in Chouinard *et al.*, 2005. They investigated the hypothesis that increased predation by a growing number of Grey seals *Halichoerus grypus* resulted in increases in the natural mortality (*M*) of Atlantic cod *Gadus morhua*, thereby playing a role in the decline of this species. Rather than explicitly modelling seals, their approach entailed estimating trends in *M* using sequential population analysis (SPM) within an ADAPT framework.

2.2.3 MSVPA approach
Multi-species Virtual Population Analysis (MSVPA) is a technique that uses commercial fisheries catch-at-age and fish stomach-content data to estimate both the past fishing mortalities and the predation mortalities on some of the major fish species of interest

(see e.g. Sparre, 1991; Magnússon, 1995). Unlike VPA (Virtual Population Analysis) which assumes that the natural mortality rate remains the same over time and usually also age, here natural mortality is split into two components: predation due to predators explicitly included in the model (*M2*) which depends on time and age because of variations in predator abundance and residual mortality (*M1*) due to all additional factors which are customarily taken to be constant. Based on the estimates of *M2* that result, forward-looking simulations (MSFOR) are then used to determine the average long-term consequences of changing patterns of fishing.

One disadvantage of this approach is that it requires substantial data pertaining to the predation ecology of the predators included in the model, to the extent that tens of thousands of stomachs were sampled in the North Sea in 1981 and 1991, the "Years of the Stomach", under the auspices of the International Council for the Exploration of the Sea (ICES). MSVPA applications have mainly focused on the North Sea, with the considerable data requirements generally impeding the application of this approach to other areas, although similar approaches have been applied to the Baltic Sea (Sparre, 1991), Georges Bank (Tsou and Collie, 2001), Eastern Bering Sea (Livingston and Jurado-Molina, 2000; Jurado-Molina and Livingston, 2002) and Barents Sea as well as to the Gulf of Maine.

A second potential problem with MSVPAs in general is that they concentrate on the impacts of predators on prey but ignore any potential effects that changing prey populations may have on the predators themselves (because of the approach's constant ration assumption – see below). Nonetheless, the approach has some utility in quantifying the relative losses in prey biomass attributable to other predatory fish, marine mammals and commercial fisheries. Moreover, the MSVPA studies have made a start (e.g. Rice *et al.*, 1991, Rindorf, Gislason and Lewy, 1998, Jurado-Molina, Livingston and Ianelli, 2005) in trying to determine the extent to which the consumption of a given prey is a simple linear function of its relative abundance in an ecosystem (the constant suitability assumption). "Suitability" is an important input to MSVPA and specifies the relative preference that a predator would have for different prey species, if all were present in equal abundances.

Although most areas lack sufficient data to permit the application of a full MSVPA approach (for which collection of all necessary data is exorbitantly expensive [Hilborn and Walters, 1992]) such as that applied in the North Sea, there is the possibility of applying a slightly simpler or even hybrid version. The data intensive requirements of MSVPA could be reduced (obviously at the expense of increasing model uncertainty) by restricting the focus to a smaller subset within the ecosystem and by making various assumptions regarding the length of the time period over which data such as age-length keys and stomach samples are assumed to be adequately representative.

Hybrid MSVPA approaches

Mohn and Bowen (1996) used a hybrid-type approach to model the impact of Grey seal (*Halichoerus grypus*) predation on Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf. Their approach involved first running a standard VPA using commercial landings and research survey data and then adding the consumption of cod by grey seals to the commercial landings and repeating the VPA which was retuned to take grey seal predation into account. They incorporated two alternative models of food consumption by seals (a constant ration predation model in which the fraction of cod in the diet was assumed constant and a proportional ration model in which the fraction of cod in the diet was assumed proportional to cod abundance), with these two predation models yielding substantially different estimates of the amount of cod consumed by grey seals.

A further limitation for MSVPA in some contexts is that it is age- rather than length-based and the latter is frequently inescapable for tropical areas for example. However,

age/length hybrid MSVPA versions have been produced (Christensen, 1995b). These approaches are based on length-based catch information as well as a number of other relationships such as the mean weight of length classes, length-age growth parameters and prey size selection functions.

2.2.4 MULTSPEC, BORMICON and GADGET

These models (and others not described in detail here such as Scenario Barents Sea (Schweder, Hagen and Hatlebakk, 2000), Seastar (Lindstrøm, Tjelmeland and Haug, 2002) and FLEXIBEST (IWC, 2004a)) are all of Northern Hemisphere origin and have variously incorporated predation by marine mammals. A common feature is that they are area-disaggregated which is a definite advantage given the migratory behavior of many marine mammals and the consequent importance of considering spatial-temporal overlaps between fisheries, marine mammals and shared prey species. In brief, MULTSPEC (see Bogstad, Hauge and Ulltang, 1997) is a length-, age- and area-structured simulator for the Barents Sea that includes cod, capelin, herring, polar cod, harp seal and minke whales. Predation interactions are modelled only as one-way in the case of marine mammals, which in the model do not react to changes in prey availability. BORMICON (A BOReal Migration and CONsumption model) is another area-structured approach for the multi-species modelling of Arcto-boreal ecosystems (Stefánsson and Palsson, 1998).

