



Review

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Modelling marine protected areas: insights and hurdles

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Models provide useful insights into conservation and resource management issues and solutions. Their use to date has highlighted conditions under which no-take marine protected areas (MPAs) may help us to achieve the goals of ecosystem-based management by reducing pressures, and where they might fail to achieve desired goals. For example, static reserve designs are unlikely to achieve desired objectives when applied to mobile species or when compromised by climate-related ecosystem restructuring and range shifts. Modelling tools allow planners to explore a range of options, such as basing MPAs on the presence of dynamic oceanic features, and to evaluate the potential future impacts of alternative interventions compared with 'no-action' counterfactuals, under a range of environmental and development scenarios. The modelling environment allows the analyst to test if indicators and management strategies are robust to uncertainties in how the ecosystem (and the broader human–ecosystem combination) operates, including the direct and indirect ecological effects of protection. Moreover, modelling results can be presented at multiple spatial and temporal scales, and relative to ecological, economic and social objectives. This helps to reveal potential 'surprises', such as regime shifts, trophic cascades and bottlenecks in human responses. Using illustrative examples, this paper briefly covers the history of the use of simulation models for evaluating MPA options, and discusses their utility and limitations for informing protected area management in the marine realm.

1. Introduction

Before discussing models and their utility as a tool for informing marine spatial management, it is important to introduce two key concepts—models and counterfactuals.

A model is an abstraction of reality, a simplified description of certain features or processes of interest. Models can be used to describe, to explain and ultimately to predict how systems work and how they might respond to human actions. Humans use models to create expectations about the future and prepare accordingly—from commuters choosing to carry an umbrella based on a weather forecast, to central bankers setting interest rates based on economic forecasts. Here, we confine our discussion to scientific models that represent marine ecosystems (or at least some parts of them), their use and their management.

A counterfactual explores what would have followed had a sequence of events or circumstances been different. In the context of modelling and

ecosystem management, the counterfactual is the past state or future evolution of a modelled system without the specific management action of interest, or under different levels of perturbation. The difference between the counterfactual and the observed or predicted state can then, with proper study design, indicate the impact on the system attributable to management or perturbation.

Spatial management is one of several tools available to managers to reduce potential conflict and cumulative impacts. It is an attractive option, being relatively straightforward to apply across different sectors of resource use [1]. This makes it an exceptionally valuable tool as the world's oceans become increasingly crowded with, and impacted by, human users. Marine resources are used for food, energy and recreational purposes. They are valued for existence and cultural reasons. The systems they are part of also play an important regulatory role in the world's climate [2–4]. Impacts from the many pressures on marine ecosystems can be both direct [2] and indirect [5], with some impacts mediated through marine food webs and biogeochemical cycles. Fishing, pollution, invasive species and eutrophication have resulted in clear impacts on coasts, estuaries and enclosed seas [6]. Open ocean impacts are also being increasingly recognized in the form of marine debris [7], ocean warming and acidification [8,9]. These pressures are typically managed through national and international forms of governance using sector- or pressure-specific management measures, such as fisheries management.

Unfortunately, the broad range of pressures inevitably leads to conflicts between sectors, such that individual sectoral objectives may not all be achievable [10]. Even relatively well-managed marine systems, such as Australia's Great Barrier Reef, are recognized as having a potentially poor future owing to the cumulative pressures of marine stressors, and impacts from terrestrial land use [11]. In more intensively used regions of the world, the desire to develop new industries, including renewable energy or seabed mining, in addition to existing uses, is increasing the complexity and magnitude of cumulative impacts. In response, integrated forms of ocean management are being attempted, with marine spatial planning becoming a more prominent tool of choice [12], particularly in crowded coastal seas [10].

Marine protected areas (MPAs), one spatial approach to managing human pressures, have been embraced globally, with goals to include 10% of the world's seas and oceans in MPAs by 2020 [13]. Modelling can be useful for informing the use of such management tools, helping to develop an understanding of how individual decisions may impact the broader ecosystem. One way in which scientific models can provide useful information on the performance of MPAs is through the use of counterfactuals. The outcomes of simulations with and without an MPA are compared to show how the properties of the ecosystem, for instance fish biomass, change when an MPA is put in place (figure 1). This can highlight the benefits of using MPAs, but in some cases, and perhaps more usefully, can help identify unanticipated outcomes that might prevent objectives from being achieved.

Models of many kinds have been used to help design and evaluate MPAs—including conceptual mental models, qualitative mathematical models, statistical algorithms and dynamic, quantitative simulation models. The optimization tools that support systematic conservation planning, such as Marxan [15] and Zonation [16], are perhaps the best-known modelling tools associated with MPAs. These approaches

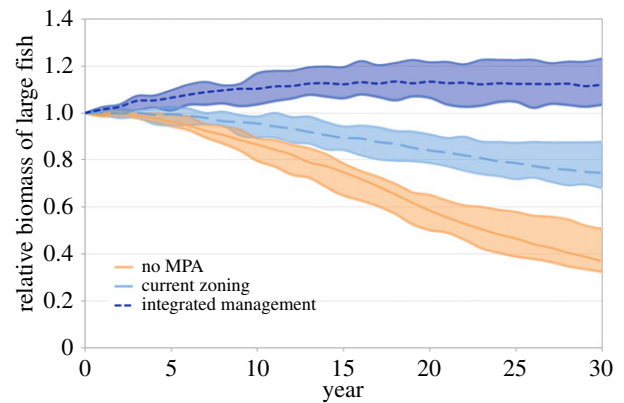


Figure 1. An illustrative example of the output from counterfactuals using an agent-based ecosystem model of Ningaloo Reef (Western Australia) [14]. The plot shows trends over the 30 years of the simulation (beginning with conditions in 2005) in the biomass of >40 cm lethinids (emperors) with a growing human population and visitor pressure and no marine reserves (orange), zoning as of 2011 (lighter blue), but no other fisheries regulations (on recreational or commercial fishers), and when zoning is in place along with a ban on fishing from the shoreline in sanctuary zones and stringent catch restrictions (dark blue). The median result in each case is shown by dashed lines, along with the 25th and 75th quartile.

have been used to map the distributions of key conservation species [17], identify bioregions to be captured in representative networks of MPAs [18] and identify locations that may simultaneously service many conservation objectives [19]. While these tools have been used quite widely and effectively to support MPA design, there is a rich literature discussing them [20,21] and we will instead focus here on dynamic modelling approaches used to predict the impacts of changed management arrangements.

This paper discusses the strengths and weaknesses of using modelling and counterfactuals to investigate the performance of (mostly) no-take MPAs, considered to be the most 'extreme' form of spatial management. The clear demarcation of no-take MPAs from areas open to extractive uses makes their impacts easier to assess. Thus, they provide an exemplar of the benefits and challenges in modelling spatial management more generally, highlighting the issues relevant to, or even amplified by, other spatial management approaches.

2. Models and their uses

Models are a good way to explore the extent to which MPAs may achieve conservation and other objectives, by synthesizing information and drawing it together in a coherent form to answer particular questions of interest.

