

Linking Ecosystem Health and Services to Inform Marine Ecosystem-Based Management

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Abstract.—A growing variety and intensity of human activities threaten the health of marine ecosystems and the sustained delivery of services provided by oceans and coasts. The Gulf of Maine (GoM) is no exception to this trend, and as such, an ecosystem-based approach to managing the region has gained traction in recent years. The ultimate aim of marine ecosystem-based management (EBM) is to maintain ecosystem health (i.e., structure and function) and to sustain the full suite of ecosystem services on which people rely. Maintaining ecosystem health and sustaining services are related goals, both from a scientific and management perspective, yet in some cases, the interplay between the two is not well understood. Here, we examine relationships between attributes of ecosystem health and ecosystem services. In particular, we explore how outputs from ecosystem models, originally developed for ecosystem-based fisheries management (EBFM), can be used to quantify and value services of particular relevance to the GoM environments and human populations. We highlight services, such as the provisioning of food from fisheries, that ecosystem models are well equipped to inform and reveal where more work is needed to value other services, such as the protection from erosion and inundation afforded by coastal habitats. EBM also requires knowledge about the costs and benefits of management decisions for humans and ecosystems. We demonstrate how ecosystem models can be used to explicitly illustrate trade-offs between attributes of ecosystem health and ecosystem services that result from alternative management scenarios. By bridging the gap between models developed for EBFM and ecosystem service models, we identify existing science and future needs for informing an ecosystem approach to managing the GoM.

Introduction

Coastal and ocean environments provide humanity with many important benefits or ecosystem services (MEA 2005). However, a growing vari-

ety and intensity of human activities threaten the health of marine ecosystems and the sustained delivery of ecosystem services. A greater awareness of the need to manage for multiple uses and interconnectedness of marine ecosystems has led to a shift toward an ecosystem approach to manage-

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ment in the United States, Canada, and elsewhere (Christensen et al. 1996; Arkema et al. 2006; Smith et al. 2007; Levin et al. 2009; McLeod and Leslie 2009). Ecosystem-based management (EBM) is an integrated approach that focuses on the influence of multiple human activities on ecosystems. The ultimate aim of EBM is to maintain ecosystem health in order to sustain the services people desire from it (McLeod et al. 2005). These two components, maintaining ecosystem health and sustaining the delivery of ecosystem services, are not independent of one other. Indeed, the provisioning of ecosystem services depends on a well-functioning ecosystem, which in turn can be modified by the demand for various services (MEA 2005). In spite of this interconnectedness, the relationships between various attributes of ecosystem health and the delivery of specific services of interest are not well defined.

“Ecosystem health” is an oft-used term in regulatory and policy documents and in the public media (POC 2003; USCOP 2004; McLeod et al. 2005; MEA 2005). Here, we operationalize and define ecosystem health as attributes of ecosystem structure (e.g., species composition, physical habitat characteristics) and function (e.g., biological and physical processes) relevant to the management goal of maintaining a productive and resilient ecosystem. Our understanding is based on various avenues of ecological research and theory, including the relationship between diversity and ecosystem function (reviewed by Srivastava and Vellend 2005), food web theory (e.g., Pimm 2002; Vermaat et al. 2009), the ecosystem-based fisheries management literature (e.g., Link et al. 2002; Fulton et al. 2005), and ecosystem ecology (e.g., Odum 1969, 1985; Likens 1985; Carpenter et al. 1995). From this literature has emerged an enormous list of attributes that scientists use to characterize an ecosystem, including the relative abundance and diversity of species with ecological and/or conservation importance, rates of primary and secondary production, community energetics, nutrient and trophic cycling, and resilience (Samhour et al. 2009). These attributes describe the status of the ecosystem irrespective of the human dimension.

In contrast with ecosystem health, the goal of maintaining ecosystem services focuses on endpoints that relate directly to human needs and

desires (NRC 2005; MEA 2005). Scientific understanding of the relationship between management decisions, ecosystem processes, and the delivery of benefits for humans is improving. These benefits include not only provisioning services of fish and shellfish, but also regulating services, such as control of damage from storms or floods, supporting services of nursery habitats and forage fish, and cultural, aesthetic, and recreational values (Daily 1997; MEA 2005). The Millennium Ecosystem Assessment (MEA) of the status of ecosystem services around the globe (MEA 2005) spawned a flurry of academic research and action by nongovernmental organizations and some international governments to increase understanding and awareness of the linkages between our activities and what benefits we can expect to reap from ecosystems (e.g., Hayhoe et al. 2004; examples in Turner and Daily 2008). Although the MEA raised awareness of ecosystem services on a global scale, much scientific work remains to be done. Decision support tools, predictive models, and more detailed understanding of specific services and the relationships among them are needed to inform management decisions on local, regional, and national scales. Moreover, until recently, the focus of ecosystem services research has largely been on terrestrial ecosystem services, although advances are being made in the marine arena (Ruckelshaus and Guerry 2009; reviewed in Kareiva et al. 2011). Quantitative approaches developed for ecosystem-based fisheries management (EBFM) may be able to provide an initial step toward quantifying the delivery of at least a subset of services provided by coastal and ocean ecosystems under alternative management scenarios.

In this paper, we explore the relationship between ecosystem health and ecosystem services and seek to bridge the gap between ecosystem models developed for EBFM and modeling currently in development to map and value ecosystem services. First, we outline relationships between ecosystem attributes and ecosystem services, highlight which services existing ecosystem models are well equipped to inform, and reveal where more work is needed. Second, we use an ecosystem model to elucidate trade-offs that arise among ecosystem health attributes, among services, and among attributes and services under rep-

representative management strategies. Throughout the paper, we focus on ecosystem health attributes and services of importance in the Gulf of Maine (GoM). We discuss implications of the relationship between health and services and identify future needs for an ecosystem-based approach in the region.

Models for Understanding Ecosystem Health

The past few decades have seen the development of a variety of marine ecosystem models, especially in the domain of fisheries science and management (reviewed by Fulton et al. 2003; Plaganyi 2007; Fulton 2010; Rose et al. 2010). These models attempt to incorporate the dynamics of species from many trophic levels (e.g., bacteria, primary producers, primary consumers, intermediate consumers, and apex predators), in addition to capturing some of the physical processes, fluxes, and/or forcings (e.g., habitat heterogeneity, nitrogen cycling, and sea surface temperature) most relevant to the biota. Plaganyi (2007) identified at least five classes of marine ecosystem models that fit our definition and differ in their data requirements, complexity, biological detail, handling of uncertainty, integration of climatic and oceanographic effects, incorporation of biogeochemistry, and inclusion of a spatial dimension. Many, if not all, of these frameworks initially were designed to inform EBFM, though they are increasingly capable of modeling new fisheries management scenarios (e.g., catch shares), other types of anthropogenic pressures (e.g., pollution, habitat loss, and climate change), socioeconomic dynamics, and the assessment and management processes themselves. In order to explain how such models can be used to examine relationships between attributes of ecosystem health and ecosystem services, the authors describe in more detail one of the most commonly used modeling frameworks, Ecopath with Ecosim (Polovina 1984; Christensen and Walters 2004), and another, Atlantis, which is gaining traction in a variety of locations worldwide because of its comprehensiveness and versatility (Fulton et al. 2005; Kaplan and Levin 2009; Link et al. 2010). Indeed, an Ecopath model for the Gulf of Maine was constructed nearly a decade ago (Heymans 2002) and has since been elaborated (Link et al.

2008) concurrently with the development of an Atlantis model for the northeast U.S. Continental Shelf (Link et al. 2010).

