Challenges of Modeling Ocean Basin Ecosystems
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With increasing pressure for a more ecological approach to marine fisheries and environmental management, there is a growing need to understand and predict changes in marine ecosystems. Biogeochemical and physical oceanographic models are well developed, but extending these further up the food web to include zooplankton and fish is a major challenge. The difficulty arises because organisms at higher trophic levels are longer lived, with important variability in abundance and distribution at basin and decadal scales. Those organisms at higher trophic levels also have complex life histories compared to microbes, further complicating their coupling to lower trophic levels and the physical system. We discuss a strategy that builds on recent advances in modeling and observations and suggest a way forward that includes approaches to coupling across trophic levels and the inclusion of uncertainty.

Our perception of the importance of interannual and decadal variability in the oceans has grown with an ever-expanding body of physical, chemical, and biological data (1, 2) and numerical modeling (3, 4). Reported correlations between time series of annual indices of biological constituents and climate are routine in the literature but often turn out to be ephemeral. For example, the annual average abundance of the copepod *Calanus finmarchicus* in the North Sea was highly correlated with the North Atlantic Oscillation (NAO) index between 1960 and 1996, but subsequently the relationship broke down (5). Correlations do not prove direct causal links, and their lack of persistence makes them unreliable. For higher trophic level taxa, which live for one or more years, annual abundance indices will be autocorrelated, potentially generating misleading cross-correlations with other variables that have different time scales. Nevertheless, when we see parallel changes in time series of climate indices, physical oceanographic properties, and chemical and biological components of an ecosystem, one is forced to accept that there must be strong connectivity between decadal variability in the Earth climate and the structure, function, and productivity of the marine ecosystem (Fig. 1). Although our understanding of the governing processes and our ability to model interannual variability is emerging for large-scale climatic events such as El Niño (6), modeling and prediction at decadal time scales remains a challenge because of sketchy understanding of the underlying processes.

Long life cycles of target organisms (7), their migratory behavior, and the decadal scales of environmental changes define the ocean basins as a natural spatial scale (6). Large-scale circulation features often define the geographical distributions of species (Fig. 2). Changes in physical oceanic conditions at basin scales will affect organism growth and survival directly by the transport of larvae or prey and by changes in temperature that affect vital rates, and can affect them indirectly by changes in nutrient or food supply (Fig. 2) that result from mixing and stratification (3, 8).

Continental shelf and marginal sea ecosystems are affected by basin-scale forcing on decadal scales and cannot be studied in isolation (9). Modulations in the circulation and feeding environments of marginal seas—imposed by variability in the neighboring ocean basin—can result in increased connectivity of distinct, previously isolated populations (10), or they can affect growth and possibly population recruitment through changes in the feeding environment (11). For example, the spatial patterns in the variability of *C. finmarchicus* appear to be related both to the North Atlantic circulation and climate change (12, 13). In turn, variations in populations of several North Sea fisheries target species have been related to the supply of *C. finmarchicus* (Fig. 2).

The Rhomboidal Modeling Approach

Advances in modeling marine ecosystems will require coupling numerical formulations across trophic levels that have differing degrees of resolution and embedding these in a basin-scale representation of the physics and biogeochemistry (Fig. 2). We must also adapt our modeling approaches to account for uncertainties in the data and in our representation of processes (14).

There is no single, fully integrated model that can simulate all possible ocean ecosystem states. The biological resolution of early attempts at marine trophic modeling (15) was dictated more by the extent of knowledge rather than by conscious decision about the structure and function of the model (16). The biological detail of most models increases with trophic level, probably because there is more knowledge of the larger, more easily handled organisms. However, this structure is not optimal, and it risks artifacts arising from competitive interactions implied by the lack of food web resolution in the lower trophic levels. Even a simplified food web, such as for North Sea herring (fig. S1), cannot be completely simulated numerically because of the absence of data and the difficulty of parameterizing interactions. Some simplification of the structure and predator-prey relations is invariably necessary; however, the traditional approach of representing trophic or functional groups of species by bulk biomass variables is not adequate for all trophic levels (17). Taxa such as zooplankton and fish, where juveniles and adults differ in body size by many orders of magnitude and there is the potential for long-distance active migration, require a different approach that resolves the developmental changes in diet, physiology, and behavior.

