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[Article]

End-To-End Models for the Analysis of Marine Ecosystems: Challenges, Issues, and Next Steps

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Abstract.—There is growing interest in models of marine ecosystems that deal with the effects of climate change through the higher trophic levels. Such end-to-end models combine physicochemical oceanographic descriptors and organisms ranging from microbes to higher-trophic-level (HTL) organisms, including humans, in a single modeling framework. The demand for such approaches arises from the need for quantitative tools for ecosystem-based management, particularly models that can deal with bottom-up and top-down controls that operate simultaneously and vary in time and space and that are capable of handling the multiple impacts expected under climate change. End-to-end models are now feasible because of improvements in the component submodels and the availability of sufficient computing power. We discuss nine issues related to the development of end-to-end models. These issues relate to formulation of the zooplankton submodel, melding of multiple temporal and spatial scales, acclimation and adaptation, behavioral movement, software and technology, model coupling, skill assessment, and interdisciplinary challenges. We urge restraint in using end-to-end models in a true forecasting mode until we know more about their performance. End-to-end models will challenge the available data and our ability to analyze and interpret complicated models that generate complex behavior. End-to-end modeling is in its early developmental stages and thus presents an opportunity to establish an open-access, community-based approach supported by a suite of true interdisciplinary efforts.

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There is growing interest in models of marine ecosystems that include descriptors of climate as it affects higher trophic levels (Travers et al. 2007; Cury et al. 2008). These so-called end-to-end models typically combine submodels of physicochemical oceanographic processes with descriptors of lower- and higher-trophic-level organisms into a single modeling framework (Travers et al. 2009). There are currently several established modeling efforts along this line, including OSMOSE (Shin and Cury 2001), Ecospace (part of Ecopath with Ecosim; Walters et al. 1999; in press), ATLANTIS (Fulton et al. 2004a, 2004b), and SEAPODYM (Lehodey et al. 2003). These models and others were recently reviewed in Plagányi (2007). Newer efforts are also under way, such as a multispecies fish extension to the NEMURO family of models. While none of these newer models yet constitutes a comprehensive end-to-end model, the great variety in their underlying approaches and details provides a promising foundation for the development of the next generation of end-to-end models.

Traditionally, in marine ecosystem modeling models of lower trophic levels (LTLs) and higher trophic levels (HTLs) have been developed quasi-independently (Jennings et al. 2001; Travers et al. 2007). The LTLs have been modeled in terms of single-element (typically nitrogen or carbon) dynamics among the various forms of nutrients and multiple functional groups of autotrophs (i.e., phytoplankton) and heterotrophs (i.e., bacteria and zooplankton), as typified by nutrient–phytoplankton–zooplankton (NPZ) models (Fasham et al. 1990; Fennel and Neumann 2004).[1]

Models of HTL organisms (e.g., fish) are typically based on biomass or age-, stage-, or size-classes (e.g., Tuljapurkar and Caswell 1997; Quinn and Deriso 1999) and embody simplified physical (environmental) conditions and LTL (ecological) representations (Latour et al. 2003). These models include single-species population dynamics models (Quinn and Deriso 1999) and multispecies models that represent the predator–prey and competitive interactions among the HTL species (Pauly et al. 2000; Rose and Sable 2009). When included, humans are typically represented in a highly simplified manner in such models. However, several models have begun to include more dynamic representations of human activities, mostly in terms of the dynamics of harvesting (Plagányi 2007). End-to-end models attempt to meld the physical–LTL and HTL modeling approaches and include important feedbacks among these three factors. Ultimately, end-to-end models should more broadly include humans as members of the HTL community that react and adjust to changing conditions (Liu et al. 2007; Perry et al. 2010).

The increasing interest in developing end-to-end models is the result of several developments: the worldwide movement toward ecosystem-based management, advances in ecosystem modeling, improvements in computing power, and the ever increasing appreciation of the complexity of the interacting factors that control ecosystem dynamics. A major driver is the demand for quantitative tools to support ecosystem-based management initiatives (Pikitch et al. 2004). It has long been recognized that there are strong interactions and feedbacks among climate, upper-ocean biogeochemistry, and the LTL components of marine food webs. Ecosystem approaches are now considered necessary because of the growing appreciation of the interconnectedness between climate and fish and other HTL organisms and because of the recognized deficiencies in the commonly used single-species approach to fisheries management (Latour et al. 2003). Climate scale variability and its impact on fish population dynamics have been documented in many ecosystems (e.g., Chavez et al. 2003; Beamish et al. 2004; Lehodey et al. 2006). Regional and global climate change can affect HTL organisms in a multitude of ways. For example, the growth, mortality, reproduction, and movement of fish are directly affected by changes in the physical and chemical properties of the ocean (temperature, salinity, mixing, advection, and pH) and directly and indirectly by changes affecting phytoplankton, zooplankton, benthos, and other fish in their roles as predators, prey, and competitors (Ito et al. 2010).

