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Lessons in modelling and management of marine ecosystems: the Atlantis experience

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Abstract

Models are key tools for integrating a wide range of system information in a common framework. Attempts to model exploited marine ecosystems can increase understanding of system dynamics; identify major processes, drivers and responses; highlight major gaps in knowledge; and provide a mechanism to 'road test' management strategies before implementing them in reality. The Atlantis modelling framework has been used in these roles for a decade and is regularly being modified and applied to new questions (e.g. it is being coupled to climate, biophysical and economic models to help consider climate change impacts, monitoring schemes and multiple use management). This study describes some common lessons learned from its implementation, particularly in regard to when these tools are most effective and the likely form of best practices for ecosystem-based management (EBM). Most importantly, it highlighted that no single management lever is sufficient to address the many trade-offs associated with EBM and that the mix of measures needed to successfully implement EBM will differ between systems and will change through time. Although it is doubtful that any single management action will be based solely on Atlantis, this modelling approach continues to provide important insights for managers when making natural resource management decisions.

Keywords Atlantis, ecosystem modelling, ecosystem-based management, exploited marine ecosystems

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Introduction

An ecosystem perspective towards the management of marine living resources has been widely espoused for some time (e.g. Baird 1872), yet until relatively recently implementing such approaches has been limited. Improved understanding of marine systems and breakthroughs in computing capacity over the last 40 years (Beck 1999) has lead to substantial interest in a holistic understanding of entire ecosystems. Our improved understanding and capability have contributed to whole-of-system (or end-to-end) ecosystem models becoming an increasingly used tool for informing the management and understanding of a wide range of natural resources (Watt 1975; Halfon 1979; Walters *et al.* 1997; Sainsbury *et al.* 2000; Plagányi 2007; Travers *et al.* 2007; Fulton 2010). Building these models for marine ecosystems is a challenge, as the coupled dynamic representation of the biophysical, economic and social components of a system and its major environmental and anthropogenic drivers means modelling critical processes whose characteristic spatio-temporal scales span up to 14 orders of magnitude (from microbial to ocean basin scales). This pushes the bounds of scientific understanding, model size and complexity.

Here, we summarize insights gleaned from the application of one model (Atlantis) to reveal generalities that might be applied to the broader issue of ecosystem-based fisheries management. The Atlantis modelling framework (Fulton *et al.* 2004a) is one end-to-end model presently being used to support marine ecosystem-based management (EBM) and system understanding. Its use in the last decade has centred on questions regarding model construction, system understanding, indicators of the effects of fishing and effective forms of strategic EBM. The diversity of Atlantis applications provides an opportunity to learn from its implementation, specifically providing insights about the context within which these tools are most useful and also the likely form of best practices for EBM.

A brief overview of Atlantis

Atlantis (Fulton *et al.* 2004a) is a modelling framework intended for use in management strategy evaluation (MSE) studies (see Plagányi *et al.* 2007 for a summary of the MSE approach). It therefore includes representations of each significant component of the adaptive management cycle (Jones 2009), including the biophysical system, the human users of the system (industry), the three major components of an adaptive management strategy (monitoring, assessment and management decision processes) and socioeconomic drivers of human use and behaviour. Atlantis includes dynamic, two-way coupling of all these system components. Although a brief general overview of this structure is given below, readers may find it useful to step through the schematic in Fig. 1 to clarify how the modules are connected.

A full exposition of the Atlantis equations is not possible here as the modelling framework includes many alternative model formulations for each major process and model component included (full documentation is available on a wiki at http://atlantis.cmar.csiro.au/). The choice of formulation is an application-specific decision made by the user, who has the freedom to set complexity at any desired level. This can range from a small number of groups with simple trophic interactions and a Baranov catch equation to highly complex models with sophisticated stock structure, multiple fleets, detailed social and economic effort drivers and

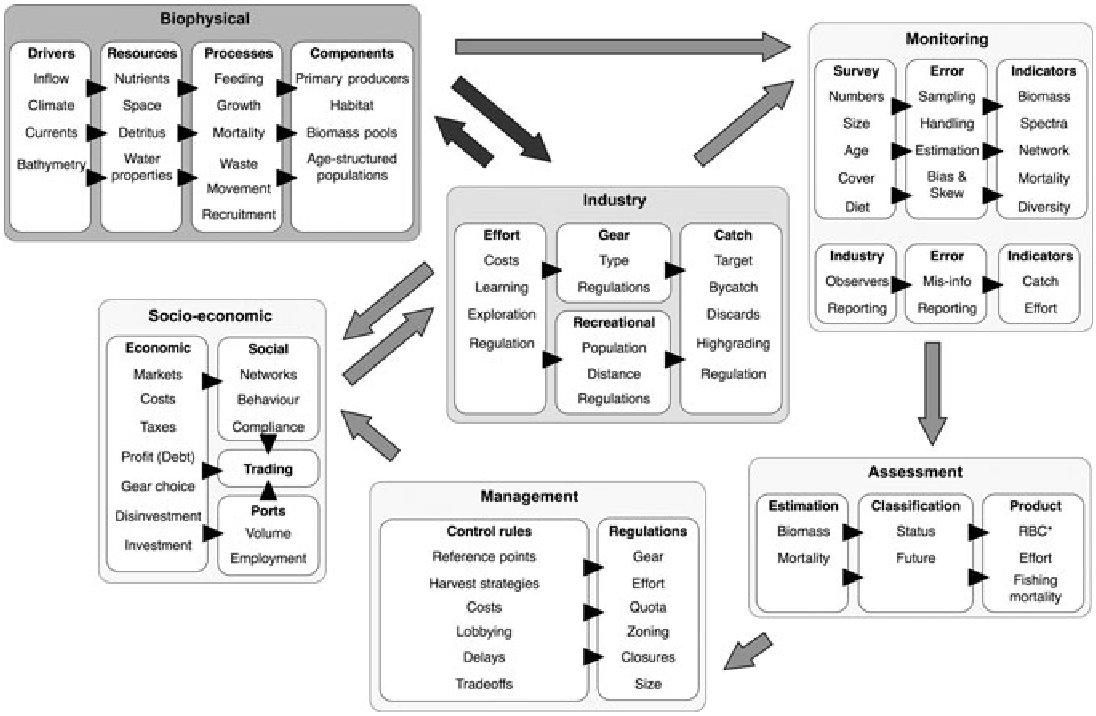

Figure 1 Schematic diagram of the connections, components and major processes included in the Atlantis modelling framework. RBC stands for recommended biological catch.

multiple management options. This modular structure was deliberate given the model's intended use for MSE (where alternative candidate models are used to cover system uncertainty) and its history as a platform for exploring the effect of model complexity on performance (Fulton *et al.* 2003a,b, 2004a,b,c).