The importance of scale as a structural issue in ecological model design is well established (16). The key steps in representing extended food webs in complex marine systems are (i) to concentrate the biological resolution, or detail of representation, in the main target species, and (ii) to make increasing simplifications, or decrease the resolution, with distance both up and down the trophic scale from the target species. The target species of a model might be represented by developmental stage–structured representations in which the key life-history stages and their links to the environment are explicitly formulated. Competitors, prey, and predators might be represented by less detailed structures, perhaps based on species-aggregated, bulk biomass properties or on

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empirical representations derived from external forcing data, leading to a rhomboid-shaped representation of detail (Fig. 3). The coupling between levels of differing biological resolution or representation requires special consideration. Different classes of model will be required, depending on the temporal, spatial, and biological focus. The physical model, in which the biological representation is embedded, should have resolution and complexity appropriate to the biological models.

Processes that occur below the resolution of models, either in time or space, require implicit representation. Fluid dynamics models routinely include "sub–grid scale" processes, but such representations are less well developed for biological models (17), as evidenced in the increased primary productivity in a North Atlantic model (18) obtained with an increase in spatial resolution. To ensure that the dynamics of simulated populations are as independent of grid resolution as possible, parameterization of the sub–grid scale processes needs to be such that the mean fluxes are correct even if the detailed spatial structure is not fully resolved.

How Can We Apply the Rhomboid Approach to Develop Models?

We have outlined some principles for simplifying the food web structure that make the task of simulating populations of marine organisms at the scale of ocean basins more tractable. We illustrate this approach with two examples. In both cases, biological resolution has been concentrated at the level of primary interest and decreases with distance both up and down the trophic scale.

Our first example refers to simulations of the population dynamics of the copepod *C. finmarchicus* in the North Atlantic (Fig. 2). We chose this copepod as a target species because of its dominance in the mesozooplankton of the northern North Atlantic, its impor-

tance in the diet of many fish species, and its inclusion as an indicator species in climate impact monitoring studies. The target taxon spans a wide range of relative body sizes, demanding the application of a structured demographic model to effectively represent the population dynamics, with the additional complication that the species undergoes a diapause resting phase for up to 6 months of the year (19). During diapause, development is arrested and the copepods descend to depths of 500 to 2500 m in the ocean, whereas the reproductive phase is spent in the upper 100 m. Computational overheads were simplified by introducing advection and diffusion terms as separate transition matrices for an upper layer of the ocean and for a deep

layer that corresponds to the winter diapause depth. These were computed off-line from the hydrodynamic data for each time-step of the population model (20). The gain in computational speed was needed to permit iterative fitting of the model to observational data. The focus of biological resolution in our model of the North Atlantic *Calanus* is in the representation of the target species and less in the underlying food web. However, previous investigations have shown that inclusion of stage development in the life-history representation is necessary to capture the essential diagnostic features of the demography (21).

The second example is a model of skipjack tuna (*Katsuwonus pelamis*) population dynamics in the Pacific Ocean (22) (figs. S2 and S3). Tuna are the target species by virtue of their economic importance. The resolution of biological detail reduces with distance down the trophic scale, the food of tuna being represented by a simulated bulk-biomass variable representing all prey species. The prey model is driven by a biogeochemical model of the Pacific Ocean, which is coupled to a three-dimensional ocean circulation model that captures El Niño events and the regime shift in the late 1970s (8, 22). Preliminary studies using this same approach have also been applied at a longer time scale, showing possible species distributional shifts for global warming caused by anthropogenic change (23). The strengths of this strategy are that it simulates skipjack dynamics over its geographic range in the Pacific Ocean, and it links statistically based fishery-stock assessment models and biogeochemical modeling. The food web successfully retains key elements of space-time dynamics with minimal taxonomic resolution. The clear weaknesses are the failure to fully close the life cycle and the absence of dynamic density-dependent processes of life history.
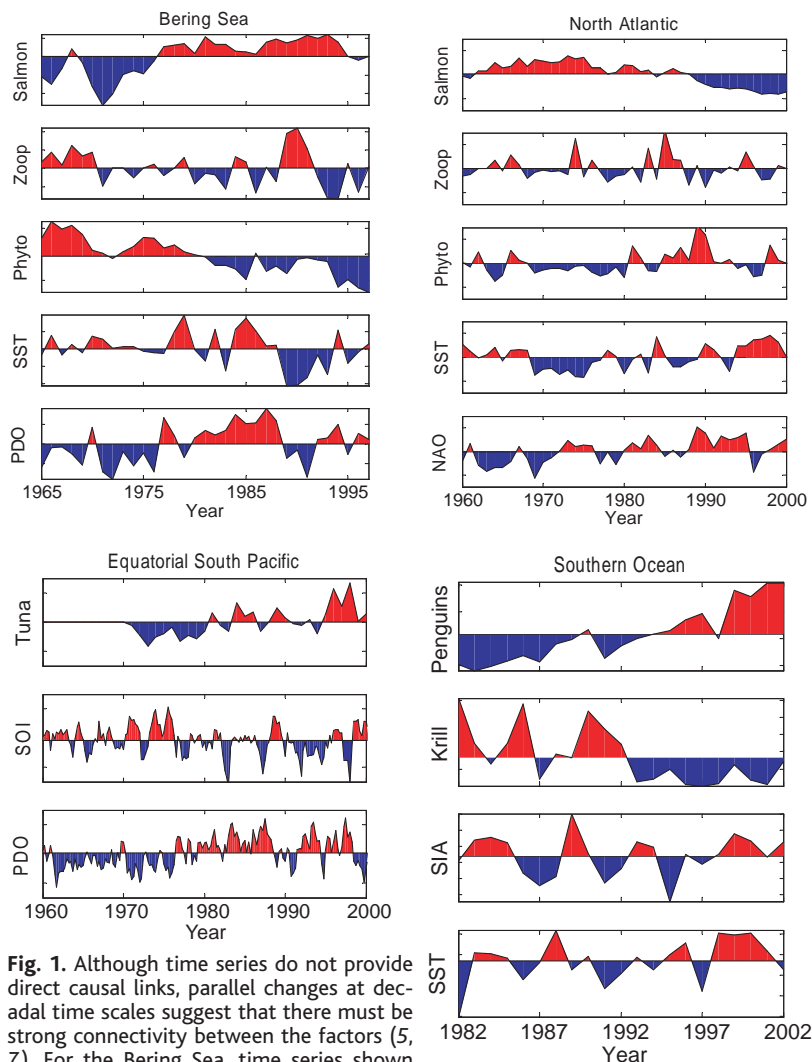
Modeling with Uncertainty