As illustrated in table 1, many forms of model can be used to evaluate MPA performances. The continuum of models (figure 2) can be classified into three main types or roles:

- *Conceptual*: descriptive, 'mental models' (often presented in a discursive or graphical form) that capture the broad conceptual understanding of a system's main components and how they are connected.
- *Tactical*: precise models focused on specific aspects of the system (the main elements are captured in detail but others are typically omitted or heavily abstracted), used to inform tactical decisions in the near term (less than a few years) or in specific geographical locations. Typically,

Table 1. Objectives for modelling studies of MPAs and examples of model types used to address the questions.

objective type	objective	appropriate model types	
conceptual understanding	conceptual	synthesize understanding (and communication)	conceptual models; qualitative mathematical models [22] (which can be visualized using signed digraphs), or fuzzy cognitive maps [23]
MPA design/planning	tactical	determine species vulnerability or relative protection (e.g. overlap of fishing, habitat, and species distributions)	species distribution model (e.g. Maxent [24])
MPA design/planning	tactical	determine effective MPA network design	connectivity models (e.g. biophysical larval dispersal model [25,26]); geostatistical or GIS models [17,19]; spatial optimization (e.g. Marxan [15])
MPA design/planning	strategic	optimal no-take MPA size	population (and harvest) model [27]
MPA assessment (ecological); MPA planning; conceptual understanding	strategic conceptual	assessment of ecological effects of no-take MPAs ^a (often considering the influence of life-history parameters or trophic interactions on outcomes)	population models [28], IBM [29] or multispecies models (e.g. predator–prey [30]); qualitative mathematical models [31]; implicitly spatially partitioned food web model (e.g. Ecosim [32]); or explicit ecosystem model (e.g. Ecospace [33]; or OSMOSE [34])
MPA assessment (fisheries or bioeconomic)	strategic	assessment of fisheries or bioeconomic effects of no-take MPAs ^a (often aimed at finding optimal harvesting policy in combination with no-take MPAs, or exploring the implications for effort allocation)	single or multispecies bioeconomic models [35]; effort allocation models [36,37] or Ecospace [33]; game theory based behaviour (e.g. fleet cooperation [38]; interactions between countries, industries and objectives [39])
conceptual understanding	conceptual	assess influence of a ban on collections in no-take MPAs on data streams used to inform other industries (e.g. influence on information content of catch statistics) ^a	single or multispecies bioeconomic model or other model containing effort dynamics [40]; coupled population-effort allocation models [41]
EBM planning and use of MPAs	strategic	evaluation of role of MPAs in fisheries or conservation management, EBM and integrated coastal zone or ocean management	empirically based GIS-Bayesian belief network models [42]; process-based models including: spatial single or multispecies models (e.g. ELFsim [43]); ecosystem models (e.g. models of intermediate complexity [44]); coupled models [45]; end-to-end ecosystem models (e.g. Atlantis [46])
MPA evaluation (overall)	tactical	evaluate performance of MPAs	empirical statistical and GIS models (generating system diagnostics and test effects); spatially resolved multispecies or ecosystem models of intermediate complexity [47]
MPA evaluation (economic)	tactical	economic assessment of performance and effects of no-take MPAs	econometric model (e.g. travel cost model [48])
MPA evaluation; conceptual understanding	strategic (for later tactical use)	identify performance measures for assessing MPAs	qualitative mathematical models [31,49]; quantitative population, multispecies or ecosystem model (e.g. Atlantis [50]); spatially finely resolved statistical models [51]
experimental design	tactical	adaptive management experiment design	spatial population, multispecies or ecosystem model [52]

(Continued.)

Table 1. (Continued.)

objective type	objective	appropriate model types
evaluate modelling tools	all	all (figure 2)
	review model types appropriate for modelling MPAs	

^aThese may be hypothetical abstracted representations (e.g. implicitly representing spatial effects or simplifying space to one cell representing an MPA and one cell representing an area open to harvesting, as in reference [30]) or a highly detailed representation of a real geographic location (e.g. the Great Barrier Reef resolved to individual reefs and shoals [43]); habitat may be represented implicitly via modifications to carrying capacities [35] or explicitly [46]; and they may be run under historical, current or future environmental conditions and external shocks [53].

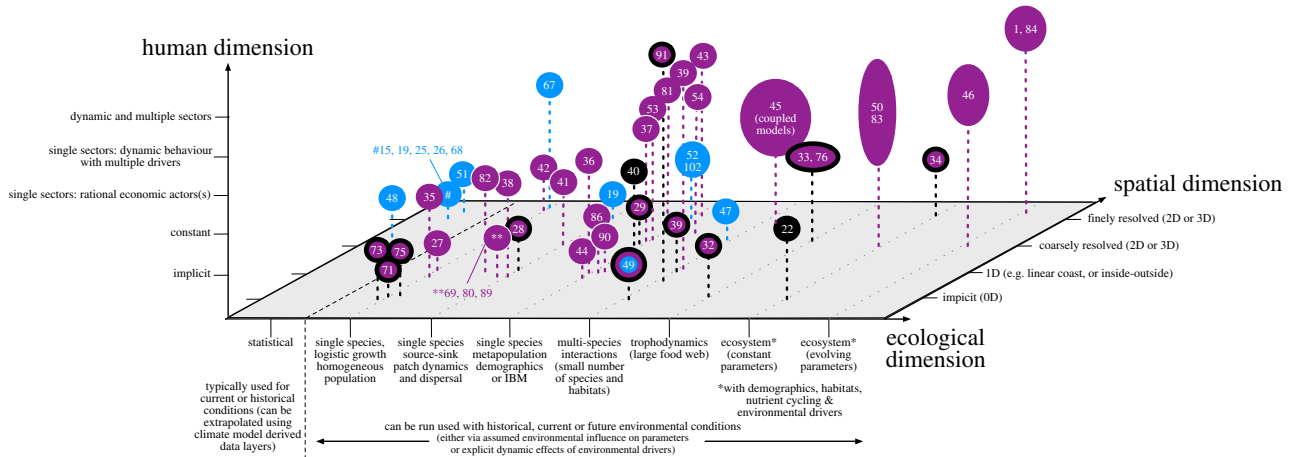


Figure 2. Schematic of the broad classes of model used to consider MPAs, showing the range of model types. The three main axes for describing models are their spatial resolution, how much ecological detail they include (from a simple single-species model through to more complex population models to multispecies and entire food webs), and finally how human activities are represented (either as a simple overall pressure or whether individual or multiple human activities are represented dynamically). Black circles represent conceptual models, blue indicates tactical models and purple indicates strategic models. Circles of more than one colour have more than one use. Reference numbers are provided, so that interested readers can follow up on specific models in the text and tables of this paper or in the original publications. Note that the relative density of the models on the plot is reflective of the literature—there are many more examples in the lower left-hand side of the plot, with less ecological detail, simpler representation of human pressures, and coarser spatial resolution. Such models are easier to create. The data and computing needs become much greater on the upper right and, so there are fewer examples, though numbers may grow as more complex questions about the future utility of MPAs are asked.

a good deal of effort is made to ensure that these models reflect the detailed dynamics of the parts of the system they are focused on, but they can lose relevance outside a small spatial and temporal window.

- **Strategic:** broad and generally more inclusive in scope, these models usually include more elements of the system (for example, more species or functional groups in the food web or more human uses) and provide information in support of strategic planning and decision-making, typically in the long term or at large spatial scales. They may include the same elements as tactical models (usually in less detail and often with less precision), but often also go much broader, drawing in a wide range of aspects of interest to managers, and represent more features of the whole system. The broader scope of these models allows the modeller to consider a larger number of scenarios, drivers, interactions and trade-offs.

While in reality, there is no clear demarcation between these categories or roles, models of different kinds are typically better able to address one role or the other, but not all three simultaneously. Selection of criteria for the appropriate model for a given problem is beyond the scope of this paper and has been tackled elsewhere in depth [54–57]. In brief, we concur that the nature of the question should dictate the type of model used.

The availability of data also has a role to play in shaping model choice—mainly by filtering out models where there simply is not enough data to validly use the approach. However, data-rich situations should not immediately default to one model type over another. Rather the different modelling approaches provide complementary interpretations of the world and lead to more robust understandings and predictions [58]. This is because the different model types are constrained by the impossibility of simultaneously maximizing all three of Levins' modelling attributes: generality, precision and realism [58]. This constraint endures despite the advances in modelling methods and resources—such as data assimilating methods [59] and whole-of-system (also known as end-to-end) models [46]—which now allow for observations and models to be coupled, and ecosystems to be represented at temporal and spatial scales undreamt of previously.