Biophysical

The Atlantis biophysical submodel is a deterministic (differential equation), spatially resolved (albeit coarsely), three-dimensional model, which is based on a system of irregular spatial polygons (so that the spatial resolution can be matched to the dominant scale of the processes at any one location). This box representation facilitates tracking the flows of limiting nutrients (typically nitrogen and silica, although others are possible) through the main biological groups in the system (as defined by the user), with the system of differential equations typically solved on 6-, 12- or 24-h time steps (finer adaptive substeps are executed for high turn-over rate groups like plankton and microbes) using a simple forward difference integration scheme. The primary ecological processes modelled are consumption, production, waste production, movement and migration, predation, recruitment, habitat dependency and mortality. Ecological components are represented as either biomass pools (which are largely used for the lower trophic levels) or age-structure populations (typically for vertebrates) where the average size and condition of individuals in each age class are tracked in each box. Representation of the physical environment occurs within the polygonal boxes, matched to the major geographical and bioregional features of the marine system, coupled with an oceanographic transport model. Seabed type (proportions of soft, rough and flat) and features such as canyons are represented in each box, as well as the vertical temperature, salinity, pH and oxygen profiles, advective and diffusive flows and influence of eddies. The biological components may inhabit the substrate or any vertical layer of the water column according to environmental preferences.

Industry and socioeconomic

The human impacts submodel deals primarily with the dynamics of fishing fleets – allowing for multiple fleets, each with its own characteristics (including gear selectivity, habitat association, targeting, effort allocation and management structures). The fleet dynamics model can be tailored to each fleet using formulations ranging from simple catch equations to forced effort, or catches, through to a quasi-agent-based approach. In the latter, subfleets (boats of similar size with common home ports, socioeconomic backgrounds or other aggregate behavioural feature) explicitly step through effort allocation decisions based on a memory of past conditions, current economic conditions, distance to fishing grounds, management regulations and social networks. The more complex variants can include explicit handling of taxes, markets, compliance decisions, exploratory fishing, fuel prices, employment, learning, information sharing, quota trading and investment/disinvestment.

The industry submodel can also include the impact of pollution, coastal development and broad-scale environmental change. However, at present, each of these is handled as a simple forced change or magnitude through time rather than as part of an adaptive management process.

Monitoring and assessment

To allow for evaluations of adaptive management options, 'simulated data' are generated from the biophysical and industry submodels. Given a user-specified monitoring scheme, the sampling submodel generates fishery-dependent data (e.g. catch rates) and fishery-independent data (e.g. biomass surveys) with specified levels of measurement uncertainty (bias and variance). These data can be used to calculate 25 types of ecological indicators (e.g. relative biomass, size spectra and network-based indices) or can be fed directly into simulated assessment models. The output of the assessment submodel is fed into a management submodel, which is typically a set of decision rules and management actions that respond to the current assessed state of the system. Atlantis includes formulations for all major fishery management instruments (including gear restrictions, days-at-sea, quotas, spatial and temporal zoning, discarding restrictions, size limits, economic incentives and by-catch mitigation) as well as decision rules such as the tiered harvest decision rules used in Australian federal fisheries (Smith *et al.* 2008) and the within-year revision of management regulations used by some US fishery councils.

Applications to date

There are currently 13 Atlantis models in use (Table 1; a selection of their maps is shown in Fig. 2), and there are several others (7+) under development. Together these models cover a broad range of ecosystems and emphases (Table 1). These applications have led to a number of important insights about system function as well as the possible forms of effective (or best practice) EBM approaches. These findings are summarized in Table 2 and discussed further later.

Lessons learned about EBM in practice

EBM in practice

As science, industry, the public and management bodies have embraced the concept of EBM, the question of what form this might take has become increasingly pressing. Most discussions of the topic have focused on a single 'silver bullet' solution such as spatial management (Worm *et al.* 2006) or individual transferable quotas (ITQ) (Costello *et al.* 2008; Grafton *et al.* 2008). Work with the many different Atlantis implementations has shown that the performance of different types of management is far more complex than these arguments project. There are a myriad of complex trade-offs that exist between the various ecological, economic and social objectives within EBM. In particular, there is a tension between conservation and economic objectives that are at the heart of EBM. This means that no single lever is sufficient for addressing the trade-offs, as any one lever can be circumvented. Performance is improved if an integrated package of management levers – which draws on a variety of input, output and technical management levers – is implemented, but even this will not be 'best at everything' (Fulton *et al.* 2007, in press). Moreover, it is not possible to create a 'recipe book' form of EBM that can be universally applied. The form of EBM for a system will depend on the state of that particular natural system and the culture exploiting it and will need to evolve through time along with the system (a finding reinforced empirically, Worm *et al.* 2009). The point is that EBM, by its very nature, will require evaluation of trade-offs.

A good illustrative example of this comes from Atlantis-SE (Fulton *et al.* 2007), which was used as the basis for a whole-of-ecosystem MSE in support of

Table 1 List of Atlantis model applications in use (models currently only in the early stages of planning have not been included here) and their main purposes (or topics covered).

