

## Construction Kits or Virtual Worlds; Management Applications of E2E models

John Steele, Woods Hole Oceanogr. Instn., Woods Hole MA 02543, [jsteele@whoi.edu](mailto:jsteele@whoi.edu)  
Kerim Aydin, Alaska Fisheries Science Center, NOAA, Seattle, Washington 98115  
Dian J. Gifford, Graduate School of Oceanography, University of Rhode Island,  
Narragansett, RI, USA.  
Eileen Hofmann, Center for Coastal Physical Oceanography, Old Dominion University  
Norfolk, VA 23508

### Abstract

We review briefly the diversity of modeling activity that comes under the rubric of end-to-end (E2E) models, but the focus of this paper – of joint concern to researchers and to managers - is on applications to management and decision making. The models and applications span a range from “construction kits” that identify particular management issues and use comparisons across ecosystems; to “virtual worlds” that immerse managers in the details of strategic evaluations for particular systems. The general conclusion is that “application” is not a straightforward transition from theory to practice but a complex interactive process.

Note This review is based on the proceedings of a workshop, held at Woods Hole Oceanographic Institution, 19-22 April 2010, as part of CAMEO (Comparative Analysis of Marine Ecosystem Organization), a program supported jointly by NOAA (U.S. National Oceanic and Atmospheric Agency) and NSF (U.S. National Science Foundation). A full report of the Workshop is available at (IMBER website).

Key words: end-to-end models; management applications; ecosystem-based management

### Introduction

The main impression from any survey of recent work on end-to-end modeling of marine ecosystems (e.g. Travers et al., 2007; Rose et al., 2010; Moloney et al., 2010) is of the great variety in types of model that may be considered as “end-to-end”. This variety derives from the very broad range of questions we ask about ecosystems – from effects of climatic change, and decreases in diversity, to declines in fish populations. Many of the questions focus on the relation between model performance and potential application.

*Do we require a different model for each ecosystem?* The proliferation of ECOPATH models (Christensen and Pauly, 1993) depends on the applicability of this method to any ecosystem without extensive reprogramming; and illustrates the advantages of a general protocol.

*Is there an optimal level of complexity for “portability”?* Hannah et al (2009) argue “the case for marine ecosystem models of intermediate complexity” in terms of the balance between number of interacting components and details of individual processes. This has been demonstrated in relation to Nutrient- Phytoplankton-Zooplankton-Detritus (NPZD) models used in carbon budgeting (Friedrichs et al, 2006, 2007).

*What is gained and lost by aggregation of species into guilds representing functions?* In part this concerns methodology (Hofmann, 2010), in part data availability (Garrison and Link, 2000) but also relates to different types of application.

*How much better does the model do than just measuring your observations?* There is great interest in “metrics” and “indicators” as management tools (Shin, et al, 2010). Do these interactions between modeled components explain trends better than simple correlations?

*How can we use predictions at the species or the community level?* Scenarios in terms of changing patterns for functional groups or guilds, may be more acceptable than estimates of abundance of individual species (Mangel and Levin, 2005; Meuter and Megrey, 2006; Auster and Link, 2009; Steele and Gifford, 2010).

*How can E2E models complement stock assessments?* This is, perhaps, the central issue in creating protocols for ecosystem-based management (Larkin, 1977; Mace, 2001; Aydin et al, 2005)

Nearly all the answers to these questions will relate to the potential or actual consequences of human activities. There is a very wide range of possible uses of the models – from insight into underlying processes that are the probable causes of change, through description of possible outcomes, to provision of statutory controls. The details of methodology are adequately reviewed elsewhere (e.g. Travers et al., 2007; Plaganyi, 2007; Rose et al., 2010; Moloney et al., 2010; Fulton, 2010). Here we focus on the applications of end-to-end models to management, and especially on the constraints that management impose on the models.

In this paper we shall (1) review extant end-to-end models in relation to their underlying rationales, (2) consider the range of applications to management and decision making, (3) enumerate the constraints imposed on managers in the use of models, and (4) recommend developments, such as skill assessment, needed to increase the relevance of end-to-end models. We shall propose that the variety of models and their various applications can be subsumed under two general categories “Construction Kits” and “Virtual Worlds”. These define the overall range but also an emerging dichotomy in application that can be valuable but needs to be recognized.

