Food for Thought

Why compare marine ecosystems?

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Effective marine ecosystem-based management (EBM) requires understanding the key processes and relationships controlling the aspects of biodiversity, productivity, and resilience to perturbations. Unfortunately, the scales, complexity, and non-linear dynamics that characterize marine ecosystems often confound managing for these properties. Nevertheless, scientifically derived decision-support tools (DSTs) are needed to account for impacts resulting from a variety of simultaneous human activities. Three possible methodologies for revealing mechanisms necessary to develop DSTs for EBM are: (i) controlled experimentation, (ii) iterative programmes of observation and modelling ("learning by doing"), and (iii) comparative ecosystem analysis. We have seen that controlled experiments are limited in capturing the complexity necessary to develop models of marine ecosystem dynamics with sufficient realism at appropriate scales. Iterative programmes of observation, model building, and assessment are useful for specific ecosystem issues but rarely lead to generally transferable products. Comparative ecosystem analyses may be the most effective, building on the first two by inferring ecosystem processes based on comparisons and contrasts of ecosystem response to human-induced factors. We propose a hierarchical system of ecosystem comparisons to include within-ecosystem comparisons (utilizing temporal and spatial changes in relation to human activities), within-ecosystem-type comparisons (e.g. coral reefs, temperate continental shelves, upwelling areas), and cross-ecosystem-type comparisons (e.g. coral reefs vs. boreal, terrestrial vs. marine ecosystems). Such a hierarchical comparative approach should lead to better understanding of the processes controlling biodiversity, productivity, and the resilience of marine ecosystems. In turn, better understanding of these processes will lead to the development of increasingly general laws, hypotheses, functional forms, governing equations, and broad interpretations of ecosystem responses to human activities, ultimately improving DSTs in support of EBM.

Keywords: comparative marine ecosystem analysis, decision-support tools, EAM, EBM, ecological modelling, ecosystem approaches to management, ecosystem-based management.

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Introduction

Success in marine ecosystem-based management (EBM), or alternatively ecosystem approaches to management (EAM), requires (i) a governance system that engages appropriate stakeholders to attain shared objectives and goals, (ii) clearly articulated principles for decision-making, and (iii) science tools that support decision-making, characterize uncertainty, benchmark progress, and articulate benefits and risks of alternative management paths (Larkin, 1996; USCOP, 2004; FAO, 2005; Rice, 2005; EC, 2006; Murawski, 2007). Scientifically derived decision-support tools (DSTs; Kangas *et al.*, 2008) are key elements for documenting progress in the attainment of those objectives and for guiding adaptive approaches to management. Such tools can be quantitative models of ecological interactions (Daan and Sissenwine, 1991; Pope, 1991; Christensen and Walters, 2004), optimization methodologies for allocation of goods or space (Crowder *et al.*, 2006; Barbier *et al.*, 2008), and forecasts of various types (NRC, 1998; Brandt *et al.*, 2006).

Current forecast skill in marine ecosystem decision support is largely sectoral (e.g. fishery stock assessment forecasts, harmful algal bloom forecasts) and near-term (Brandt *et al.*, 2006). EBM requires DSTs that can be used to assess strategic outcomes for more complex interactions among humans and the ecosystem over the medium to long term. Experimental approaches and locally adapted observation and modelling programmes for individual ecosystems do not lead to generally applicable DSTs, although eventually they may provide competent support for local management. Comparative analysis of marine ecosystem organization and dynamics has a long history in marine science (Megrey *et al.*, 2009) and provides a complementary and potentially efficient pathway to develop and test candidate DSTs for use in a wide variety of settings (ICES, 2001).

Here, we outline a structured hierarchical programme of ecosystem comparisons using both empirical and model-based hypothesis-testing for key relationships. The aim is to develop better DSTs supporting EBM/EAM. First, we identify examples of challenges posed by abrupt ecosystem change ("black swans"); problems of scale, complexity, and non-linearity; and response to ecosystem perturbations through intervention. Next, we propose a hierarchy for the comparative approach, and finally, we suggest a framework for the scientific research that is needed.