Given that work is not currently continuing on MULTSPEC and that BORMICON is being incorporated as a special implementation of GADGET, the focus here falls instead on a brief review of GADGET (Globally applicable Area-Disaggregated General Ecosystem Toolbox) (Begley, 2005; see also webpage http://www.hafro.is/gadget; coordinator G. Stefánsson). Current case studies include the Celtic Sea, Icelandic waters, southern Benguela hake populations and the North Sea and North Atlantic herring. Plagányi and Butterworth (2005) note that GADGET is still being developed but shows great promise for modelling indirect interactions between marine mammals and fisheries (and has been recommended for such – NAMMCO, 2002).

In GADGET, populations can be split by species, size class, age group, area and time step. The model platform is flexible in permitting the easy addition/substitution of alternative model components of biological processes such as growth, maturation and predator-prey interactions. Thus, for example, there are currently seven growth functions from which to choose, including forms such as a simplified "MULTSPEC" type growth equation, a von Bertalanffy equation, two simplified forms of this as well as an extended version which allows for spatial and temporal growth differences, an extended form of the Jones growth function which includes the concept of starvation and a simple power-based growth equation (Begley, 2005). The beta statistical distribution is then used to distribute the growths around the mean.

GADGET's consumption formulations

Prey consumption rate C_p is modelled as dependent on the length of both the predator and the prey p, as well as the relative abundance of the prey (when compared to the total amount of food available). Values of C can affect predator growth depending on the growth function selected. The consumption equations are of interest as they are formulated in a particularly flexible form as follows (Begley, 2005):

$$C_p(l,L) = \frac{N_L M_L \varphi_L F_p(l,L)}{\sum_p F_p(l,L)} \tag{25}$$

where $F_p(l,L)$, which governs the amount of prey consumed by a predator, depends on the product of prey biomass, energy content E_p and the suitability S, such that:

$$F_p(l,L) = \left(S_p(l,L)E_p N_l W_l\right)^{d_p} \qquad (26)$$

and M_L, the maximum possible consumption rate by a predator, depends on temperature and length as follows:

$$M_L(T) = m_0 e^{\left(m_1 T - m_2 T^3\right)} L^{m_3} \qquad (27)$$

where m_1, m_2 and m_3 are constants.

Finally φ, the "feeding level" is:

$$\varphi_L = \frac{\sum\limits_p F_p(l,L)}{HA + \sum\limits_p F_p(l,L)} \qquad (28)$$

where:
L is the length of the predator;
l is the length of the prey;
H is the half feeding level (pre-specified value representing density of prey corresponding to half maximum consumption level);
A is the size of the feeding area;
d is the preference of the predator for the prey;
N is the number of prey in the length cell l, or number of predators in lenght cell L;
W is the mean prey weight in the length cell; and
T is the ambient temperature.
GADGET currently includes five or more suitability functions (Begley, 2005), ranging from a constant suitability function (the proportion of the prey length group that a predator can consume is independent of predator length) to the Richards (logarithmic dependence on both predator and prey length) and Andersen (dependent on the ratio of predator length to prey length) suitability functions. Similarly, a number of options are available to model recruitment, with the following four recruitment functions currently included (Begley, 2005): a fecundity-recruitment function, a simple spawning stock biomass (simpleSSB), a Ricker relationship and a Beverton-Holt recruitment function. Fishing fleets are modelled in an analogous manner to predators and hence suitability functions are defined for fleets to reflect which stocks are caught.

Movement is implemented by either directly specifying migration matrices, or calculating these based on migration ratio input information describing the proportions of the stock that will migrate between different areas. These matrices can for example be used to capture broad seasonal patterns, even if the finer details are not known. A particularly useful aspect of GADGET is its tagging experiment feature that can keep track of the number and proportion of fish in an age-length cell that have been tagged. A number of tags can be lost from the population at each timestep as a consequence of capture, natural mortality or tag loss.

Statistical fits to data
Appreciable improvements in representing uncertainty are possible given the inclusion of a range of options in the construction of penalised likelihood functions that are maximized to obtain parameter estimates and can also serve to provide associated confidence intervals when fitting to data. There are currently 12 penalised potential likelihood contributions incorporated in GADGET (Begley, 2005). These cover the very wide range needed for multi-species models and are as follows (Begley, 2005):

Data likelihood contributions:

(1) Catchdistribution (age, length or age-length grouped catch data); (2) Catchstatistics (biological data such as mean length at age or mean weight at age); (3) StockDistribution (biological properties of different stock components (e.g. immature and mature components)); (4) Surveyindices (standardized indices of abundance or age-length indices); (5) SurveyDistribution; (6) StomachContent; (7) Recaptures (data from field tagging experiments); (8) RecStatistics, and (9) CatchInKilos.