Conceptual models continue to be the fundamental building blocks of all modelling exercises. An end in themselves for synthesizing understanding across many knowledge types, these models are also the means of defining the content of other modelling approaches. There is, however, a limit to which conceptual models can adequately account for complex ecological and socio-economic systems [60]. The graphical nature of signed digraphs, increasingly used as a means of codifying conceptual models as qualitative mathematical models

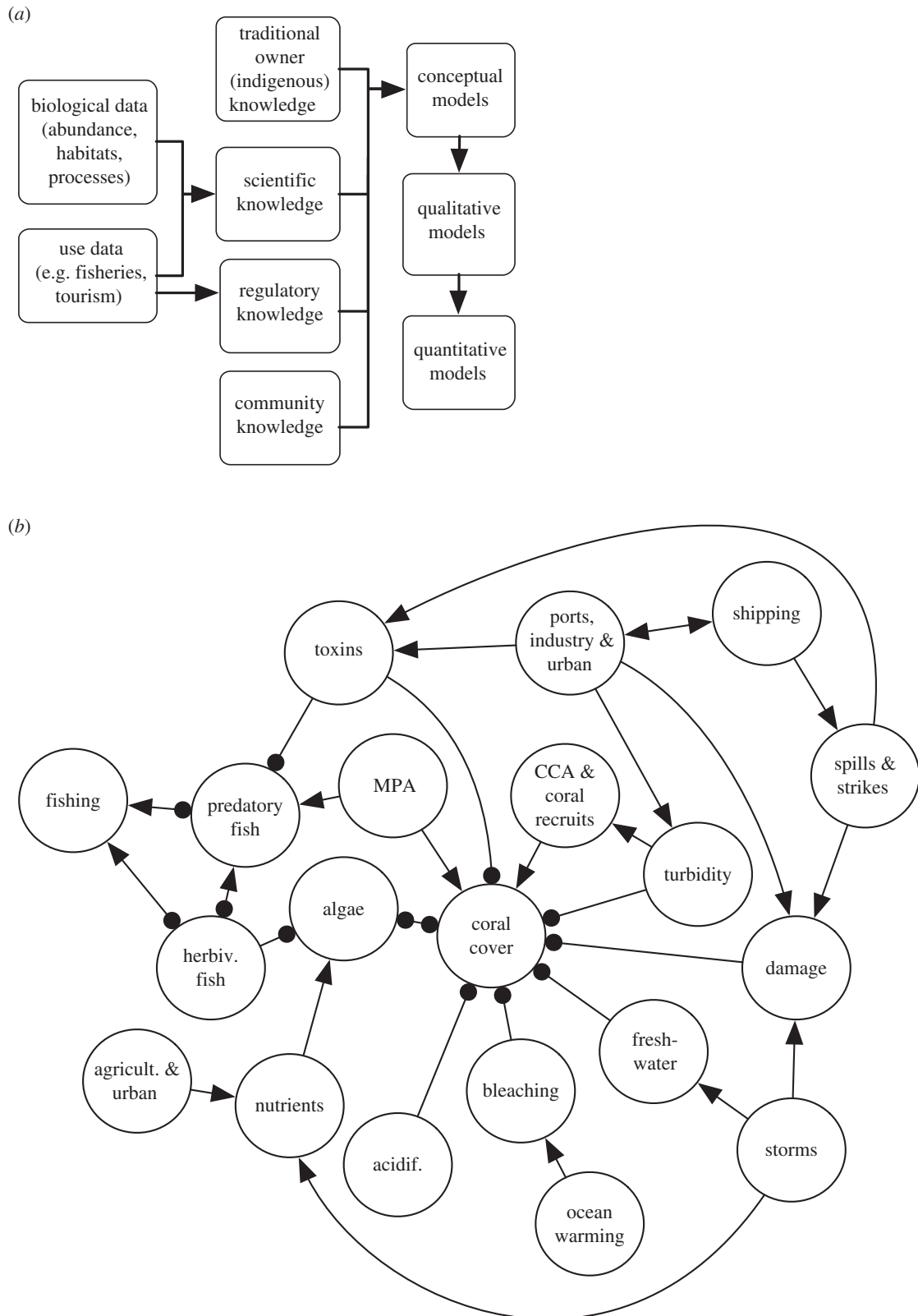


Figure 3. Information inputs and structure of conceptual and qualitative models. (a) Schematic diagram of data types used in conceptual and qualitative mathematical models of an MPA: this approach can feed into quantitative models, but does not have to. (b) An example of a qualitative MPA model (modified from [62]): arrows indicate positive effects and the dots indicate negative effects.

[61], is a particularly effective way of understanding and predicting the qualitative dynamics of complex systems that transcend the boundaries and backgrounds of different stakeholder groups (figure 3). This common understanding of connections and potential feedbacks and trade-offs can then act as a useful starting point for planning and discussions of options, which can be used directly to inform conservation management and improve the scientific content of outcome of

stakeholder-driven processes [63]. This approach was applied for the Gulf of California Biosphere Reserve, where qualitative models were used to explore how the reserve functions, how it responds to perturbations and what combination of management options might achieve conservation objectives [49]. Qualitative mathematical models focus on generality and realism at the expense of precision. They can be constructed and analysed relatively quickly, and can be used in isolation, or in

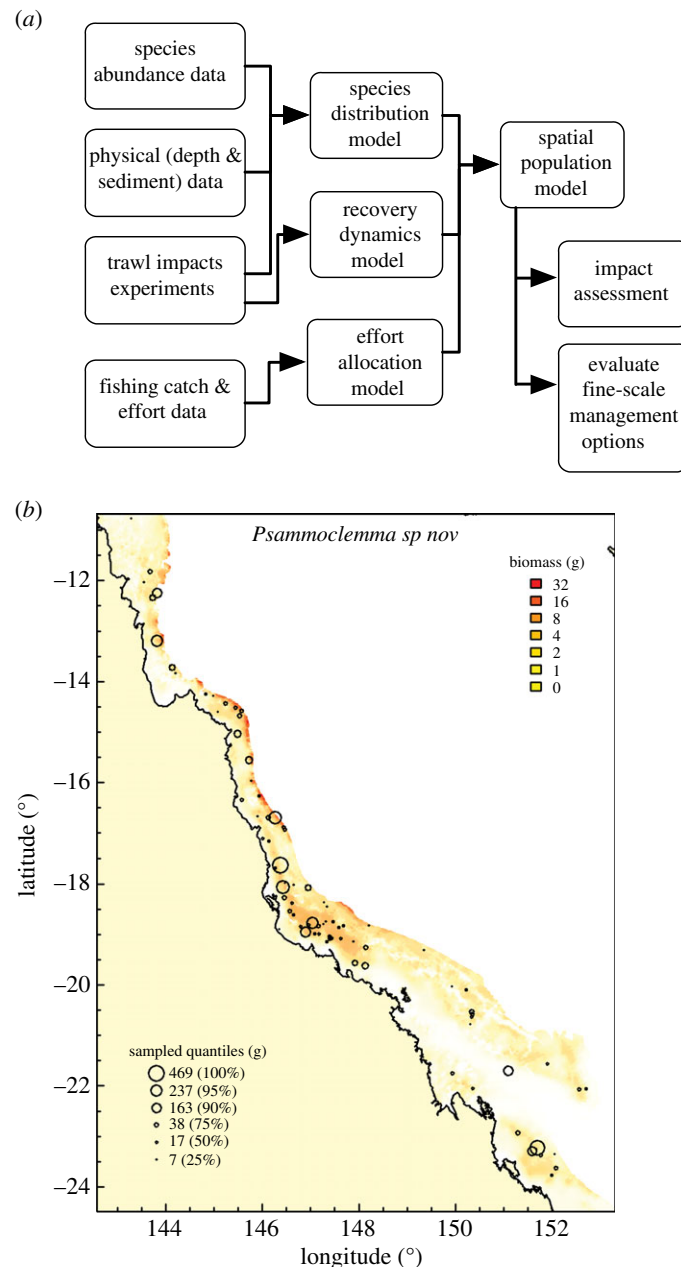


Figure 4. Tactical model applied to the Great Barrier Reef. (a) Schematic diagram of data used in an illustrative tactical MPA model [66]. (b) An example output map from that model for a species of sponge: the map colouring indicates biomass in grams per hectare and the circles show quantiles of sampled species abundance data used to condition the model.

combination with quantitative models. Qualitative mathematical models have a role as rapid-deployment assessment tools that provide testable (but imprecise) predictions about system responses, but these models can also identify critical model structural uncertainties, thereby helping to specify what components and interactions should be included or varied in quantitative models and what can be omitted without compromising predictions for the specific issue being addressed.