Model (system)	No.	Ecological components	Fisheries	Geometry, drivers (hydrodynamics series length)	Max depth (m)	Complexity	Understanding	Systemlevel MSE	Fisheries	Nutrients	Mining	Climate impacts	Catchments	Indicators	Management	Reference
Australia																
Atlantis-SE (SE Australia)	1	4 pp, 20 inv, 14 targ, 22 other vert	33 gear-based fleets	71 boxes, 5 layers; nutrients, climate, inflow, sediments, pH (10 years)	2400		P	P	P			S		P	P	Fulton *et al.* 2007
Atlantis-SM (Victoria/Tasmania)	2	4 pp, 18 inv, 9 targ, 23 other vert	1 aggregate fleet	80 boxes, 6 layers; climate (10 years)	2400		P		S	S		S		P	P	Smith *et al.* 2010
Atlantis-PPB (Port Phillip Bay)	3	6 pp, 11 inv, 4 targ, 4 other vert	1 aggregate fleet	60 boxes, 1 layers; nutrients (5 years)	45	P			S	S				P		Fulton *et al.* 2004b
Atlantis-WPT (Westernport)	4	2 pp, 13 inv, 5 targ, 5 other vert	1 aggregate fleet	27 boxes, 1 layers; nutrients (1 year)	30		P			P			P			Savina *et al.* 2005
Atlantis-ET (Eastern Tasmania)	5	4 pp, 14 inv, 4 targ, 23 other vert	1 aggregate fleet	11 boxes, 6 layers (10 years)	2400	P	P		S			E			E	Johnson *et al.* 2008
Atlantis-TasCERF (Tasmania)	6	4 pp, 21 inv, 7 targ, 20 other vert	1 aggregate fleet	45 boxes, 5 layers (10 years)	2400		E		E						E	–
Atlantis-STORM (Derwent-Huon)	7	15 pp, 21 inv, 8 targ, 21 other vert	1 aggregate fleet	70 boxes, 4 layers (5 years)	150		P	E	E	E		E	E		E	Savina 2009
Atlantis-NSW (New South Wales)	8	4 pp, 20 inv, 11 targ, 21 other vert	1 aggregate fleet	43 boxes, 5 layers (10 years)	800	P	P		P		S				S	Savina *et al.* 2008
Atlantis-CR (Clarence River)	9	2 pp, 7 inv, 5 targ, 10 other vert	1 aggregate fleet	47 boxes, 1 layer (40 years)			P		E	E		E	P	P	E	Hayes *et al.* 2007
North America																
Atlantis-NEUS (NE United States)	10	2 pp, 15 inv, 9 targ, 15 other vert	18 gear-based fleets	30 boxes, 4 layers; nutrients (1 year)	200		P	P	P					S	P	Link *et al.* 2010, in press
Atlantis-EMOCC (California Current)	11	4 pp, 18 inv, 14 targ, 21 other vert	13 gear-based fleets	62 boxes, 7 layers; climate (7 years)	1200		P	P	P			S		S	P	Brand *et al.* 2007
Atlantis-ECCAL (Central California)	12	4 pp, 18 inv, 14 targ, 21 other vert	20 gear-based fleets	82 boxes, 7 layers; climate (50 years)	1200		P		S						P	Horne *et al.* 2010
Atlantis-GOC (Gulf of California)	13	4 pp, 18 inv, 9 targ, 21 other vert	14 gear-based fleets	66 boxes, 6 layers; climate, inflow (23 years)	2025		P	P	P	S		E	E	E	P	Ainsworth *et al.* in press

The ecological components show the number of primary producer (pp), invertebrate (inv), target species (targ) and other vertebrate groups (other vert) included in the model.
P, primary use of the model; S, secondary use; E, exploratory use beginning; MSE, management strategy evaluation.

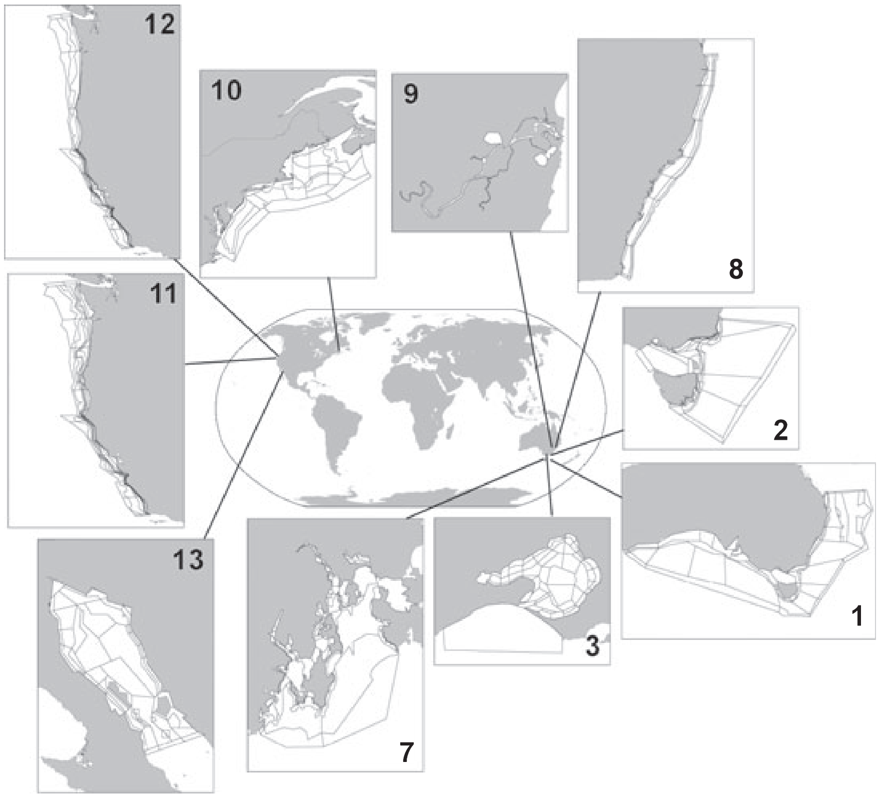

Figure 2 Maps for a representative selection of the Atlantis models (see Table 1 for numbering and a more complete list).

a strategic restructuring of south-east Australian federal fisheries. This study developed and tested EBM solutions for this complex of multispecies and multigear fisheries, which are legally required to meet an extended list of objectives. Each of the strategies tested involved an integrated package of management measures, although most focused on a particular type of management. One represented the management measures in place in 2003 (limited entry and vessel restrictions, some (ineffective) gear restrictions, generally unconstraining quotas, and largely ineffective spatial management); another focused on enhanced quota management; a third was largely structured around spatial management; and a fourth represented a balanced combination of quotas, spatial management and gear controls. No single strategy outperformed the others across all objectives, and each strategy had its own strengths and weaknesses. However, the integrated strategy had the fewest shortcomings, consistently ranking in the top 20% across all objectives and avoiding the (potentially catastrophic) pitfalls that marred the performance of the other strategies (which all scored well only on a subset of objectives). Importantly, neither quota nor spatial management emerged as a solution by itself.