Penalty functions:

(10) Boundlikelihood (assigns a penalty weight to parameters that move outside pre-specified bounds); (11) Understocking (penalty term for overconsumption by a predator or fleet), and (12) MigrationPenalty (penalty term for nonsensical values in the migration matrices).

Formulations are available to deal with data that are aggregated into either age, length or age-length groups. The "goodness of fit" of the model is assessed using a weighted sum of penalised likelihoods for a range of individual components. The use of a powerful algorithm to conduct global maximization of the penalised likelihood is a definite advantage as is the continuing work to derive improved statistical measures of uncertainty.

A large range of variants are available to define the type of linear regression equation (e.g. linear or log-linear regressions with fixed or estimated slope and intercept) to be used in the likelihood calculations or the choice of assumed statistical distributions for the error components of the (implicit) models relating data to model variables (Multinomial, Pearson, gamma or log).

GADGET is thus extremely flexible in terms of methods for fitting to data, being comprehensive and incorporating state-of-the-art features, with the only disadvantage of these being that it is foreboding for a novice user! Although the GADGET manual is fairly comprehensive, it doesn't always include the underlying equations for some components making it difficult to follow these. New users will battle to get going on their own, suggesting the need for more workshop type sessions as is successfully done for EwE. Advanced users will greatly appreciate the fact that GADGET is capable of running on multiple computers in parallel using PVM (Parallel Virtual Machine) (Begley and Howell, 2004).

As with the other modelling approaches, a major impediment to applying this approach in many cases is the current lack of adequate data to describe feeding relationships, especially when considering situations where resource abundances and their ratios differ greatly from those of the recent periods for which data are available. A strong advantage however is that GADGET incorporates a data warehouse that provides the flexibility for ready use of data at the different levels of aggregation that may be required across a number of investigations.

Some of the recent changes (GADGET versions 2.1.01 and 2.1.02) (Begley, 2005) to the model include the addition of the Richards and Gamma suitability functions, a capability to deal with catch information by number rather than mass, of a prey energetic content component and of parameters to allow for a Type III functional response.

2.2.5 Multi-species statistical models

One of the most well-known and utilized fisheries assessment methods is VPA or cohort analysis which is a recursive algorithm utilising catch-at-age information with no underlying statistical assumptions. Hilborn and Walters (1992) distinguish between this method and so-called "Statistical Catch-at-Age Methods" which rely on the formal statistical estimation of parameters. Single-species statistical catch-at-age models are widely used in fisheries management but there have been fewer attempts

to extend these approaches to multiple species models. Unlike more traditional multi-species models such as MSVPA, Multi-species Statistical Models (MSM) are forward-fitting and hence use likelihood maximisation algorithms for parameter estimation. This is the same general approach as employed by models discussed elsewhere in this report, such as Punt and Butterworth (1995), Livingston and Methot (1998) and Hollowed *et al.* (2000). However, the MSM approach currently being developed by Jurado-Molina, Livingston and Ianelli (2005) is categorized separately here because unlike these other statistical catch-at-age models discussed in this report, it includes predator-prey feedback dynamics. Thus, changes in the prey population can impact the predator population and *vice versa* rather than a one-way interaction only in which the predator ration is fixed and changes in prey abundance have no effect on predator populations. The initial application includes only walleye pollock and Pacific cod *Gadus macrocephalus* (including cannibalism), but there are plans to incorporate more species in future model versions (Jurado-Molina, Livingston and Ianelli, 2005).

A distinct advantage of the MSM approach is the use of formal statistical methods for estimating the parameters of multi-species models and quantifying the associated uncertainty.

2.3 INDIVIDUAL-BASED MODELS
Individual-based models (IBMs) (e.g. DeAngelis and Gross, 1992; Van Winkle, Rose and Chambers, 1993; Grimm, 1999) follow the fate of individuals through their life cycle, under the assumption that individual behaviour has an appreciable effect on a population's dynamics. They are thus useful in situations in which an understanding is needed of how individual behaviour might affect the dynamics of a system. These models are sometimes referred to as "agent-based" models with the "individual/agent" being represented by either individual animals and plants, or composite units such as fish schools or fishing fleets. They have typically been applied to investigate the dynamics of a single population within the marine environment, but a number of applications extend these analyses to consider multi-species dynamics as well (e.g. Shin and Cury, 2001; Ginot, Le Page and Souissi, 2002; Ginot *et al.*, 2006; Alonzo, Switzer and Mangel, 2003; Kirby *et al.*, 2004; Gray *et al.*, 2003). Megrey, Hinckley and Dobbins (2002) developed a visualization tool that can be useful in analysing the outputs from IBM simulations, given that these are often voluminous and complicated. Grimm *et al.* (2006) propose a useful standard protocol for describing individual-based and agent-based models, although only minor mention is made regarding higher-level entities such as communities consisting of populations. Attention is focused here on the multi-species individual-based model OSMOSE (Object-oriented Simulator of Marine ecOSystem Exploitation) (Shin, Shannon and Cury, 2004) and the agent-based ecosystem model INVITRO (Gray *et al.*, 2003; 2006).

