An Overview of Ecosystem Models Germane to Whale Population Issues

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ABSTRACT

A plethora of ecosystem models have been developed for marine ecosystems in the past couple of decades; many of them have been developed and applied in the context of either biogeochemical cycles (coupled biophysical models) or living marine resource management (fisheries ecosystems). Yet not all of them are relevant to the issues facing whale populations, nor are all ecosystem models applicable to all types of questions being posed in a whale-oriented context. Some of the key questions for whales in an ecosystem include: What species and fisheries can potentially compete with whale feeding? How would one evaluate the potential magnitude of such competition? What are the potential, indirect food web effects on whales? What are the ecosystem tradeoffs that most warrant evaluation? What are the best scenarios (to model) to mitigate any of these concerns? How well do such (simulated) scenarios perform? Here I provide a brief review of the major ecosystem model classes being employed globally in an ecosystem-based management context, provide a map of ecosystem model classes as they relate to these and similar questions, and note how global best practices are being adopted in the use of these ecosystem models. I note that other environmental features are also possible to elucidate with these models, but here largely focus on ecological interactions from a trophodynamics perspective. Several commentaries on strengths and weaknesses of these models have been developed in other venues, and a brief review and summarization is warranted. Arguably one of the key observations is to ensure that intended model uses map to the questions being addressed, and I thus note the ecosystem modeling universe to do so.

KEYWORDS

Bioenergetics, multi-species, trophodynamics, environmental effects, ecosystem-based management, model use, living marine resources

Ecosystem Models: A Brief Introduction

The use of models has recognized value in marine science, particularly for living marine resources (Fennel and Neumann 2004, Megrey and Moksness 2009). Modeling approaches provide a means to: (1) collate and integrate a broad array of data; (2) evaluate the relative importance of several concurrent processes; (3) test hypotheses concerning ocean system structure and functioning; (4) formalize hypotheses; and (5) produce predictions of both scientific and resource management interest.

There are a plethora of ecosystem models (EMs) used in a living marine resource (LMR) management context. As such, several reviews of EMs have been conducted, with best practices for conducting, executing and using EMs and their outputs emerging (Hollowed et al. 2000, Whipple et al. 2000, Plagányi 2007, FAO 2008, Townsend et al. 2008, Link et al. 2010a). There are several types of uses of these EMs, but typically the rationale and application of EMs in this context tends to be for one of few general reasons: to provide further ecological or environmental realism to stock assessments of LMRs; better capture the dynamics of processes impacting stock dynamics; better characterize the role of a particular species, stock or group of species in the marine food web/ecosystem; or to better explore tradeoffs among component biota or ocean-uses for a particular ecosystem. Certainly there are other possible applications, but these general topics cover the majority of EM uses that have been reviewed. Essentially, the scientific community realizes that there are broader impacts to LMR populations than solely harvest and that LMRs, or harvesting thereof, can have notable impacts to the broader ecosystem (Link 2010a).

Certainly each class of EM has its own strengths and weaknesses (Plagányi 2007, FAO 2008, Link et al. 2010a). One of the key lessons for EM best practices is to ensure that the class of EM chosen matches an appropriate use. Further discussions as to best practices for fitting, tuning, addressing uncertainty, handling EM output, structuring EMs, evaluating best functional forms, presenting EM results, validating EM outputs, and use of EMs and their outputs for both tactical and strategic LMR management are clearly ongoing. Yet these discussions are beginning to coalesce about themes and protocols that are increasingly acceptable to the marine EM community at large as standards for use (FAO 2008, Hill et al. 2007, Link et al. 2010a, in press, Lynch et al. 2009, Regan et al. 2005, Steele et al. in press, Stow et al. 2009). Engagement with climate and physical oceanographic modeling communities (e.g. Stock et al. 2011) has informed some of the best practices for LMR-oriented ecosystem modeling. Here I do not repeat the range of best practices found in the cited references, but briefly note the main strengths and weaknesses of each general model class typically applied in LMR contexts.