Ecopath with Ecosim (EwE) is composed of two linked parts. Ecopath, introduced by Polovina (1984), is a static, mass-balanced food web model consisting of trophically connected functional groups represented in terms of biomass density and fishing fleets that impose an additional source of mortality on a user-defined subset of the functional groups. Ecosim, developed by Christensen and colleagues (Christensen and Walters 2004; Christensen et al. 2005), is a dynamic simulation model driven by coupled equations that are initialized from the Ecopath mass-balance solution and influenced by specified predator-prey relationships (in addition to dynamic harvest rates, physical forcings, and recruitment processes, if desired). Though not a prerequisite, Ecosim can also represent multiple age-/size-classes for each functional group using Deriso-Schnute equations (Walters et al. 2000) and nontrophic interactions (such as the reduction in vulnerability to predation of species that seek shelter in structure-forming organisms like kelp). EwE is used widely to predict the direct and indirect effects of fisheries practices on targeted and nontargeted species throughout an ecosystem, the relative importance of top-down and bottom-up factors in structuring food webs, qualitative outcomes of alternative management strategies, and the reliability of candidate indicators of ecosystem health (Plaganyi and Butterworth 2004; Fulton et al. 2005; Field et al. 2006; Heymans et al. 2007; Österblom et al. 2007; Plaganyi 2007; Link et al. 2008; Mackinson et al. 2009; Samhoury et al. 2009; Shannon et al. 2009; Worm et al. 2009).

Atlantis, originally introduced as a biogeochemical box model (Fulton 2001; Fulton et al. 2004), consists of several submodels. At its core is a spatially explicit, biophysical submodel that tracks the transport of nutrients through functional groups in a three-dimensional ecosystem. Like EwE, the Atlantis biophysical submodel is driven by consumer-resource interactions, recruitment processes, and physical forcings, but it also allows for migration and habitat preferences to be influenced by physical habitat features (e.g., canyons). Also, as in EwE, Atlantis functional groups can be represented as biomass pools or as

age-structured populations. The biophysical sub-model is coupled to an oceanographic transport model, a human-impacts model (primarily fishing fleets, but also coastal development, pollution, etc.), a sampling and assessment submodel that simulates real-world monitoring programs, a management submodel consisting of decision rules and management actions, and a socioeconomics submodel that handles a range of features from compliance decisions to taxes to social networks among fishing vessels. Thus, a variety of nontrophic effects can drive the dynamics of an Atlantis ecosystem model. Because it treats such a wide range of biological, physical, and socioeconomic components of the ecosystem, Atlantis is quite useful for management strategy evaluation (MSE; Smith et al. 2007). MSE is used to project alternative management scenarios into the future, via simulation, to reveal insights into the ecosystem's dynamics, trade-offs among management objectives inherent to specific policy actions, and unintended consequences of particular management choices (Sainsbury et al. 2000; Levin et al. 2009). In addition, Atlantis has been used to evaluate the influence of model complexity on ecosystem understanding, identify robust indicators for monitoring programs, consider cumulative impacts of multiple human pressures, and examine the consequences of spatial management (Fulton et al. 2003, 2005; Kaplan and Levin 2009).

A major benefit of ecosystem models such as EwE and Atlantis is that they capture the dynamics of multiple attributes of ecosystem health in a single model domain. In this way, it is possible to examine changes in different aspects of ecosystem health while accounting for interactions and linkages between them. For example, the biomass of harvested species and the areal extent of biogenic habitat each may be considered ecosystem attributes, and if biogenic habitat serves as a structural refuge from predation for some species, it will also influence their biomass. Though many ecosystem attributes are challenging to measure empirically, these models capably predict changes in both ecosystem structure and function. For instance, Fulton et al. (2005), Shannon et al. (2009), and Samhouri et al. (2009) used EwE and Atlantis models to measure the effects of different types and magnitudes of human perturbation

on changes in ecosystem attributes ranging from structural characteristics like mean trophic level and diversity to functional aspects such as trophic cycling, the ratio of ecosystem respiration to ecosystem biomass, and resilience. Examples of other attributes of ecosystem health, well represented by EwE and Atlantis, are listed in the columns of Table 1, though this list is by no means exhaustive. While some attributes, like the biomass of harvested species, are directly related to ecosystem services, like the food obtained from fisheries, in other cases, the relationships between ecosystem health attributes derived from ecosystem models and ecosystem services are indirect or unknown (e.g., the rate of nutrient cycling and recreational use of the ecosystem) (see Linking Health Attributes to Services section below).

Framework for Modeling Ecosystem Services

An important component of EBM is to understand how alternative management strategies will influence the full suite of services provided by marine ecosystems. A promising approach, recently forwarded in terrestrial ecosystems, has been the development of ecosystem service models that are sufficiently general to be applied systematically in various sites at temporal and spatial scales relevant to management (Nelson et al. 2009; Tallis and Polasky 2009; Kareiva et al. 2011). Such models must combine the rigor of small-scale studies, which tend to focus on one habitat type or ecosystem service, with the breadth of broad-scale assessments to integrate across multiple services. Here, the key aspects of such an ecosystem service modeling framework are described.

A fundamental component is the application of sound ecological models and understanding to develop "ecological production functions." Essentially, a production function specifies the output of services that are provided by an ecosystem, given its condition and characteristic processes (NRC 2005). Such a modeling approach relies on descriptions of the relationships between ecosystem structure (e.g., distribution and abundance of biogenic habitats and key species, water temperature, and concentrations of particulate organic matter and sediments) and function (e.g., sediment erosion and accretion, production and growth rates of

TABLE 1. Example attributes of ecosystem health (columns) and marine ecosystem services (rows). Existing ecosystem models capture the dynamics of all of the ecosystem attributes. Some of the ecosystem services can be valued with existing models (e.g., food from fisheries), whereas models for valuing some of the other services (e.g., control of erosion and inundation) are currently under development. Grey shading indicates which attributes of ecosystem health have a primary influence on the delivery of a specific service. These attributes would likely be included in simple production function models that describe the aspects of ecosystem structure and function that are most fundamental to the delivery of provisioning, regulating, and cultural services. Some of these attributes have been described as supporting services (MEA 2005).

Ecosystem service	Ecosystem attribute ^a														
	Charismatic species ^b	Harvested species	Biogenic habitat	Primary production	Secondary production	Mean trophic level	Diversity	% top predators	% intermediate species	% Basal species	Nutrient cycling	Connectance	Resilience	Respirator/total biomass	Food chain length
Provisioning															
Food for humans (fisheries, aquaculture)															
Biochemicals, natural medicines, pharmaceuticals															
Biofuels															
Regulating															
CO ₂ sequestration and storage															
Bioremediation of toxins															
Control of erosion and inundation															
Cultural															
Recreation															
Aesthetics															
Cultural heritage values															
Supporting															
Nursery habitat for harvested/forage species															
Food for target species															
Primary production															
Nutrient cycling															

^a Units for charismatic and harvested species = density or biomass; units for biogenic habitat = density or area; units for primary and secondary production = density, biomass, or rates; and units for trophic and nutrient cycling = rates. Percentages of different types of species refer to the percent of total ecosystem biomass. Resilience can be expressed as a return time following perturbation or as a proportional change in density/biomass of individual taxa relative to the entire ecosystem. Other attributes are labeled with their units or are unitless.

^b Charismatic species may include marine mammals, sea turtles, and/or seabirds.

key species, wave attenuation, and consumption/ filtration rates of organic matter) that are the basis for the delivery of a service (Tallis and Polasky 2009).