The intent of the ITQ-based management system was undermined by incentives to high grade and misreport quota species and to target species not in the quota management system. These behaviours – along with lags in the quota setting cycle, non-constraining quotas, unaccounted sources of mortality (e.g. discards), partial spatial or life-history coverage and stock influences not addressed by quotas (e.g. habitat) – led to unsustainable biomass levels [less than half the target groups had biomasses at or above 40% of unfished levels ($B_{0.4}$)]. Other incentive-based approaches designed to improve economic performance were also less effective than standard rationalist economic theory would suggest (Fulton *et al.* 2007, in press). For instance, despite expectations that allowing flexibility in choice of gears would allow the tailoring of fleets to the most efficient gear mix, this option instead necessitated heavy subsidies (without these, the costs of the infrastructure needed and the lease costs

Table 2 Major findings to date from Atlantis models.

Model	Findings
Atlantis-SE (SE Australia)	There is no single management lever provides a complete solution to EBM Complex trade-offs exist when trying to satisfy the various ecological, economic and social objectives present in EBM Human behavioural uncertainty produces unanticipated outcomes of management decisions (ecosystem state and the noneconomic or interacting pressures on fisheries operators mean that economic solutions often do not have clear cut outcomes) If TACs are linked across species (with the TAC of one species increased/decreased based on the size of the TAC of another species), this leads to the ecological decline of weak stocks or significant economic costs (e.g. 75% of the catch foregone) Despite past trends where fishing moved further offshore, future target shifting back to popular shelf species is likely as fisheries are squeezed by management constraints and rising costs (causing unintended increases in pressure on the already intensively fished shelf species) Relative biomass indicators, ratios of biomass (e.g. pelagic:demersal), size-structure and size at maturity are consistently the most robust indicators of the effects of fishing
Atlantis-SM (Victoria/Tasmania)	Relative biomass indicators are consistently the most robust indicators of the performance of spatial management Universal reference points are unlikely to work (because different systems are under different pressures and respond in different ways) Some indicators (e.g. biomass ratios) are only effective at small or very large scales (because of how species are aggregated and distributed) Monitoring design (both temporal and spatial) is critical for long-term interpretation of time series Not all groups benefit from spatial management
Atlantis-SETas (Eastern Tasmania)	There are differential impacts of exploiting mid-trophic species (e.g. off Tasmania, there appears to be minor effects of fishing squids, but large impacts of targeting myctophids, suggesting a wasp-waist system)
Atlantis-NSW (New South Wales)	The size of no-take marine protected areas can be important for their ultimate success, but the redistribution of the catch and effort outside the closed areas is even more important (simply displacing effort is insufficient and will undermine the effectiveness of spatial management) Not all species benefit from spatial management (e.g. prey species do not) Moderate levels of fishing pressure can lead to an increase in biodiversity The explicit representation of ontogeny can be important for correctly representing the dynamics of marine species that show large spatial or habitat shifts with age
Atlantis-NEUS (NE United States)	Multiple factors affect large marine ecosystems (production and fisheries), and for understanding, they need to be considered simultaneously; even when focusing on fisheries impacts, overlooking the role of nutrients, primary and secondary production can lead to erroneous conclusions (ecosystems grow fish, but the only the right kinds of ecosystem grow bigger fish) Despite their complexity, clear patterns are detectable in large complicated biophysical systems (making calibrated predictions feasible) Trade-offs are central to both modelling and successful marine management, optimizing everything is impossible (in the management realms this means simpler management is usually better) Modelling squid and shrimp is extremely difficult (a finding recurring in many ecosystem models), but should be attempted as it can lead to new system understanding

Table 2 (Continued).

Model	Findings
	Modelling ecology is much simpler than modelling a coupled ecological-anthropogenic system
	When modelling whole systems concentrate on the general accuracy of what's being done, do not become overly fixated on (potentially spurious) precision
Atlantis-EMOCC (California Current)	Catch shares are more economically efficient than 2008 status quo management arrangements, even if catch levels remain unchanged
	There are differential impacts of the introduction of catch shares (and costs) across some fleets (and communities)
	Monitoring and enforcement are critically important for fisheries management and for guiding the use of incentives to achieve desired fleet behaviours
	Ocean acidification is likely to lead to the reduction in biomass (by an order of magnitude potentially) of predators dependant on shelled invertebrate prey; in contrast, other groups (e.g. jellyfish) are likely to increase in biomass
	Ratios of functional group biomass (e.g. piscivore:planktivore) are strong indicators of community restructuring under fishing
Atlantis-ECCAL (Central California)	Trade-offs exist between economic and ecological objectives when comparing spatial management, gear switching (from trawl to pots and longlines) and effort control scenarios
	Fleets are differentially affected by the scenarios (some suffer significant economic declines, while others see substantial increases)
	Shifting gears to minimize by-catch and habitat destruction does not restore age-structures, but spatial closures can
Atlantis-GOC (Gulf of California)	Reported catch values are insufficient to cause observed declines in species biomasses (by 3–5 times for most species)
	Full enforcement of existing regulations, as opposed to instituting new regulations, would satisfy a broad range of conservation objectives

EBM, ecosystem-based management.

of adjusting packages of quota across species to match catch compositions proved prohibitive), delays in fleet downsizing (as operators under stress tried switching gears rather than exiting the fishery) and flocking behaviour (with many operators making similar decisions to switch gears). Together these responses dissipated any potential gains and ultimately led to worse economic performance (by >20%) than when gear switching was banned.

Spatial management was insufficient as the dominant management lever because it proves quite difficult to strike the balance between protecting areas that are of a size sufficient to produce any conservation benefit and providing sufficient fishing grounds to sustain an economically viable industry (which is not possible in many fisheries if closures on the order of 70–80% or more are imposed, Fulton *et al.* 2007). Moreover, Savina *et al.* (2008) found that effort displaced by closures potentially undermines any benefits coming from the zoning. For instance, strong improvements in diversity (by nearly 20%) under heavy fishing pressure occurred if effort outside a marine protected area (MPA) was controlled. However, without effort control, there was a significant (>20%) drop in overall diversity. Fulton *et al.* (2007), Savina *et al.* (2008), Smith *et al.* (2010) and unpublished work associated with Horne *et al.* (2010) all found that while spatial management appears to be an effective means of satisfying conservation objectives concerning habitat and restoring age-structures of less mobile species, benefits from closures for individual species depend on its trophic position, degree of mobility, geographical distribution and extent of ontogenetic shifts in habitat use and depth (highly mobile or prey species do not benefit in the way that more site attached or predatory species do).