With the advent of enhanced computing power (Megrey and Moksness 2009) and widely available software, problems of misuse and misparameterization of EMs are also increasingly encountered (e.g. Link 2010b). Often this misuse, general lack of rigor and poor treatment of EM results has limited the utility—or perceptions thereof—of EMs and the ability of their outputs for informing LMR management bodies. Several best practices are emerging to add rigor to the evaluation and review of EMs (Link 2010b, Link et al. 2010a, Stow et al. 2009). Yet the EM community also does not want to apply standards of use that are inappropriate or needlessly constraining depending upon the intended use of any particular EM application. Striking the balanced between analytical rigor and pragmatic application of EM use is warranted. My aim here is to help the Whaling EM Working Group's examination of EMs see the need for that balance, doing so by highlighting a few suggested steps for ensuring that any choice of EM to use in a whale management context is both rigorous and appropriate.

A Brief and General Description of Model Classes

Again, there have been very useful summaries of the range of ecosystem models that are germane for EBFM (Hollowed et al. 2000, Whipple et al. 2000, Plagányi 2007, Townsend et al. 2008, FAO 2008). These models cover the gradient noted in Link (2002b; his Figure 1) from single species (SS) to full system models, with numerous modeling options along that gradient of complexity and realism. At various points along that gradient, multiple models can address a range of questions or issues. Again and as noted in Townsend et al. (2008, their Table A.3), the types of model classes being employed need to correspond to the appropriate set of questions and issues.

A number of extended single species assessment models (ESAMs) have been developed (Hollowed et al. 2000, Whipple et al. 2000, Plagányi 2007, Townsend et al. 2008) through add-ons to single species formulations to account for predation, consumptive demands, or the environment in a single species assessment model. These have been both age- or stage-structured and bulk biomass or production models. The purpose of these ESAMs has ranged from providing context for stock biomass estimates, providing tuning indices, serving as sources of other mortality, informing modifications to key parameters, serving as "reality checks" for estimates of magnitude of population estimates, and even providing explicitly modeled estimates of predation mortality. Typically for a whale context, these have been to link various biophysical features to whale abundance and to a lesser extent whale population vital rates. The positive aspects of this approach are that such models are relatively simple conceptually and operationally, use extant data, are implemented in a familiar assessment and management context, provide familiar (albeit modified) model outputs amenable to calculating biological reference points (BRPs), improve the biological realism of assessment models, and help to inform and improve stock assessments for species that may have been difficult to assess in the past. The negative aspect is that, like all minimal realistic models, they may be missing a suite of non-linear responses caused by not including the full suite of complex interactions involved in a real-world ecosystem. They also have the potential to be controversial, by producing more conservative BRPs and emphasizing the potential for competition between predators and fleets that target these stocks. Further, they do not have the fuller modeling capability to completely address the full set of trade-off issues.

A suite of multispecies models are another class of "minimal realistic models" similar to ESAMs, have similar constraints and properties, but are distinct from single species focused ESAMs in that they model a group of organisms, and their population dynamics, simultaneously. The pros of this approach are that it captures more processes and species simultaneously and provides BPRs commonly used. The negatives are that it still does not capture every process that can affect LMRs, nor is it able to model tradeoffs among stocks or ocean-uses, and several of the functional forms of key processes are highly debated. Examples germane to whaling are the documented use of marine mammals in MSVPA, GADGET, MS-Production approaches. There are aggregated versions of the general MRM approach that are having increasingly demonstrated utility (e.g. Link et al. 2010b).

Biophysical and biogeochemical models are employed that include upper trophic levels like whales. However, only the former tends to explore how oceanographic features such as frontal boundaries influence whale distribution. One is hard pressed to think of an example where either model class has been used to inform LMR management advice, and these tend to be more heuristic or exploratory in nature.