Ecosystem functions are fundamental to the delivery of benefits from natural environments, but ecosystem structure and function do not equate with services. Although critical for quantifying and valuing services, this distinction is often overlooked. Humans must benefit from an ecological process in order for it to be a service (Luck et al. 2009) and the value of a service depends both on *supply* and *demand*. Ecosystem functions influence the supply of ecosystem services, but they do not account for demand. Where are the people who enjoy services, and how much do they use? How will their use of a service change with different management decisions or policies? The combination of supply and demand generates use of ecosystem services. Defined quite broadly, the service is that portion of the ecosystem function that is used, not only via the consumption of physical goods, such as fish and timber, but also inclusive of the recreational and aesthetic appreciation of nature (i.e., nonconsumptive use values).

Management actions may influence service value through either their effects on supply or on demand (Vira and Adams 2009). Thus, models of ecosystem services must integrate analysis of the supply of the ecosystem function of interest with analysis of the location, type, and intensity of demand for services (Beier et al. 2008). Particularly useful outputs from ecosystem service models include maps of the availability and distribution of ecosystem services that indicate both areas where services are provided and where they are used (Tallis and Polasky 2009; Kareiva et al. 2011). For example, service maps that display the spatial distribution of metric tons of carbon sequestered have great utility in the context of climate change mitigation planning, while maps that display the spatial distribution of the volume of water yield available for hydropower production are critical to land use and development strategies. In some management contexts, it may be sufficient to quantify ecosystem services in biophysical units, as in the two preceding examples. For instance, some agencies make decisions about what activities will be allowed based on whether or not they meet a water quality standard or an allowable

catch. Other decisions are tied to financial costs and benefits, and thus presenting policy alternatives in terms of the net benefits measured in a monetary currency is preferred. In these cases, it can be very useful to combine ecological production functions with economic valuation methods to estimate and report the monetary value of ecosystem services. The value of the changes in marketed services (e.g., fish, aquaculture, and avoided storm damage) can be quantified using market prices for marginal changes. Nonmarket valuation methods, including revealed preference and stated preference methods, can be used for ecosystem services that are not traded in markets (e.g., esthetic or cultural values; Freeman 2003; NRC 2005).

Integrating ecosystem and valuation modeling tools can help managers understand how trade-offs in ecosystem services may be modulated by trade-offs in the values of services. The framework discussed here could be described as a promising first step toward linking ecosystem health and services because it focuses on unidirectional effects of management decisions on the supply and demand of services. More work is needed to account for feedbacks between management decisions and ecosystem components by dynamically linking (1) models that deal with human behavioral responses to policies (e.g., dedicated behavior models) to (2) biophysical models that account for effects of management actions on the ecosystem functions that underlie the supply of services (Fulton 2010).

Linking Health Attributes to Ecosystem Services

The framework we use to link ecosystem health attributes to ecosystem services (Figure 1A) is based on connecting human actions to changes in ecosystem structure and function, ecosystem structure and function to the delivery of services, and the delivery of services to their values (NRC 2005; Daily et al. 2009). We focus on the extent to which outputs from ecosystem models can be used to generate information about the delivery of a suite of services under alternative management strategies. For the purposes of illustration, Figure 1 has been simplified so as not to include all the possible ecological and socioeconomic feedbacks and interac-

General framework for modeling ecosystem services (adapted from Daily et al. 2009)

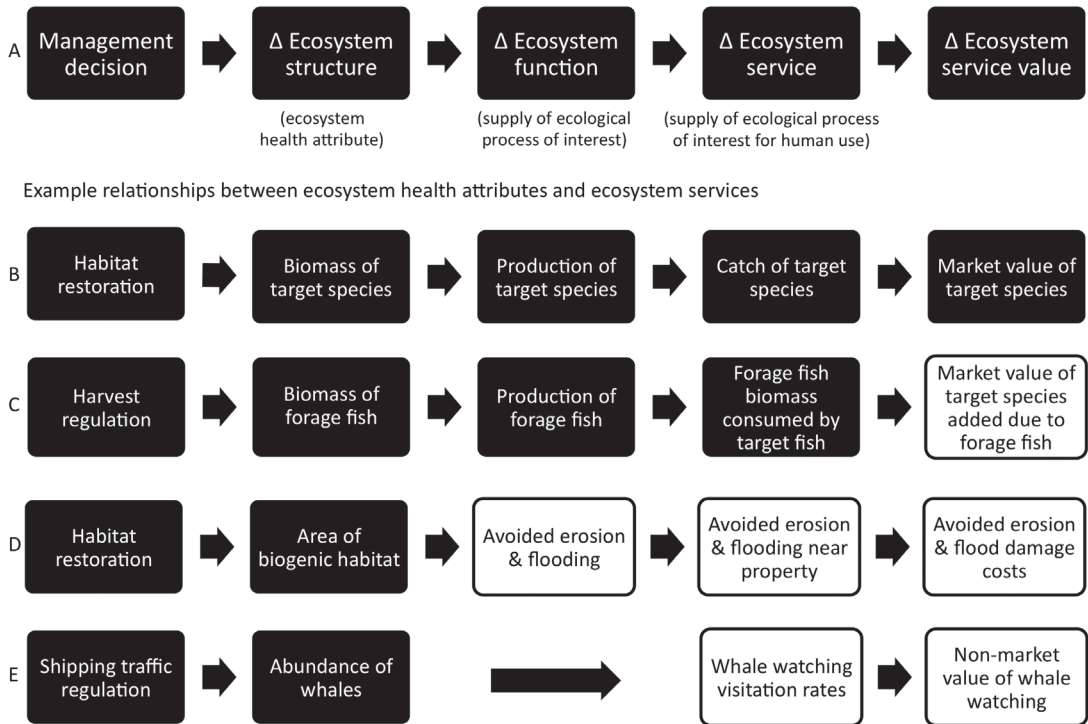


FIGURE 1. (A) A general framework for modeling ecosystem services (adapted from Daily et al. 2009). Note: in some cases, ecosystem health attributes are functional as well as structural (e.g., production of fish). (B–E) Example relationships between ecosystem health attributes and ecosystem services. Shaded boxes indicate that ecosystem models, developed largely for ecosystem-based fisheries management (EBFM), can be used to quantify a step in the logical chain. White boxes indicate a gap in current modeling capabilities. For the purposes of illustration, we have excluded the many possible ecological and socioeconomic feedbacks that may occur among steps.

tions that may occur among steps in the modeling framework (see last paragraph in previous section and Fulton [2010] for further discussion of feedbacks). We discuss three types of decisions (harvest regulation, habitat restoration, and shipping traffic) and four examples of services (catch of target species, production of forage species consumed by target species, the amount of erosion or inundation prevented via wave attenuation by biogenic habitat, and whale watching) that are significant in coastal and marine ecosystems. Our focus is on the relationship between management decisions and ecosystem attributes and services in light of examples relevant to the GoM ecosystem.

In the first example, we explore the influence of habitat restoration on the catch and mar-

ket value of a species targeted for human food (Figure 1B). Our thought experiment is relevant in the GoM where Atlantic cod *Gadus morhua* young of the year recruit to structurally complex eelgrass and kelp habitat for protection from predation (Lazzari et al. 2003). An increase in the abundance of macrophytes and seaweeds, as a result of restoration activities, may lead to increases in the biomass and production of target species like Atlantic cod. Depending on current harvest regulations, the total catch and total market value of the target species should increase. Ecosystem models can predict outputs of the service in biophysical terms (i.e., kilograms of Atlantic cod) or in economic terms (i.e., the total market value of the catch). The health attribute in this example

(biomass of target species) is closely related to the provisioning service (catch of target species), and ecosystem models are well equipped to assess changes in both factors. Worth noting, however, is that for examples like this one, where nontrophic effects are important, ecosystem models such as Atlantis and EwE may require enhancements to account for the influence of biogenic habitat on the production of target fish species.