Another driver for the development of end-to-end models is concern about the overharvesting of many fish populations. Much attention has been given to a series of controversial papers purportedly showing that many of world's fish populations have been overharvested (e.g., Myers and Worm 2003; but see Hilborn 2007). Whether or not the dire state of fisheries has been exaggerated, there is no doubt that overharvesting and low population biomasses are a concern (Mullon et al. 2005; Worm et al. 2009). As a result, current fisheries management practices, which rely heavily on single-species approaches (Rose andCowan 2003), are

[1] Throughout this paper, we use the term "NPZ" to refer to a common class of mass-based models of LTL organisms that simulate the dynamics of nutrients, phytoplankton, and zooplankton. We also include models that represent multiple nutrients, multiple functional groups of phytoplankton and zooplankton, and detritus under this term. The term "LTL models" is a more general one that includes NPZ models as well as other types of models, such as stage-based population dynamics models of copepods.

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being called into question, and multispecies and ecosystem approaches are being advocated (Latour et al. 2003; Plagányi 2007; Cury et al. 2008).

The emergence of end-to-end models is also timely because advances in the modeling of hydrodynamics and HTL organisms, combined with improvements in computing power, now make it possible to link component submodels explicitly. Recent advances in physical modeling include accurate and efficient solution schemes, sufficient spatial resolution to simulate mesoscale features, the nesting of grids to enable fine-scale simulation within a relatively broad spatial domain, and the ability to reproduce patterns in field data for nearshore and coastal areas (e.g., upwelling regions) that are utilized by many HTL organisms during their life cycle (Ito et al. 2010; Lett et al. 2009). We are now able to simulate mesoscale phenomena in the physical and LTL models, which provides more realistic spatial and temporal temperature, salinity, and food fields for the simulation of the reproduction, growth, mortality, and movement of individual fish as well as the short-term population dynamics. The physical and LTL models can also reconstruct decadal-scale phenomena (e.g., regime shifts) critical for simulating the low-frequency variation in HTL organisms. We do not want to overstate the current abilities of the physical and LTL models. The degree to which simulations with these models match reality can always be questioned. For example, artificial numerical "fixes" are still used in many LTL models to ensure that certain behaviors are realistic (Cropp and Norbury 2009). However, recent advances in physical and LTL modeling have partially shifted the emphasis from inadequate modeling methods to the lack of appropriate data for parameterization and validation (see Anderson 2005; Flynn 2005).

There have also been advances in the modeling of HTL organisms. There is now far greater appreciation of the ways to handle ontogeny at scales that are appropriate for end-to-end models. While the differential and difference equation representations are still very useful in many situations, especially for the low and mid trophic levels (e.g., Gentleman et al. 2008), an individual-based approach that simulates discrete Lagrangian entities offers several advantages over the more traditional age- and stage-based approaches at the higher trophic levels. The individual-based approach has become very popular in ecology (DeAngelis and Mooij 2005) and is well suited for representing HTL organisms in end-to-end models. The individual-based approach allows for conceptually straightforward linking of the HTL processes of growth, mortality, and reproduction to the detailed spatial and temporal scales of the physical and NPZ submodels. Competitive and predatory food web interactions can be represented on local scales, and physical-based and behavioral movement can be implemented (DeAngelis and Rose 1992; Breckling et al. 2006). The individual-based approach has been used in single- and multiple-species models (DeAngelis and Mooij 2005), but far less in community-level analyses because of computational costs (Rose and Sable 2009). Data collection has also progressed, the advances including remote sensing that permits synoptic measurements to be made over broad areas, the ability to obtain spatially resolved measurements in the field, and the ability to acquire fine-scale information (such as that obtained through acoustic and sonic tagging) on the movements of animals (Rose et al. 2001). A mix of stage-, age-, and individual-based modeling approaches will probably be needed to represent the complex food webs and community dynamics of HTL organisms in end-to-end models.

Computing power is ever increasing, such that end-to-end models are now computationally feasible. We have the computing power to simulate physical phenomena at fine scales using highly resolved models with the spatial coverage (domain) and ability to perform the decadal-length simulations that are needed to capture the dynamics of HTL organisms. Computing limitations will always be present, however. High-end computing is not widely available and requires special expertise, and there are issues related to the storage of and efficient access to the massive data and model output that can be generated. One could easily formulate an end-to-end model that would be limited by computing power, especially in terms of data fitting and uncertainty analysis. At present, however, uncertainty about biological processes is more limiting than computing power.