Many of the Atlantis studies have found trade-offs between economic and conservation goals, which can also shape the response of fishers in the system. For example, there was a quite striking trade-off between economic and ecological objectives in Atlantis-SE – where the greatest improvements in relative biomasses, habitat cover and stock structure were only possible if the fishery was reduced to the point it was no longer economically viable (despite a 1.2–5.4× increase in catch rates, insufficient catch was landed to cover management, variable, capital and onshore costs) or where the use of a companion quota system either caused the ecological decline of weak stocks (which can not withstand the fishing pressure associated with efficiently exploiting strong companion stocks) or was associated with significant economic costs (as heavy restrictions on the catch of productive stocks, to maintain all stocks above their individual reference points, can see as much as 75% of the catch foregone). The tension between objectives was also found when using Atlantis [and Ecopath with Ecosim (EwE; Christensen and Walters 2004)] to consider ecosystem level reference points (Worm *et al.* 2009). In that case, the exploitation rates that produced system-level maximum sustainable yield were typically 2.5–5× (but as much as 200×) higher than that causing 10% of the groups in the model to suffer a 90% decline in biomass.

Atlantis-based analyses have also consistently revealed differential impacts of management among fleets – typically consistent with their overall cost structure and projected need to employ policies such as the purchase of expensive by-catch quota (Fulton *et al.* 2007; unpublished application of the model by Horne *et al.* 2010). Furthermore, the modelling in Australia and the California Current has also illustrated that the addition of management levers can create new management issues, particularly around compliance and enforcement issues (something also observed in real fisheries; Healey and Hennessey 1998; Hilborn *et al.* 2004; Grafton *et al.* 2008). For instance, in Atlantis-EMOCC (Brand *et al.* 2007), a model used to evaluated alternative management strategies for the California Current groundfish trawl fleet, while by-catch of overfished species generally declined under ITQs in the models, significant drops (of 20–90%) were strongly dependent upon penalties for exceeding quota. Penalties needed to be >$500/kg, but at that point, ITQs did outperform the status quo (as of 2008) management system in terms of both overall net revenue (with 80% of the vessels having net profits that exceed status quo returns) and the status of overfished species (with biomasses of these rising by 30–400%).

Realization of the conflict between objectives, compliance issues and the mismatch of management intent and realized outcomes is not possible without direct consideration of uncertainties because of human behavioural responses (a feature of the system included in Atlantis, but omitted in many models). This is highlighted by a comparison of the results of the Atlantis modelling and a qualitative assessment by experts with >100 years combined experience in the Southern and Eastern Scalefish and Shark Fishery (SESSF) (Smith *et al.* 2004). In 35% of the cases considered, the predicted trajectories derived through the two approaches did not correspond. The most common difference was that Atlantis-SE suggested differential results across sectors or species, where the experts gave a single response. Also important were differences over the magnitude or inflection of non-linear responses. In few cases (1%), the predicted trajectories were in complete contradiction of each other. In all cases, these mismatches in expected response arose because Atlantis indicated indirect and non-linear ecological dynamics or differences in costs and behaviours between fishery sectors that the qualitative evaluation did not explicitly contemplate.

Monitoring in support of EBM

Monitoring and assessment are key components of any adaptive management approach, including EBM. Atlantis has frequently been used to evaluate these two components of management, as MSE testing of indicators is an effective means of evaluating indicator performance under a range of circumstances (e.g. alternative levels of fishing, climate forcing or cumulative pressures). These evaluations compare indicators calculated from 'sampled' data with 'true values' of key variables (attributes) of interest from the Atlantis biophysical submodel.

An enormous number of candidate ecological indicators have been proposed in the literature (e.g. Rochet and Trenkel 2003; Trenkel and Rochet 2003; Link 2005; Rice and Rochet 2005; Rodionov and Overland 2005), but a wide range of Atlantis models (from both Australian and US systems) show that not all indicators are equally robust in identifying the effects of fishing or summarizing system status. Fulton *et al.* (2005) undertook an in-depth analysis of the efficacy of indicators using Atlantis-PPB and an early version of Atlantis-SE, and Kaplan and Levin (2009) undertook a similar analysis using Atlantis-EMOCC. These analyses showed that there were a few key functional groups (such as gelatinous zooplankton, cephalopods, seagrass, forage fish, piscivorous fish, demersal fish and top predators like large sharks) that provide a useful system-level characterization and that are sensitive to effects of exploitation or system modification. These studies provided general guidelines on effective indicators for marine systems, including:

1. indicators should be cost-effective and easily measured and interpreted (indicators that require large amounts of data or employ intermediate models in their calculation are unlikely to be consistently reliable for monitoring);
2. there is no definitive set of indicators that will work universally, but suites of simple indicators (e.g. relative biomass of indicator groups, size spectra, proportional habitat cover, maximum length of fish in the catch and simple physical measures such as temperature, turbidity and chlorophyll *a*) appear to provide robust measures of the overall state of an ecosystem, and biomass ratios (particularly piscivore:planktivore and benthic:pelagic fish biomass) are effective means of detecting shifts in community composition;
3. to ensure maximum efficiency, reliability and interpretability, the suite of indicators used should span a wide range of processes (with different associated rates), biological groups (plankton, target species, habitat and top predators) and indicator types and use data from a range of temporal and spatial scales; and
4. monitoring schemes benefit from the collection of fisheries-independent information on unfished reference sites (to improve signal detection and attribution) as even the most careful uses of fisheries-dependent data are unable to detect significant effects of fishing given typical short-term time series and moderate system fluctuations.

Interestingly, an empirically based study reached similar conclusions (Link 2005) giving credence to the 'realism' of these Atlantis results.

The work with Atlantis has also cast doubt on some commonly recommended indicators. For instance, mean trophic level has been proposed as an effective indicator of the effect of fishing by many studies (e.g. Greenstreet and Hall 1996; Russ and Alcala 1996; Jennings *et al.* 2001), but Kaplan and Levin (2009) found it did not decline with harvest intensity in Atlantis-EMOCC, largely because some species that are resilient to fishing (such as mackerel, sardines and anchovies) have trophic levels similar to many of the rockfish species that are highly susceptible to overfishing.