"Black swans" in marine ecosystem research and management

A prevalent theme in ecosystem studies is the occurrence of abrupt ecosystem change (Collie *et al.*, 2004). These "black swan" events (Taleb, 2007) can often reveal basic properties of ecosystems and second-order interactions not interpretable from small perturbations from *status quo*. A compelling example is the collapse of the Atlantic herring (*Clupea harengus*) stock on Georges Bank and adjacent areas in the early 1970s (Fogarty *et al.*, 1991). Because herring was a primary food source for many species of predatory fish and mammal, the assumption was that the herring collapse would produce cascading impacts through the ecosystem. What was not anticipated was a compensatory release of other small forage species, principally the sand lance (*Ammodytes americanus*). Cod (*Gadus morhua*) and marine mammals shifted their attention to this increasingly abundant prey, and growth rates of fish were maintained and mammals continued to use the Bank for feeding. Experimental removal of herring solely for the sake of science would have created unacceptable risk given the assumed obligate relationships between predators and prey, but in retrospect, the overfishing scenario provided a rich set of new hypotheses concerning the functional stability of high diversity ecosystems generated by the serendipitous black swan of the collapse of the herring stock.

Another black swan with ongoing consequences is the collapse and minimal recovery of Atlantic cod off Newfoundland and in the North Sea. The lack of a recovery of cod off Newfoundland is apparently explained by depensatory natural mortality and by increases in the abundance of seals and other species (Bundy, 2001). In the North Sea, the same absence of a significant recovery has been linked with increases in pelagic fish, principally herring and mackerel (*Scomber scombrus*; Heath, 2005). Could the relationships between cod and other components of the foodweb have been predicted from past events or from mechanistically driven ecological modelling of these systems? Put another way, can we collect the global set of such black swans into a generalized theory of ecosystem response to human drivers? If so, how might functional redundancy and depensatory mortality have been incorporated into management, had they been understood better?

Taleb (2007) describes three characteristics of these black swan events. First, they are often treated as outliers, likely to recur infrequently, and rarely predicted in advance. Second, they carry extreme impact both on the system itself and our perceptions of how systems function. Third, even if considered rare events, they are often viewed retrospectively as predictable outcomes, with theories and models developed after the fact to explain them. All these attributes are applicable to the historical record of fisheries collapses. Can we use such experiences to make them retrospectively predictable using more robust quantitative tools, as a basis to inform future management strategies that are more robust to uncertainty in ecological processes driving these collapses?

Modes of learning about marine ecosystem dynamics

> *You could not step twice into the same rivers; for others are ever flowing on to you.*
>
> Heraclitus

Unlike many physical systems that obey clearly defined laws, it is often argued that for natural ecosystems there are few generalizable laws or tenets upon which predictive models can be built (Murray, 2000; Turchin, 2001). Although both Murray and Turchin argue against such a simplistic view, critical ecosystem properties, such as resilience to perturbations, levels of species richness and primary productivity, which are influenced simultaneously by human activities such as fishing, nutrient pollution, and variations in ocean climate (NRC, 2006), have not generally been incorporated into practical models supporting decision-making. Moreover, marine ecosystems are structured by complex spatial patterns of marine geography (Longhurst, 1998). The scales at which we need to evaluate ecosystem interactions are therefore hierarchical in both space and time, which creates the need for models to reflect this continuum of "scalability".

Marine systems exhibit a "reddened" (higher variance at low frequency) spectrum (Steele, 1985), so focusing attention on phenomena at longer and larger scales. These simple conclusions derived from comparisons of marine and terrestrial systems lead to an emphasis on linking the larger scales of physical variability to the evolutionary mechanisms that allow long-term persistence of marine life under varying oceanic conditions (e.g. Francis, 2002). Management of human activities in the oceans must conserve persistence mechanisms that ensure long-term stability in biodiversity (Yachi and Loreau, 1999) in the face of occasional rapid regime shifts, trophic cascades, and species replacements (Collie *et al.*, 2004).

Understanding the interactions between properties of ecosystems can lead to important insights that have practical importance. For example, an evolving body of theory in terrestrial ecology (e.g. Hubbell, 1997; Tilman, 1999) resolves Robert May's diversity: stability paradox (May, 1973) by proposing that "diversity increases (temporal) stability at the community level but decreases stability at the population level" (Lehman and Tilman, 2000). If this holds for marine systems, there are implications for our desire to maintain diversity while taking "maximum sustainable yields" from individual populations.