### **End-to-end models**

We consider first those studies that focus on gaining some insight into factors determining changes at the community or ecosystem level, rather than the traditional population studies that underpin management in terms of individual species. Then we describe studies that focus on the fluxes of energy within ecosystems as partially distinct from approaches that begin with detailed model of the physics. Lastly we review the emergence of very large models that attempt to embed population demography and community dynamics in detailed spatial models of the physical system combined with lower trophic level processes.

Process studies.

These studies can be considered as building blocks or construction kits for other studies. Insight into the complicated processes within food webs and their interaction with the physical and chemical environment requires a relatively simplified or integrated definition of components for both physical and ecological processes. One major trade-off involves the decision on whether to emphasize complex food web structure, or the detailed demographics of individual populations (de Young et al, 2004; Steele and Gifford, 2010). In this context an important distinction concerns the use of “guilds” rather than individual species, to represent the fish community. The lower trophic levels in food web models typically are represented by broad aggregate groupings such as micro/meso/macro zooplankton, or benthic in- and epi-fauna. For fish, should we use feeding guilds such as planktivores, benthivores and piscivores (Garrison and Link, 2000)?

An alternative is to use size as a measure of trophic status where predation is a function of the prey/predator size ratio. This is now commonly used for lower trophic levels, with phytoplankton characterized as small and large; zooplankton as micro, meso and macro. Some early food chain models (Platt and Denman, 1978) used size throughout the trophic range. Recent work (Pope et al, 2006; Hall et al, 2006) is generally restricted to fish populations, with the larger fish at higher up the trophic levels. Then there can be equivalence between size categories and diet guilds (Steele and Gifford, 2010), so that planktivores, benthivores and piscivores correspond to increasing size categories..

Are these depictions of food webs in terms of community or size structure rather than species composition (Steele et al, 2009) just a convenience for relatively simple and rapid modeling and for comparisons between ecosystems? Or is this approach a consequence of unpredictable longer-term variability in the species mix (Gifford et al, 2009)? We may consider community metrics as more appropriate for longer term analysis and prediction (Jennings and Blanchard, 2004; Mangel and Levin 2005; Perry et al. 2010; Steele and Gifford 2010), with obvious implications for management.

There is a comparable concern about a focus on physical processes. We recognize the dominant role that oceanographic processes play in the life history of nearly all marine species. Do we need to combine simulation of the details of horizontal advection with detailed representation of the vertical processes that determine nutrient input? For those parts of the food web, labeled planktonic, that are at the mercy of physical transport, there can be a direct relation between physics and population dynamics. This is of particular importance for larval fish survival where variations in advection can affect access to feeding areas or nursery grounds (Wiebe et al, 2001). In terms of fisheries management, the assumption behind the proliferation of studies of physical/biological coupling, is that events during the larval phase of the life cycle of individual fish species play a prominent role in determining recruitment and therefore the population dynamics of individual commercially important stocks. On the other hand, transport of nutrients from deep water reservoirs into the euphotic zone drives the flux of energy up the food web to fuel adult stocks and determine overall fish production, with the larger fish higher up the trophic levels.

These two themes, direct physical effects on planktonic populations, and indirect effects through nutrient fluxes to communities or guilds; underlie different ecological concepts as well as different perspectives on processes controlling fishery yields. The desire to integrate these concepts and develop management applications is the basis for the construction of end-to-end models. We first consider those approaches that have emphasized the structural aspects.

### Energy flow within food webs

Ecosystem structure has been a dominant interest of theoretical, mainly terrestrial, ecologists. Much of this interest is topological (Pascual and Dunne, 2006) and not really relevant to ecosystem management, particularly since recycling is usually excluded or minimal; whereas nutrient recycling in marine systems is recognized as an essential feature of the microbial food web (deAngelis et al, 1975). The interest in quantitative energy or nutrient fluxes through food webs began with aquatic studies (Lindeman, 1942) and has flourished in relation to estimation of fish production and fisheries yields. Early studies of food web fluxes (Steele, 1974; Sissenwine et al, 1984) were back-of-the-envelope, but recent work has developed specific methodologies. One methodology epitomizes this approach and has dominated fisheries studies, *ECOPATH with ECOSIM (EwE)*.