Related to the catch of target fish and shellfish is the supporting service of forage species for higher trophic levels. Recent work has considered the trade-offs between harvest of a commercially valuable fish species (Pacific sardine *Sardinops sagax*) and its importance as prey for other species of commercial, recreational, and ecological significance (Hannesson et al. 2009). In the second example, a harvest regulation (e.g., catch quotas, area and seasonal closures) directly influences the biomass and production of a target species that is also a forage fish (Figure 1C). As pointed out by Hannesson et al. (2009), indirect effects may play a role in determining the biomass of forage species (see Trade-offs among Ecosystem-Based Management Goals section below). But for the sake of illustration, the simplest expectation is that a reduction in harvest of the forage fish species will positively influence its biomass and production, and this effect should increase prey availability for forage fish predators, which may also be target species. Because EBFM models were largely developed to increase the understanding of community-wide impacts of harvest practices and are based on trophic relationships, they are well equipped to assess changes in the catch of a higher trophic level species as a result of changes in fishing effort for lower trophic level species. One limitation, however, is that some ecosystem models do not include the final step in the framework for modeling ecosystem services: valuation of forage fish as a supporting service (indicated by white box in Figure 1C). This quantity can be calculated as the added market value of the target fish species due to an increase in its biomass and catch as a result of the addition of forage food (similar to the approach of Hannesson et al. (2009)).

In the third example, restoration activities increase the area of biogenic habitat, an ecosystem health attribute that also provides a variety of services (Figure 1D). In addition to the sup-

porting service of acting as nursery habitats, eelgrass beds, estuaries, and saltmarshes (which are all foci of restoration efforts in the GoM (Gulf of Maine Council Habitat Restoration Committee 2004) have the ability to attenuate wave action and protect coastal areas from storm surge and erosion processes (reviewed in Irish et al. 2008; Koch et al. 2009). Unlike the previously discussed services, ecosystem models generally do not include nearshore hydrodynamic processes, such as wave attenuation, sediment transport, and water flow across inland areas, that are essential for quantifying avoided erosion or flooding in coastal areas (Komar 1998; reviewed in Irish et al. 2008). Moreover, these models generally lack the capacity to value coastal protection services via avoided sea defense costs (Moller et al. 2001), damages to property (FEMA 2009), affected people (Nicholls 2004), and/or lives lost (Das and Vincent 2009; indicated by white boxes in Figure 1D).

The effects of shipping traffic regulation on whale watching provides another example of a relationship between ecosystem attributes and services, for which there is a gap in our modeling capacity. Recent reports have implicated vessel traffic for sustained injuries and mortality caused by ship strikes to whales (Vanderlaan and Taggart 2006). Thus, we might expect traffic regulations, such as the designation of "areas to be avoided" or speed caps on specific routes, to lead to an increase in the abundance of whales. One service provided by whales is simply their existence value, which is essentially the benefit people receive from knowing that a particular environmental resource, such as marine mammals, exists (Krutilla 1967; NRC 2005). In this case, the ecosystem attribute, whale abundance, is the same as the service. However, whales also provide a recreational service, which can be determined using both market and non-market valuation approaches (Fisheries and Oceans Canada 2008; L. H. Pendleton, Ocean Foundation unpublished manuscript). The ecosystem models discussed in this paper currently lack the socioeconomic approaches necessary for predicting changes in recreational services and values of whale watching. Mortality from whale strikes due to shipping traffic is quite relevant in the GoM where the U.S. and Canadian governments have changed shipping routes in and out of Boston and the Bay of Fundy in an attempt to re-

duce whale strikes, in particular to the North Atlantic right whale (Right Whale Recovery Team 2000; Kraus et al. 2005).

Here, we have discussed just a few of the health attributes that reflect the ecosystem structure and function that are fundamental to delivering a full suite of services and predicting the influence of alternative management actions. Numerous other attributes of ecosystem health may have a primary influence on specific and broad categories of ecosystem services. Examples of these are indicated with gray shading in Table 1. Shaded attributes are likely to be included in simple production function models describing the aspects of ecosystem structure and function that are most fundamental to the delivery of provisioning, regulating, and cultural services. Some of these attributes have been described as supporting services (MEA 2005). The ecosystem health attributes that are not shaded may also be related to the delivery of services. In some cases, we may lack the scientific understanding to directly link changes in these attributes with services. In other cases, such as resilience, the ecosystem attribute may relate to temporal variability in the delivery of services. Increasingly complex ecosystem services models should be able to take into account such attributes in order to forecast fluctuations in services as a result of various perturbations.

Trade-offs among Ecosystem-Based Management Goals

The implementation of EBM raises policy questions about how one human use will affect others and how a policy focused on addressing one EBM goal (e.g., maintaining ecosystem health) will influence other goals (e.g., sustaining the delivery of ecosystem services) (Rosenberg and Sandifer 2009). Existing ecosystem models can provide insights into how alternative management actions affect such trade-offs among attributes of ecosystem health, among ecosystem services, and among ecosystem attributes and services (Walters and Martell 2004; Gerber et al. 2009; Kaplan and Levin 2009; Samhuri et al. 2010). Introduced below is a heuristic example of trade-offs among EBM goals using an EwE model for northern British Columbia (2000 AD; Ainsworth et al. 2008). The British Columbia model consists of 53

trophically linked functional groups (including 4 marine mammal, 32 fish, 12 invertebrate, 1 seabird, 2 primary producer, and 2 detritus groups). We chose to use this model because we are familiar with it (Samhuri et al. 2009, 2010); because it includes a biogenic habitat group in the food web (kelps and eelgrass), which allowed us to examine the effects of nearshore habitat management decisions; and because many of the functional groups have analogs in the GoM ecosystem. A similar approach could be employed using the recently developed Atlantis model for the northeast U.S. Continental Shelf (Link et al. 2010) within the GoM.

We measured the change in four attributes of ecosystem health and three ecosystem services under three different management scenarios. The ecosystem attributes we examined were drawn from the columns of Table 1 and include the abundance of charismatic species (specifically, the biomass of seals, sea lions, and seabirds); resilience, measured as the amount of change in the biomass of individual species (or functional groups) relative to the change in biomass of the entire ecosystem over the course of each simulation (Samhuri et al. 2009); one measure of the abundance of harvested species, groundfish biomass; and, the ratio of ecosystem respiration to ecosystem biomass, a measure of the maintenance costs in the ecosystem (Odum 1985). The ecosystem services we evaluated fall under the “food for humans” and “recreation” categories in Table 1 and include the recreational catch of lingcod *Ophiodon elongatus*, the recreational catch of Pacific halibut *Hippoglossus stenolepis*, and the catch of Pacific herring *Clupea pallasii* by the commercial gill-net and seine fisheries.

We compared the status quo management (i.e., harvest rates estimated for the year 2000; Ainsworth 2006) to three alternative management scenarios at the end of 25-year simulations. The management scenarios included (A) a 50% reduction in fishing mortality induced by the groundfish trawl fleet, (B) a 50% increase in kelp production (e.g., due to nearshore habitat restoration, Reed et al. 2006), and (C) the combined effects of reduced fishing as in (A) and increased kelp production as in (B). We highlight two points regarding these simulations. First, in this EwE model the groundfish trawl fleet targets lingcod and Pacific halibut,

in addition to 14 other functional groups. Second, as in Samhouri et al. (2010), in scenarios B and C the authors incorporated a nontrophic, positive effect of macrophytes on several functional groups (juvenile herring and rockfishes, small crabs, shallow water benthic fish, and adult lingcod) that use the structural complexity of these habitat-forming organisms as a refuge from predation.