Similarly, comparisons of species, communities, and ecosystems along such attributes as body size, metabolic rate, population interactions, and trophic dynamics (primarily considering terrestrial problems) have resulted in the development of new comprehensive theories about how ecosystems work (e.g. the metabolic theory of ecology, Brown *et al.*, 2004; Hildrew *et al.*, 2007). Only by comparing attributes in structured ways do such patterns emerge.

Management questions often concern the relative influences of human and natural factors contributing to observed changes in natural ecosystems. Because of the pervasive effects of advection and diffusion, most marine ecosystems have no clearly defined boundaries, and experimental manipulations with classical controls, treatments, and replicates give us only limited ecosystem-level information. The enormity of natural ecosystems makes inferences from small-scale experiments difficult. Experimental approaches using laboratory and mesocosm studies remain essential to quantify certain processes (such as physiological effects of environmental change), but other methods may be more appropriate to analyse whole-ecosystem response.

Marine ecosystems have been described as both complex and complicated—the former emphasizing non-linear relationships between components such as predator–prey switching behaviour and the latter emphasizing the large number of interacting parts, any one of which can have a dominant influence on outcomes relevant to people. The technical challenge in modelling ecosystems is to combine these two approaches. Detailed mechanistic understanding (e.g. Brown *et al.*, 2004) imbedded in complex models is likely to be a more robust learning approach than are simple correlations among complicated ecosystem drivers and states. Although complex models may initially fail to improve predictive skill compared with simpler correlation or time-series approaches, the process of refining mechanistic models by comparing ecosystem behaviours across a wide range of ecosystem types may eventually lead to a deeper understanding of general laws, principles, and behaviours of ecosystems that have wide application across ecosystems in various states of human-induced change. Therefore, there is a need to widely apply both empirical and modelling approaches in ways that allow understanding of the unique and general mechanisms underlying the patterns of species and ecosystem change (Power, 2001).

Comparative analyses of ecosystems have a long history as the basis for formulating hypotheses about control mechanisms and their impacts on systems (Megrey *et al.*, 2009). There are two modalities for these comparisons: (i) retrospective interpretation following the imposition of significant interventions (either planned or unplanned), and (ii) formal comparative analysis of ecosystems structured to use time, spatial replication, or spatial contrast as the basis for learning. Below we discuss these learning approaches.

Interventions in marine ecosystems

Ecosystem interventions have provided significant insights into the factors controlling marine species and ecosystem variability. They are generally categorized as unplanned or planned events that may have significant impacts on ecosystems. For example, for North Sea groundfish stocks, population abundance, as measured by commercial trawler catch per unit effort (cpue), increased substantially just after both World Wars, compared with preceding years (Borley *et al.*, 1923; Margetts and Holt, 1948; Smith, 1994; Pope and Macer, 1996). Likewise, when fishing pressure is rapidly and significantly increased, the decline in individual species, alone or in patterns of sequential depletion, presents strong evidence for top-down control by fisheries, such as on Georges Bank (Brown *et al.*, 1976; Fogarty and Murawski, 1998). Natural disasters can similarly change our perceptions about how ecosystems and their components respond to other human activities and natural drivers.

Planned interventions can have similar impacts on our knowledge of factors controlling ecosystems. Marine protected areas (MPAs) generally produce some form of "reserve effect" that results in accumulation of sessile or relatively sedentary animal biomass within well-enforced boundaries (FAO, 2006). Often, the imposition of MPAs can validate or refute long-held views concerning the role of human impacts and the expected benefits from decreasing them. Hence, sea scallop (*Placopecten magellanicus*) biomass increased 9–14-fold in the 5 years following imposition of closed areas on Georges Bank, consistent with predictions based on assumed low natural mortality and rapid growth rates (Murawski *et al.*, 2000). Most analyses heretofore have examined MPAs in relation to individual species effects, and the field is ripe for additional community and ecosystem response work. The so-called BACI design, i.e. before–after-control–impact (Stewart-Oaten *et al.*, 1986; Faith *et al.*, 1991; Scheiner and Gurevitch, 2001), may be particularly amenable to MPA studies, as long as it is recognized that the open (control) regions may be subject to ensuing increases in human activities as they are precluded within the MPA. For whole-ecosystem comparisons, time-series intervention analyses (Carpenter *et al.*, 1989; Mantua, 2004) are often employed to detect human and natural drivers of ecosystems and their impacts on ecosystem attributes. Further, comparison of effects of MPAs in different regions can enhance understanding of such planned interventions.