Most tactical models focus on maximizing precision of particular aspects of the system of interest, so that information from the models can be used to provide precise advice, such as identifying locations that meet the performance criteria for MPAs, or to assess what the current, historical or future state of a property such as species richness might be. These models are typically statistical or simulation models that focus on a few key attributes of the system. The most commonly used tactical models in the MPA context are species distribution models [64] and larval dispersal and connectivity models [65]. Species distribution models are statistical models based on

observed relationships or correlations between physical properties (such as temperature, depth or seabed type) and species abundance. These relationships are used as surrogates to map distributions over broader areas, identifying potential hotspots for species of interest. Larval dispersal models [65] are used in the same way but are based on mechanistic descriptions of ocean currents and larval behaviour to plot the potential movement from source (starting) to sink (destination) locations, which can influence the value of a location as an MPA. The two approaches can even be combined to answer specific questions. For instance, work on the Great Barrier Reef (and elsewhere) in Australia has used a combination of species distribution models for sessile megabenthos (sponges, gorgonians and corals), logistic population and impact models for the benthos, and fisheries effort allocation models to look at (i) trawl effects on tropical benthos, (ii) the role of MPAs in species recovery, and (iii) whether management interventions are in line with the stated objectives for the World Heritage Area (figure 4; [66]). These kinds of tactical models need not be confined to the assessment

of the biological aspects of MPAs. Work in Fiji, for example, used habitat and species abundance models developed from survey data, along with catch, fishing effort, market value, fishing cost and profit models to produce maps of opportunity costs on local reefs. These maps were then used as inputs to the Marxan conservation planning software to identify socially acceptable configurations for community-managed MPAs [67].

Abstract and more theoretical models and large-scale mechanistic (e.g. end-to-end) models can be used to examine broader strategic issues around MPAs. Theoretical models looking at MPAs and idealized single-species populations distributed along linear coastlines have been used to identify guidelines around reserve placement and design and the influence of activities in the surrounding region such as fishing [68]. At the other extreme, complex end-to-end models that represent physical properties of ecosystems, the food web, habitats and human use are also being used to investigate marine reserve design and the roles played by MPAs (and spatial management more broadly) in regional- or national-scale conservation and resource management. An example of this type of modelling exercise was undertaken in the Gulf of Carpentaria in northern Australia [45]. This combined extensive fisheries and scientific survey data to create an Ecospace (spatial ecosystem) model of the region as well as age-structured stock-specific models for the prawn species targeted by fisheries in the region (figure 5*a*). An effort allocation model was also developed using the catch and effort data for the region. This first allocated effort per stock and from there to the fine spatial grid used by the Ecospace model. Other models were created to represent the monitoring, assessment and management decision processes for the system. All of these models were coupled to represent the entire system and the management processes. This set of coupled models was then used to simulate alternative spatial and fisheries management options, ultimately providing advice on how each option met conservation, fisheries, stock and economic objectives (figure 5*b*). This work highlighted trade-offs among biodiversity, benthic impacts, ecosystem function, fished species, economic and sustainability objectives. It indicated that MPAs were necessary to meet habitat objectives, and they assist with biodiversity protection, but also have negative ripple effects on protected species and trophic levels (figure 5*b*). These findings demonstrate that MPAs need to be used in combination with other management tools, applied to surrounding ('off-reserve') regions, to address the broader set of sustainability objectives for the Gulf.

3. A brief history of the modelling of marine protected areas

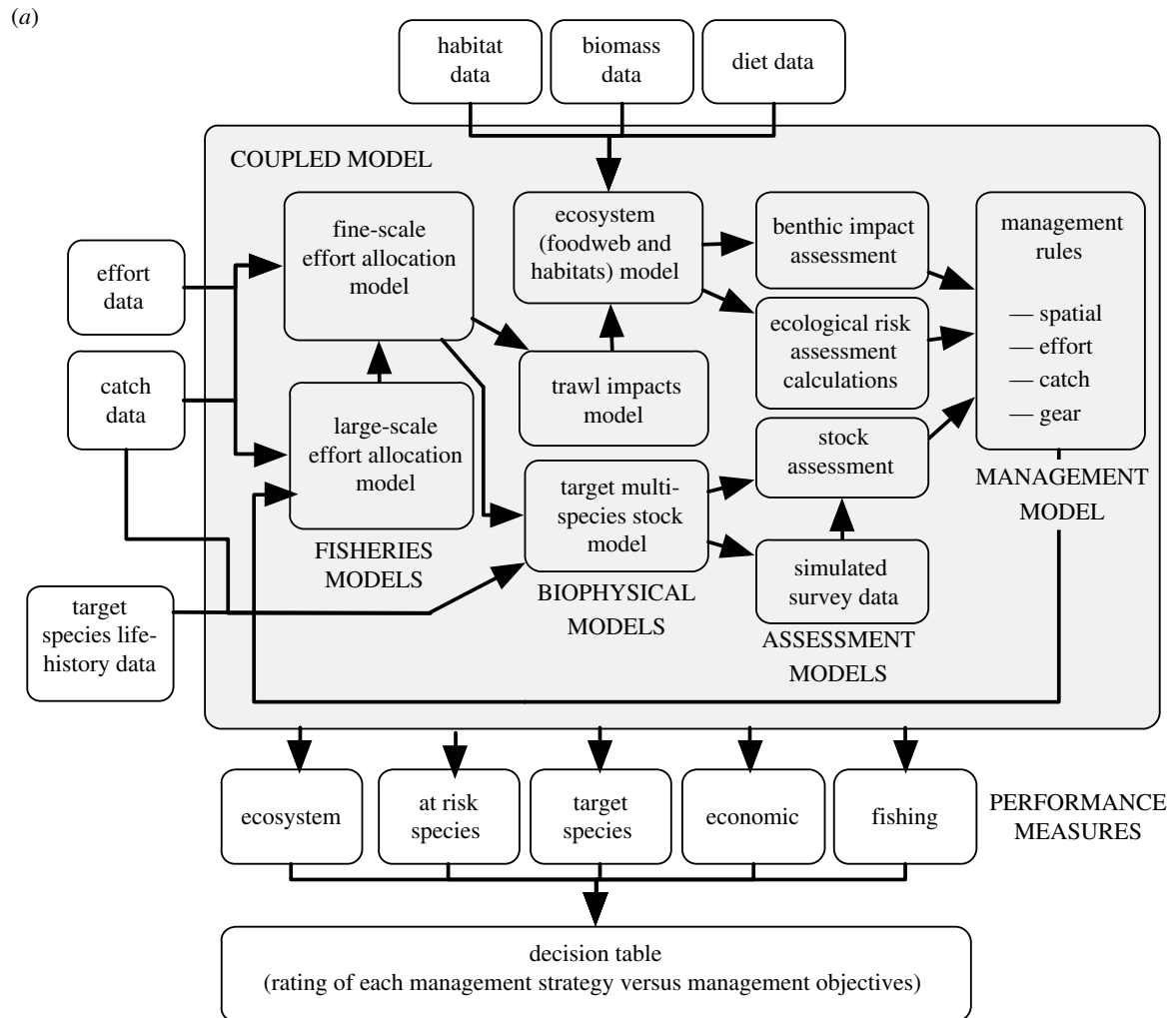
The content and the complexity of quantitative models has typically grown through time, as computational capacity has increased, but is still largely dictated by whether the tool is being used to help in the initial design of a network of MPAs or to investigate the performance of MPAs over time. The former may be spatially detailed on quite fine scales, but contain few physical or ecological processes, whereas the latter can be quite complex once trophic, habitat and human uses and behavioural responses have been added, though data availability might limit their resolution (figure 2).