Reducing mortality induced by the groundfish trawl fishery by half led to a 36% decline in that fleet's catch relative to status quo management but only a 3% change in the groundfish stock size (i.e., biomass; Figure 2A). This somewhat counterintuitive result occurred largely because predator-prey interactions among the 16 functional groups constituting the groundfish guild reduced the expected beneficial effects of a decline in fishing-induced mortality. For instance, in this EwE model Pacific halibut make up a substantial portion of the diet of lingcod, but the reverse is not true (Ainsworth 2006). Thus, lingcod biomass increased in part due to increased availability of Pacific halibut prey when both species were released from trawl fishing pressure, whereas Pacific halibut biomass declined, though less so, for the same reason. Correspondingly, this management scenario caused a 7% decline in the recreational catch of Pacific halibut and a 34% increase in the recreational catch of lingcod (Figure 2A). Additionally, because several of the groundfish functional groups that benefited from a reduction in the trawl fishery (e.g., Pacific cod, lingcod, and turbot) prey on herring, the commercial catch of this forage species declined by 13% as well. These responses illustrate how a single management decision focused on one sector, the groundfish trawl fishery, can, through direct and indirect effects, produce trade-offs among other ecosystem services, in this case the recreational catch of lingcod and Pacific halibut and the commercial catch of herring.

In terms of attributes of ecosystem health, the 50% reduction in fishing mortality induced by the groundfish trawl fleet caused an increase in resilience; a slight decline in the biomass of seals, sea lions, and seabirds; and no change in the ratio of ecosystem respiration to ecosystem biomass relative to status quo management (Figure 2A). The 33% increase in resilience implies that restricting the groundfish trawl fishery caused a

smaller change in the abundances of individual functional groups relative to the overall change in ecosystem biomass than would have occurred under status quo management. The 4% decline in the abundance of charismatic species is a consequence of prey depletion (these groups forage on herring and a subset of the groundfish; Ainsworth 2006). The lack of response in the respiration to biomass ratio suggests that ecosystem maintenance costs were not altered by the change in the groundfish trawl fishery. As in the case of the ecosystem services, taken together these responses demonstrate that a management decision focused on one component of the ecosystem can lead to trade-offs among ecosystem health attributes (e.g., resilience versus charismatic species abundance). The responses also reveal trade-offs among ecosystem attributes and services (e.g., commercial groundfish and herring catches versus resilience).

The second management scenario, in which we simulated a 50% increase in kelp production, had marginal effects on the ecosystem attributes and services (Figure 2B). Indeed, only two of the ecosystem attributes and none of the ecosystem services differed by more than 2% from the status quo scenario. Resilience increased somewhat, by 13%, as did the respiration to biomass ratio (4%). Importantly, even changes of relatively small magnitude like these may be quite valuable to managers and stakeholders. Nonetheless, comparison of scenarios A and B suggests that either (1) changes in structure-forming nearshore habitat groups have small effects on the ecosystem relative to fishing, or (2) it is difficult to model accurately the nontrophic effects of macrophytes using EwE. Though we cannot distinguish between these two possibilities at this time, the Atlantis modeling framework treats both space and nontrophic effects of biogenic habitat explicitly and would be well suited to do so.

Finally, in the third management scenario, we explored the combined effects of reduced groundfish trawl fishing mortality and increased kelp production (Figure 2C). Because scenario B only had marginal effects on the ecosystem attributes and services, the responses of the ecosystem attributes and services appear qualitatively similar to those in scenario A (Figure 2A), which examined reduced fishing effects exclusively. Quantitatively, the combined effects of fishing and changes

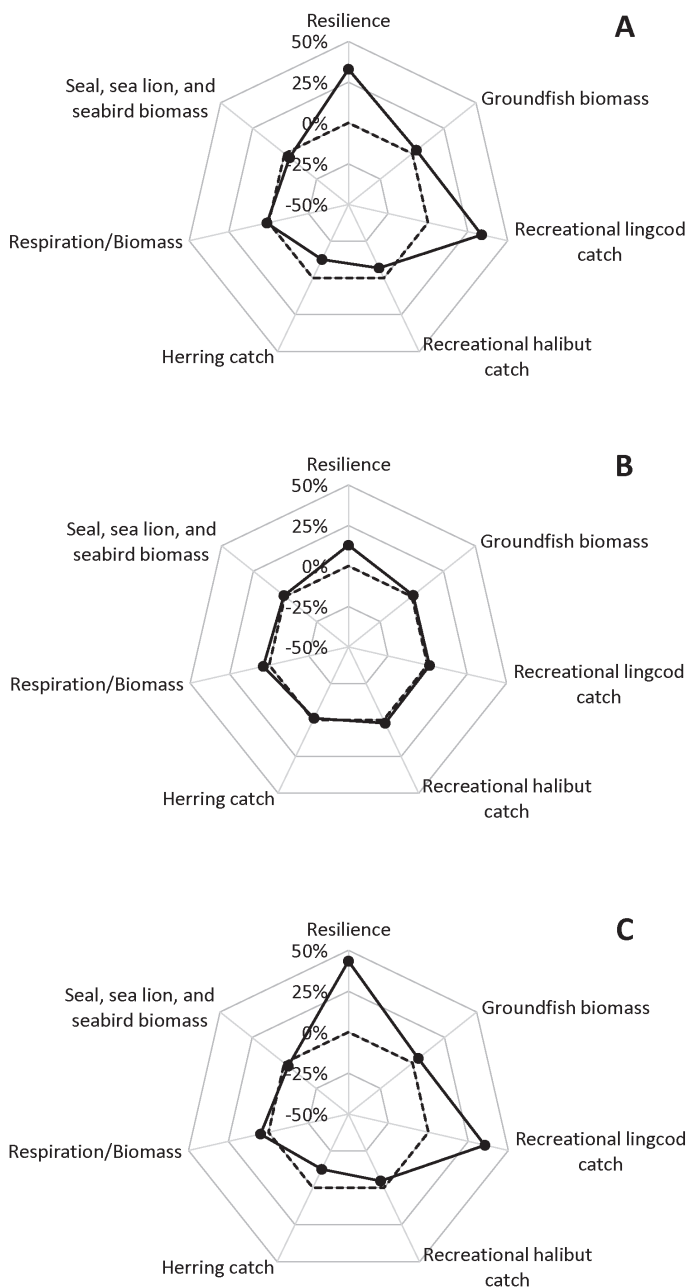


FIGURE 2. Spider plots depicting trade-offs among four attributes of ecosystem health (seal and bird biomass, resilience, groundfish biomass, and the ratio of ecosystem respiration to ecosystem biomass) and three ecosystem services (recreational lingcod catch, recreational halibut catch, and herring catch) predicted by an Ecopath with Ecosim model of northern British Columbia. The three scenarios represent (A) a 50% reduction in fishing mortality by the groundfish trawl fleet, (B) a 50% increase in kelp production (e.g., due to nearshore habitat restoration or reduced nutrient inputs), and (C) the combined effects of reduced fishing as in (A) and increased kelp production as in (B). Note that for each scenario, values of attributes and services are plotted as percentage differences from status quo management (indicated by the dashed line at zero) and rescaled so that positive values indicate improvements and negative values indicate declines.

in structure-forming nearshore habitat groups in scenario C were essentially additive. As the effects of multiple human impacts are frequently synergistic or antagonistic in nature (Crain et al. 2008), it is possible that the additivity seen here is a consequence of EwE model structure.