The EwE modeling framework, introduced by Christensen and Pauly (1993), has been very widely used and has been the main tool to provide a top-down or fishery focus for the analysis of marine ecosystems, usually incorporating a comprehensive set of fish species. The use of a linear steady state food web calculation (ECOPATH) to drive a spatially integrated dynamic simulation (ECOSIM, Christensen and Walters, 2004) allows a variety of metrics to be calculated (Gaichas et al, 2009; Link, 2008).

One strength of EwE is that the “common currency” of biomass and flow rates through food webs (regardless of units) facilitates a strong ability for interregional comparisons, and the development of “toolboxes” (standard techniques that could be applied across multiple systems with minimal modifications). Also, the scale of the models from a fisheries perspective (whole stock or ecosystem without spatial considerations) allows direct comparison of results with standard single-species stock assessment techniques and allows the models to be built with data already available from long-term stock assessment efforts. Recent developments have included the introduction of spatial compartments for the higher trophic levels (Pauly et al, 2000). Finally, the relatively quick run-time of these models, allows complex analysis of outputs, including Monte Carlo methods and formal statistical fitting techniques.

There are other energy flow models for food webs (Steele, 2009). The *INVERSE* method introduced by Vezina and Platt (1988) has had applications to various coastal environments (Richardson et al, 2004).

### Spatially focused pelagic systems

Advances in coupled physical/biological models (Wiebe et al, 2001) have focused on detailed spatial representations of the planktonic realm and on pelagic fish species, ignoring the shelf benthos. These models build on the ability to simulate physics at eddy resolving scales using circulation models, such as the Regional Ocean Modeling System (ROMS; Haidvogel et al, 2000). The focus of the dynamics in these models is primarily planktonic, with extensions to planktivore species (forage fish) through approaches such as Individual-Based Modeling (Rose et al, 2010). The dominance of fisheries for anchovy and sardine in eastern boundary upwelling has led to extensive modeling efforts (Shannon et al, 2000), showing how these can be used for multi-decadal historical simulations, and potentially for management applications. The great concern with the world-wide collapse in certain tuna stocks, has increased the interest in modeling their trans oceanic movements (Lehodey et al, 2003). A principal interest is in investigating the consequences of climatic change on patterns of mid-level pelagic production.

The increasing concerns with sustainability of some vertebrate species highlight the need for food web models to include a focus on the top trophic levels, particularly marine mammals and sea birds. These top predators can be regarded as indicators that integrate effects at lower trophic levels, as well as being very visible and iconic representatives of their ecosystems.

### Spatial Fisheries Models

The ECOPATH system of models has a spatial component for the fish populations (Pauly et al, 2000) but the main deficits in the EwE framework are the lack of structure for the microbial food web and the neglect of physical forcing of the ecosystem. These deficits can be rectified by linking different models, such as a ROMS, with a nutrient-phytoplankton-zooplankton (NPZ) module, and with the upper trophic levels from ECOPATH. (Aydin et al, 2005; Heath, 2005; Heath and Beare, 2008)

However the main new approach is a very comprehensive and detailed simulation, ATLANTIS, developed by Fulton in Australia (Fulton et al, 2004) and now being adapted for several US ecosystems (Brand et al, 2007; Link et al, 2010;). Unlike previous approaches where the physical, NPZ and fish components are developed separately and then loosely coupled, ATLANTIS has complete integration of the circulation, derived from the ROMS type physical models, with a detailed comprehensive non-linear representation of the whole ecosystem including all significant fish species. A distinguishing aspect is that these models focus on details in the spatial patterns in fisheries and economics. The development time and effort for these types of modeling system can involve a large group of researcher and programmers over three years or more (Plaganyi, 2007; Plaganyi and Butterworth, 2004). There are several hundred parameters, generally unconstrained by data. These parameters are used to “calibrate” the system to the available observations, principally the fish species. The output can represent the spatial distribution of individual fish species, their interaction with fishing fleets and their “response” to regulation. The general aim of these models in a fisheries management sense is to provide a platform on which realistic management strategy evaluations (MSE’s) can be played out (Fulton et al, 2007).