Another development that favors an end-to-end approach is the dynamic and spatially variable nature of the factors that control marine ecosystem dynamics. Knowing the relative roles of bottom-up, top-down, and wasp-waist controls (Cury et al. 2000; Frank et al. 2005; Bakun 2006; Field et al. 2006)—and how they operate simultaneously and vary in time and space—is vital for making accurate projections of the responses of ecosystems to changing conditions (Cury et al. 2008). Evidence of the complexity of inter–trophic level controls in coastal and marine systems (Hutchings et al. 1998; Hunt and Stabeno 2002; Frank et al. 2005; Ware and Thompson 2005) and the complexity of the relationships between environmental conditions and fish population dynamics (Rose 2000; Breitburg et al. 2009) is accumulating. While it has long been known that nutrients are related to fish production (Caddy 1993; Nixon and Buckley 2002), some studies have

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suggested that fish themselves can affect nutrient availability (Hjerne and Hansson 2002; Wilson et al. 2009). How to represent the complexity of the food web continues to be investigated for NPZ models (e.g., Friedrichs et al. 2007), and it is even more complicated when HTL organisms are added to the model. End-to-end models will need to have the structure and feedbacks to represent a complex mix of controlling processes (e.g., an alternation of bottom-up and top-down processes). In some situations, this will involve feedbacks among the physical, NPZ, and HTL components.

In this paper, we discuss nine issues related to the further development and application of end-to-end models. These are (1) the role of zooplankton as a link between the lower and upper trophic levels, (2) the inclusion of new organisms such as macroinvertebrates and humans, (3) the melding of multiple temporal and spatial scales across submodels, (4) acclimation and adaptation by organisms, (5) the behavioral movement of upper-trophic-level organisms, (6) the software and technology for coding and sharing algorithms in an open-access community, (7) one-way and two-way solution techniques, (8) the assessment of model performance and forecasting, and (9) the challenges posed by the interdisciplinary aspects of end-to-end modeling. We conclude with a general statement about the future of end-to-end modeling and its relevance to management decision making. This paper is based on the discussions at a workshop entitled "Bridging the Gap between Lower and Higher Trophic Levels" that was held February 2009 in Plymouth, England. This paper is not meant to be an exhaustive review of end-to-end modeling of marine ecosystems. Our goal is to make the participants' deliberations at the workshop on this rapidly advancing field available to a wider audience.

Zooplankton as the Link between Lower and Upper Trophic Levels

A major topic of discussion at the workshop was whether the current representation of zooplankton in the traditional NPZ models is an appropriate to way link LTL organisms to fish and other HTL organisms. Zooplankton will be a linchpin as we develop end-to-end models because of their importance as a consumer of primary production and as prey for HTL organisms. Historically, zooplankton was included in NPZ models mostly to achieve realistic biogeochemical cycling (Le Quere et al. 2005), while in models of fish population dynamics, food (LTL) dynamics were either not considered explicitly (e.g., age-structured models; Caswell 2001) or represented very simply (e.g., Ecopath with Ecosim; Walters et al. 1997).

In end-to-end models, the goal of representing zooplankton shifts from obtaining realistic nutrient and chlorophyll concentrations in a biogeochemical context to representing the quantity and quality of food available to multiple species of fish over their lifetimes. Two likely differences between traditional NPZ models and end-to-end models are the representation of biogeochemical processes and the definition of functional groups.

Shifting the focus of zooplankton means that many of the processes represented in traditional NPZ model formulations need to be revisited. For example, traditional NPZ simulations (e.g., Fasham et al. 1990) have either made reference to a single nutrient (typically nitrogen) or assumed fixed, Redfield-like stoichiometry. Setting aside the question whether Monod–Redfield models can sufficiently describe phytoplankton growth (Flynn 2010), variable elemental stoichiometry has been shown to be important in controlling NPZ dynamics (Andersen et al. 2004; Mitra et al. 2007). Whether stoichiometry is a first-order problem or not is unknown, but the importance of this issue (and others) needs to be assessed in the context of incorporating NPZ models into end-to-end models.

Another issue is the amount of detail needed in the algorithms that represent prey selection by zooplankton. Relating prey selection to food quality in a simplified manner in NPZ models is a nontrivial matter (Mitra and Flynn 2006), while including it in structured copepod models can have profound impacts on copepod dynamics (Flynn and Irigoien 2009). We do not know the extent to which the traditional representations of processes in NPZ models will require revision in the context of the demands imposed by end-to-end models, but we caution against simply adopting existing formulations.

A second major issue that arises with end-to-end modeling is the representation of zooplankton functional groups. Much of the literature still focuses on ways to represent functional groups with respect to biogeochemical cycling (Hood et al. 2006); end-to-end modeling will dramatically shift the focus to ways to represent LTL organisms because the emphasis will be on their linkage to HTL organisms. Most real LTL dynamics operate through microzooplankton, as represented by protistan grazers and the juvenile states of mesozooplanton. Biogeochemically oriented NPZ models typically employ closure terms that operate on the mortality component of the zooplankton groups, which (often without being stated explicitly) describe the activities of HTL organisms (see Mitra 2009). End-to-end modeling provides explicit description of predatory activity in place of general closure terms.