An Ecosystem Health and Services Approach for the Gulf of Maine

The GoM is well known as one of the world's richest marine ecosystems. Flanked by Massachusetts, New Hampshire, Maine, New Brunswick, and Nova Scotia to the north and west, and Georges Bank to the south and east, the GoM region has a long tradition of fishing, marine transportation, coastal development, and recreation. Indeed, seafood, recreational opportunities, and aesthetics are perhaps the most recognized services provided by coastal and marine ecosystems in the GoM. Additionally, a suite of important regulating and supporting services are provided by the diversity of environments (e.g., salt marshes, rocky intertidal, mudflat, eelgrass beds, sandy beaches, and nearshore and offshore subtidal habitats) characterizing the region (Gulf of Maine Council Habitat Restoration Committee 2004; Taylor 2008). As in other coastal areas around the world, a growing variety and intensity of human activities have increased the demands on the GoM marine ecosystem while threatening its historical functioning (Steneck et al. 2002) and overall health. Proposed and existing activities in the GoM include aquaculture, coastal development, discharge of sewage and other pollutants, energy production and distribution (wind farms, pipelines, and liquid natural gas terminals), fishing, tourism and recreation, seabed mining, telecommunications, and transportation (Taylor 2008). Balancing the numerous ocean uses, maintaining ecosystem health and services, and considering the current and future needs of stakeholder groups require comprehensive approaches.

Current EBM and marine spatial planning processes at the federal (e.g., Interagency Ocean Policy Task Force, www.whitehouse.gov/administration/eop/ceq/initiatives/oceans), regional (e.g., Massachusetts Ocean Management Plan, www.mass.gov), and local levels (e.g., Taunton Bay Management Plan, www.maine.gov/dmr/council/

tauntonbay/index.htm) will benefit from incorporating an ecosystem services framework and an understanding of how attributes of ecosystem health interact with and sustain services (see also Hale and Westhead 2012, this volume). Spatial information about the provisioning, delivery, and use of ecosystem services can make explicit information regarding human activities and their effects on the coastal and ocean ecosystems of the GoM and identify target areas and beneficiaries for restoration. Ecosystem models can, and have, been used to assess trade-offs among a subset of services, especially related to fisheries, and among attributes of ecosystem health (Kaplan and Levin 2009; Samhuri et al. 2010). However, an assessment of trade-offs among a full set of ecosystem services will require tailoring models to predict changes in these services as a function of a variety of human uses of ocean ecosystems.

A variety of modeling approaches and efforts to synthesize information about marine services are underway at various institutions (e.g., Stanford University, World Wildlife Fund, The Nature Conservancy, University of Minnesota, University of Vermont, Conservation International, and United Nations Environmental Programme, to mention a few), and these may be of use to EBM efforts in the GoM. One suite of models, with which the authors are most familiar, is called Marine InVEST, and is being developed by the Natural Capital Project (Integrated Valuation of Ecosystem Services and Trade-Offs, Ruckelshaus and Guerry [2009]). Marine InVEST shares a number of key attributes with the original, terrestrial InVEST tool (Nelson et al. 2009; Tallis and Polasky 2009; Kareiva et al. 2011). The models allow users to map and value ecosystem services under current and future management and climate change scenarios. Highly flexible, for use with diverse habitats, policy issues, stakeholders, data limitations, and spatial and temporal scales, Marine InVEST comprises models for a variety of services (food from fisheries and aquaculture, recreation, coastal protection, and wave energy generation). The InVEST modeling framework includes key aspects of the approach discussed in this paper and, with site-specific calibration and parameterization, will be transferable to the GoM. A particularly powerful approach would be to link outputs from the recently developed

Atlantis model for the GoM (Link et al. 2010) with outputs for a full suite of services provided by Marine InVEST.

Implementing EBM in the GoM presents unique governance challenges, as doing so will require coordination among multiple states and across an international border. It is suggested that the ecosystem health and services models discussed in this paper can provide common ground and common currencies for tackling questions about the consequences of alternative management actions in the GoM. Key lessons from other systems in which these approaches have been used are as follows:

- Though they may not have a primary influence on endpoints of direct use to humans, attributes of ecosystem health are important for sustaining the delivery of ecosystem services. Existing models can be used to ask how different components of these two EBM goals change in relation to one another. A greater mechanistic understanding of the interplay between ecosystem health and services is a fertile area for future research.
- Existing data sources and models can provide guidance toward the mapping and valuation of ecosystem services but must be integrated across disciplines and synthesized within a cohesive framework to be useful for resource managers and policy makers.
- Ecosystem models like EwE and Atlantis, and ecosystem service models currently under development, can assist policy makers by exposing the trade-offs and counterintuitive results of alternative management decisions. Any one management action is likely to produce benefits for some attributes of ecosystem health or some ecosystem services and costs to others. The models discussed in this paper can alert managers to potential trade-offs and help them to reduce the likelihood of unintended consequences with detrimental effects on ecosystem structure and function. It is important to recognize and understand how single-sector management decisions alter species interactions and influence ecosystem health and services in direct and indirect ways (Mangel and Levin 2005; Tallis et al. 2008).

It is suggested that obtaining and integrating mechanistic information about the relationships between ecosystem health and ecosystem services into EBM science will produce compelling, useful, and transparent advice for resource managers and policy makers in the GoM region and beyond.

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References

- Ainsworth, C. H. 2006. Strategic marine ecosystem restoration in northern British Columbia. Doctoral dissertation. University of British Columbia, Vancouver.
- Ainsworth, C. H., T. J. Pitcher, J. J. Heymans, and M. Vasconcellos. 2008. Reconstructing historical marine ecosystems using food web models: northern British Columbia from pre-European contact to present. *Ecological Modelling* 216:354–368.
- Arkema, K. K., S. C. Abramson, and B. M. Dewsbury. 2006. Marine ecosystem-based management: from characterization to implementation. *Frontiers in Ecology and the Environment* 4:525–532.
- Beier, C., T. Patterson, and F. Chapin. 2008. Ecosystem services and emergent vulnerability in managed ecosystems: a geospatial decision-support tool. *Ecosystems* 11:923–938.
- Carpenter, S. R., S. W. Chisholm, C. J. Krebs, D. W. Schindler, and R. F. Wright. 1995. Ecosystem experiments. *Science* 269:324–327.
- Christensen, N. L., A. M. Bartuska, J. H. Brown, S. Carpenter, C. D'Antonio, R. Francis, J. F. Franklin, J. A. MacMahon, R. F. Noss, and D. J. Parsons. 1996. The report of the Ecological Society of America Committee on the scientific basis