## Communicating with Users, Managers and Stakeholders

Fishing provides examples of a relatively small scale and distinct social and economic activity. For this reason the socio-economics of fisheries have elicited much theoretical consideration and a large literature in appropriate professional journals (Marine Resource Economics, Marine Policy). The practical issues involved in converting the concepts to actions by fishers, managers, regulators and other “stakeholders” is less easily referenced. This topic arouses the most interest among “hands-on” managers. Specifically, debate focuses on the problems associated with communicating the output of models to “managers and decision makers”, especially in representing the uncertainties inherent in the results. It is necessarily an interactive process requiring the construction of an agreed set of questions in a common language. The many issues and unknowns associated with this process are illustrated by the following questions:

*Do decision makers want to be given uncertainties?* There is a general sense that the output of models giving single values for Maximum Sustainable Yields (MSY) for each species are not only mandated, but are accepted by many as “the truth”. It is not the practice to put statistical limits on the MSY.

*Should capability of estimating levels of risk be a necessary criterion?* Although there is acceptance of the need to estimate risk (as probability x consequence), the inability to determine rare but extreme “black swan” events (Murawski et al, 2009) has precluded management uses. The concept of large “regime shifts” (Scheffer, 2001; Scheffer and Carpenter, 2003) is frequently used as a model for abrupt changes in fish stocks but does not yet have management application.

*Would it be useful for researchers and managers to examine jointly model scenarios?* A range of scenarios is often favored as an alternative to predictions or forecasts since these scenarios do not commit the researcher or the manager. Yet, for them to be useful as management support tools, they will need to be available at time scales appropriate for the decision makers. This can place constraints on the types of model and the resources needed to implement them.

*What approaches and safeguards need to be in place to transition a research model to one that can be used for operational or regulatory applications?* The normal scientific process of peer review may not be sufficient or even appropriate. The concept of “ecosystem based management” is accepted but more as a general framework rather than as a protocol: for example the Integrated Ecosystem Assessments (IEA’s) for Puget Sound and Chesapeake Bay (NOAA, 2008). It may take a long time before E2E models are accepted as part of the management protocol.

*Do we need experts to act as cultural facilitators between the modeling, regulatory and management communities?* It is accepted that most scientists do not communicate effectively outside their profession, and need either help from experts or training, particularly in dealing with the press on sensitive issues (Elzinga et al, 1998; Lee, 1999).

There is awareness of the need to communicate effectively to a diverse range of stakeholders but no obvious simple solutions. We need to start a long term dialog with potential stakeholders to see what they want and what would be appropriate as E2E models for IEA's.

### **Skill Assessment, Validation and Calibration**

Model skill assessment “requires a set of metrics and procedures for comparing model output with data. A model starts to have skill when the model and data uncertainty halos overlap” (Stow et al. 2009). These methods depend on data sets independent of parameter estimates for the model and on values for means and errors. Friedrichs et al (2006, 2007) has described the process of skill assessment that was applied to a suite of 12 models used in ocean biogeochemistry. Methods developed to compare the skills of different models in terms of the number of state variables (4-12), their parameter requirements and their portability (application to other systems) were estimated. The usual procedures compare: (1) different models applied to the same system, (2) the same model in different systems, or as a compromise, (3) construct the model using part of a time series and test against other parts of the time series. Data assimilation procedures can provide a valuable adjunct. Problems in adapting these types of analysis to E2E models arise in part for technical reasons; particularly the large number of heterogeneous variables, and the inadequacy of data sets. But a major issue is that these methods for skill assessment may not fit with some of the aims of E2E practitioners.

For ATLANTIS, and probably for other large complicated models such as the European Regional Seas Ecosystem Model (ERSEM: Baretta et al, 2005), the management purpose is primarily defined as providing an operational model, with some “basis of truth”, for Management Strategy Evaluations (MSE). MSE's use scenarios where, for example, different methods and levels of fishing can be simulated in varying geographical regions within an ecosystem. For these purposes, very detailed descriptions of individual fish populations are needed. To get these details, all available data for a given system are used for “calibration”.

We should recognize that calibration is quite different from skill assessment. Skill assessment does not appear to be a requirement where the focus is on recreating a very detailed representation of a particular system. In addition, a primary issue with these models would be run-time for repeated sensitivity testing. The increased development of high-performance computing (HPC) resources could facilitate these approaches.