What can be learned from these interventions relevant to the development of ecosystem DSTs? The focus on comparisons of ecosystem interventions provides specific opportunities to identify critical factors and evaluate their impacts on ecosystem attributes (Table 1). In the best of circumstances, the BACI design for MPA effects offers spatial contrast, pseudo-controlled experimentation, and replication (Oksanen, 2001). The types of DST that may result from such comparisons can be used to inform adaptive management programmes, to interpret impacts of extreme perturbations that would not otherwise be undertaken in planned interventions, and to model human behaviour as it relates to ecosystem dynamics. To date, most MPA studies have documented the obvious reserve effects (FAO, 2006). A more compelling set of DSTs would include analysis of the timing of changes after the establishment of MPAs and the trophodynamics associated with those changes, allowing models of ecological succession, as well as human reactions, to be evaluated (Table 1).

A proposed hierarchy for comparative analyses of ecosystems

Within ecosystem studies

The creation of prediction tools for marine ecosystems must be largely an exercise in inductive reasoning, building on experiences within ecosystems. The focus of such studies is temporal comparison of the impacts of changes in life history, abrupt climate change, and ecosystem response to various scales of perturbation. Long time-series of observations from monitoring programmes within particular ecosystems can be interpreted for insights into the relative impacts of human activities and climate forcing (Table 1). Most studies of human behaviour in relation to ecosystem change take place within the context of whole ecosystems. The focus on within-ecosystem comparisons of different sections of time-series allows analysis of covariance among species (i.e. recruitment patterns in relation to climate deviations), regime-shift detection, and predator–prey evaluations over time. The within-ecosystem scale makes up the bulk of published studies. The DSTs developed from such studies include system-specific models of predator–prey reactions, spatial planning methods, portfolio analysis of goods and services to competing use sectors, and ecosystem restoration (Table 1).

Between similar ecosystems

The second level in the hierarchy is comparisons of ecosystems with common features (Table 1). Although no two ecosystems are pure replicates, they can be grouped in terms of common attributes. For example, upwelling systems along the western continental margins share many common attributes and responses, as do

Table 1. Hierarchy of comparative ecosystem analysis studies.