The evolution of MPA modelling is instructive, as it mirrors both technological capacity and an increasing realization of how complex the questions of interest are. Models have

moved from abstract conceptualizations to issues of MPA design and quantitative evaluation of conservation benefits conferred by the implementation of MPAs [54]. Until the late 1990s, the model-based consideration of no-take MPAs was dominated by the use of largely abstract, idealized or theoretical models (i.e. approaches such as differential equations applied on linear coastlines or simple grids representing a generic ocean) to explore the potential fisheries and conservation benefits of closures to individual species [70,71]. A consistent finding was that reserves benefit overfished stocks, but that these benefits (and costs) were dependent on the rate of fish movement [55] and how fishers reallocated the displaced effort [72]. Improved computing capacity and improved data availability (especially physical data) saw more and more species distribution models [64] or connectivity models [65] developed to explore MPA network design. Models linked limited biological data to extensive physical data (including model outputs) to predict biological distributions and dynamics over broader areas; this shift in focus and extent paralleled a broadening of societal desires for MPAs to be used for marine conservation more generally rather than to simply combat fishing effects. The turn of the twenty-first century saw a step change in the use of dynamic simulation models for exploring issues associated with MPAs, driven by an increasing focus on integrated spatial management as a conservation tool by non-governmental organizations and international legal requirements [73]. This, in turn, spurred the growth of models from analytical considerations [74] to include habitats, multiple species or food webs and more sophisticated fleet dynamics [43,75]. While some conservation questions remain focused on single-species issues, others address more complicated issues associated with one or more aspects of the multitude of marine genotypes, species and ecosystems with their varied distributions, abundances and life histories, i.e. a broader representation of biodiversity. In parallel to expanding ecological scope, bioeconomic models used to consider MPAs have extended beyond straightforward treatments of economic costs of no-take MPAs [35] to consider the role of spatial management as part of integrated management regimes within and outside marine reserves [76]. This approach is taken further still in management strategy evaluations (where both the natural world and the individual steps of the adaptive management cycle are explicitly modelled) to consider MPAs along with other management options [45,77,78], some of which consider how MPAs may be designed in the first place [63].

4. Impact evaluation

MPAs can be a divisive political issue. As they constrain what can be done in an increasingly crowded ocean, there is continuing interest in whether, or under what conditions, MPAs are an effective management tool. When MPAs are considered as part of a broader adaptive management approach, there are additional demands to understand their contribution to overall management performance. Evaluations are desired both to check retrospectively on the performance of existing MPAs, but also in a predictive sense—to see if MPAs will deliver the desired conservation benefits, whether the results are worth any social and economic costs incurred, or whether alternative management approaches could provide similar conservation benefits at a reduced cost.



(b)

objectives	performance measures	management options			
		baseline	MPA	hotspot closures	bycatch min.
protected species	dugong biomass	yellow	red	yellow	yellow
	sea snake biomass	yellow	green	yellow	green
	sawfish biomass	yellow	green	yellow	yellow
commercial species	cephalopod biomass	yellow	green	red	yellow
	prawn biomass	yellow	green	yellow	yellow
habitats	filter feeder biomass	yellow	green	yellow	yellow
	seagrass cover	red	green	red	red
biodiversity	Kempton's Q	yellow	green	yellow	yellow
	overall biomass	yellow	yellow	yellow	yellow
	average trophic level	yellow	red	yellow	yellow
fishing	area closed	green	red	yellow	green
	displaced effort	green	yellow	yellow	green
ecological risk	number of groups at risk	red	yellow	green	red
	sharks at risk	red	yellow	yellow	red
	rays at risk	yellow	green	yellow	green

Figure 5. Strategic MPA model for the Gulf of Carpentaria. (a) Schematic diagram of data used [45], with the components of the coupled model shown in the shaded area. (b) An example output decision table from the model taken from [69]. The colours in the table indicate how well the management objectives were met (red, failure; yellow, partial; green, full) for the four management options considered: *baseline* (status quo) management arrangements in place in the region in 2008; a conservation network of MPAs across the region; adaptive closures triggered in fishing effort *hotspots*; and new management arrangements (including targeted area closures) focused on fisheries *bycatch minimization*.

(a) Retrospectives

The majority of retrospective evaluations of MPAs have relied on field observations—typically time-series (or snapshots) of

conditions inside and outside the MPAs. The challenges faced when trying to monitor large areas for long periods have meant that the majority of such comparisons have relied

Table 2. Examples of model-based lessons learnt regarding the performance of MPAs. Extensive review of lessons from literature up until 2008 available in reference [53].

lesson	example/ reference(s)
no-take MPAs service the conservation of key habitats (e.g. canyon heads, shelf reefs, seamounts and key substrates), and potentially slow-growing localized or highly aggregated species (or life-history stages), but may not guarantee healthy stocks of mobile predator or prey species, particularly under changing large-scale anthropogenic and environmental pressures	[30,55,70,80]
single-species spillover from no-take MPAs has the maximum conservation effect when dispersal rates are moderate and source locations are protected	[28,81]
spillover from no-take MPAs provides significant contributions to biodiversity conservation and fished stock status if the MPAs are large (hundreds of square kilometres or more than 30–50% of an ecosystem type), well demarcated and well enforced	[38,45,54]
no-take MPAs may cause the displacement of fishing effort, though this is not a universal outcome. When it does occur, then this effort can ultimately depress overall productivity, system state or biodiversity if not removed from the area	[54,66,72,82]
removal of fishing pressure owing to the introduction of no-take MPAs in highly perturbed systems has clear, positive, and mostly direct, effects on biomass and functional biodiversity	[83]
in systems under light to moderate fishing pressure the level of disturbance may provide for a higher coexistence of species; the introduction of no-take MPAs can cause both direct positive effects, but also indirect negative effects through trophic cascades, ultimately leading to a drop in overall functional biodiversity	[68,83]
human behaviour (such as poaching or fishing the edges of MPAs to benefit from any spillover) can undermine the performance of MPAs and as such must be accounted for in MPA models and management plans	[54,84–86]
no-take MPAs may have a dual influence on the assessment of fish stocks or system state, by either (i) providing reference locations that contrast with exploited areas or (ii) degrading information content or terminating data streams (via a ban on collections)	[40,87]
the multi-faceted nature of ecosystems and the multitude of potentially conflicting objectives held for them means that spatial management is an important part of ecosystem-based management, but that, by themselves, no-take MPAs cannot deliver across all objectives ^a . Integrated management across areas inside and outside of reserves is required	[45,46,49,87–89]
no-take MPAs may confer an economic benefit via improved ecosystem service status, but there is a nonlinear relationship between MPA area and fishery yield (yield increases as MPA area increases population persistence, but beyond that threshold further increases in area can lead to declines in yield by constraining access to fishing grounds)	[54,80,90,91]
a suite of indicators for monitoring MPAs is required to characterize overall system state, with simple indicators (such as the relative biomass of key functional groups, or proportional area of habitats) typically performing with more accuracy (skill) than complex or abstracted indicators (like complicated diversity measures or compound statistical indices that aggregate many data sources)	[45,50,92]
regional-scale observations and understanding of system dynamics will be necessary to define performance measures for MPAs (as indicator–attribute relationships can change on scales of a few hundred kilometres)	[49,50]

^aThese may be combinations of social, economic, and ecological objectives from different stakeholder groups, or even simply conservation objectives across interacting species.

upon the evaluation of small MPAs [79]. Modelling has the potential to move understanding beyond the sometimes misleading comparison of conditions immediately inside and out of small no-take MPAs (see examples in table 2). It allows for the evaluation of marine ecosystems and how they evolve after the establishment of an MPA with a comprehensiveness that is not possible in the field, especially under conditions where field surveys can be expensive (whether due to the large size or remoteness of the MPA) or where the ecosystem's components are difficult to observe (e.g. highly mobile pelagic predators such as tuna). The modeller can rapidly and reversibly test what happens under different management actions. Models can help us to answer questions about the conservation, social and economic outcomes of

having MPAs in place relative to the counterfactual of no MPAs.