End-to-end models inevitably require the inclusion

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of at least two zooplankton types: protistan zooplankton for realistic LTL dynamics and mesozooplankton (notably copepods) for the HTL link. The zooplankton groups need to be represented so that key shifts in the prey types eaten as fish develop can be realistically simulated. Larval fish often require small prey sizes and certain types (e.g., Checkley 1982; Munk 1997; Kühn et al. 2008), and subtle changes in mortality arising from growth differences or episodic events can dramatically affect annual recruitment (Houde 1989). Adult fish tend to eat larger prey and often consume a mix of invertebrate and fish prey (e.g., Scharf et al. 2000). Detailed stage-based models of specific copepod species have been successfully imbedded into three-dimensional spatial models (e.g., Moll and Stegert 2007), and others have invoked postprocessing of NPZ model output to obtain sufficiently detailed prey fields for modeling fish feeding (e.g., disaggregating biomass into size structure; Daewel et al. 2008). Several plankton–fish models have essentially abandoned the functional group approach and represented LTL organisms by means of size distributions (e.g., Zhou and Huntley 1997; Maury et al. 2007). Defining planktonic functional groups remains a longstanding challenge in NPZ modeling (Anderson 2005; Le Quere et al. 2005), and the additional requirement of accurately representing the energy flow pathways and phenology of multiple groups of zooplankton will further complicate it. The extent to which multistage LTL models will be required to describe the development of important LTL species groups (e.g., copepods) is a major unknown. Indeed, from a biological standpoint, the modeling of mesozooplankton may have more in common with modeling the more challenging HTL organisms than with modeling single-celled microbes (Carlotti and Poggiale 2010).

A critical element of making end-to-end models realistic is correctly describing the LTL organisms. In this regard the demands of end-to-end modeling differ from those for biogeochemical cycling. We anticipate that, at least in some situations, significant changes to traditional NPZ model formulations will be needed to fulfill the demands of end-to-end models. In other situations, more moderate changes may suffice. Data that describe the flux of materials and energy up through their pathways are needed to confirm the simulated dynamics of the fish-oriented zooplankton functional groupings. This will reinforce the drive for changes in the ways that phytoplankton and zooplankton are traditionally represented. We will need NPZ models that deal with multiple nutrients, that generate energy flows through functional or size-groups that provide a sound basis for ontogenetic changes in fish prey demands, and that are robust to changing environmental conditions. This issue will become especially important as we extend the use of models to conditions (e.g., global climate change) that are well outside the domain in which the models were calibrated and validated.

New Organisms

Two groups of organisms that have not been the focus of marine ecosystem modeling to date but that are likely to become important under changing climate scenarios are macroinvertebrates and very-high-trophic-level organisms. Macroinvertebrates such as salps, appendicularians, and jellyfish seem to fall in-between most NPZ and HTL modeling efforts. Salps can channel small-sized phytoplankton and aggregate them into large, fast-sinking particles, thereby making them unavailable to the small stages of crustaceans and interfering with the trophic link between zooplankton and fish (Le Fèvre et al. 1998). Given the worldwide concerns about jellyfish blooms (Mills 2001; Purcell 2005) and how they alter the energy flow through the food web (Brodeur et al. 2002) and affect zooplankton community dynamics (e.g., Kremer 1979) and fish growth and survival (Purcell and Arai 2001), the representation of jellyfish in end-to-end models requires careful consideration.

Demersal fish species are another group of organisms that will need to be considered in end-to-end models. While HTL models of demersal fish species have been developed (e.g., Bryant et al. 1995), they have tended to include simplified physical conditions and benthic prey dynamics. Most LTL–fish models that include detailed physical conditions have focused on the early life stages of pelagic fish species (Werner et al. 2001; Lett et al. 2009; North et al. 2009), while the initial attempts to formulate end-to-end models that include demersal organisms have been simplified in other aspects, such as the physical conditions or behavioral movements (see Plagányi 2007). In many situations, end-to-end models will need to consider demersal fish species as integral parts of the HTL community. This presents new challenges as to how to represent the interface not only with LTL organisms in the overlaying waters but also with the hydrodynamics and physical conditions near the bottom and the associated benthic food web. Some of the existing benthic modules within ecosystem models (e.g., Ebenhoh et al. 1995; Blackford 1997) and the spatially simplified models that include demersal species (e.g., Bryant et al. 1995; Okey et al. 2004) will provide a starting point, but much further work is required to determine the appropriate formulations for demersal-related processes and linkages to the physical conditions and pelagic food web.

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Finally, many of the models that include LTL and HTL organisms have shifted the mortality closure term problem further up the food chain. We have moved from specifying zooplankton mortality in NPZ models to achieve realistic biogeochemical cycling to specifying HTL mortality in terms of predation by other HTL organisms and human activities such as fishing. In most models, fish mortality is treated in a simplified manner by assuming constant annual natural and fishing mortality rates. In end-to-end models, marine mammals, birds, and humans may need to be included as full members of the food web in order to obtain realistic representations of the mortality and dynamics of their prey. Integrating closure terms with model-generated predation rates for functional groups whose suite of possible predators is only partially represented by explicit simulation might require model-specific solutions (Fulton et al. 2003a). Representing very-high-trophic-level organisms can require very different modeling approaches than the traditional fish-oriented approaches (Perry et al. 2010) and result in model behaviors that would not be expected from the study of the natural and social systems separately (Liu et al. 2007).

