Models for an ecosystem approach to fisheries

FAO
FISHERIES
TECHNICAL
PAPER
477

by
Éva E. Plagányi
University of Cape Town
South Africa

FOOD AND AGRICULTURE AND ORGANIZATION OF THE UNITED NATIONS
Rome, 2007

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):

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

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*:

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

---

[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),

---

[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:

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

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 ($\mathrm{P}_{\mathrm{prey}}$, 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:

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

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 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.