### **Data requirements**

The general proposition that we are data limited underlies marine ecosystem research. Within this context there are a number of specific points about data that are common to most end-to-end modeling exercises:

- The major inadequacies in data to define the food web, determining overall uncertainties, are at intermediate trophic levels such as meiobenthos, gelatinous zooplankton, squid and pre-recruit fish
- Rate processes determining growth and reproduction can limit flux calculations
- Experimental data for functional responses of trophic groups, rather than individual species, are needed
- The food web effects of behavioral responses (e.g. aggregation) are lacking for fish and other top trophic levels
- Historical data for fish populations and other food web components are essential for skill assessment and for estimation of recovery measures

Present systems for data acquisition and retrieval (R. Groman, pers.comm) may not be appropriate for the problem of handling the potentially very large output from models. The requirements could be comparable to or greater than traditional data handling. A further unresolved issue for existing scientific data centers concerns the protocols for archiving sensitive and often confidential data sources related to management policies.

### **Discussion: Virtual Worlds or Construction Kits**

The range of issues raised in this brief review reflects the diversity of interests of the user in terms of insight gained versus practical application. Yet there is an aggregation around two rather different approaches – different in model structure, application and skill assessment – that might be termed *Virtual Worlds* and *Construction Kits*.

*Virtual Worlds*. One important use of models is as intermediaries or decision support tools between the “researcher” and the “decision maker”. For such models to play a full role, the questions that can be asked of them and their answers, or scenarios, should appear as realistic as possible. However, the large number of parameters, spatial detail, and extensive calibration associated with these models are likely to make them opaque to other practitioners. In certain situations, this may be a minor inadequacy compared with the value as a communication tool, similar to what has been done with climate models. The “skill” is in the ability to convey, realistically, possible consequences of management actions involving interventions in fishing practice, particularly, Marine Strategy Evaluations and Marine Spatial Planning. For example Fulton et al (2007) have used the south-eastern Australia model to quantitatively evaluate alternative management packages of quotas, protected areas and closed seasons. Kaplan et al (2010) have used an ATLANTIS model for the California Current ecosystem to determine the consequences of ocean acidification exemplified by increased mortality of shelled benthos. The authors point out that model results in terms of long term reduction in catch of specific fish stocks is more likely to have an impact on managers than forecasts of community effects. This has to be set against the complexity and long run times of ATLANTIS that deter the estimation of uncertainty (Kaplan et al, 2010). Given the great detail and the effort



required to build these large models, it is not clear how they could be used routinely to explore the causes of differences between ecosystems, or the consequences of large changes within ecosystems such as those arising from climatic trends. This aspect is a challenge for future work.

*Construction Kits.* The alternative approach covers the variety of possible food web models that can be assembled; and the consequences for input/output relations of changing internal processes such as variable nutrient recycling, seasonal and inter-annual patterns in upwelling, and the effects of increases in gelatinous zooplankton or rare species on the rest of the food web. For these purposes, and for portability, the physical processes determining nutrient input are caricatured to emphasize particular critical features, and the trophic components are kept at the functional or guild scale of aggregation (Hofmann, 2010). Concepts such as the “Minimum Realistic Model” and “Intermediate Optima” (Hannah et al, 2009) attempt to capture this approach but it is not apparent how such concepts relate to possible uses or applications. The various types of simplification can aid comparison of ecosystems or skill assessment but it is often difficult to see how such models relate directly to management questions. This is a major challenge in the context of programs for ecosystem-based management.

To use a cliché, the elephants in discussions are the highly developed single species stock assessment methods that are, and will remain, the mainstay of regulatory measures. For “managers” these methods are closest to “truth”. Alternate E2E models must compete for that role. In an ecosystem context stock assessment models may be considered as an end point of the so-called “rhomboid” approach, (de Young et al., 2004) that proposed focusing attention on one trophic level, using age structured populations; and restricting detail above and below this level. The construction kits are intended to complement the single species models. The virtual worlds attempt to incorporate them.

## Conclusions

Certain general, and generally accepted, conclusions emerge from this review.

- (1) There is a wide range of models that can fit under the E2E rubric. Many potential proponents are not represented here; in particular the more conceptual and topological approaches to food web theory (Pascual and Dunne, 2006).
- (2) This diversity is valuable and should be encouraged. There is consensus that no single package of models is preferable.
- (3) The diversity arises from the variety of possible applications or uses. Simple categories such as “tactical” and “strategic” seemed inadequate

- (4) The applications require long-term interaction with stakeholders. These processes merit more study across research and user communities. It should not be assumed that the interactions will happen automatically after the modeling science is done.
- (5) In particular, specialist help or instruction in the transfer from research to regulation may be necessary. This is not cheap but is not usually budgeted.
- (6) Testing of the models is a complex process and differs for different models. There needs to be more work on skill assessment and, particularly, on risk analysis – a topic barely touched on here.