Comparison type	Focus	Analysis	Leading to DSTs, including
Significant ecosystem interventions (planned or unplanned)			
BACI; time-series intervention analyses	Impacts of large-scale events (wars, hurricanes, tsunamis, and other unplanned interventions) on ecosystem attributes, biodiversity response, and resilience Impacts of significant planned change in human-based factors (fishing effort, water quality improvements, coastal alterations, habitat restoration) on marine ecosystems and specific components	Isolation of a single factor or a small number of varying factors affecting ecosystems (pseudo-controls for management "experiments") Testing of hypotheses regarding TD, BU, WW* control, large-scale reductions in human activities not feasible under traditional management Large-scale perturbations incorporating serendipitous before/after data	Structure adaptive management programmes using hypothesis identification and priors on likely strengths controlling factors affecting outcomes Models of ecosystem resilience under extreme perturbation
Inside/outside MPAs	Specific and generic demonstration of reserve effects, spill-over, and larval export in relation to MPAs and resource goals for species Population effects of MPA placement (overall exploitation rates, genetic modifications, density-dependence in vital rates) Human behavioural response and projected benefits (income, costs, profitability) in relation to MPA placement Projected changes in patterns of diversity, productivity, and stability in relation to MPA placement	Proper meta-analyses considering ecosystem type, scale of MPAs, multispecies impacts, in relation to multiple drivers Analysis of ecological succession inside and outside closed areas including bentho-pelagic coupling, density-dependence, trophic structure, bioenergetics, and disturbance	Siting tools for placement of closed areas and for evaluating and projecting impacts and benefits on species and communities Models of human behaviour and reaction to the placement of closed areas Models of ecological succession allowing projections of "climax" ecosystem states and timing of resource change in relation to MPA placement
Whole ecosystem comparisons			
Within specific ecosystems	Temporal change Life history/genetic adaptation Abiotic drivers Abrupt and trended climate change Response to management change Coherence in recruitment patterns among species Spatial relationships and biodiversity Resilience to human and natural perturbations Valuation under alternative use scenarios	Retrospective analysis Density-dependence Regime shift detection Multivariate correlation Non-linear relationships among species and between species and environment Covariance in species abundance Changes in species distribution in relation to abundance and climate Patterns of human use (sectoral and spatial)	Multispecies interaction models (system specific) Multispecies forecasting tools Spatial planning tools Portfolio analyses for allocation decisions within and between use sectors Ecosystem restoration investment decision tools (e.g. for evaluating the relative merits of habitat restoration, fish stocking, nutrient abatement)
Within ecosystem "types"	Defined by latitude; TD/BU/WW*, unique type (e.g. seamounts, shallow coral reefs, upwelling) Degree of abiotic influence on ecosystem organization and productivity Degree of human influence on ecosystem organization and productivity Degree of commonality among similar ecosystems in outcomes between ecosystem drivers and responses (probability of similar response)	Spatial pseudo-replication among ecosystem types defining the range of outcomes and responses to perturbations Relationships between basin- or global-scale abiotic change and ecosystem-type response Application of risk assessment in response to management actions Analysis of regulatory systems and human use patterns contributing to similarities or differences in ecosystem response and organization	Ecosystem models adapted to specific ecosystem types (e.g. high latitude, few species, upwelling) Projection models incorporating process uncertainty in key ecosystem relationships

Continued

Table 1. *Continued*

Comparison type	Focus	Analysis	Leading to DSTs, including
Among ecosystem "types" or global analyses	General laws, governing equations, and relationships determining the scope of marine ecosystem response to human and natural factors Patterns of biodiversity of the oceans and trends and variability in abiotic and human factors Relationships between diversity and stability and resilience of marine ecosystems Frequency of abrupt change in relation to variation in drivers and general patterns of biodiversity Responses of human communities and economic sectors to ecosystem change Articulation of ethical and moral questions regarding use, intergenerational equity, and social welfare issues in terms of ocean ecosystems	Meta-analyses of patterns of productivity, trophic levels, and demography Characterization of the unique aspects of ocean ecosystems (compared with terrestrial), and implications for marine ecosystem management Responses of various ecosystem types in relation to the degree of precaution as a consequence of uncertainty and the use-protection continuum	Development of general classes of ecosystem models (trophic, demographic) allowing projections of the impacts from alternative uses and conservation efforts for marine biodiversity Generic spatial planning tools applicable to a wide variety of ecosystems Framing tools for the development of policies in legislation and regulation of the oceans Generic allocation tools for among-sector allocation and optimization

Each type of analysis focuses on different ecosystem attributes, supports unique analyses, and enables development of different decision support tools supporting EBM.
*TD, top-down; BU, bottom-up; WW, wasp-waisted ecosystem types.

groups of boreal ecosystems (ICES, 2001), coral reefs, and temperate shelves in the North Atlantic or North Pacific. There is much to be learned from these comparisons. They share physical and some ecological attributes, but human interventions are often quite different. The research focus of these comparisons is the commonality of ecosystem response in relation to contrasts in human uses of the ecosystems. If the studies can assume some degree of replication of common ecosystem function, then we can apply risk-assessment techniques to the analysis of responses to basin- or global-scale abiotic changes (Table 1). From these comparative analyses, modelling approaches are being developed that respond to particular attributes of like ecosystems, such as high-latitude fishery systems, upwelling systems, and coral reefs.

Global comparisons

A third level of ecosystem comparisons involves the contrast across ecosystem types from coral reefs to boreal environments. This is the most general level of ecosystem comparison, and it requires evaluation of the broadest set of ecosystem questions. For example, questions about the patterns of biodiversity, variability, and productivity in relation to human use and climate are addressed in their most general form by such comparisons. These broad studies inform the development of overall laws determining the scope of marine ecosystem responses (Table 1). At this level of comparison, global meta-analyses of ecosystem response can be developed and generic or "framing" tools supporting policies for marine ecosystems can be tested for their generality. There are many analyses produced at this level of organization that emphasize the diversity of response and the general patterns of life in the oceans and its potential vulnerability, and resilience, to human effects.