Work with Atlantis-SM (Smith *et al.*2010), a model developed to evaluate ecological indicators and the power of alternative monitoring regimes, is also highlighting that monitoring for EBM performance may be far from simple. Monitoring schemes with small spatial coverage or infrequent temporal repetition (on the order of 3–5 years or more) had no power to rapidly detect changes in the system. In contrast, intensive sampling was confounded by natural system variation and shifts through time, unless carefully planned around stratified sampling schemes. Moreover, indicators, such as pelagic: demersal fish biomass, that have been found to be useful across different system types proved sensitive to scale. These indicators were informative in the immediate area of closures (as the data at this scale is within habitat patches and individual species ranges and so avoids species-scale mismatches) and globally (because at such large scales the ratio integrates across many species effectively smoothing out any potential mismatches). However, they do not work at intermediate scales because these exceed the typical spatial range of individual species, yet do not span a wide enough area to include a large enough number of species in the aggregate biomasses to smoothly integrate across patchiness in individual groups. Atlantis-SM also suggests that variation in community dynamics between regions can lead to locally specific indicator–attribute relationships; meaning that while indicator signals are representative of the attribute at a specific locale, they may not always be consistent site-to-site. For instance, the relationship between the indicator relative lobster biomass and the attribute diversity was linear (with $R^2 > 0.92$), but in opposite directions (in one case, there was a positive correlation, and in one, a negative) at sites less than 300 km apart. This difference in direction of response is because of locally specific environmental drivers and community dynamics and has significant implications for monitoring and management, as it shows that an understanding of system dynamics at regional scales will be necessary to understand the signal obtained from indicators. This suggests that universal reference points (analogous to $B_{0.4}$ in fisheries) or directions, which do not take into account local specificity, may not be feasible. This finding is at odds with recent literature on indicators (Rochet and Trenkel 2003; Cury *et al.* 2005; Jennings and Dulvy 2005; Trenkel *et al.* 2007; Bundy *et al.* 2010), which not only recommends a definitive set of indicators across many systems and scales but also recommends the use of reference points that are intended to be consistent across systems. Instead, suites of indicators drawn from the main general classes of indicators noted earlier (e.g. relative biomass, biomass ratios, relative habitat cover) will need their associated reference points or directions adjusted to suit status and processes at the locations of interest (and potentially through time as the system changes). Crucially, this also means that a lack of a temporal dimension in monitoring cannot be completely compensated for by periodically applying very intensive surveys across broad spatial scales.

Lessons learned about using models to inform EBM

Policy and legal framework requirements

Statutes and policies under different jurisdictions provide differing levels of latitude to use ecosystem models to inform management. There has been considerable uptake of the Atlantis modelling framework in Australia, particularly in the SESSF, where an MSE built around Atlantis-SE discussed above contributed to major changes in the breadth and scope of management tools being adopted in the fishery. This degree of uptake was possible for two reasons. Australia has enabling legislation (the Environment Protection and Biodiversity Act), which demands that all export fisheries and federally managed fisheries demonstrate they are ecologically sustainable, and this requires an ability to measure the ecological effects of fishing. Australia also has a well-developed, participatory fishery management system (Smith *et al.* 1999, 2001). This combination has enabled resource managers and industry representatives to become increasingly familiar with MSE and, in the case of fishers, to develop a level of comfort that ecosystem models can reflect their own 'on the water' experience.

In contrast, the uptake of Atlantis within management circles in the United States has progressed at a slower pace, largely because the United States still retains a greater focus on single-species assessments (and their associated outputs with management largely based on reference points). This is because in parts of the United States, such as the East Coast and Gulf of Mexico, fishery management has been controversial for decades if not centuries (Smith 1994). Stocks have commercially collapsed, and fleets have sequentially depleted resources (Fogarty and Murawski 1998; Link 2007) despite a wide array of increasingly stringent and complex management measures that attempt to mitigate such over-exploitation. This has seen the management process become quite heavily structured from a regulatory perspective, with the contentious (and often litigious) circumstances surrounding it leading to very high standards for model use, documentation and review. This need poses unique challenges to data- and parameter-intensive ecosystem modelling approaches, including Atlantis. However, these issues are being addressed, and Atlantis is beginning to be used in US management, where it has the potential to provide specific recommendations to address the mandates in the Ecosystem Fishery Management Plans, Essential Fish Habitat plans and 'cumulative impacts' sections of documents prepared under the National Environmental Policy Act (NEPA). Moreover, Atlantis is one of the identified tools for NOAA's Integrated Ecosystem Assessments, which are a new framework for synthesizing and organizing science to inform EBM decisions (Levin *et al.* 2009) – for example by quantitatively evaluating management options relative to ecological, economic and social objectives.

When is Atlantis a useful tool?

Atlantis is best suited to the investigation of cumulative impacts, as a strategic tool to explore ecosystem dynamics and to test general management approaches. As indicated in the examples earlier, Atlantis has proven particularly useful for highlighting how ecological feedbacks, and human behavioural responses can derail the adaptive management process and EBM more generally.

At the time of Atlantis' inception, few marine models attempted to join processes and components from the biogeochemical to fish or higher trophic level and fisheries components (Fulton 2010). While more end-to-end models are being developed (e.g. the coupled models being developed under the Bering Ecosystem Study and Bering Sea Integrated Ecosystem Research Program (BEST-BSIERP)) and with models such as OSMOSE (Travers *et al.* 2009) and EwE (Christensen 2010; Walters *et al.* 2010) also being extended to cover more system components, consideration of cumulative impacts remains one of Atlantis' advantages. The majority of these considerations have revolved around impacts of industries other than fishing on water quality, productivity and the availability of suitable habitat in the coastal zone, which can all modify the system and thereby undermine or counteract the effects of fisheries management. For instance, work with an early form of Atlantis-PPB showed that in enclosed bays 80% of the fished groups (vertebrate and invertebrate) are more strongly impacted (typically by a factor of 50% or more) by eutrophication and associated changes in production than they are by fishing (Fulton and Smith 2004). Atlantis' explicit representation of the nutrient cycle also means that Atlantis can help clarify the implications of climate impacts both for the ecological system and for effective forms of EBM, topics which are of growing concern for resource managers (Brander 2007; Benoit and Swain 2008). For example, work with Atlantis-EMOCC by has considered ecological, management and economic implications of potential declines in shelled benthos and other calcifying invertebrates that may result from ocean acidification. The simulations showed differential outcomes for different food web members, some of which were quite severe. This led to a system restructuring with an 80% drop in the biomass of invertebrate-feeders such as English sole (*Pleuronectes vetulus*), a 10% drop in the biomass of small demersal sharks and a 30% decline in biomass of skates and rays. In turn, these changes impacted yields from the fisheries, with an order of magnitude decline in the potential level of sustainable yield for English sole meaning that catches that are currently sustainable would lead to severe depletion under the acidification regime. Such shifts in species biomasses, distributions and habitat and associated fisheries yields under climate effects reinforce the message found with Atlantis-SE that the strategy to achieve the goals of EBM will need to change along with the system being managed.