Food web or energy transfer models have had a wide use in LMR contexts. Chief among them would be the Ecopath with Ecosim (EwE) model has been widely used to describe aquatic systems and to explore the impacts of fishing ecosystems (Christensen et al. 2005). It is composed of a mass balance model (Ecopath) from which temporal (Ecosim) and spatial (Ecospace) dynamic simulations can be developed. Yet I would be remiss if I did not note that there are several other food web models, with a degree of similarity to EwE like Econetwrk but also including qualitative food web models that explore signed digraphs. Typically data requirements for these models include estimates of biomass, production and consumption rates, catch and diets. The major advantages of this approach are that it encompasses the whole ecosystem and is conceptually simple, versatile, accessible and adaptable. The cons of this approach are that because of the widespread availability EwE, it can be misused. It also requires a plethora of data and parameters to initialize the model that are not routinely collected, either in terms of process or taxa group, in a LMR context.

Finally, there are full system or "whole of system" models that seek to evaluate LMRs in the context of all the potential uses of a marine ecosystem. Examples include Atlantis, In Vitro, NEMURO.FISH, SEPODYN, APECOSM, and similar approaches that all seek to model the full range of dynamics of a marine ecosystem. The data and inputs needed to parameterize and calibrate these full system models are too numerous to list in detail here, but we provide a general outline. Flowfields and physical forcing time series (temperature, salinity, etc.) are required for the hydrodynamics. Nutrient inputs and primary productivity estimates are required for the lower trophic levels. Geographically proportioned biomass, catch, effort and discard time series are required, as are vital rates (growth, consumption, etc.) for each of the functional groups at the mid to upper trophic levels. More detailed information on parameterization, calibration and scenario testing is typically required in each case. The advantage of system models is that they can generally incorporate multiple forms of myriad processes, can emphasize those considerations and processes most appropriate for a given system, and can be used to evaluate management decisions to provide insight into what might happen in a real system; i.e., as an operating model in an MSE context. Another advantage is that they cover a wide range of biota and can be flexible or adaptive to a range of key factors. The chief negative aspect of these system models is that they can be unwieldy in their complexity and take an inordinate amount of time to parameterize, initialize, calibrate, and run any particular application. Additionally, the validation routines and capabilities of are minimal at best, requiring much further improvement. Further exploration of appropriate model skill metrics to validate calibration is still quite rudimentary.

From this rather brief description, one can see that there are indeed a wide range of EMs appropriate for a wide range of LMR uses.

Whale-Oriented Issues

Based upon first principles and discussions with the EM Working Group organizers, there are a suite of questions that arise when thinking about ecosystem issues that can affect or be affected by whales.

The first question is: what species and fisheries can potentially compete with whale feeding? This can be thought of in two parts: Directly there are forage/lower trophic level species (fishes & invertebrates) eaten by whales and targeted by fisheries. Examples include species such as herrings, hakes, sardines, anchovies, mackerels, squids, krill, shrimp, capelin, etc. Indirectly there are fishes targeted by fisheries that consume the same forage as whales. These include many upper trophic level species and their associated fisheries. Identifying the probable areas for competition among whales and fisheries is somewhat trivial. How to address it is not.

How would one evaluate the potential magnitude of such competition? For a first order examination, I submit that one would need an evaluation of: forage demand for whale populations, and diet compositions and hence predatory removal of prey by whales; fisheries catches; size composition of eaten and caught prey helps; and biomass estimates of prey/targeted species; spatio-temporal overlap among whales and fisheries. There are a suite of both statistical and simulation approaches germane here that one could employ. I should also note that a range of functional forms are an important consideration, particularly if predicting consumption based upon prey density. The salient point is that here one is attempting to evaluate the following inequality:

$$\rho_{is} \cdot \alpha M_{is}^{\beta} \cdot N_{is} \cdot DC_{ijs} \geq q_{jf} \cdot E_f \cdot B_j \geq \psi? \qquad \text{(EQ 1)}$$

where the first combined term is whale prey consumption, the second is fishery removal, and the final is some threshold (ψ) beyond which the prey population would collapse.