- for ecosystem management. *Ecological Applications* 6:665–691.
- Christensen, V., and C. J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* 172:109–139.
- Christensen, V., C. Walters, and D. Pauly. 2005. Ecopath with Ecosim: a user's guide. University of British Columbia, Fisheries Centre, Vancouver. Available: www.ecopath.org. (February 2012)
- Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11:1304–1315.
- Daily, G. C., editor. 1997. *Nature's services: societal dependence on natural ecosystems*. Island Press, Washington, D.C.
- Daily, G. C., S. Polasky, J. Goldstein, P. M. Kareiva, H. A. Mooney, L. Pejchar, T. H. Ricketts, J. Salzman, and R. Shallenberger. 2009. Ecosystem services in decision making: time to deliver. *Frontiers in Ecology and the Environment* 7:21–28.
- Das, S., and J. Vincent. 2009. Mangroves protected villages and reduced death toll during Indian super cyclone. *Proceedings of the National Academy of Sciences of the United States of America* 106:7357.
- FEMA (Federal Emergency Management Agency). 2009. Multi-hazard loss estimation methodology. Hurricane Model HAZUS*MH MR3 technical manual. Department of Homeland Security, Federal Emergency Management Agency, Mitigation Division, Washington, D.C.
- Field, J. C., R. C. Francis, and K. Aydin. 2006. Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the northern California Current. *Progress in Oceanography* 68:238–270.
- Fisheries and Oceans Canada. 2008. Estimation of the economic benefits of marine mammal recovery in the St. Lawrence Estuary. Fisheries and Oceans Canada, Policy and Economics Regional Branch, Quebec.
- Freeman, A. M. I. 2003. *The measurement of environmental and resource values: theory and methods*. Resources for the Future, Washington, D.C.
- Fulton, E. A. 2001. The effects of model structure and complexity on the behavior and performance of marine ecosystem models. Doctoral dissertation. University of Tasmania, Hobart, Tasmania, Australia.
- Fulton, E. A. 2010. Approaches to end-to-end ecosystem models. *Journal of Marine Systems* 81:171–183.
- Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2003. Effect of complexity on marine ecosystem models. *Marine Ecology Progress Series* 253:1–16.
- Fulton, E. A., A. D. M. Smith, and C. R. Johnson. 2004. Biogeochemical marine ecosystem models I: IGBEM—a model of marine bay ecosystems. *Ecological Modelling* 174:267–307.
- Fulton, E. A., A. D. M. Smith, and A. E. Punt. 2005. Which ecological indicators can robustly detect effects of fishing? *ICES Journal of Marine Science* 62:540–551.
- Gerber, L., L. Morissette, K. Kaschner, and D. Pauly. 2009. Should whales be culled to increase fishery yield? *Science* 323:880–881.
- Gulf of Maine Council Habitat Restoration Subcommittee. 2004. *The Gulf of Maine habitat restoration strategy*. Gulf of Maine Council on the Marine Environment.
- Hale, S. S., and M. Westhead. 2012. Ecosystem services in the Gulf of Maine. Pages 1–8 in R. L. Stephenson, J. H. Annala, J. A. Runge, and M. Hall-Arber, editors. *Advancing an ecosystem approach in the Gulf of Maine*. American Fisheries Society, Symposium 79, Bethesda, Maryland.
- Hannesson, R. G., S. Herrick, Jr., and J. Field. 2009. Ecological and economic considerations in the conservation and management of the Pacific sardine (*Sardinops sagax*). *Canadian Journal of Fisheries and Aquatic Sciences* 66:859–868.
- Hayhoe, K., D. Cayan, C. B. Field, P. C. Frumhoff, E. P. Maurer, N. L. Miller, S. C. Moser, S. H. Schneider, K. N. Cahill, E. E. Cleland, L. Dale, R. Drapek, R. M. Hanemann, L. S. Kalkstein, J. Lenihan, C. K. Lunch, R. P. Neilson, S. C. Sheridan, and J. H. Verville. 2004. Emissions pathways, climate change, and impacts on California. *Proceedings of the National Academy of Sciences of the United States of America* 101:12422–12427.
- Heymans, J. 2002. *The Gulf of Maine, 1977–1986. fisheries impacts on North Atlantic ecosystems: models and analyses*. Fisheries Centre Research Reports 9:128–150.
- Heymans, J. J., S. Guenette, and V. Christensen. 2007. Evaluating network analysis indicators of ecosystem status in the Gulf of Alaska. *Ecosystems* 10:488–502.

- Irish, J. L., L. N. Augustin, G. E. Balsmeier, and J. M. Kaihatu. 2008. Wave dynamics in coastal wetlands: a state-of-knowledge review with emphasis on wetland functionality for storm damage reduction. *Shore and Beach* 76:52–56.
- Kaplan, I. C., and P. S. Levin. 2009. Ecosystem-based management of what? An emerging approach for balancing conflicting objectives in marine resource management. Pages 77–96 in R. Beamish and B. Rothschild, editors. *The future of fisheries science in North America*. Springer Press, Secaucus, New Jersey.
- Kareiva, P., H. Tallis, T. Ricketts, G. Daily, and S. Polasky. 2011. *Natural capital: theory and practice of mapping ecosystem services*. Oxford University Press, Oxford, UK.
- Koch, E. W., E. B. Barbier, B. R. Silliman, D. J. Reed, G. M. E. Perillo, S. D. Hacker, E. F. Granek, J. H. Primavera, N. Muthiga, S. Polasky, B. S. Halpern, C. J. Kennedy, C. V. Kappel, and E. Wolanski. 2009. Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment* 7:29–37.
- Komar, P. D. 1998. *Beach processes and sedimentation*, 2nd edition. Prentice Hall, Englewood Cliffs New Jersey.
- Kraus, S. D., M. W. Brown, H. Caswell, C. W. Clark, M. Fujiwara, P. K. Hamilton, R. D. Kenney, A. R. Knowlton, S. Landry, C. A. Mayo, W. A. McLellan, M. J. Moore, D. P. Nowacek, D. A. Pabst, A. J. Read, and R. M. Rolland. 2005. North Atlantic right whales in crisis. *Science* 309:561–562.
- Krutilla, J. 1967. Conservation reconsidered. *American Economic Review* 57:777–786.
- Lazzari, M., S. Sherman, and J. Kanwit. 2003. Nursery use of shallow habitats by epibenthic fishes in Maine nearshore waters. *Estuarine Coastal and Shelf Science* 56:73–84.
- Levin, P. S., M. J. Fogarty, S. A. Murawski, and D. Fluharty. 2009. Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean. *PLoS (Public Library of Science) Biology* [online serial] 7:e14. DOI: 10.1371/journal.pbio.1000014.
- Likens, G. E. 1985. An experimental approach for the study of ecosystems: the fifth Tansley lecture. *The Journal of Ecology* 73:381–396.
- Link, J. S., J. K. T. Brodziak, S. F. Edwards, W. J. Overholtz, D. Mountain, J. W. Jossi, T. D. Smith, and M. J. Fogarty. 2002. Marine ecosystem assessment in a fisheries management context. *Canadian Journal of Fisheries and Aquatic Sciences* 59:1429–1440.
- Link, J. S., E. A. Fulton, and R. J. Gamble. 2010. The northeast US application of ATLANTIS: a full system model exploring marine ecosystem dynamics in a living marine resource management context. *Progress in Oceanography* 87:214–234.
- Link, J., W. Overholtz, J. O'Reilly, J. Green, D. Dow, D. Palka, C. Legault, J. Vitaliano, V. Guida, M. Fogarty, J. Brodziak, L. Methratta, W. Stockhausen, L. Col, and C. Griswold. 2008. The northeast U.S. Continental Shelf energy modeling and analysis exercise (EMAX): ecological network model development and basic ecosystem metrics. *Journal of Marine Systems* 74:453–474.
- Luck, G. W., R. Harrington, P. A. Harrison, C. Kremen, P. M. Berry, R. Bugter, T. P. Dawson, F. de Bello, S. Diaz, C. K. Feld, J. R. Haslett, D. Hering, A. Kontogianni, S. Lavorel, M. Rounsevell, M. J. Samways, L. Sandin, J. Settele, M. T. Sykes, S. van den Hove, M. Vandewalle, and M. Zobel. 2009. Quantifying the contribution of organisms to the provision of ecosystem services. *BioScience* 59:223–35.
- Mackinson, S., B. Deas, D. Beveridge, and J. Casey. 2009. Mixed-fishery or ecosystem conundrum? Multispecies considerations inform thinking on long-term management of North Sea demersal stocks. *Canadian Journal of Fisheries and Aquatic Sciences* 66:1107–1129.
- Mangel, M., and P. S. Levin. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. *Philosophical Transactions of the Royal Society B* 360:95–105.
- McLeod, K. L., and H. Leslie. 2009. *Ecosystem-based management for the oceans*. Island Press, Washington, D.C.
- McLeod, K. L., J. Lubchenco, S. R. Palumbi, and A. A. Rosenberg. 2005. Scientific consensus statement on marine ecosystem-based management. Signed by 221 academic scientists and policy experts with relevant expertise and published by the Communication Partnership for Science and the Sea. Available: www.compassonline.org/sites/all/files/document_files/EBM_Consensus_Statement_v12.pdf. (February 2012)
- MEA (Millennium Ecosystem Assessment). 2005. *Ecosystems and human well-being: current state and trends*. Island Press, Washington D.C.
- Moller, I., T. Spencer, J. R. French, D. J. Leggett, and M. Dixon. 2001. The sea-defence value of salt marshes: field evidence from north Norfolk.