2.3.1 OSMOSE
OSMOSE (Shin and Cury, 2001; Shin, Shannon and Cury, 2004) is a spatial individual-based model that uses simple individual predation rules to model trophic interactions. It is thus an excellent framework to explore the hypothesis that predation is a size-based opportunistic process, depending only on size suitability and spatial co-occurrence between predators and their prey. Given the need as motivated in this review for alternative representations of species interactions, OSMOSE has a potentially important role to play as an alternative modelling approach that can help to identify consistent patterns in attempting to understand the ecosystem effects of fisheries (Shin, Shannon and Cury, 2004). It is however limited to some extent in this regard, in that, for example, when comparing model outputs to those produced by EwE, OSMOSE is initialized using ECOPATH-based estimates of biomass, annual natural mortality and fishing mortality values (Shin, Shannon and Cury, 2004). This

constrains OSMOSE somewhat in the extent to which it can posit an entirely different ecosystem make-up. Also, estimates from one modelling approach are usually specific to that approach and hence great caution should be taken when transplanting estimates into another approach or even when assuming the same inputs.

The focus of OSMOSE is on piscivorous fish species, with fish schools moving in a two-dimensional square-celled grid with closed overall boundaries. In the model, fish move to adjacent cells with the highest biomass of potential prey. Plankton and other invertebrate species are represented through a total carrying capacity term and top predators such as marine mammals and seabirds are represented simply using an additional natural mortality term.

As with the other multi-species models discussed, OSMOSE requires a large number of input parameters in the form of growth, reproduction and survival parameters. Some of these parameters are common to different species and ecosystems which facilitates the parameterisation process. However, there are a number of influential parameters upon which the model is based and the sensitivity of results to alternative defensible choices needs to be examined. Specifically, the model assumes a minimal predator-prey size ratio (τ) of 3.5 (the theoretical ratio between predator and prey body lengths) (from Froese and Pauly, 1998) and that individual fish of all species require 3.5g of food per body gram per annum (based on Laevastu and Larkins, 1981; Gislason and Helgason, 1985; Longhurst and Pauly, 1987 – cited in Shin, Shannon and Cury, 2004). The constant maintenance food ration assumption adopted here needs to be borne in mind in interpreting model outputs because it does not account, for example, for differences between species, for effects due to temperature or for energetic differences of diverse prey types, or the potentially seasonal nature of major feeding opportunities. However, a useful feature of the model is that the mean fish growth rate depends on the quantity of food ingested and if this quantity falls below the basic maintenance requirement, fish are assumed to die of starvation. A predation efficiency (ξ_i) coefficient is computed based on the ratio between the food ingested by a group and the maximal ration requirement. When this falls below a critical threshold level, the starvation mortality rate is modelled as a linear function of the predation efficiency.

The values which are possibly the most problematic and difficult to obtain are those for the relative fecundity (ϕ_S) parameters which are input for each species and represent the number of eggs spawned per gram of mature female. The reproduction formulation is one of the simplest possible, with the abundance of recruits of species S at time t (assuming an equal sex ratio) determined by simple linear proportionality:

$$N_{S,0,t+1} = \phi_S SSB_{S,t} \quad with \quad SSB_{S,t} = \frac{1}{2} \sum_{a=a_{M_S}}^{A_S} B_{S,a,t} \tag{29}$$

where a_M is the age at maturity, A the terminal age for a species S, *SSB* is spawning biomass and *B* is biomass. The current formulation does not permit exploration of scenarios in which fecundity is a non-linear function of size. Instead of directly modelling recruitment levels, these emerge from the annual survival of eggs and juveniles based on modelled predation pressure and the carrying capacity term in the model. By explicitly modelling predation pressure on fish larval stages, the model provides a useful comparison with the results obtained from other modelling approaches. However, without further development, it seems unlikely that OSMOSE will be accepted into the realm of models contributing to practical fisheries management advice.

A similar age- and size-structured individual-based model termed MOOVES (Marine Object-Oriented Virtual Ecosystem Simulator) (Colomb *et al.*, 2004) is being applied to the ecosystem of Guinea.