For a second order examination of the same issue, one would need an evaluation of: forage demand for whale populations, fishery catches, etc. (same as 1st order exam), but also; have this information embedded in some network/food web model with measured flows over time; and would need to track throughput and indirect effects metrics. Again, there are a suite of both statistical and simulation approaches germane here. The point of this evaluation is to examine the indirect and unanticipated, often termed “counter-intuitive”, effects of fishing and whale population competition and the associated results of various levels that explore scenarios thereof. A key test here, one that I have never seen examined, would be to attempt to “crash” a system in a food web or full system model by iteratively adding in whale populations to see what the system could support (historical sensitivities) before effects trickle through to other facets of the food web. And the converse, whereby whales are iteratively removed until indirect measures of tropic balance are exceeded. Not that either extreme would be actually practiced nor recommended, rather that it would afford a virtual, simulated test to bound the question.

On a related note, what are the ecosystem tradeoffs that most warrant evaluation? Some issues worth exploring are noted here: adequate food for whale populations, especially those undergoing recovery; estimates of mortality (predatory removal) on key forage stocks; and identification and preliminary scoping of potential areas (in time and space) and resources (i.e. forage) of competition or conflict between whales and human uses (fisheries, navigation). These would all be considered cognizant of the effects of climate change and other marine ecosystem drivers. Specific evaluation of the tradeoffs is a strategic, not tactical, exercise. But one can see that competing objectives would need to be assessed concurrently.

I note that to address many of the facets of these issues, an evaluation of whale feeding is needed. A more detailed treatment of this topic (and the first term in EQ 1 above) is covered in WP/SC64/EM2. In that WP, the following questions are addressed: How much do whales eat (and how do we measure this)? What is adequate forage for whales (and what to look for)? How does whale distribution and abundance effect these estimates?

These and similar issues are arguably the core set of data and parameters from which one can begin to address these other issues.

From these types of issues, how to evaluate scenarios arises. Thus, what are the best scenarios (to model) to mitigate any of these concerns? Without going into specifics, bracketing the issues associated with these tradeoffs into best, worst, median case scenarios tends to be a recommended best practice. One can imagine the full range of scenarios to explore, but one would need to do so very much recognizing that although the scenarios are going to provide directional and strategic advice, they are generally not likely apt to be able to provide tactical thresholds. Thus, usually an energy transfer or full system model helps here, beyond a more statistical approach. Further, an adaption of an MP approach could be applied here to explore a range of tradeoff scenarios, using the more complex model types. Additionally, one would need to examine how well do such (simulated) scenarios perform. Where possible, statistical diagnostics are preferred; but that is not always possible. So *a priori* tolerance criteria, agreed upon before presenting EM scenario results, are needed. Here a wide range of vetting and calibration techniques are possible, but using at least some form of them for use of these EMs would be mandatory.

The prior issues addressed the issue of competition between whales and fisheries or the broader system context within which tradeoffs need to be explored. Both are important and often gain high public profile. Another important issue is to examine how whale populations themselves are impacted by other factors in an ecosystem beyond solely harvesting or other, direct mortality events. That is, what are the potential, indirect food web effects on whales? Examples of how this could influence whale populations include: inadequate forage base; slower growth; lowered reproduction; shifting to sub-optimal prey; shifting to feeding grounds further afield; shunting of energy to alternative pathways; subtle but critical increase in energetic costs; indirect, cascading effects; trophic collapses of a system; or delayed population recoveries. How these subtle effects of the food web impact whales merits consideration but has not commonally been reported.

I also note that there are several other issues worth noting beyond the more ecological or trophic-focused items raised here. I briefly note them, but have not addressed them in any fuller extent. For instance, how do/will/are whales responding to climate change? How does whale distribution respond to environmental shifts? How does whale abundance, mortality and growth respond to environmental shifts? Clearly these questions warrant continued consideration and merit thorough examination as singular topics.