Our *Calanus* and tuna examples are purely deterministic. An important challenge in the development of a

Fig. 1. Although time series do not provide direct causal links, parallel changes at decadal time scales suggest that there must be strong connectivity between the factors (5, 7). For the Bering Sea, time series shown include the winter Pacific Decadal Oscillation (PDO); sea surface temperature (SST); a proxy phytoplankton abundance (Phyto), based on average isotope ratios in long baleen plates from bowhead whales that feed in the Bering Sea; zooplankton abundance (Zoop); and western Alaska sockeye salmon abundance. For the northeastern North Atlantic (55°N to 65°N, 30°W to 10°W), time series include the NAO, winter SST, phytoplankton abundance, *C. finmarchicus* abundance (Zoop), and Atlantic salmon abundance. For the Equatorial South Pacific, time series include the PDO, the Southern Oscillation Index (SOI), and abundances of skipjack tuna. For the Southern Ocean, time series are for austral winter SST anomaly (°C), austral winter sea-ice concentration anomaly (SIA), austral summer log10 of the total krill catch anomaly at South Orkney, and the austral Gentoo penguin numbers.

new generation of ocean basin scale models is the incorporation of uncertainty (*24*). Uncertainty arises because of limitation in the data, in the process representations of the model, and in the parameterizations of the model. Simulations should be probabilistic rather than deterministic, such that our endemic lack of knowledge of processes and structure at these scales can be acknowledged. This philosophy has been adopted in fisheries modeling (*25*), because of the management need for uncertainty estimates, and by physical oceanographic climate modelers whose results also have management implications. Uncertainty is inherent to individual-based modeling approaches (*26*), but it has not yet been applied to ecosystems and carries a high computational cost. Monte Carlo, ensemble, and data assimilation modeling are all well developed, but their application in spatially explicit ecosystem models is just beginning (*27*).