2.3.2 INVITRO

Traditionally two main types of ecological models have been used: aggregate state models (like EwE) and individual based models (such as OSMOSE). Formal separation of these model types is not always easy. For instance, within the latter form of model, the individuals may represent schools, patches of homogeneous ground cover, flocks, patches of reef, or some other subset of a population that could be treated as equivalent to an entity. From this it is clear that most aggregate state models can be seen as a special case of an individual (or more properly agent) state model. Consequently, we can treat aggregate state models as agents within an Agent-Based Model (ABM) system. This is the approach that has been taken in INVITRO (Gray *et al.*, 2006), which is currently used as the basis for MSE-based studies focusing on the multiple-use ecosystem-level management questions within the coastal waters of Australia (e.g. on the Northwest Shelf of Australia, Little *et al.*, 2006).

Until recently decision-based ABMs have usually been tightly focused on a small subset of a system (e.g. a single fish in DeAngelis *et al.,* 1991, or a small part of the food web, as in Van Nes, Lammens and Scheffer, 2002). Advances in the use of hybrid models, has (within the last five years) seen the incorporation of a wide variety of ecosystem components into ABMs - facilitated by the coupling of classical dynamic models, using differential equations and decision-based agents. In this way, the best means of representing each ecosystem component can be used - for example in INVITRO classical metapopulation models are used for habitats while IBMs are used for higher trophic levels or species of conservation concern, such as whales.

To make this conjunction of aggregate state and individual-based models seamless, INVITRO embeds them in a time-sharing universe. With each model-type (i.e. each instance of an agent) allowed operating at the most appropriate time and space scales – the scales that match the native resolution of the processes and their associated data sets. Seasonal cycles, for example, do not adhere to time steps appropriate for tidal larval migration. This treatment does have its consequences, not least of which was that it demanded the development of a sophisticated (operating system-like) scheduler.

INVITRO includes a range of alternative agent types, which can be modularly combined to create the final ecosystem (the open source nature of the code means additional modules can also be written by interested users). Currently it contains modules for three dimensional physical and environmental forcing (not just of typical fields like temperature, light and currents, but also more unusual fields such as catastrophic storms), larvae, mobile and sessile fauna from many trophic levels (including top predators), primary producers, biogenic habitat (such as reefs, seagrass beds and mangrove forests) a wide range of human activities (including commercial and recreational fishing, nutrient pollution, salt extraction, shipping, tourism, coastal development, conservation and oil and gas exploration) and their associated assessment and management tools (including standard options like spatial management, but also more hypothetical structures such as alternative management institutions that may be confined to single sectors or span across multiple sectors). The behaviour and representation of each agent is specific to its type. Consequently, mobile agents may be represented as individuals (e.g. turtles and sharks), or small groups (e.g. schools or sub-populations of fin-fish and prawns), while sedentary habitat-defining agents represent entire patches (e.g. an entire reef complex).

While this array of agent types is fairly comprehensive (and allows for immense flexibility) the computational costs of constructing an ecosystem in this way mean that in practice an MRM approach is taken to model structure, with only a subset of the ecosystem that incorporates the dominant system components included explicitly in the model. To date this has meant that only the commercially valuable fish and crustaceans, top predators, species of special interest (e.g. vulnerable species such as turtles), benthic communities (or forage communities if in the pelagic system) and primary producers

have been included. Ongoing work will see a wider set of "supporting" species included, but it is unlikely that the complete coverage offered by EwE or ATLANTIS will ever be possible. ABMs are also faced with all the same complexity, uncertainty and interpretation issues as the other forms of ecosystem models.

2.4 BIOENERGETIC MODELS

A separate suite of models include those based on bioenergetic and allometric reasoning, which involves parameterising a model using power functions of individual body mass (Yodzis and Innes, 1992). Yodzis (1998) used a 29-species foodweb model incorporating allometric reasoning to investigate the effects of a reduction of fur seals on fisheries in the Benguela ecosystem. However, the model structure implemented was arguably too linear and lacked age-, spatial- and seasonal structure.

More recently, an improved bioenergetics model has been constructed to describe interactions between squid, anchovy, hake and sea lions off the Patagonian shelf (Koen-Alonso and Yodzis, 2005). They used a system of four ordinary differential equations, with basal equations to model squid and anchovy and consumer equations for hake and sea lions. The form of equation used for a consumer is very general and could readily be adapted for other systems:

$$\frac{dB_j}{dt} = B_j\left(-T_j + \sum_k e_{kj} F_{kj}\right) - \sum_i B_i F_{ji} - m_j B_j - \mu_j B_j^{v_j} - H_j \qquad (30)$$

where:

B_j is the biomass of consumer species j;

T_j is the mass-specific respiration rate of species j (modelled as $T_j = a_{T_j} w_j^{-0.25}$ with a_{T_j} an allometric coefficient and w_j the mean individual biomass of species j);

e_{kj} is the assimilation efficiency for species as a predator j when feeding on prey k;

F_{kj} is the functional response (i.e. amount of prey species k consumed by predator species j per unit of time);

m_j is the "other natural mortality" rate of species j (due to species not explicitly included);

H_j is the harvest rate of species j; and

u_j, v_j are constants specifying the density dependence in other natural mortality.