General

These levels of ecosystem comparisons, within individual ecosystems, among similar ecosystem types, and across ecosystem types, are mutually supporting and provide a framework for integration at regional to global levels. A fourth level compares marine and terrestrial systems not only in ecological terms, but in a management context. The long transition on land from hunter-gatherers to monoculture of a few species of plants and animals, required not only modification of ecosystems, but greatly altered social structures; now, we have increasing demand for more areas devoted to nature reserves. The same issues arise frequently, and with much shorter time-scales, in the sea, both for allocation and for ownership of fish stocks, farms, and marine reserves. The ecological and economic challenges involve choices between intensive harvesting of selected species by capture fisheries or by mariculture. Despite the differences between regimes on land and in the sea (Steele, 1985; Carr *et al.*, 2003), comparisons of success and mistakes in management at this level can enhance long-term decisions about the "global" implications of the different options.

Where are we now?

A number of previous and ongoing efforts has proposed broad ecosystem comparisons as the basis for developing greater insights into the impacts of human activities. We note two relevant examples.

GLOBEC (the Global Ocean Ecosystem Dynamics Programme) is a long-term field and modelling programme aimed at understanding links between climate variation and marine productivity. The objective of the programme (GLOBEC, 1988) was "To understand ocean ecosystem dynamics and how they are influenced by physical processes so that the predictability of population fluctuations in a changing global climate can be assessed". The focus has been on physical–biological coupling and its consequences for the dynamics of target populations, principally zooplankton and pelagic fish. The GLOBEC programme has undertaken a number of ecosystem comparisons as part of its intra- and inter-basin synthesis activities (GLOBEC, 2007) and described a number of important questions that could be addressed through structured comparisons within and among ecosystem types:

(i) which systems are the most variable and why?

(ii) which systems are the most diverse, and why?

(iii) which systems are the most productive, and why?

These three questions focus on important properties of ecosystems—biodiversity, productivity, and resilience—and can be related to human interventions that affect these properties (Figure 1).

A systematic approach for ecosystem comparison was suggested by an ICES Planning Group to evaluate the potential for structured ecosystem intercomparisons to assist in the interpretation of ecosystem processes (ICES, 2001). The planning group listed four specific reasons for conducting structured ecosystem comparisons:

(i) we need an ability to compare different ecosystems to predict what may happen in one by analogy with what has already happened in others;

(ii) we need the ability to compare ecosystems through time to define ecosystem status (ecosystem health) and to understand ecosystem structure;

(iii) we need to compare ecosystems to determine the factors affecting biodiversity;

(iv) we need to compare to understand the relative importance of anthropogenic impacts and natural processes on ecosystem behaviour.

The ICES Planning Group proposed using biomass-based comparisons, *K*-dominance curves (cumulative percentage composition by species), size-spectrum comparisons, and Ecopath models (Christensen and Walters, 2004). They also proposed to extend the relevant comparisons back six decades to the end of World War II. They considered the proper scales and species groups required to develop ecosystem comparisons, with the final choices being problem and issue-dependent. These objectives and approaches, which are still relevant 8 years later, are consistent with the need to develop a greater variety of DSTs supporting marine ecosystem management.

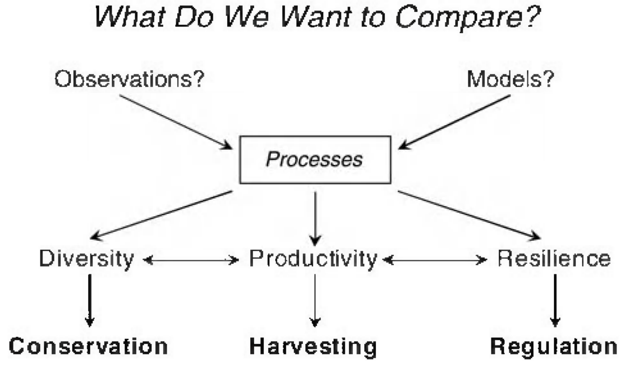

Figure 1. Relationships between ecosystem-level information and the processes affecting the management of ecosystems. We propose a comparative analytical framework with ecosystem processes as the focus to better elucidate those processes for use in marine DSTs.