The central mandate of the IWC Ecosystem Modeling Working Group is to consider models that are relevant to the IWC's evaluation of special permit whaling (the Revised Management Procedure (RMP) for setting catch limits). This generally falls under the scope of stock assessment and management science more than EMs, as such some of the ESAMs seem particularly germane. Yet specifically this mandate would lead one to prioritize those ecosystem effects that can influence estimates whale populations as measured by key BRPs (e.g. MSY). This leads the conversation to focus upon how best to map EMs to intended uses.

Mapping uses to models

If one peruses Table 1, four features emerge. First, the effects of the ecosystem, be they ecological or environmental, on LMRs are different than the effects of LMRs on the ecosystem and in some instances require different types of models. Second, evaluating a suite of system-level features tends to emphasize the more aggregative, food web or systemic types of models, which can actually be quite useful for whale-oriented issues. Third, addressing tradeoffs at various levels similarly tends to suggest application of more complex models than SS or MS approaches. Finally, most of the models can serve as operating models for a management procedure/ management strategy evaluation context, particularly the more complex models, but only the SS and MS classes of models directly address issues impacting BRPs for individual stocks. None of this is surprising or revealing. Yet it is worth noting to avoid potential misuse of EMs.

Expanding this more general approach to specific questions pertinent to the IWC, one can examine Table 2. Therein whale-related issues are mapped to the various EM model classes. Those issues exploring impacts to whales tend to require the more species or stock-oriented approaches. Those issues exploring tradeoffs at a broader level tend to require the more aggregated, food web or system level models. Of note is that almost all the questions here could benefit from a food web or full system model, save those evaluating specific, tactical outputs for an RMP context. Multispecies models also have multiple applications germane to the issues noted here. Even the RMP evaluation would benefit from broader context provided by the more complex models. Again, nothing in these tables is novel or particularly insightful, but the exercise merits doing solely to force one to think about the intended use of a model for a particular question.

As the IWC EM Working Group focuses upon those features most apt to influence BRPs for an RMP context, it is apparent that some form of a minimal realistic model seems warranted, be it an ESAM or MS model. Yet the need for contextual and background information, and especially evaluating tradeoffs and indirect effects from the RMP scenarios, would also imply the need to explore a food web or full system model as well. Of course all these generalities depend upon the specific questions being posed, the data available, and the particular EM modeling package being proposed for use in any given situation. How one would execute any ecosystem modeling effort in a particular instance would benefit from following the general protocols, principles and emerging best practices, but the LMR community has been adamant about retaining flexibility for any particular situation so as to best model a set of species, questions and hypothesis. I concur with that need for flexibility and provide this cataloguing of models with potential uses as a suggested guideline to help inform and ensure EM best practices are considered.

Recommendations and Future Work

To conclude, I provide a set of recommendations that the IWC EM Working Group could consider as guidelines for future ecosystem modeling efforts. First, I strongly recommend that an EM application map the question to an appropriate class of model. Failure to do so could result in spurious results, mis-application of model outputs, and continued lack of rigor and hence application of EMs in situations where they could be useful. Ultimately there will be continued pressure to use EMs to support a wide range of positions and hypotheses. What I am recommending is to ensure that EMs are used for the correct and intended purposes they were designed for.

Second, I would recommend that the when EM output requires evaluation in specific cases, that the right review venues and protocols be establish and empanelled. Too often EM outputs are reviewed in the wrong venue or by the wrong set of expertise. Consideration of how ecosystem features impact whale stocks could be evaluated in existing review venues, but the review panel would by necessity require those with oceanographic, ecological or environmental expertise beyond the standard stock assessment experts. Conversely, if the considerations were focusing upon broader tradeoffs and systemic-level issues, perhaps a similar but distinct venue would be warranted apart from the typical stock assessment review procedures as these EM outputs would be much more strategic in nature. In either case, I endorse an MP/MSE approach as it would help frame the issues under review.