The density-dependent mortality form can be used to represent strong nonlinearities in mortality rate, for example as a function of density due to overcrowding of sea lion colonies during the breeding season (Koen-Alonso and Yodzis, 2005). A particularly useful feature of the differential equation (30) above is that it is easy to substitute different functional response variants using the general form derived by Koen-Alonso and Yodzis (2005):

$$F_{ij} = \frac{C_{ij}}{1 + \sum_i h_{ij} C_{ij}} \qquad (31)$$

where

h_{ij} is the handling time per unit of prey i and

C_{ij} is the capture rate of prey i by predator j, the formulation of which varies depending on the functional response assumed.

Difficulties in achieving management-quality multi-species models

Koen-Alonso and Yodzis (2005) stressed the importance of correctly specifying the form of the functional response and experimented with five different formulations (see

Table A1a-d). Apart from the allometry-derived parameters, they estimated the model parameters by minimising the negative log-likelihood for observed (from a database compiling all the time-series data) biomasses. Particularly commendable is that, unlike most of the multi-species models presented, they attempted a detailed analysis of parameter uncertainty using the sample-importance-resample (SIR) algorithm (Punt and Hilborn, 1997; McAllister *et al.*, 1994). The major contribution of this approach thus far resides in it having highlighted the dangers of drawing definitive conclusions from a single model structure.

The Koen-Alonso and Yodzis (2005) multi-species trophodynamic modelling approach is both time-consuming and data intensive, but is a useful tool in systems where biomass (and catch) estimates are available for a subset (at least) of the ecosystem. Bjørge *et al.* (2002) present another data intensive approach that uses a combined Geographic Information System GIS and energetics modelling approach. They used radio-tracking data to construct an energetics simulation model of a population of harbor seals in Norway. By integrating their results into a GIS model, they were able to analyse the co-occurrence of fishing operations and seals. They showed that harbor seal predation probably negatively impacted some fisheries but had a positive effect on shrimp catches due to the removal of benthic-feeding fishes by seals. More recently, Cornick, Neill and Grant (2006) used a bioenergetics modelling approach to project Steller sea lion (*Eumetopias jubatus)* population trends under various scenarios of walleye Pollock harvest. Their model included a sea lion life history component, a sea lion bioenergetics component and a groundfish energetic component. The last component did not explicitly model the groundfish population – instead it converted randomly-drawn standing stock biomass into energy available to the Steller sea lions. It provides an interesting example of a tailored approach including only as much detail as required to address a specific question. Their simulations were unable to produce energy deficits sufficient to account for the observed declines in the western US stock of the Steller sea lion.

2.5 CCAMLR MODEL DEVELOPMENT

2.5.1 Predator-prey models
The adoption of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR) and particularly Article II thereof (for a discussion of the implications see, e.g. Butterworth, 1986), was a crucial step forward in acknowledging the importance of maintaining the ecological relationships between harvested, dependent and related populations of marine resources. Krill is the primary food source of a number of marine mammal species in the Antarctic and concern has been expressed that a rapidly expanding krill fishery might negatively impact (retard) the recovery of previously overexploited populations such as the large baleen whales of the Southern Hemisphere.

Predator-prey modelling procedures have been developed through CCAMLR to assess the impact of Antarctic krill harvesting on krill predator populations and to explore means of incorporating the needs of these predators into the models that are used for recommending annual krill catch levels. Initial modelling procedures estimated the level of krill fishing intensity that would reduce krill availability and hence the population of a predator to a particular level (Butterworth and Thomson, 1995; extended in Thomson *et al.*, 2000). More recently models such as KPFM, EPOC and SMOM have been developed to consider these krill predation issues (see more details below). Hill *et al.* (2006) also present a recent review of models pertaining to the Southern Ocean.

A particular concern in CCAMLR has been the potential negative effects of concentration of krill fishing in the vicinity of land-based predator breeding colonies, for which the foraging ranges of parents are necessarily restricted. Mangel and Switzer

(1998) developed a model at the level of the foraging trip for the effects of a fishery on krill (*Euphausia superba*) predators, using the Adelie penguin (*Pygoscelis adeliae*) as an example. Their approach of incorporating advection and diffusion processes in a spatio-temporal framework to model krill availability in relation to the location of breeding colonies could usefully be extended and applied to situations involving seal populations. Given the large interannual fluctuations observed in krill biomass, these models may also need to include the capacity to incorporate physical forcing of prey dynamics (Constable, 2001; Atkinson *et al.*, 2004). Alonzo, Switzer and Mangel (2003) have developed a model using individual-behaviour to predict the indirect effects of Antarctic krill fisheries on penguin foraging.