Scaling

There are scale differences between LTL and HTL dynamics that will need to be accommodated in end-to-end models. Dealing with multiple biological, spatial, and temporal scales is fundamental to all ecological modeling (Levin 1992) and becomes even more acute with end-to-end models. Deciding the best temporal and spatial scales and processes is the art of modeling. A model should be tailored to the specific questions to be addressed, but because there are no general guidelines for deciding the scales and processes to be included for a given question, model development includes judgments on the part of the model developers.

End-to-end models exacerbate the uncertainty in model building because they include a more diverse set of processes that operate on different scales and organisms that span a wide range of sizes and life histories. Examples include how to generate temperature and prey fields in an LTL model on scales that harmonize with the way that fish feeding is represented in the HTL model; how to include behavioral responses when modeling the movement of fish and other HTL organisms on a spatial grid dictated by hydrodynamics; and how to have sufficient temporal and spatial resolution in the physical conditions to realistically represent fast-reaction dynamics (e.g., phytoplankton and fish foraging) while simulating decadal dynamics over a broad enough spatial domain to allow for changes in large-scale migration and movement patterns. We are challenged to harmonize fine-scale physical models with biological processes that span a wide range of temporal and spatial scales for fish (Mullin 1993) and other HTL organisms. We are confident that working on a single temporal and spatial scale will not be sufficient (Fulton et al. 2003b). The issue of scaling is not new, but with end-to-end modeling it becomes even more challenging.

End-to-end models will probably create situations of complex systems behavior that will complicate the interpretation of model results. Complex systems behavior occurs when the composite has properties that are not obvious from the properties of the individual components (Auyang 1999). Models do not need to be complicated to exhibit complex systems behavior. For example, very simple models can generate chaotic and irregular patterns of population dynamics over time (e.g., May 2001). The wide range of scales in end-to-end models and the fact that the individual-based approach allows simple rules to be scaled up to the population and community levels via local interactions provide fertile ground for the emergence of complex systems behavior (Railsback 2001). While such model behavior is often beguiling, we must be prepared to detect and diagnose it—via analysis of model output and simulation experiments (Grimm et al. 2005)—to ensure that the output is indeed realistic and to fully understand the reasons for our results.

Acclimation and Adaptation

Acclimation refers to the biochemical, morphological, and behavioral ways an organism responds to reoccurring changes in its environment. Acclimation responses are usually short term and rapid and involve the expression of phenotypic plasticity (see Scheiner 1993). If the response results in genotype changes, then adaptation has occurred. The need to include acclimation and adaptation is not unique to end-to-end models; it arises from the general problem of how to model responses to changing environmental conditions.

Phytoplankton and zooplankton have relatively rapid turnover rates, so that the typical 50–100-year simulations needed for HTL organisms could include evolutionary adaptation on the part of plankton (Fussmann et al. 2003; Yoshida et al. 2003). Large-scale changes in plankton functional type dominance is possible. High-trophic-level organisms can also exhibit adaptive responses to selective pressures from harvest and global climate change within 50–100-year simulations (Jørgensen et al. 2007), although distinguishing between phenotypic (acclimation) and genetic responses (adaptation) is difficult (Naish and Hard 2008). The

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trade-offs among species traits as environmental conditions change can affect species' spatial distributions and productivity, predator–prey dynamics, and community structure (Litchman and Klausmeier 2008). Examples of the incorporation of acclimation and adaptation into models include photoacclimation by phytoplankton in response to changing light and nutrient environments (Geider et al. 1996; Flynn 2003; Pahlow 2005; Armstrong 2006); optimal acclimation of nutrient uptake by phytoplankton (Flynn 2003; Smith et al. 2009); the emergence of alternative phenotypes in phytoplankton (Follows et al. 2007); changes in the migration of fish (Mullon et al. 2002; Huse and Ellingsen 2008); and changes in the age at maturity of fish as a result of selective pressures and inheritability (Jager 2001). Methods are being developed, such as structural dynamic models (see Jorgensen 1997), which relate model structure and parameters to recent environmental and other conditions (e.g., Bendoricchio and Jørgensen 1997; Solidoro et al. 2010).

Long-term simulations under potentially highly variable environmental conditions and the diverse mix of organisms in end-to-end models will heighten the need for mechanistic representations of acclimation and adaptation. This is an active area of research, and the examples cited above (and others) should provide a basis for the eventual inclusion of acclimation and adaptation into end-to-end models. The challenge will be to avoid unsupportable and deleterious model complexity.