Such counterfactual model-based comparisons have been used in South Africa to investigate spatial management in the context of investigating the consequences of no-take MPAs for the South African deep-water hake *Merluccius paradoxus*, a relatively mobile species. [44]. In this instance, the specific interest was on the hake, and so a tactical age-structured model was used in the analysis. It showed that area closures were of negligible benefit for the hake fishery in the area. A more complex model would have been required if there had been interest in fully quantifying whether there were any concomitant conservation benefits of MPA implementation. The counterfactual modelling tool needs to be chosen

carefully, so that the scope of the model matches the scope of the question being asked.

Dynamic system models (where habitats, food webs, fishers and MPAs are all represented in the model) have been used to consider the broader ecosystem objectives of MPAs and whether these have been met by existing MPAs. A particular strength of using a dynamic simulation model in this way is that the evolution of the system can be explored with and without the MPA but also under differing levels of perturbation (e.g. differing fishing pressure to see how the MPA performed given what did happen in the system, but also what the performance would have been had fishing pressure been higher or lower). This can provide a dynamic context to the observed outcomes, highlighting how the performance of a management option, such as an MPA, may vary through time and be dependent on context. For instance, an ecosystem model of the shelf and slope waters off New South Wales, Australia, was used to investigate the effect of the level of fishing disturbance on the ecosystem response to the establishment of marine reserves [83]. In scenarios where the level of fishing pressure increased quite strongly (as it did in that region between the 1970s and 1990s), the ecosystem was strongly perturbed, and the introduction of a network of no-take MPAs had clear, positive and mostly direct effects on regional-scale biomasses and functional biodiversity (mainly owing to the removal of fishing pressure). However, under low-to-moderate fishing pressure (i.e. if fishing pressure had stayed at 1970s levels indefinitely), the introduction of MPAs caused both direct positive effects, mainly on shark groups, and indirect negative effects through trophic cascades (e.g. increased predation on small territorial demersal fish), ultimately leading to an overall drop in functional biodiversity. This is because at large scales the low levels of fishing generated an intermediate level of disturbance in the model, which sustained relatively high levels of functional biodiversity. In this context, the potential positive effect of reducing fishing pressure on functional biodiversity was offset by the effect of an increased large predator biomass, leading to stable or even mildly declining levels of broader-scale functional biodiversity (as has been observed empirically on coral reefs [92]).

Models can also be used to assess the costs associated with the use of MPAs and society's ability and willingness to pay [67]. Fairly conventional economic models have traditionally been used to quantify the cost–benefit trade-offs of no-take MPAs, such as benefits from tourism, but also the cost to industry of placing no-take MPAs in previously fished areas [90]. Models can also be used to quantify costs of novel forms of management, such as dynamic ocean management, where the location of an MPA is tied to an oceanic feature, for instance, and moves in time and space [93]. This dynamic form of MPA has potential conservation benefits, but it typically relies on continuously updating data streams (e.g. continuous oceanographic observations from satellites or mooring networks) to track the location and integrity of the oceanic feature and ensure that human users of the system comply with restrictions associated with the MPA. Models can be used in a retrospective sense to explore the conservation value of such an intensive management method, but they can also indicate how those costs may be ameliorated via the use of proxy-based approaches. For example, the scientific basis for associating an MPA with a particular type of feature may be predicated on a property

that is not easily observed remotely (e.g. oxygen content or pH), but modelling can clarify whether management would still meet objectives if another correlated property that is more readily observed (and forecast) is used instead, such as temperature. These considerations are important, as the cost of monitoring is an ongoing concern for modern evidence-based decision-making and is difficult to estimate at the system level without the use of models [94].

There is undoubtedly uncertainty associated with any model-based assessment (and with the data the models are based on). Nevertheless, the approach remains a useful one, because there is no capacity, in reality, to get perfect replicates of ecosystems with and without MPAs. Models give us that capacity, at least to some extent. Concern over uncertainty can be minimized by calibrating against independent field-based time-series, targeted sensitivity analyses and running multiple realizations (e.g. parametrizations or model structures) to evaluate robustness in results across the model ensemble. Moreover, retrospective analyses of the effects of real-world MPAs can be used to condition the model for use in informing model dynamics and projections, thereby anchoring them in real-world understanding.

(b) Projections

Models are most useful when they are used to project into the future. Model findings allow stakeholders to anticipate challenges to the effective use of MPAs ahead of time, providing time to prepare or adapt—a key capacity given global change. The future is highly uncertain, and there may be processes or species whose role and importance are yet to be recognized. Nevertheless, even though models (like decision-makers) have to operate within a world of much uncertainty, models have much to offer in terms of considering both the potential effects (ecological, social and economic) of any proposed MPAs versus the counterfactual of no new MPAs, and the role of MPAs more broadly in marine biodiversity conservation and sustainable management of marine ecosystems. Models provide a tool to formalize and communicate the thought experiments that decision-makers regularly engage in. For example, can MPAs reduce pressure on ecosystems, or particular species, thereby providing them with the adaptive capacity to cope with additional pressures that MPAs cannot directly restrict, such as invasive species, climate change, ocean acidification and water quality?

Global ecosystem models, the ecological equivalent of general circulation ocean–atmosphere (climate) models are in their infancy. However, regional-scale (strategic) models are already being used to provide counterfactuals under impending global change and project the future role of no-take MPAs in ocean management. For example, whole-of-system (or end-to-end) ecosystem models—which include climate drivers, physical ocean properties such as temperature and salinity, ocean currents, habitats, the food web, fishing fleets, monitoring, management decision-making processes, and the development and expansion of coastal industries and urban centres—are being used in Australia to explore alternative ocean management options, including no-take MPAs, and how robust they may prove to be to global change [46]. At the core of the work in south-east Australia are two ecosystem models, with differing taxonomic and spatial resolution (one focused on inshore waters and one extending more broadly over the offshore area). Multiple productivity and food web parametrizations of

the two models have been run in combination with nine management strategies, three climate (emission) scenarios (RCP 3, 4.5 and 8.5 [95]), and eight system scenarios, including low, moderate and high industrial development and population growth scenarios, with and without market shifts and catastrophic extreme events. Among the hundreds of combinations considered were cases where there were no MPAs at all, others where there were extensive no-take MPAs, and still others where MPAs were part of integrated management strategies that used many regulatory tools (e.g. quotas, gear restrictions) to attempt to address a suite of social, economic and ecological objectives. The models' results showed that targeted management options, such as no-take MPAs, can perform well for individual management objectives (e.g. extensive spatial management can lead to improved stock status for large-bodied habitat-associated predatory fish), but they do not successfully meet minimum requirements across multiple objectives (such as the status of prey species, catch composition, equity of access or employment). These ecosystem models clearly demonstrated that reducing the physical extent of spatial management along Australia's south-east coastline was a universally poor management action, even in this area with well-established and monitored sustainable fisheries. However, the models also indicated that static spatial zoning, currently used as the basis of conservation management in the region, was not well suited to the more fluid nature of future marine ecosystems. If current reserves were retained, many would become less effective for currently high-profile species, and some reserves retained no conservation benefit at all for these species, although other conservation values could persist.

The model highlighted two ways in which the efficacy of MPAs could be undermined. The first was a direct result of species range shifts. The system of Commonwealth Marine Reserves in Australia includes consideration of key ecological features—areas of high productivity or species richness. The models showed that some of the MPAs designed to protect specific vulnerable habitats retained their value under climate change, either because the sessile habitat-forming species were tolerant of the new conditions, or because the feature was associated with a geological or physical property that was unaffected by the changed state of the overall system. However, the models also showed that shifts in species composition and distribution could undermine the original intent of protecting key ecological features. The feature may still be a productive ecosystem or assemblage, but it may no longer contain the key species of initial interest. In some instances, the oceanography of the system changed so much that the original feature no longer existed at all. Moreover, the list of species that would be deemed 'at risk' had evolved along with the system, especially under high emission scenarios, such that static conservation measures ultimately failed to keep up with the new demands. The second way in which the efficacy of Commonwealth and State MPAs was undermined in the models was due to human behaviour. Even when shifting species distributions (range shifts) did not directly degrade the level of protection provided by no-take MPAs, the performance of MPAs could be degraded by non-compliance—where human users of the system ignored or circumvented the management rules and exploited or impacted no-take areas regardless. This is a situation that the modelling suggests is more likely with an increasing number of uses of the marine environment and an increasing intensity of use. Competition for space and resources sees

support for MPAs decline as the community, or industry, believes that no-take MPAs are unduly constraining their ability to respond to new circumstances and opportunities, and so they simply ignore the constraints and operate in the MPAs anyway (even under the risk of penalties) or lobby to have the MPAs' regulations weakened.