Discussion of these general conclusions often relates to the two categories of models – construction kits and virtual worlds. These two main approaches might be labeled *academic* and *operational*. As discussed, there are significant questions relating to improvements in both approaches in terms of skill assessment and in the ability to communicate results. But the major unresolved issue is whether these two approaches should continue on parallel tracks. Thus, a central issue for ecosystem-based management is how to focus activities on integrating these two approaches (and their associated research communities) so that they became complementary rather than parallel, non-interacting activities.

#### **Acknowledgements**

We wish to thank the following for discussions that provided essential material for this review.

Tosca Ballerini, Richard Brodeur, Fei Chai, Daniel Costa, Jeremy Collie, Jerome Fiechter, Marjorie Friedrichs, Sarah Gaichas, Watson Gregg, Robert Groman, Michael Heath, Porter Hoagland, Thomas Ihde, Di Jin, Isaac Kaplan, Kelly Kearney, David Mountain, Raghu Murtugudde, Kenneth Rose, Tammi Richardson, Eric Thunberg, Howard Townsend.

#### **References**

- Auster, P.J. and Link, J.S. 2009. Compensation and recovery of feeding guilds in a northwest Atlantic shelf fish community. *Mar. Ecol. Prog. Ser.* 382, 163-172.
- Aydin, K., McFarlane, G. A., King, J. R., Megrey, B. A., and Myers, K. W. 2005. Linking oceanic food webs to coastal production and growth rates of Pacific salmon (*Oncorhynchus* spp.), using models on three scales. *Deep Sea Research, II*, 52: 757–780.
- Baretta, J.W., Ebenhoh, W., and Ruardig, P. 1995. The European-Regional-Sea-Ecosystem-Model, a complex marine ecosystem model. *Neth. J. Sea. Res.* 33:233-246.
- Brand, E.J., Kaplan, I.C., Harvey, C.J., Levin, P.S., Fulton, E.A., Hermann, A.J., Field, J.C. (2007) A spatially explicit ecosystem model of the California Current's food web and oceanography. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-84, 145 p.
- Christensen, V. and Walters, C.J. (2004) Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.*, **172**, 109-139.

- Christensen, V., Pauly, D. (Eds.), 1993. Trophic models of aquatic ecosystems. The International Center for Living Aquatic Resources Management (ICLARM) Conference Proceedings, vol. 26. ICLARM, Manila, Philippines
- DeYoung, B., Werner, F., Chai, F., Megrey, B. & Monfray, P. 2004. Challenges of modeling ocean basin ecosystems. *Science*, 304: 1463-1466.
- Elzinga, C.L., Salzer, D.W. and Willoughby J.W. 1998. Measuring and monitoring plant populations. Bureau of Land Management. BLM Tech. Ref. 1730-1.
- Friedrichs, m., Dusenberry, J., Anderson, L., Armstrong, R., Chai, F., Christian, J., Doney, S., Dunne, J., Fujii, M., Hood, R., McGillicuddy, D., Moore, J., Spitz, Y. and Wiggert J. 2007. Assessment of skill and portability in regional marine biogeochemical models; the role of multiple planktonic groups. *J. Geophys. Res. Oceans*. 112, C08001.
- Friedrichs, M Hood, R. and Wiggert, J. 2006. Ecosystem model complexity versus physical forcing; quantification of their relative impact with assimilated Arabian Sea data. *Deep-Sea Res.* 52, 576-600.
- Fulton, E.A. 2010 Approaches to end to end ecosystem models. *J. Mar. Sys.* 81, 171-183.
- Fulton, E., Smith, A., Johnson, C. 2004. Biogeochemical systems models I: IGBEM – a model of marine bay ecosystems. *Ecological Modelling*. 174, 267-307.
- Fulton, E. A., and Smith, A. D. M. (2007). Lessons learnt from a comparison of three ecosystem models for Port Phillip Bay, Australia. *African Journal of Marine Science*, 26: 219-243.
- Gaichas, S., Skaret, G., Falk-Petersen, J, Link, J., Overholtz, W., Megrey, B., Gjørseter, B., Stockhausen, W., Dommasnes, A., Friedland, K. and Aydin, K. 2009. A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics *Prog. In Oceanogr.* 81, 47-62.
- Garrison, L.P. and Link, J.S. 2000. Dietary guild structure of the fish community in the north-east United States continental shelf ecosystem. *Mar. Ecol. Prog. Ser.* 202:231-240.
- Gifford, D. J., Collie, J. S., Steele, J. H. 2009. Functional diversity in a marine fish community. *ICES Journal of Marine Science*, 66, doi:10.1093/icesjms/fsp076
- Haidvogel, D. B., H. G. Arango, K. Hedstrom, A. Beckmann, P. Malanotte-Rizzoli, and A. F. Shchepetkin 2000, Model evaluation experiments in the North Atlantic Basin: Simulations in nonlinear terrain-following coordinates, *Dyn. Atmos. Oceans*, 32, 239-281.
- Hall, S.J., Collie, J.S., Duplisea, D.E., Jennings, S., Bravington, M., Link, J. 2006. A length-based multispecies model for evaluating community responses to fishing. *Can. J. Fish Aquat. Sci.* 63, 1344-1359.
- Hannah, C., Vezina, A. and St John, M. 2010. The case for marine ecosystem models of intermediate complexity. *Prog. Oceanogr.* 84, 121-126
- Heath, M.R. 2005. Changes in the structure and function of the North Sea fish food web, 1973-2000, and the impacts of fishing and climate. *ICES Journal of Marine Science*, 62, 847-868.
- Heath, M.R. and Beare, D.J. (2008). New primary production in northwest European seas, 1960- 2003. *Mar. Ecol. Prog. Ser.* 363: 183-203.
- Hofmann, E.E. 2010. Plankton functional groups – an assessment. *Prog. Oceanogr.* 84, 16-19
- Jennings, S. and Blanchard, J. 2004. Fish abundance with no fishing: predictions based on macroecological theory. *Journal of Animal Ecology*. 73:632-642.
- Kaplan, I., Levin, P., Burden, M. and Fulton, E. 2010. Fishing catch shares in the face of