Behavioral Movement

End-to-end models that include the juvenile and adult stages of HTL organisms will need to deal with behavioral movement. Movement based on physical conditions has been investigated for a long time, often as particle tracking. This approach has been used extensively with the early life stages of fish (North et al. 2009), the swimming abilities of which can be simplified (i.e., vertical only) in favor of relying on advective and dispersive transport to move the particles around a spatial grid (Lett et al. 2009). Similar approaches can be taken (with caution) to simulating the transport of copepod stages (Speirs et al. 2006). As we include the juvenile and adult stages of HTL organisms, we must deal not only with movement based on physical conditions but also significant movement related to behavior. In contrast to the movement of plankton, that of adult fish and other HTL organisms (e.g., marine mammals) is poorly approximated by treating them as passive particles. Behavioral movement plays a strong role in many HTL organisms and is a function of both environmental factors and the state of the organism itself (Burrows 1994; Tyler and Rose 1994). Modeling behavioral movement has involved a diverse set of approaches (Giske et al. 1998) and is receiving increasing attention (Sugden and Pennisi 2006). Several of the commonly used approaches are fitness based (Railsback et al. 1999), kinesis (Humston et al. 2004), neural network with genetic algorithm (Huse and Giske 1998), rule based (Vabø and Nøttestad 1997; Roth et al. 2008), random walk (Huse 2001; Zhang et al. 2007), and event driven (Goodwin et al. 2006). There are also approaches that relate algorithms to the optimality of the overall spatial distribution (e.g., ideal free distribution; Kacelnik et al. 1992). At present, there are no general guidelines as to which approach is appropriate in certain situations or how the approaches relate to each other within a general framework. Yet the choice of a specific movement algorithm can affect the predictions of fish growth and spatial distribution (e.g., Wildhaber and Lamberson 2004). We recommend that a group effort be made to examine the methods of modeling behavioral movement. The group's charge would be to identify the approaches that are available, indicate how they relate to each other, and determine the conditions under which each shows promise.

Software and Technology

End-to-end models require a substantial amount of custom computer code, and an "off-the-shelf" end-to-end model is neither realistic nor desirable. For large-scale, complicated modeling, languages such as FORTRAN and C are still preferred, mostly for reasons of processing speed (Barnes and Hopkins 2003) and ease of coupling to existing model code. We cannot declare a single programming language the best for end-to-end models, but we do foresee continued reliance on sequential languages. End-to-end models will require extensive computer programming skills into the foreseeable future. Common data standards (including common units) and interfaces would make sharing, exchanging, and testing model codes easier.

We anticipate new algorithms for one-way and two-way coupling solutions, predator–prey interactions, behavioral movement, and evolutionary adaptation, to name a few. However, end-to-end models (and individual-based models in general) are still very much custom computer programs known and available only to the model developers and perhaps some of their collaborators. This creates challenges in comparing results and sharing the lessons learned about algorithms (Lorek and Sonnenschein 1999; Ropella et al. 2002). As the building of end-to-end models is still in its infancy, we have the opportunity to develop a

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community-based approach with open-source computer code and rapid exchange of information. Data standards, such as that of the Network Common Data Form (NETCDF), would enable easy sharing of input and output files. The community involvement in the Regional Ocean Modeling System (ROMS) modeling effort (Shchepetkin and McWilliams 2005) is a good example of an open-source, community approach to model development. If there is ever a time to establish a common framework for end-to-end modeling, it is now, when we are at the beginning of what we expect to be a substantial effort in this area.

Solution Techniques: One-Way Linking or Two-Way Coupling

The components or submodels of end-to-end models can be solved by means of either one-way linking or two-way coupling. Two-way coupling involves the solution of all submodels simultaneously, thereby allowing for dynamic feedbacks among them. Thus, the hydrodynamic, LTL, and HTL submodels can exchange information as the solution proceeds. Feedbacks are critical for the accurate simulation of HTL population dynamics because of the important role played by density-dependent processes in those dynamics (Rose et al. 2001). The simulated dynamics of HTL organisms, in turn, affect the realism of the dynamics of LTL organisms. Typically, fish consumption (and thus growth) is determined from the available zooplankton at that time step and then summed over the HTL individuals and fed back into the LTL submodel as zooplankton mortality (e.g., Travers et al., in press). In a tightly coupled system, fish consumption affects the population dynamics of the zooplankton, which then has a density-dependent effect on fish growth. Density-dependent feedbacks, which occur throughout the entire LTL–HTL system, impose bounds on the population dynamics and enable assessment of sustainable harvest levels of commercially and recreationally important HTL organisms. It is the compensatory density dependence in fish populations that allows increased mortality from harvesting to result in a stable population over time and makes possible the evaluation of sustainable harvest options (Rose and Cowan 2003).

One-way linking involves using the output of one submodel as input to another submodel without feedbacks. A common example is running the hydrodynamic component and then using the stored velocity, temperature, and other environmental fields to drive the LTL model. In another type of one-way coupling the output from one submodel is summarized in terms of aggregate indicators and input into the other submodels (e.g., Aydin et al. 2005). If the LTL submodel is solved with the physical conditions submodel but separately from the HTL submodel, the consumption of zooplankton by fish has no effect on the availability of zooplankton for other fish (i.e., the crowding of fish has no effect on food availability). The implicit assumption is that the ecological linkage is also unidirectional.

