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

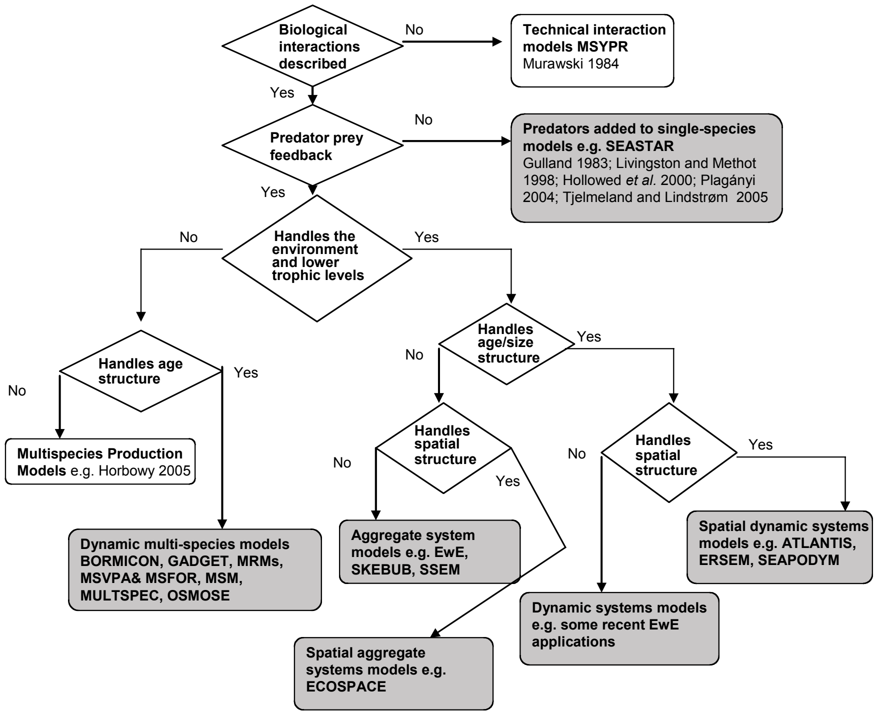


TABLE 1

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

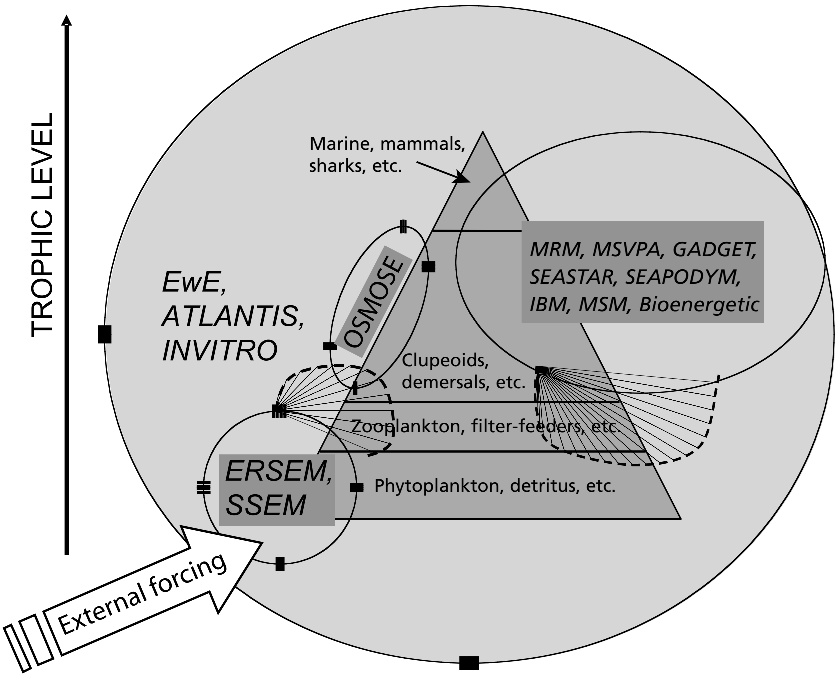
The tables in the Appendixes can be consulted to further examine the above models. The models are compared (Tables A1 a-d) based on the following criteria:

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

a) General ecosystem



b) Antarctic ecosystem

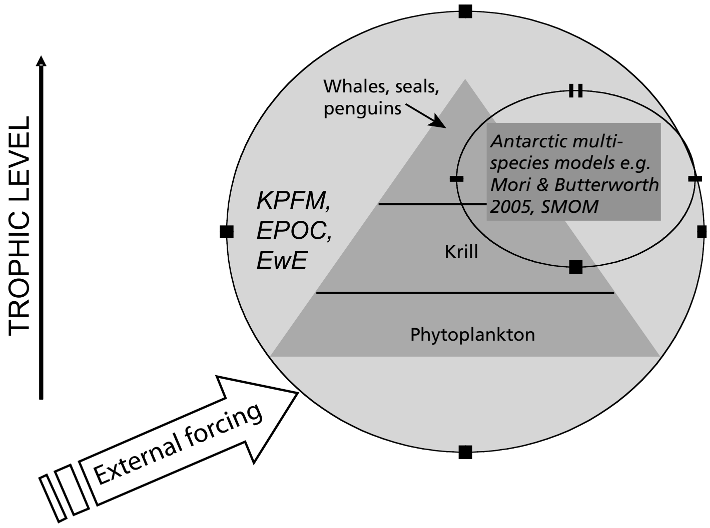
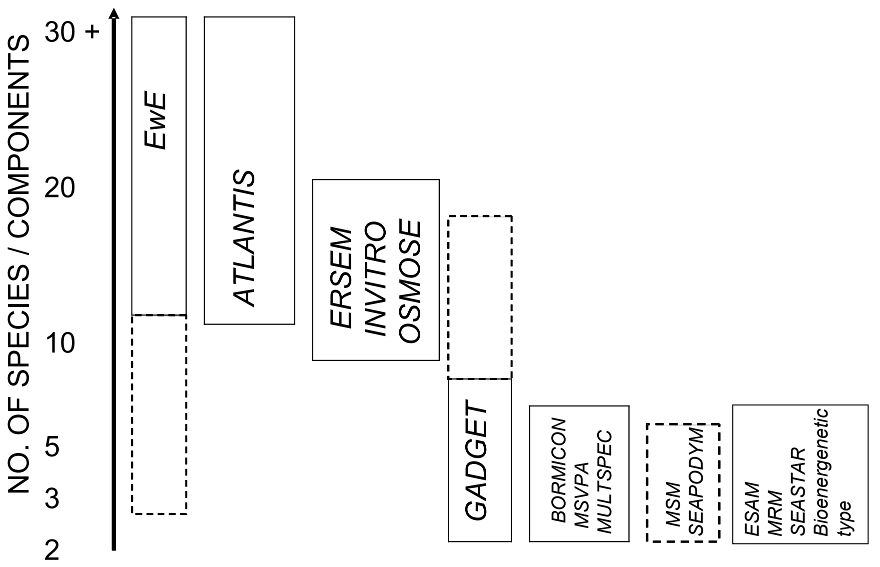


FIGURE 3

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):

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

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*:

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

---

[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):

$$\frac{d\left(FX_{\mathrm{i,s}}\right)}{dt} = G_{\mathrm{FX}_{\mathrm{i,s}}} \tag{8}$$

$$\frac{d\left(FX_{\mathrm{i,r}}\right)}{dt} = G_{\mathrm{FX}_{\mathrm{i,r}}} \tag{9}$$

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

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:

$$P_{prey,CX} = \frac{CX \cdot \mathrm{k}_{\mathrm{CX}} \cdot \mathrm{p}_{\mathrm{prey,CX}} \cdot \delta_{refuge} \cdot prey}{1 + \mathrm{k}_{\mathrm{CX}} \cdot \dfrac{\varepsilon_{CX} \cdot \left(\sum\limits_{\mathrm{j=prey}} \mathrm{p}_{\mathrm{j,CX}} \cdot \mathrm{j} \right) + \varepsilon_{\mathrm{CX,DL}} \cdot \mathrm{p}_{\mathrm{DL,CX}} + \varepsilon_{\mathrm{CX,DR}} \cdot \mathrm{p}_{\mathrm{DR,CX}}}{\mu_{CX}}} \tag{11}$$

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:

$$s_{\mathrm{FX}_i} = \begin{cases} \mathrm{U}_{\mathrm{FX}_i} \cdot \boldsymbol{max}\left(0, \left(\mathrm{Z}_{\mathrm{FX}} \cdot (1+\mathrm{X}_{\mathrm{RS}}) \cdot FX_{\mathrm{i,s}} - \mathrm{Y}_{\mathrm{FX}}\right)\right) & , \; FX_{\mathrm{i,s}} + FX_{\mathrm{i,r}} > (1+X_{\mathrm{RS}}) \cdot FX_{\mathrm{i,s}} \\ \mathrm{U}_{\mathrm{FX}_i} \cdot \boldsymbol{max}\left(0, \begin{pmatrix} \mathrm{Z}_{\mathrm{FX}} \cdot (1+\mathrm{X}_{\mathrm{RS}}) \cdot FX_{\mathrm{i,s}} + (FX_{\mathrm{i,s}} + FX_{\mathrm{i,r}}) \\ -\mathrm{Y}_{\mathrm{FX}} - (1+\mathrm{X}_{\mathrm{RS}}) \cdot FX_{\mathrm{i,s}} \end{pmatrix}\right) & , \; FX_{\mathrm{i,s}} + FX_{\mathrm{i,r}} < (1+X_{\mathrm{RS}}) \cdot FX_{\mathrm{i,s}} \end{cases} \tag{12}$$

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:

$$b_{tj} = \frac{\left(\dfrac{\alpha \cdot L_{tj}}{\beta + L_{tj}}\right)}{t_x} \tag{13}$$

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:

$$L_{\mathrm{tj}} = \sum_{\mathrm{i=age\ class}} s_{\mathrm{FX_i}} \cdot FX_{\mathrm{i,d}} \cdot \left(1 + \omega_{recruit} \cdot \delta[t]\right) \tag{14}$$

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:

$$\begin{aligned} D_a &= D \times L_a \times \left[1 - \left(H_a / \left(g_2 + H_a\right)\right)\right] \\ \chi_a &= \chi_0 \times L_a \times \left[1 - \left(H_a / \left(g_1 + H_a\right)\right)\right] \end{aligned} \tag{15}$$

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.

$$F_{i,j,t,a} = s_a q E_{i,j,t} \tag{16}$$

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