The efforts above highlight the importance of structured comparisons as a method to reveal important control mechanisms: top-down for ICES or bottom-up for GLOBEC. Implicit in them is the challenge of integrating top-down and bottom-up forcing in ways relevant to end-to-end ecosystem management and prediction.

A way forward

Although a number of regional marine science organizations and programmes has identified ecosystem comparisons as a goal, often these comparisons emphasize a particular ecosystem type or human driver. We propose a broader framework emphasizing hierarchical, whole-ecosystem comparisons at individual, regional, and global levels, as well as a framework for evaluating a range of ecosystem interventions. Each set of comparisons offers unique insights into the relative importance of human drivers on ecosystems, from specific to general. Ultimately, our ability to predict ecosystem functional response to human interventions is dictated by the extent to which the basic patterns of diversity, productivity, and resilience (Figure 1) can be characterized, and the key factors influencing them identified.

A programme of systematic comparisons focusing on both whole-ecosystem evaluation and ecosystem interventions could produce profound benefits to researchers for a wide variety of ecosystem-orientated problems. A conceptual framework for comparative analysis of marine ecosystems involves selecting appropriate ecosystem types that are comparable in terms of structure and function, drivers of change, and characterization of socially relevant properties. A simple schematic (Figure 2) suggests the various levels of organization at which comparisons can be made.

Key drivers of ecosystem variability and change include:

(i) extraction of living resources, such as fishing;

(ii) introduction of exotic predators, parasites, diseases, and competitors;

(iii) alteration and loss of living and non-living habitat; and

(iv) environmental change including natural variability, climate change, eutrophication of coastal ecosystems, and ocean acidification.

Socially relevant outputs of marine ecosystems can be expressed as ecosystem goods and services characterized in terms of

(i) diversity of species, genetics and stock structure, trophic structure, and habitats;

(ii) ecological interactions between species, such as predation, competition, facilitation, other interactions (e.g. parasites and diseases);

(iii) patterns of energy flow and utilization;

(iv) magnitude of biological productivity and yield at both species and community levels;

(v) resilience (e.g. the ability to adapt or rebound from ecosystem shifts to different regimes or multiple stresses and/or irreversible or slowly reversible changes); and

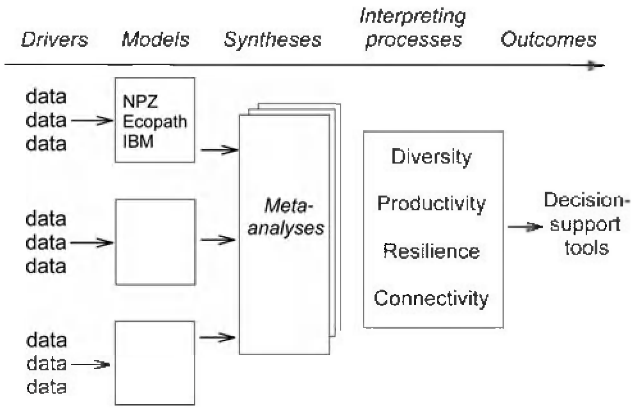

Figure 2. A schematic of possible steps relating data, models, meta-analyses, and process interpretation to the development of DSTs for EBM. Each ecosystem can have different models, such as NPZ (nutrient, phytoplankton, zooplankton), Ecopath, and IBM (individual-based models), evaluated through some meta-analysis, to inform DSTs relevant to essential ecosystem properties.

(vi) spatial distributions and connectivity of biota and habitat (including hydrography, circulation, and other basic oceanographic processes).

These processes, emphasizing diversity, productivity, resilience, and connectivity (Figure 2) are prime focal points for model development. Between these inputs and outcomes lie the technical and scientific challenges in using a variety of models to encompass the range of space–time-scales and ecological processes required for end-to-end representation of the drivers from climate change to overfishing. It is likely that more than one type of model is needed to describe each ecosystem and that different models will be used for different ecosystems. Therefore, the comparisons of systems will require some form of meta-analysis, either as a conceptual framework or as a meta-model whose inputs are the outputs from the individual ecosystem component models.