Such review processes for EMs would generally need to ensure that there is adequate rigor to the review of EM outputs, but also EM inputs such as structural choices, input data and parameterizations. Ensuring such inputs and initial values are as robust and rigorously evaluated as EM outputs is critical. These EM initializations need to be supportable with extant data and theory and clearly document how tuning or calibration occurred, and what such tuning criteria actually were. Uncertainty of EMs also needs to be characterized for evaluation in such reviews. Finally, for reasonable acceptance for use, EM outputs require some form of validation or vetting. Clearly these are good practices for any LMR modeling context, but the EM community has only recently begun to adopt them. Insistence on reasonable levels of such standards would add robustness for the outcomes of such modeling exercises and imbue increasing confidence in EM use. Given this level of review, one would need to be cognizant that the degree of rigor in which these considerations was applied would again be highly dependent upon the intended use of the EM outputs. Broad scenarios, sensitivity analyses or background context would by nature require less initial rigor than using EMs to inform tactical BRPs.

As the central mandate of the IWC Ecosystem Modeling Working Group is to consider models that are relevant to the evaluation of the RMP, some suggestions regarding how ecosystem considerations could be included in such a context are in order. Clearly those effects that can influence estimates of whale populations would be germane to consider, as in an ESAM. By analog to fish examples that have included other ecosystem factors, it is unlikely that predation mortality or direct thermal effects to growth are going to notably influence whales. Yet changes in habitat, foraging base, prey density, or similar such features could readily be envisioned to impact various parameters influencing either whale vital population rates or carrying capacities. This topic merits further consideration.

Finally, I provide a last recommendation in the form of a comment. We collectively need to recognize that “right” answers may indeed be a range or region, not a point. In some of the ESAM, Aggregated, or MS model instances, a point may indeed be obtainable, defensible and appropriate. But in a lot of the questions and issues surrounding the need to invoke EMs, the output should really be viewed as bracketing the question. Defining regions of technical infeasibility or impossibility, regions that are undesirable, and regions that are acceptable is actually not trivial and a useful outcome of an ecosystem modeling exercise. Using a modified MP or MSE to explore many of the questions noted herein will result in wise consideration of this strategic output. This type of output would be used very differently from output to help determine next year’s catch limits. But both are important for enhanced understanding and management of LMRs.

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Table 1. Mapping of general ecosystem model classes to general management issues influencing living marine resources (LMRs; here implicitly whales). SS = single species, MS = multispecies MSY = maximum sustainable yield, Agg = aggregate, BRP = biological reference points, MSE = management strategy evaluation, similar to management procedures approach.

	Env on LMRs	LMRs on Env	Ecology on LMRs	LMRs on Ecology	System level Production	Thresholds for SS LMR Mgt	Estimation of MS MSY & other BRPs	Estimation of Agg MSY & other BRPs	Estimation of Systemic MSY & other BRPs	Evaluate Tradeoffs among Biota	Evaluate Tradeoffs among Ocean uses	Simulations and Scenario Testing	Operating Models for Strategic Testing (MSE)
Single Species						√							
Single Species w/add-ons	√		√			√							√
Multi-species			√	√		√	√						√
Biophysical	√				√								
Food Web			√	√	√		√	√		√	√	√	√
Aggregate Biomass					√			√	√	√		√	
Biogeochemical	√		√		√								
Full System	√	√	√	√	√				√	√	√	√	√

Table 2. Mapping of general whale issues to ecosystem model classes. RMP = revised management procedure.

	Single Species	Single Species w/add-ons	Multi-species	Biophysical	Food Web	Aggregate Biomass	Biogeochemical	Full System
What species and fisheries can potentially compete with whale feeding?		√	√		√			√
How to evaluate the potential magnitude of such competition?			√		√			√
What are the potential, indirect food web effects on whales?					√			√
What are the ecosystem tradeoffs that most warrant evaluation?					√	√	√	√
What are the best scenarios (to model) to mitigate any of these concerns?			√		√	√		√
How well do such (simulated) scenarios perform?			√		√	√		√
Influence RMP directly	√	√	√	√				
Inform RMP indirectly					√	√	√	√