If this kind of performance failure of no-take MPAs was observed, in reality, there could be pressure to reconsider the location of existing MPAs instituted to help protect particular vulnerable species or ecological communities and a move to establish them elsewhere. Unfortunately, there is significant inertia associated with the declaration of MPAs, e.g. in Australia, where their boundaries have to be formally gazetted in parliament. Consequently, the models identified regulatory inertia as one of the greatest barriers to long-term adaptation [46]. Results such as this have inspired the scientific proposition of pelagic MPAs and dynamic ocean management, under which MPAs (i) are defined around dynamic oceanographic features (such as fronts) in addition to static geological features (such as seamounts), or (ii) focus on community states (i.e. specific ecological assemblages or ecosystems in a particular state) rather than strict geographical coordinates [96–98]. This does not mean there would be no static MPAs—the models suggest that protection of some static features may still confer a conservation benefit (versus no MPAs) even under changed climate and ecosystem states—but it does mean that our concept of an MPA has to become more dynamic and adaptive.

Models can further assist MPA management and evaluation by identifying informative monitoring schemes and quantifying the associated costs [99]. A whole-of-system ecosystem model has been used to determine appropriate monitoring schemes (in terms of frequency and spatial extent) for marine reserves in temperate waters such as those found off south-east Australia. The simulation-based analysis also identified indicators that could be used to assess the performance of spatial management which were robust to a wide range of environmental and anthropogenic scenarios [50]. The results of this work indicated that monitoring MPAs under global change may be far from simple. Sampling schemes of low temporal frequency or sparse spatial coverage could detect change inside and outside closures provided sufficient time-series had accumulated to enable causes of the signal to be evaluated. However, such samplings had little power to detect change across broader spatial scales (i.e. the thousands to millions of km² typical of bioregional planning in Australia) and they had no power to rapidly detect changes in the system [50]. Moreover, the modelling showed that a lack of a temporal dimension in monitoring cannot generally be completely compensated for by periodically applying very intensive surveys across broad spatial scales, as intensive sampling is confounded by natural system variation and shifts through time. The modelling results also showed that ecosystem shifts in response to changing climate drivers mean that reference points (or indicator–attribute relationships) will need to be adjusted as the system changes, otherwise, they run the risk of becoming irrelevant or misguided.

We acknowledge that projections are uncertain, with uncertainty increasing the further the projection extends. Much of this uncertainty is related to human responses and decisions, and how they will shape the system. Management of MPAs can be very complicated, involving a large number of ill-defined and potentially contradictory contributions accumulated over

time and from groups with differing objectives. Fine-scale details about the tactical management of MPAs (and other human uses of surrounding areas)—such as a complex mix of different regulations being applied at very small scales and potentially varying seasonally or under specific conditions—are difficult to implement in models, yet that kind of detail may significantly influence human behaviour and hence the effectiveness of the overall management package. It is possible to model some aspects of human behaviour, thereby reducing some forms of uncertainty [100]. Agent-based models have been an effective means of capturing the nuances of human behaviour, information sharing and learning, both at the level of individual actions, but also for entire communities [84]. These models use sets of empirically derived behavioural rules (or decision trees) to dictate behaviour rather than equations, though both can be used in combination. The approach has been used in models of fisheries operating within marine reserve networks [43], but also for marine tourism and protected area management [101]. Nonetheless, uncertainties remain, as this is still a relatively new discipline and it shares the common model challenges when projecting forward into novel (previously unobserved) conditions. These impediments do not mean that human responses to the implementation of no-take MPAs should be ignored, as they will be a key determinant of success. Here again, attempting to predict their impact with models informs how MPAs might work in the broader socio-political setting and which aspects of management or compliance could be influenced to improve the benefits of spatial management under a variety of future scenarios [33] (table 2).

5. Benefits

The examples discussed in §4 show us how models can represent MPAs at scales beyond the capacity of field studies to observe directly (e.g. at large regional and potentially global scales). Models can help elucidate (i) general patterns of performance; (ii) the potential for unintended consequences that inadvertently undermine management intentions, and (iii) how MPA networks in combination with other management actions can influence system state and service conservation and fisheries, and satisfy other social, economic and environmental objectives (see table 2 for examples of model-based MPA findings). These insights can then be used to inform future decision-making and adaptive management.

A modelling-based approach is a means of exploring options in safety, under conditions that are hard to observe or have yet to be experienced. This has made the method particularly appealing as a way to discern future barriers and the nature of future opportunities, and the trade-offs associated with alternative management options under uncertainty. This leads to an increased willingness to go beyond minor modifications to existing arrangements, to explore novel ideas and substantial changes to potential management arrangements. In addition, the influence on management outcomes of decision uncertainty and ambiguity around system structure and function can be dealt with explicitly [102]. This is typically done by considering the overlap in outcomes across ensembles of models (encapsulating different theories about system processes, including climate). Ensembles of models can indicate whether similar outcomes are repeatedly realized or whether performance is sensitive to poorly understood system details. Understanding built up in this way,

from a set of diverse models, can be used to establish a common understanding of a system's characteristics, promoting more informed discussion over contentious issues, regardless of whether or not one particular model prediction is accepted.

Perhaps the greatest strength of a model-based approach is that the simulation environment can act as common ground for discussions between people with different backgrounds and objectives. Models can catalyse discussion between conflicting parties, enabling critical questions to be addressed and acting as important precursors to evidence-based decision-making. Even when the model results are not sufficiently reliable to inform specific decisions, the process of assembling the data will synthesize information and theories, identify missing and contradictory information, and highlight beliefs and opinions that are not currently supported by data. Patchy or incomplete data (i.e. data insufficient for the creation of quantitative tactical or strategic models) are not a barrier to the use of models in this role. Qualitative mathematical modelling using signed digraphs [22,61] is one method for synthesizing understanding in the absence of sufficient data for fully quantitative dynamic models. This approach has been usefully applied in support of conservation planning [31], climate change implications [60,103] and conceptual understanding of the reasons for success and failure of MPAs [49].

One of the greatest challenges to the assessment of MPA performance illuminated by modelling is a lack of clearly defined operational objectives for MPAs [104]. It is almost impossible to demonstrate that objectives as vague as 'increasing biodiversity' have been achieved. The formality of modelling clearly identifies such vagueness and provides a means of addressing it. Defining objectives in an explicit way, so that they can be used in modelling provides clarity also for their real-world use. For instance, high-level objectives such as 'manage the reserve in a manner that is consistent with maintaining the reserve's values' is opaque from a modelling standpoint. In contrast, clear statements like 'fish biomass in sanctuaries should be above 90% of pre-exploitation levels 75% of the time' or 'visitors should have a greater than 90% chance of seeing fish greater than 50 cm in length' or 'reserves should see no drop in species richness' are all far more tractable from a modelling perspective.

6. Drawbacks

Scale is both a blessing and a curse for models. Models can easily extend up to scales beyond most monitoring schemes, but going to finer scales is more challenging. It is difficult to capture the fine spatial scales typical of many MPAs in tactical or strategic models, as there are insufficient data or understanding at such spatial, temporal or taxonomic scales. These technical impediments mean that it is hard to resolve and represent small no-take MPAs in models. Despite the difficulty of working at fine scales, there is nevertheless a demand for such information, as these can be the most management-relevant scales (globally the median area of individual MPAs is less than 5 km² [105]). One way of addressing this problem is to constrain model extent; to choose not to attempt to resolve complex ecosystem function, but instead concentrate on specific ecosystem aspects such as the abundance of specific fauna or the distribution of habitats. This approach is known as the 'minimum realistic' or 'intermediate complexity' approach [47], or 'relevant subsystem' [22,61] approach.