- global change: a framework for integrating cumulative impacts and single species management. *Can.J. Fish. Aquat. Sci.* 67, 1968-1982.
- Larkin, P.A. 1977. An epitaph for the concept of maximum sustainable yield. *Trans. Amer. Fish Soc.*, 106, 1-11.
- Lee, K.N. 1999. Appraising adaptive management. *Cons. Ecol.* 3, 3.
- Lehodey P., Chai F., Hampton J. (2003). Modelling climate related variability of tuna populations from a coupled ocean-biogeochemical-populations dynamics model. *Fisheries Oceanography*, **12**(4): 483-494
- Lindeman, R.I. 1942. The trophic-dynamic aspect of ecology. *Ecology*, 23: 399-418.
- Link, J.S, Fulton, E.A. and Gamble, R.J. 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., Overholtz, W., O'Reilly, J., Green, J., Dow, D., Palka, D., Legault, C., Vitaliano, J., Guida, V., Fogarty, M., Brodziak, M., Methratta, L., Stockhausen, W., Col, L., Griswold, C. 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  
doi:10.1016/j.jmarsys.2008.03.007
- Mace, P.M. 2001. A new role for MSY in single-species and ecosystem approaches to fisheries assessment and management. *Fish and Fisheries*, 2, 2-32.
- Moloney, C., St John, M., Denman, K., Karl, D., Koster, F. Sundby, S., Wilson, R., 2010. Weaving marine food webs from end to end under global change. *J. Mar. Sys.* 84, 212-229.
- Mangel, M. and Levin, P.S. 2005. Regime, phase and paradigm shifts: making community ecology the basic science for fisheries. *Phil. Trans. Roy. Soc. B* 360:95-105
- Meuter, F.J. and Megrey, B.A. 2006. Using multi-species surplus production models to estimate ecosystem-level maximum sustainable yields. *Fish. Res.* 81, 189-201.
- Murawski, S., Steele, J., Taylor, P., Fogarty, M., Sissenwine, M., Ford, M., Suchman C. 2010. *Why compare marine ecosystems? ICES Journal Marine Science*; 67, 1-9.
- NOAA. 2008. Integrated ecosystem assessments. NOAA Tech. Memo. NMFS-NWFSC-92
- Pascual, M. and Dunne, J.A. 2006. *Ecological Networks: linking structure to dynamics in food webs.* Oxford University Press, USA.
- Pauly, D., Christensen, W. and Walters, C. 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries *ICES J. Mar. Sci.* (2000) 57 (3): 697-706.
- Perry, R.I., Cury, P., Brander, K., Jennings, S., Mollmann, C. and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and management response. *J. Mar. Sys.* 79, 427-435.
- Plaganyi, E.E. 2007. Models for an ecosystem approach to fisheries. *FAO Fisheries Technical Paper* 477.
- Plaganyi, E.E. and Butterworth, D.S. 2004. A critical look at the potential of ECOSIM with ECOPATH to assist in practical fisheries management. *Afr. J. Mar. Sci.* 26, 261-287.