In general, initiatives such as these pursued under CCAMLR recognize the need to balance the needs of predators with the socio-economic pressures underlying fishery harvests.

2.5.2 KPFM (Krill-Predator-Fishery Model)

The krill–predator–fishery model (KPFM) of Watters *et al.* (2005, 2006) is being developed specifically to address options for subdivision of the precautionary krill catch limit in the Antarctic Peninsula region (Statistical Area 48) amongst SSMUs (Small Scale Management Units) with areas in the range 10^4 to 93×10^4 km^2. The model is a whole ecosystem model in that it can be used to investigate the roles of transport, production, predation and harvesting, but it also resembles a MRM in some aspects as it focuses on aspects considered to be most important rather than fully specifying the entire spectrum of ecosystem processes and species. The model is spatially resolved to the level of SSMUs and surrounding oceanic areas and it uses a transition matrix approach to model the transport of krill between areas (Watters *et al.*, 2005). Spatially-explicit delay-difference models are used to describe krill and predator population dynamics. In the model krill populations are split into juvenile and adult stages and predators are split into juveniles, breeding adults and non-breeding adults. The model is currently set up to include from one to four stocks of predators per spatial cell. These are typically generic seals, penguins, whales and fish, but specific rather than generic groups may be included instead. Recent modifications (KPFM2) include extensions to represent seasonality and a structure for allowing predators to move between SSMUs (Watters *et al.*, 2006). The model has an interesting formulation pertaining to the way in which predator recruitment (but not survival) depends on krill consumption. Associated work has focused on compiling data and input parameters for ecosystem dynamics models of the region (Hill *et al.*, in press), facilitating the comparison of outputs from different modelling approaches (see below).

A notable feature of the approach is that a Monte Carlo simulation framework is being used to integrate the effects of numerical uncertainty (Watters *et al.*, 2005, 2006). Multiple simulations employing alternative assumptions are run to assess structural uncertainty. Performance measures are being developed both to evaluate catch-allocation procedures and to assess tradeoffs between predator and fishery performance.

The model thus has a number of very useful features, but also some disadvantages such as that krill in transit between SSMUs do not suffer predation and fishing mortalities and the delay-difference dynamics do not capture full age-structured complexity. An important assumption that is being tested and is a big unknown in the model is the extent to which predators and the fishery are equal competitors and hence are equally efficient at competing for limited resources.

The KPFM will permit evaluation of a wide range of management options that account for the needs of other species when deciding krill catch limits in different regions. This modelling work is being complemented to some extent by a krill flux model (Plagányi and Butterworth, 2005b) that is currently being developed to quantify the flux of krill past islands in the Antarctic Peninsula region and by the SMOM

described below. CCAMLR (2006) noted the broad agreement in trajectories between SMOM and KPFM2 in simulation trials when the parameterisation of the two models was consistent, increasing confidence in these modelling approaches for evaluating different fishing options.

2.5.3 EPOC model (Ecosystem Productivity Ocean Climate Model)

An Ecosystem Productivity Ocean Climate (EPOC) model (Constable, 2005, 2006), initially applied only to krill, is being developed using an object-oriented framework built around the following modules: (i) biota; (ii) environment; (iii) human activities; (iv) management; (v) outputs, and (vi) presentation, statistics and visualization. Each element within a module is an object carrying all its own functions and data. It is thus designed to be a fully flexible plug-and-play modelling framework in response to a need to easily explore the consequences of uncertainty in model structures as well as widely varying knowledge on different parts of the ecosystem. The model is being set up to easily examine the sensitivity of outcomes to changes in model structures, not only in terms of the magnitudes of parameters but also in the spatial, temporal and functional structure of the system. An added advantage is that within the same simulation, different species can be modelled at different spatial and temporal scales as well as with different biological and ecological levels of complexity (Constable, 2005).

The model is currently being used for developing a Heard Island whole ecosystem model that will also include oceanographic features (A. Constable, Australian Antarctic Division, pers. comm.).

2.5.4 Mori and Butterworth multi-species model

Mori and Butterworth (2004, 2005, 2006) developed a model to investigate whether predator– prey interactions alone can broadly explain observed population trends in the Antarctic ecosystem since the onset of seal harvests in 1780. The final model components include krill, four baleen whale (blue, fin, humpback and minke) and two seal (Antarctic fur and crabeater) species in two large sectors of the Antarctic. The Atlantic/Indian and Pacific sectors are differentiated because of much larger past harvests in the former, which consequently shows far greater changes in species abundances in the model outpat. Unlike most of the other models discussed, the Mori and Butterworth krill-whale-seal model is fitted to available data on predator abundances and trends, whilst acknowledging that these data are not without their problems. The model is successful in explaining observed population trends in the Southern Ocean on the basis of predator– prey interactions alone, though some difficulties were encountered.