The scientific challenges in the development of better DSTs that policy-makers and managers need and will use, include

(i) how the provision of goods and services by ecosystems with different characteristics responds to natural and anthropogenic pressures and drivers of change;

(ii) limits to ecosystem resilience, and thresholds that, when crossed, lead to "tipping points", phase or regime shifts, and the nature of reversibility of such shifts;

(iii) relative performance of different management "treatments" (such as MPAs) by comparing similar ecosystems or sub-ecosystems subjected to different treatments; and

(iv) relationships between the human dimension of ecosystems, drivers of change, and the willingness and ability to apply management alternatives.

Initial efforts could involve a mix of activities, including

(v) modelling studies focused on specific concepts, such as connectivity, resilience, or thresholds, the intent of which should be to unify comparative analyses and to generalize some of the key scientific questions to be addressed by comparative analyses;

(vi) retrospective studies that analyse or re-analyse or synthesize existing information (historical, time-series, ongoing programmes, etc.) using a comparative approach;

(vii) short-term empirical studies based around existing or proposed observation systems designed to demonstrate how such a system could be leveraged towards ongoing comparisons, such studies perhaps utilizing MPAs contained within coastal observation systems;

(viii) development of strategies and methodologies for comparative analyses, including modelling frameworks that can be applied consistently across ecosystems and that facilitate the design of DSTs.

Beyond this, there are many socio-economic factors, such as culture, governance structures, and access to alternative livelihoods, that need to be taken into consideration in comparative analyses. These include

(i) the demand for ecosystem goods and services;

(ii) how services are valued (in both the short and long term);

(iii) the feasibility of management alternatives and the socio-economic attributes associated with management alternatives;

(iv) the attitudes about the risks of undesirable changes in ecosystems; and

(v) responses to management applications (e.g. redeployment of fishing effort displaced by an MPA).

We propose a three-pronged approach to a general programme of comparative analysis. First, many national programmes support ocean monitoring and research efforts aimed at both sectoral approaches to management and EAM. Such programmes continue to generate data applicable to comparative ecosystem analysis, even if not explicitly articulated as such. Organization and integration of relevant data facilitating ecosystem intercomparison, as well as development, testing, and application of relevant statistical methods and mathematical models using these data at a national level, represent a key first step leading to next-generation ecosystem tools. Second, we propose that regional international marine science bodies assist in facilitating collaborations, particularly for ecosystems under their specific remit (e.g. ICES, 2001). Collaborations among relevant bodies (e.g. ICES and PICES) in sponsoring workshops, working groups, and expert consultations will allow the limited worldwide marine ecosystem modelling expertise to be used to distil and develop generic approaches for ecosystem comparisons. Third, we emphasize that a focus on the processes influencing marine ecosystems is most important, rather than simple comparisons of data or models (Figure 1). Understanding the processes that affect biodiversity, productivity, and ecosystem resilience leads directly to DSTs that influence strategies for conservation, harvesting, and regulation (Figure 1).

The importance of better science support for ecosystem management is emphasized in the US National Academy of Sciences Study "Dynamic Changes in Marine Ecosystems: Fishing, Food Webs and Future Options" (NRC, 2006), viz.

> "Scientific advances will need to incorporate new ideas, analyses, models, and data; perhaps, more importantly, new social and institutional climates will need to be established that catalyze a creative, long-term, comparative, and

> synthetic science of food webs and communities. Data needed to support ecosystem-based management will likely be more than the sum of currently available single-species information. Where species interact and to what extent will be as important as determining stock biomass. Furthermore, a rich array of social science, economic science and policy considerations will be essential, because many more tradeoffs are likely to be apparent among ecosystem components and stakeholders."

Although many to most living marine conservation problems will continue to focus on individual species, management questions increasingly require a more comprehensive ecosystem-based foundation (e.g. multisector cumulative impacts, allocation decisions, species interactions). Suitably constructed programmes emphasizing marine ecosystem organization and dynamics are a key strategy leading to more useful quantitative tools supporting EBM, and ultimately to better and more comprehensive management of marine ecosystems.

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