- Platt, T and Denman, K. 1978. The structure of pelagic marine ecosystems. *Rapp. P.-V. Reun. Cons. Int. Explor. Mer*, 173, 60-65.
- Pope, J.G. Rice, J.C., Daan, N., Jennings, S., Gislason, H. 2006. Modelling an exploited marine fish community with 15 parameters – results from a simple size-based model. *ICES J. Mar. Sci.* 63, 1029-1044.
- Richardson, T., Jackson, G, Ducklow, H. and Roman, M. 2004. Carbon fluxes through food webs of the eastern equatorial Pacific: an inverse approach. *Deep-Sea Res. I.* 51, 1245-1274
- Rose, K.A. (and 25 others). 2010. End-to-end models for the analysis of marine ecosystems: challenges, issues and next steps. *Marine and Coastal Fisheries*, 2: 115-130.
- Scheffer et al, 2001. Catastrophic shifts in ecosystems. *Nature*, 413:591-596
- Scheffer, M and Carpenter, S. 2003. Catastrophic regime shifts in ecosystems: linking theory to observations. *Trends in Ecology and evolution*. 18:648-656.
- Shannon, L. J., Cury, P., & Jarre, A. (2000) Modelling effects of fishing in the Southern Benguela ecosystem. *ICES Journal of Marine Science*, 57: 720–722.
- Shin, Y-J., Rochet, M-J., Jennings, S., Field, J.G. and Gislason. 2010. Can simple be useful and reliable? Using ecological indicators to represent and compare the states of marine ecosystems. *ICES J. Mar. Sci.* 67, 717-731.
- Sissenwine, M.P., E.B. Cohen, and M.D. Grosslein. 1984. Structure of the Georges Bank ecosystem. *Rapp. P.-v. Réun. Cons. int. Explor. Mer* 183:243-254.
- Steele, J.H. 1974. The structure of marine ecosystems. Harvard University Press. Cambridge, Mass. 128 .
- Steele, J.H. 2009. Assessment of some linear food web methods. *Journal of Marine Systems*, 76: 186-194.
- Steele, J.H., Collie, J.S. Bisagni, J., Fogarty, M., Gifford, D., Link, M., Sieracki, M., Sullivan, B., Beet, A., Mountain, D., Durbin, E.G., Palka, D. and Stockhausen, W.. 2007. Balancing end-to-end budgets of the Georges Bank ecosystem. *Progress in Oceanography* 74: 423-448.
- Steele, J.H. and Gifford, D.J. 2010. Reconciling end-to-end and population concepts for marine ecosystems. *J. Mar. Sys.* 83, 99-103.
- Steele, J.H. and Ruzicka, J.J. (2011) Constructing end-to-end models using ECOPATH data. *J. Mar. Sys.* 87, 227-238.
- Stow, C., Joliff, J., McGillicuddy, D., Doney, C., Allen, J., Friedrichs, M., Rose, K. and Wallhead, P. 2009. Skill assessment for coupled biological/physical models of marine systems. *J. Mar. Sys.* 76, 4-15.
- Travers, M., Shin, Y., Jenning, S., Cury, P., 2007. Towards end-to-end models for investigating the effects of climate and fishing in marine ecosystems. *Prog. Oceanogr.* 75, 751-770.
- Vezina, A. R. and T. Platt. (1988). Food web dynamics in the ocean I. Best estimates of flow networks using inverse methods. *Mar. Ecol. Prog. Ser.* 42:269-287.
- Wiebe, P. H., Beardsley, R. C., Bucklin, A. C., and Mountain, D. G.(Eds) 2001. Coupled biological and physical studies of plankton populations: Georges Bank and related regions. *Deep Sea*