There are trade-offs between the one-way and two-way approaches. Computational issues arise with two-way coupling because of the disaggregation and long run times needed in end-to-end models. One viable way of dealing with this is to use coarser spatial and temporal scales in the HTL submodel than in the physical and LTL submodels (Fulton et al. 2003b; Travers et al. 2007). There may also be numerical solution algorithms that partially alleviate the computational limitations (e.g., Walters et al. 1999). In a two-way system, the mortality from fish consumption must be fed back into the LTL submodel at the spatial and temporal scales of that submodel. If one uses a coarser spatial grid and longer time step for the HTL submodel, there will be a disaggregation problem: how to relate predation mortality on one scale to prey dynamics on another. One-way linking reduces execution time and avoids disaggregation issues as long as the next submodel in the chain is at the same or coarser time and spatial scales (it is easier to aggregate going up the food chain than to disaggregate going down it), but at the cost of not allowing feedbacks. Possible feedbacks that can be too important to ignore relate not only to the density-dependent responses of HTL organisms (Rose et al. 2001) but also to the interaction between biological and physical processes. For example, biota can affect sea ice dynamics (e.g., Leck et al. 2004) and water temperatures (e.g., Marzeion et al. 2005). If we assume one-way linkages, we have to be very sure not only that the linkage is really one-way but that it will remain one-way under all plausible simulation scenarios, including climate change. This seems unlikely as a general rule, but it may be the case in specific situations. One can force the feedbacks (e.g., reduce growth rates according to the fish biomass in the same spatial area), but externally defined feedbacks are often difficult to parameterize and can be a major driver of model dynamics. It is usually easier to formulate and justify feedbacks that emerge from model processes and local considerations than ones that are simply imposed (e.g., Rose et al. 2001).

An area worthy of exploration is coupling that is intermediate between strictly one-way and two-way coupling. Data assimilation techniques (Robinson and Lermusiaux 2002) may be useful in linking LTL and HTL submodels. In some situations they may permit existing models to be used without major reparameter-

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ization (e.g., one can still use the closure mortality term in NPZ models). The assimilation method would enable some correcting of the two coupled submodels during their simultaneous solution (Libralato and Solidoro 2010). Data assimilation may also allow communication between submodels at key points in time while allowing them to be run in one-way mode at others. The issue of solution techniques depends on the specific situation at hand, but in general it is a major unresolved problem in end-to-end modeling.

Other issues related to solving end-to-end models are the need for long-term simulations and the complications arising from the representation of local interactions, such as predator–prey encounters. Fish and other HTL organisms have complex life cycles that require multiple generations for changes in environmental and biological conditions to be fully expressed at the population and community levels. This translates into long spin-up times and decadal or longer simulations, especially if long-lived species (e.g., predatory fish and marine mammals) are included. Both HTL and LTL submodels require physical representations on relatively fine scales in order to capture the important spatial and temporal dynamics. For numerical reasons, the super-individual approach (Scheffer et al. 1995) is often used in models of HTL organisms that couple to LTL models. Each such super-individual is worth some number of identical individuals, which decreases through time via mortality processes. The activities (e.g., feeding) and abundance of the super-individuals are scaled up to the population level by adjusting them by their population worths (i.e., how many other identical individuals they represent). Using super-individuals addresses the problems of representing the variability within large populations (billions of fish in real populations) without representing every individual and maintaining fixed-size arrays in the computer program. However, super-individuals should be used carefully to avoid introducing unwanted numerical artifacts into the solutions (Parry and Evans 2008). Predator–prey interactions between HTL organisms and LTL groups usually involve the meshing of Lagrangian and Eulerian representations (Bian 2003; Goodwin et al. 2006). Interactions between HTL organisms (e.g., competition for food and predator–prey) introduce issues as to their spatial scale and how to maintain mass balance while super-individuals eat a diverse set of prey, including other super-individuals (e.g., McDermot and Rose 1999; Shin and Cury 2001).