- Journal of the Chartered Institution of Water and Environmental Management 15:109–116.
- Nelson, E., G. Mendoza, J. Regetz, S. Polasky, H. Tallis, D. Cameron, K. Chan, G. Daily, J. Goldstein, P. Kareiva, E. Lonsdorf, R. Naidoo, T. Ricketts, and R. Shaw. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment* 7:4–11.
- Nicholls, R. J. 2004. Coastal flooding and wetland loss in the 21st century: changes under the SRES climate and socio-economic scenarios. *Global Environmental Change Human and Policy Dimensions* 14:69–86.
- NRC (National Research Council). 2005. Valuing ecosystem services: toward better environmental decision-making. National Academies Press, Washington D.C.
- Odum, E. P. 1969. Strategy of ecosystem development. *Science* 164:262–270.
- Odum, E. P. 1985. Trends expected in stressed ecosystems. *BioScience* 35:419–422.
- Österblom, H., S. Hansson, U. Larsson, O. Hjerne, F. Wulff, R. Elmgren, and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10:877–889.
- Pimm, S. L. 2002. Food webs. University of Chicago Press, Chicago.
- Plaganyi, E. E. 2007. Models for an ecosystem approach to fisheries. Food and Agriculture Organization of the United Nations, FAO Fisheries Technical Paper 477, Rome.
- Plaganyi, E. E., and D. S. Butterworth. 2004. A critical look at the potential of ECOPATH with ECOSIM to assist in practical fisheries management. *African Journal of Marine Science* 26:261–287.
- POC. 2003. America's living ocean: charting a course for sea change. A report to the nation. Pew Trusts, Washington, D.C.
- Polovina, J. J. 1984. Model of a coral reef ecosystem. 1. The ecopath model and its application to French Frigate Shoals. *Coral Reefs* 3:1–11.
- Reed, D. C., S. C. Schroeter, and D. Huang. 2006. An experimental investigation of the use of artificial reefs to mitigate the loss of giant kelp forest habitat. A case study of the San Onofre Nuclear Generating Station's artificial reef project. California Sea Grant College Program. University of California, San Diego, California.
- Right Whale Recovery Team. 2000. Canadian North Atlantic Right Whale Recovery Plan. Prepared for World Wildlife Fund Canada, Toronto and Fisheries and Oceans Canada, Ottawa.
- Rose, K. A., J. I. Allen, Y. Artioli, M. Barange, J. Blackford, F. Carlotti, R. Cropp, U. Daewel, K. Edwards, and K. Flynn. 2010. End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science* 2:115–130.
- Rosenberg, A. A., and P. A. Sandifer. 2009. What do managers need? Pages 13–30 in K. McLeod and H. Leslie, editors. *Ecosystem-based management for the oceans*. Island Press, Washington, D.C.
- Ruckelshaus, M. H., and A. Guerry. 2009. Valuing marine ecosystems? *Marine Scientist* 26:26–29.
- Sainsbury, K. J., A. E. Punt, and A. D. M. Smith. 2000. Design of operational management strategies for achieving fishery ecosystem objectives. *ICES Journal of Marine Science* 57:731–741.
- Samhouri, J. F., P. S. Levin, and C. J. Harvey. 2009. Quantitative evaluation of marine ecosystem indicator performance using food web models. *Ecosystems* 12:1283–1298.
- Samhouri, J. F., P. S. Levin, and C. H. Ainsworth. 2010. Identifying thresholds for ecosystem-based management. *PLoS (Public Library of Science) ONE [online serial]* 5(1): e8907. DOI:10.1371/journal.pone.0008907.
- Shannon, L. J., M. Coll, and S. Neira. 2009. Exploring the dynamics of ecological indicators using food web models fitted to time series of abundance and catch data. *Ecological Indicators* 9:1078–1095.
- Smith, A. D. M., E. J. Fulton, A. J. Hobday, D. C. Smith, and P. Shoulder. 2007. Scientific tools to support the practical implementation of ecosystem-based fisheries management. *ICES Journal of Marine Science* 64:633–639.
- Srivastava, D. S., and M. Vellend. 2005. Biodiversity-ecosystem function research: is it relevant to conservation? *Annual Review of Ecology Evolution and Systematics* 36:267–294.
- Steneck, R. S., M. H. Graham, B. J. Bourque, D. Corbett, J. M. Erlandson, J. A. Estes, M. J. Tegner. 2002. Kelp forest ecosystems: biodiversity, stability, resilience and future. *Environmental Conservation* 29:436–59.
- Tallis, H., Z. Ferdaña, and E. Gray. 2008. Linking terrestrial and marine conservation planning and threats analysis. *Conservation Biology* 22:120–130.

- Tallis, H., and S. Polasky. 2009. Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. *Annals of the New York Academy of Sciences* 1162:265–283.
- Taylor, P. H. 2008. Gulf of Maine ecosystem-based management toolkit survey report. Gulf of Maine Council on the Marine Environment. Available: www.gulfofmaine.org/ebm. (February 2012).
- Turner, R. K., and G. C. Daily. 2008. The ecosystem services framework and natural capital conservation. *Environmental and Resource Economics* 39:25–35.
- USCOP (U.S. Commission on Ocean Policy). 2004. *An ocean blueprint for the twenty-first century*. USCOP, Washington, D.C.
- Vanderlaan, A. S. M., and C. T. Taggart. 2006. Vessel collisions with whales: the probability of lethal injury based on vessel speed. *Marine Mammal Science* 23:144–156.
- Vermaat, J. E., J. A. Dunne, and A. J. Gilbert. 2009. Major dimensions in food-web structure properties. *Ecology* 90:278–282.
- Vira, B., and W. M. Adams. 2009. Ecosystem services and conservation strategy: beware the silver bullet. *Conservation Letters* 2:158–162.
- Walters, C., D. Pauly, V. Christensen, and J. F. Kitchell. 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. *Ecosystems* 3:70–83.
- Walters, C. J., and S. J. D. Martell. 2004. *Fisheries ecology and management*. Princeton University Press, Princeton, New Jersey.
- Worm, B., R. Hilborn, J. K. Baum, T. A. Branch, J. S. Collie, C. Costello, M. J. Fogarty, E. A. Fulton, J. A. Hutchings, S. Jennings, O. P. Jensen, H. K. Lotze, P. M. Mace, T. R. McClanahan, C. Minto, S. R. Palumbi, A. M. Parma, D. Ricard, A. A. Rosenberg, R. Watson, and D. Zeller. 2009. Rebuilding global fisheries. *Science* 325:578–585.