Another means of modelling at finer spatial scales (where the resolution needs to be on the order of a few km² or less) is to combine a diversity of modelling approaches. To do this successfully requires taking the thinking behind process-based models (i.e. what are the key players, what influences them and how are they connected?) and using that to develop informative statistical models that can function at the scales required [106]. As with the minimum realistic process models, these statistical models focus on specific properties of the system (e.g. the relationships between seabed type, temperature, and the biomass of habitat-forming benthic invertebrates and macrophytes; or the relationship between distance to port and exposure to pressure from human activities). The information flow between the model types need not be one way, however. Once developed, statistical models can be useful for identifying patterns and thresholds. This information can suggest potential reference points for triggering management actions, which can be trialled at broader scales in process-based tactical and strategic models. Statistical models can also be used to identify trends in indicators that can be used to check the validity of the dynamics of the process-based models [51].

Empirical statistical models have been used to great effect at management-relevant scales [25], but they also have their limitations. The quantum of data needed to demonstrate significant effects can be large at the ecosystem scale or for elements with significant variation. Statistical models are also of limited utility by themselves when projecting beyond the bounds of the data used to define them, meaning that models used to inform on future MPA issues are currently often process-based.

The challenge of knowing how much faith to put in model results is a constant concern. This is especially true of models that are not fitted to data (or do not match data well) and when trying to inform on future as-yet-unobserved system states. The novel nature of potential future ecosystem states means that many models used to consider future states have an unknown veracity, even if well fitted to current data. Models considering strategic and conceptual questions are no more immune to these problems than tactical models. The lack of good empirical data hampers dynamic quantitative modelling of all kinds, which can be relatively expensive and data-intensive exercises. Data are sparse or lacking for many species or life-history stages, particularly those that are not fishery targets or of particular conservation concern. Observer programmes often deliver considerable data for marine mammals and seabirds, but entire invertebrate families, orders and even classes can be depauperate of data beyond presence/absence. This does not mean modelling is impossible, just that it has to be done carefully and with due attention to the handling of uncertainty and clear statements as to its veracity and limitations. For example, fisheries-dependent data (catch and effort) and remote-sensed data (e.g. sea-surface temperature, chlorophyll *a*, and wind speed) are available and of increasing spatio-temporal density. However, the explanatory power of correlative models based on such data is limited and typically deteriorates over longer time periods, as the measured variables are mediocre proxies for biologically relevant ocean habitats [107]. Derived variables such as eddy properties, upwelling intensity and the location of fronts may provide more reliable statistical models. Management decisions can be made in the absence of quantitative models but they will still suffer from the same knowledge gaps, and run the risk that these gaps are not recognized.

The modelling challenge is larger still when contemplating the explicit inclusion of uncertain biological processes (e.g. movement, evolution) and the complexity of human jurisdictional and regulatory arrangements and responses to them. Establishing and managing MPAs, and spatial and ecosystem-based management more broadly, are government processes, and science frequently does a poor job at interfacing with those processes. Scientists tend to focus on what is innovative, how new methods can resolve existing problems and frequently advocate adoption of their new 'optimal' approach without considering the broader social-political setting. Conversely, governments embrace established process and look for a variety of scientific options that they can choose between to satisfy a diversity of stakeholders. Models therefore not only need to provide scientific information in support of management, but new kinds of models are needed that describe the management process and the key points for the insertion of scientific information. Such models exist in other fields, where they are used for robust decision-making [108] or management strategy evaluation [109,110]. In common with the model described in figure 5, these models contain sub-models for the biophysical world, human users, monitoring, assessment and management decision-making steps. Counterfactuals run using such models can show how management can be improved by greater understanding of the biophysical world, monitoring information, transparent decision rules and a greater understanding of behavioural responses to regulations. Such models are in their infancy in the conservation and MPA arena [63]. However, extensive experience in fisheries shows such models are possible [109], but they are not simple and still require extensive explanation and communication. When used well, these kinds of models are a very effective means of defining useful questions, identifying measureable operational objectives and supporting evidence-based decision-making. In these ways, the models play the role of an honest broker, increasing the number of options available to decision-makers, so that they can identify the option that also meets their needs [111].

7. Discussion and conclusions

Marine ecosystems are under increasing pressure and threat of degradation. Spatial management is frequently used as a means of countering at least some of those pressures and threats and for managing conservation objectives. However, given what is at stake—livelihoods of people relying on the resources provided by the marine environment and the loss of vulnerable species and communities—it is important to understand both (i) when the approach works and (ii) how to make it more robust [110]. Policy-makers want to know not only about potential benefits, but also what kinds of costs (economic or social) are involved [80]. Modelling is a useful tool for addressing these questions. Management-relevant findings from models include information on: the effect of the configuration of reserves [87] and that a single configuration will not perform as well for all species in the area [80]; and when no-take MPAs have the maximum conservation effect (table 2)—e.g. when species are sessile (e.g. habitat forming) or when the aggregation points (e.g. spawning sites) of slow-growing species with moderate dispersal rates are protected [55]. Models have also shown that no-take MPAs can have a positive economic benefit for fisheries [91], but there

is a complex nonlinear relationship between the area within a network of MPAs and fisheries yields. There needs to be enough of the stock within the MPAs to enhance population persistence, which also depends on management of stocks outside the MPAs, but the MPAs cannot be so large that fishing grounds are diminished to the point that economic performance is compromised [80].

Coupling simulation and qualitative mathematical models with statistical models has the potential to provide significant insights into the dynamics and state of ecosystems and monitor their responses to the implementation of MPAs. Such combinations could, for example, see statistical models used to represent spatial distributions of biodiversity, whereas process models (e.g. agent-based models) could be used to represent the human users and management decision processes. These kinds of hybrid models are not yet common. Instead, there are six general classes of applications across the literature dealing with models of MPAs. The four most common uses are for MPA design, assessments of potential ecological benefits, bioeconomic assessments (including human responses to the establishment of an MPA) and management evaluations. Dynamic models of no-take MPAs have also been used to design adaptive management experiments [52] or to provide a basis for discussions of modelling philosophy, around the contextual usefulness of modelling types when aiming to provide insights into MPAs [29].

It is a natural next step to take the kinds of models used to explore the retrospective value of MPAs in place already, or the value of the application of MPAs today, and use those models to investigate future management approaches—their potential outcomes, benefits and when they may fail to meet management objectives. The exploration of the utility of MPAs under climate change, and associated regime shifts, has heightened debate around the value of dynamic spatial management, including dynamic MPAs. Given the shifts in marine habitats expected under climate change [96], accounting for future environments has been a recent focus of modelling studies. Climate layers are being added to Marxan to identify network designs that are robust to future shocks [112] and more attention has been given to adaptive approaches, such as slow-moving MPAs that change along with the environment [96], or to dynamic zoning based on oceanographic features [93].

Modelling is useful in such discussions but is not enough by itself, especially given the range of conflicting viewpoints about MPAs held by different societal groups. Modelling should be

used to initiate and support discussions around management options and pressures on a system, and particularly to evaluate the counterfactuals, and to identify trade-offs in meeting multiple and usually conflicting objectives. Ideally, model outputs will be an important part of the solution that managers will then adapt to fit their political and institutional circumstances. Models also allow for comparison of management processes, such as monitoring schemes and quantification of associated costs. Models support and enhance the learning that comes from such joint discussions, especially across diverse stakeholder groups, emphasizing the necessity to set clear objectives around what is desirable, or at least acceptable. What modelling has shown us is that, even in a simulated environment (far simpler than the real world), the success of MPAs depends on what you are trying to achieve (i.e. your objectives) and how clearly you express the why and the wherefore.

Modelling may have many constraints, and the representation of details of most immediate interest to managers is exceptionally challenging. However, models remain one of the most effective ways in which science can support the creative freedom necessary to find solutions for the novel situations we face in the future. To address the myriad questions being posed of models will require a diversity of complementary modelling approaches. Together, these models need to span generality, precision and realism to present an effective means of informing decision-making around MPAs, with each model addressing specific issues, rather than everything simultaneously.

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