Model Confidence and Forecasting

End-to-end models involve a very diverse set of calculations that need calibration and validation to enable one to judge a model's "skill" and how much confidence to place in it. The calibration and validation of hydrodynamics and LTL dynamics (especially in NPZ versions) differ from those usually done with HTL models. As with any modeling effort, calibration, validation, and measures of model skill depend on the questions to be addressed and the quantity and quality of the available data (Stow et al. 2009). In general, partial skill assessment can be achieved with the hydrodynamics component by using relatively short-term, spatially detailed measurements of the physical conditions. Evaluation of some phenomena (e.g., the physical responses to the El Niño–Southern Oscillation) requires long-term and broader-scale measurements. The LTL component (especially as regards mesozooplankton) is more challenging, as the temporal and spatial patchiness in species' distributions and their multiple life stages make synoptic and comprehensive monitoring more difficult. Finally, the complex life cycles and longevity of HTL organisms have always presented an enormous challenge to skill assessment for fish population models (Schnute and Richards 2001), especially when those models provide the foundation for fisheries stock assessment and management decisions (Hilborn and Walters 2001). Long-standing issues with calibration and validation carry forward and will be amplified when fish and other HTL organisms are imbedded in end-to-end models. Even if sufficient data are available (which they never are), simply getting the model to match the spatial and temporal patterns in physical conditions, nutrients, and HTL organisms will not be sufficient for some applications. Different sets of assumptions and parameter values will probably generate reasonable patterns within the resolution of the available data, and the particular assumptions and parameter values can greatly affect the predicted dynamics under new conditions. The diversity of information needed for the calibration and validation of end-to-end models also has implications for how data should be collected (e.g., common currency; sampling locations and frequency; synoptic measurements) to facilitate model–data comparisons.

While end-to-end modeling is developing at encouraging speed, we urge restraint in using end-to-end models in a true forecasting mode (Clark et al. 2001) until we gain more experience regarding their performance. In the near term, end-to-end modeling has many potential applications in strategic scenario analysis, pushing the envelope of modeling, and identifying data needs for future analyses. End-to-end models may appear to be an ideal way to meet the need for ecosystem-based approaches, but we should resist the temptation of using them to make forecasts for management until their performance and robustness are

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adequately tested. We need to develop more end-to-end models to work through the algorithms, identify the critical knowledge gaps, and evaluate model performance with different test cases. We believe that end-to-end models will eventually reach the point at which they can be used not only for scenario analysis but also for direct management applications. At present, however, there is a great deal of work to be done before they can be used in a truly predictive mode. Fisheries management has become extremely controversial (National Research Council 2002), and allowing end-to-end models to be prematurely pushed (or pulled) into that arena could hinder further model development. Certainly, end-to-end modeling can and should be used on a case-specific basis to inform management, particularly about the possible outcomes of long-term strategies. This is all the more so because there are often large uncertainties associated with the models currently being used, especially those involving long-term responses to alternative scenarios. But looking to the future, the need to forecast should be a major criterion guiding end-to-end model development.

True Interdisciplinary Efforts

End-to-end modeling will further challenge our ability to forge true interdisciplinary research teams. There are many multidisciplinary efforts under way in marine ecosystem modeling. We now need to move even further—from multidisciplinary to truly interdisciplinary efforts. We view the difference between multidisciplinary and interdisciplinary in terms of the degree of communication and feedback that occurs between the various research groups. A group of people working on the same problem but in a quasi-independent manner with periodic meetings to report on progress may be considered multidisciplinary but not truly interdisciplinary. Interdisciplinary research is characterized by groups that work together closely, with the constant exchange of information and adjustments to plans in response to the needs of the other groups.

The interdisciplinary challenge is not trivial. We must recognize that end-to-end modeling is as much a people challenge as a technical one. It requires respecting and understanding others' perspectives and approaches and involves communicating information in a form that is understandable by colleagues who speak the languages of other disciplines. At times, it will require trusting others' abilities without fully understanding what they are saying. The issues of communication and trust can be as challenging as ensuring that all of the needed disciplines are represented on the team.

End-to-end modeling will require the involvement of a wide variety of disciplines (e.g., hydrodynamics, LTL organisms, climate, fisheries, community ecology, economics, sociology, anthropology, etc.), which will challenge the classical research models. Involvement of a wide variety of disciplines will present a challenge to funding agencies as to how to evaluate proposals as well as to institutions taking the "silo" approach of grouping like disciplines together and adhering to the idea that credit is diluted when people from different organizations are involved. End-to-end modeling will be an excellent case study of interdisciplinary research and collaboration among groups comprised of disciplines with different research traditions.

Concluding Remarks

The above comments are presented in the hope that they will facilitate progress in the conceptualization and development of end-to-end models of marine ecosystems. Not all of the issues noted will be important in every situation, and our list of issues is not comprehensive. While the tasks ahead are formidable, they are feasible and many are project critical. At present, several research groups are developing large-scale end-to-end models. We envision more such groups getting involved and development activities proceeding in parallel, with close collaboration among the groups. The immediate next step is exploratory.

Most likely, the various research groups will continue their development of end-to-end models largely adhering to their own philosophies, structures, and algorithms. We are in the proof-of-concept phase to show that such models can be developed and implemented and in a learning phase about the solution techniques and algorithm development. In due course, a joining of forces that brings the experiences of the groups together will lead to the formulation of the next generation of end-to-end models. While the modeling community will grow and become more complex, we advocate a unified comparative analysis involving model intercomparisons (e.g., models applied to common systems). Early agreement on common-language issues would facilitate communication among the groups. We are at the beginning of what we think will be a growing and long-term effort toward the development and application of end-to-end modeling. We are being presented with a unique opportunity to set up a community-based effort. We urge anyone interested to get involved in what appears to be an exciting scientific, collaborative, and computational journey.

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