Atlantis' potential value as a tool for synthesis and system understanding needs not be constrained to consideration of future ecosystems. The value of cataloguing and synthesizing information from a wide range of disparate sources (whether for use in Atlantis or any other ecosystem model) should not be understated. These activities are a vital part of EBM in themselves as they give new perspectives on systems, highlighting important system features that had not been previously appreciated. For example, shrimp abundance in Atlantis-NEUS tended to substantially increase under plausible parameterizations in contradiction to single-species assessments (Link *et al.* in press a). New data sources support the pattern of increase predicted by Atlantis (NEFSC 2008).

Such system-level syntheses provide leverage points for EBM. For instance, they can indicate the relative strengths of fishing pressure and environmental drivers. Features found across the majority of extant Atlantis models are that wasp-waisted systems are only evident once individual mid-trophic level groups form a sizeable percentage of the system, bottom-up effects (from climate and trophic interactions) have their strongest exhibition at lower trophic levels and that effects of exploitation typically exhibit a top-down effect on upper trophic levels. Fulton *et al.* (2007), for example, found that in deep water systems off SE Australia fishing pressure far outweighed ecological interactions, as a determinant of ecosystem state and structure, whereas the two are more even in shelf waters. This does not mean that environmental factors or multispecies interactions are superfluous, as significant indirect effects do arise and would be missed if single-species assessments were the only tools used. This is particularly true when trying to guide and prioritize management actions or highlight trade-offs between different sectors exploiting different components of the same ecosystem. For example, consideration of the structure of the fish communities across south-eastern Australia using Atlantis-SE indicated that the biomass of small pelagic fish has risen steeply (by 38–70%) with the depletion of demersal predatory groups. This has made a fishery on that pelagic resource attractive, and indeed catches of these groups have increased substantially in recent decades. However, under management strategies where the demersal stocks are allowed to make strong recoveries, the sustainability of the small pelagic fishery becomes more tenuous from both an ecological and an economic perspective (Fulton *et al.* 2007).

When Atlantis can go wrong

While the Atlantis framework includes a wide range of options and can be used to create quite complicated models, this capacity must be used carefully. In particular, spatial and trophic resolution can have a significant impact on model stability as well as on the degree of complexity and non-linearity in model outputs (Fulton *et al.* 2004c) affecting the model's ability to represent realistic trophic structures and indirect effects. Extreme spatial aggregation can lead to trophic self-simplification, whereby it proves impossible to retain all the functional groups in the model system simultaneously, while inappropriate trophic aggregation (either across ages or trophic roles) can lead to erroneous and misleading model behaviour that bears little resemblance to actual system dynamics (Fulton *et al.* 2003a). At the other extreme, using all possible options available in the software can lead to equally aberrant behaviour, both because the model becomes severely over-parameterized and because it is potentially putting a focus on processes that are not actually important to the dynamics of the system in question.

When constructing an Atlantis model for a system, it is important to base its form on the critical drivers for that system (presuming these are known) and not to use the full functionality of the modelling framework simply because it is there. Using a complicated system structure or formulation does not automatically capture complex and non-linear system dynamics. For example, despite the immense complexity of the social, political, economic and regulatory environment of the north-east United States, the patterns of effort per fleet over the last 40 years were quite effectively captured for most fleets in Atlantis-NEUS using a very simple model based on catch-per-unit effort (CPUE) thresholds (Fig. 3), with days-at-sea by a fleet reduced if CPUE dropped below a lower threshold and days-at-sea increased if CPUE rose above an upper threshold. The single intervention required for validation and calibration was the imposition of the major regulatory restructuring that occurred in 1994 (Link *et al.* 2010). The point here is that although it is widely recognized that all models are simplified approximations of reality (Box 1979), the art of modelling is to represent a system in the simplest form consistent with realistically capturing its essential dynamics and behaviour. This will always remain

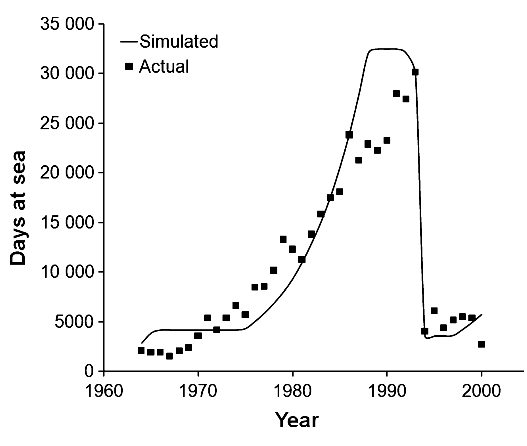

Figure 3 Simulated and actual time series of effort in the demersal squid trawl fishery from NE USA. The simulated time series comes from Atlantis-NEUS using a catch-per-unit effort-based algorithm (see text or Link *et al.* 2010, in press) for further details).

an inherent challenge for a flexible modelling tool such as Atlantis.