Early model versions (Mori and Butterworth, 2004) considered baleen whales and krill only, but an important finding was that it is necessary to also consider other species in order to explain observed trends. In particular, crabeater seals appear to play an important role.

The model equations were constructed to be as simple as possible whilst still capturing the important population dynamics features. The dynamics of krill are described by (Mori and Butterworth, 2006):

$$B_{y+1}^a = B_y^a + r^a B_y^a \left(1 - \left(\frac{B_y^a}{K_a}\right)\right) - \sum_j \frac{\lambda^j \left(B_y^a\right)^n N_y^{j,a}}{\left(Bj^a\right)^n + \left(B_y^a\right)^n} \tag{32}$$

where:
B_y^a is the biomass of krill in region a in year y;
r^a is the intrinsic growth rate of krill in region a;
K_a is the carrying capacity of krill in region a;
λ^j is the maximum per capita consumption rate of krill by predator species j;

Bj^a is the krill biomass when the consumption and hence also birth rate of species j in region a drops to half of its maximum level; and

$N_y^{j,a}$ is the number of predator species j in region a in year y.

The same basic equation is used to describe each of the predators:

$$N_{y+1}^{j,a} = N_y^{j,a} + \frac{\mu^j N_y^{j,a} \left(B_y^a\right)^n}{\left(Bb^a\right)^n + \left(B_y^a\right)^n} - M^j N_y^{j,a} - \eta^{j,a}\left(N_y^{j,a}\right)^2 - C_y^{j,a} \tag{33}$$

where

μ^j is the maximum birth rate of predator species j;

M^j is the natural mortality of predator species j in the limit of low population size;

$\eta^{j,a}$ is a parameter governing the density dependence of natural mortality and birth (and calf survival) rate for predator species j in region a;

n is a parameter that controls whether a Type II or a Type III functional response is assumed ($n=1$ for Type II and $n=2$ for Type III), and

$C_y^{j,a}$ is the catch of predator species j in region a in year y.

A likelihood function was maximized to estimate the parameters M^j, $N_{1780}^{j,a}$, λ^j, μ^j for all the predator species j and r^a for krill. K_a can be calculated analytically from the relationship between the other parameters under the assumption that all the species considered in the model were in equilibrium (balance) in year 1780, which corresponds to the co-existence equilibrium level for the species considered. An intra-specific density-dependent parameter (η) for each predator was input to admit a non-trivial coexistence equilibrium of the species considered. These terms essentially reflect the impact of limitations of breeding sites for seals and intra-species competition effects for whales (Mori and Butterworth, 2005). Through taking account of density dependent effects on feeding rates, model results suggest that Laws' (1977) estimate of some 150 million tons for the krill "surplus" resulting from the heavy depletion of the larger baleen whale species in the middle decades of the 20th century, may be appreciably too high.

The Mori and Butterworth model structure is reproduced here because it is a simple, pragmatic and self-consistent method that could be adapted for other systems as a useful starting point to understand trophic interactions. It could also be linked to an environmental effects module. One disadvantage of the model in its current state is that it is age-aggregated rather than age-structured, which can, *inter alia*, result in use of inappropriate input values for some parameters, as these likely better correspond to age-structured model constructs (Mori and Butterworth, 2004). The model also focuses on broad trends and hence lacks the smaller scale spatial structure that is required to address questions concerning options for subdivision of the precautionary krill catch limit amongst SSMUs.

2.5.5 SMOM (Spatial Multi-species Operating Model)

The Spatial Multi-species Operating Model (SMOM) (Plagányi and Butterworth, 2006 a&b) builds on the modelling work of Thomson *et al.* (2000) and Mori and Butterworth (2004, 2006) described above. The model includes 15 SSMUs and uses an annual timestep to update the numbers of krill in each of the SSMUs, as well as the numbers of predator species in each of these areas. The model currently includes four predator groups (penguins and seals, fish and whales) but is configured so that there is essentially no upper limit on the number of predator species which can be included. Given the numerous uncertainties regarding the choice of parameter values, a Reference Set is used in preference to a single Reference Case operating model (see e.g. Plagányi *et al.*, 2007, Rademeyer, Plagányi and Butterworth, 2007). The initial

Reference Set used comprises 12 alternative combinations that essentially try to bound the uncertainty in the choice of survival estimates as well as the breeding success relationship. Stochastic replicates are produced to explore different hypotheses such as those related to the transport of krill.

SMOM is intended for use as an operating model in a formal Management Procedure (MP) framework. Different MPs are simulation tested with their performances being compared on the basis of an agreed set of performance statistics which essentially compare the risks of reducing the abundance of predators below certain levels, as well as comparing the variability in future average krill catches per SSMU associated with each MP. CCAMLR (2006) has encouraged the further development of spatially-explicit management frameworks and the development and evaluation of operating models and decision rules for adjusting fishing activities (e.g. catch limits) based on field data in the future.