Most importantly, it is false to presume that Atlantis is an appropriate tool for all fisheries and natural resource use related questions simply because the model structure represents many facets of marine systems. Atlantis should not be used to dictate tactical management decisions, such as setting catch quotas or determining best location of closed areas. Atlantis is a system model that is simultaneously fit across multiple parameters and against multiple data sets (typically heuristically using pattern-oriented modelling; Kramer-Schadt *et al.* 2007). Given the uncertainty associated with so many data sources (Stow *et al.* 2009), it is important to focus on accuracy rather than precision. In turn, this means that while Atlantis is suitable for strategic direction setting, other models, such as fishery stock assessment models (e.g. Methot 2009) or extended stock assessment models (Townsend *et al.* 2008) and spatial allocation software packages such as MARXAN (Ball and Possingham 2000; Possingham *et al.* 2000), are much more appropriate for addressing specific tactical fisheries and conservation management questions. Atlantis is useful for strategic analyses at a whole-of-system level where the questions involve the intertwining of many species, biophysical processes, fleets and management levers. Even then end-to-end models like Atlantis should be considered as one tool in a properly stocked toolbox for EBM. On a case-by-case basis, advice in support of EBM will be stronger for making an active decision of whether an end-to-end model is really needed or whether simpler models (e.g. multispecies rather than full ecosystem model) may suffice. Qualitative modelling methods (Dambacher *et al.* 2002) and 'minimum realistic models' (Plagányi 2007) are examples of simpler (multispecies) model types that may be sufficient for answering focused EBM questions based around small sets of closely connected groups or processes. In cases where these simpler models are appropriate, their benefit is that they require a lot less data and computation time, and they can be rapidly applied to a variety of model structures, giving different potential perspectives on the issue of interest.

Into the future

As EBM needs and demands morph through time, so do tools like Atlantis. In this vein, the future development of Atlantis mirrors many of the remaining contentions that plague effective implementation of EBM.

Ease of use

Like many EBM tools, Atlantis can be hard to implement and understand. This is not helped by its weaknesses – poor ease of use, patchy documentation, large data demands, and long run and calibration times. Significant time and effort are being put into making Atlantis an easier tool to use and identifying effective ways to communicate results, as scientific tools are only useful if the managers of the resource comprehend the information they provide (Elzinga *et al.* 1998; Lee 1999).

Addressing multisector EBM and climate change

As EBM moves from considering sectors in the context of their connections with the natural environment to their interconnections with the complete combination of environmental and human systems, the scope of the questions and strategic tools needed to implement EBM are also likely to expand. The major form of expansion currently being explored in Atlantis is the development of generic model coupling architecture. This will facilitate dynamic coupling with biogeochemical models, climate models (beginning with regionally downscaled versions), an expanded list of assessment models (e.g. Bayesian Belief Networks used to manage resources such as river systems, Barton *et al.* 2008), food web models (e.g. EwE), oceanographic and larval connectivity models (e.g. CONNIE; Condie *et al.* 2005), individual-based and socioeconomic models. While software standards such as OpenMI are providing a technical solution for new and existing models to exchange data at run-time (Moore and Tindall 2005), there are still significant science challenges when coupling models that rival (or are related to) those at the heart of EBM (e.g. handling interconnections between components acting on different scales, dealing with uncertainty and mastering long run-times and computational costs associated with large models).

The broader context available with coupled models is increasingly necessary when addressing integrated, multisector forms of EBM. The need is particularly compelling when addressing issues associated with global climate change. As a first step, using crude 'forcing functions' to mimic the effects of a 1.8–4 °C increase in sea surface temperature and decline in pH of 0.14–0.35 (IPCC 2007) is sufficient for giving insights, as illustrated by Kaplan *et al.* (2010) using Atlantis-EMOCC. However, feedbacks drive system non-linearities, and they have been central to the need to move to EBM. Consequently, explicit handling of climate-related processes is equally likely to be necessary in future EBM analyses. This is particularly true when moving beyond simply considering fisheries effects to defining the form of management and effective monitoring as systems move away from historical baselines. Reference points are conceptually predicated on the idea of equilibrium dynamics and the use of historical system state to provide insight into future dynamics. This approach may fail as non-stationary system structure and dynamics driven by climate change may exceed system-level thresholds (Koch *et al.* 2009; Rockström *et al.* 2009).

Handling uncertainty

The cogent communication of uncertainty is a challenging and ongoing task both for end-to-end models like Atlantis and for EBM. The flexibility in model structure at the core of Atlantis means it is well suited for exploring structural uncertainty. Indeed, an early version of the modelling framework was used to consider different configurations of spatial structure (Fulton *et al.* 2004c; Johnston *et al.* submitted), functional group aggregation (Fulton 2001) and functional forms for processes such as movement, reproduction and predation (Fulton *et al.* 2003a,b, 2004a,b,c). However, without significant improvements in execution speed, thorough investigation of parameter and data uncertainty remains a significant issue. The combinatorial and feedback effects on sensitivity in all end-to-end models mean that new methods of sensitivity analysis, and more broadly uncertainty characterization, need to be developed before parametric uncertainty can really be explored in depth for any of these complex models (Pantus 2007). In the interim, bounded parameterizations, multimodel inference and 'scenario uncertainty' (e.g. Carpenter *et al.* 2005) will be the most effective means of handling uncertainty in these models and perhaps in EBM in general. Recommendations made for use of models by the Environmental Protection Agency in the United States indicate that such approaches are a much more transparent means of indicating true uncertainty (NRC 2007). This is because policy makers and regulators are less interested in statistical parameter uncertainty than in how uncertainty bounds 'optimistic' and 'pessimistic' outcomes and how these outcomes change the relative performance of different management actions. This strategic bounding, even of what is feasible and what is not, provides a sound rationale for the use of models such as Atlantis.

Conclusion

While the field of marine ecosystem modelling is now in its fourth decade, end-to-end modelling is much younger. Nevertheless, after a decade of use, Atlantis has a sufficient legacy to evaluate its strengths, weaknesses and the EBM lessons it has provided. Atlantis is a complex model that is not a suited to all problems. It is a strategic model best used to consider broad management strategies and large-scale system dynamics and should be considered as one among a range of many tools available to those interested in natural resource dynamics, exploitation and management. Atlantis has already provided some significant insights into both marine ecosystem function and structure as well as into how to implement EBM. In particular, it has highlighted that no single management lever is sufficient to address the many trade-offs associated with EBM. Complex trade-offs between ecological, economic and social objectives sit at the heart of EBM. These trade-offs and the system-specific relationships between ecosystem components mean that successfully implementing EBM will not be straightforward, static or follow a universal form. Instead, the form of EBM and associated monitoring schemes appropriate for a specific location will depend on the state and constituent structure of that particular natural system, the culture exploiting it and the evolution of both of these through time.

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