Both physical and ecological models of marine systems have, until now, been largely focused on hindcasting past observations in order to assess the quality of understanding of processes. Usually, the approach has been to evaluate, by statistics or judgement, the extent to which deterministic simulation results agree with observations (*28*). More recently, physical oceanographic models have been developed for hindcast reconstruction, involving assimilation of observations to simulate the most likely visualization of past conditions (*29*). In contrast, the requirement for forecast simulations demands a very different modeling philosophy and a trade-off between accuracy and precision. There is a high degree of uncertainty associated with the representation of processes and associated parameters in marine ecological models. The purely deterministic approaches of the past imply high precision, but the probability of
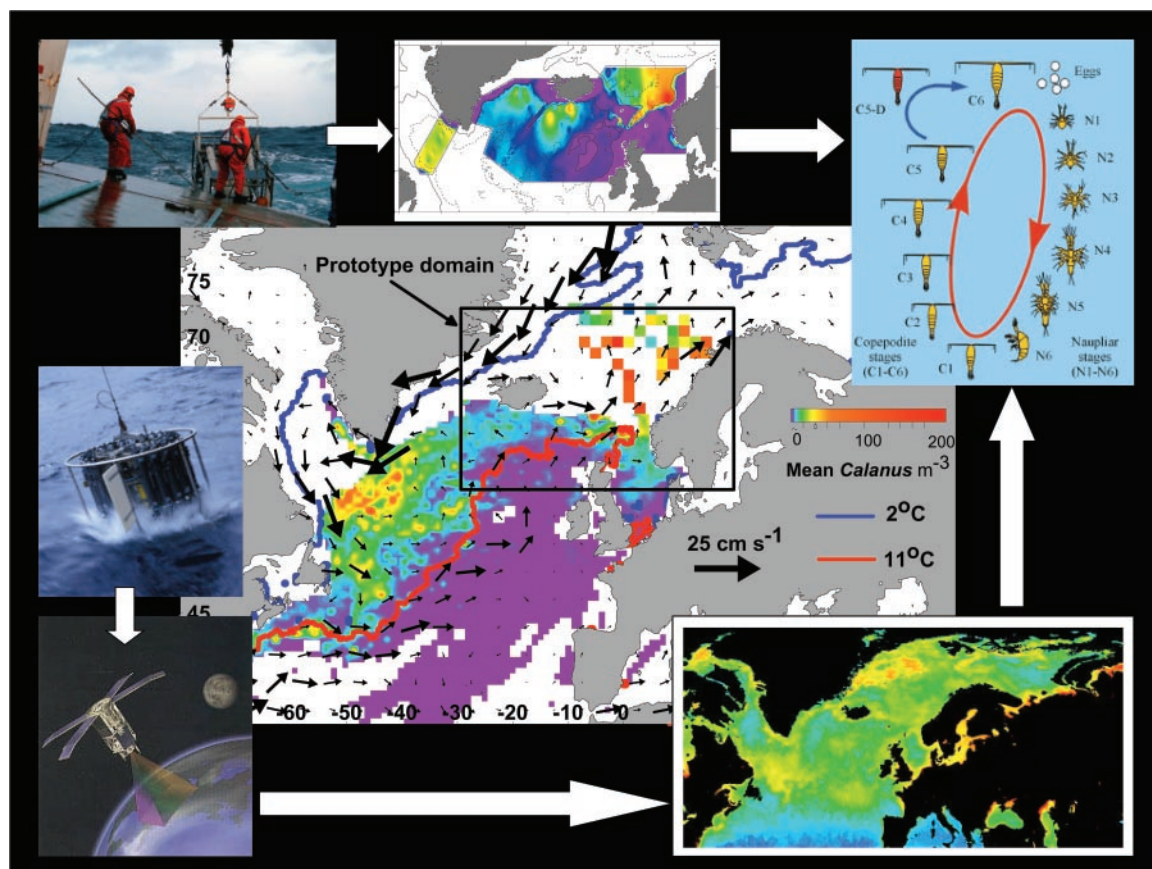

Fig. 2. Central image: 30-m-deep annual average temperature and velocities from the Ocean Circulation and Climate Modelling Program global hydrodynamic model, superimposed on the 1950 to 1999 mean abundance of *C. finmarchicus* (adults and copepodite stage 5) from Continuous Plankton Recorder (*5*, *11*) and European Union–Trans-Atlantic Study of Calanus surveys. The main centers of *C. finmarchicus* abundance are delineated by gyres in the ocean circulation system. A stage-structured life-cycle model of *C. finmarchicus* (inset, top right) is linked to the circulation model data to simulate the stage demography in space and time (*15*). Development rate, mortality, reproduction, and diapause entry are driven by temperature and food in the upper 100 m of the ocean, but the overwintering diapause stage (shown in red on the life-cycle inset) is simulated at depths of 500 to 1500 m. In the prototype system (*15*), food is provided by blended SeaWIFS and bottle data (lower insets), but a full North Atlantic version of this model is linked to output from a global simulation of phytoplankton and microzooplankton biomass. Finally, we iteratively fit the model system to archived field observations (upper insets) (*23*), using maximum likelihood functions to locate the optimum space-time distribution of mortality and diapause entry/exit parameters. [Photos: A. Mustard]

an accurate outcome is extremely low, and such forecasts are of minimal societal value. Often, sensitivity analyses are conducted with respect to key parameters to determine the dependence of the model on parameterization, but this is only achievable for relatively simple systems. The alternative is to incorporate uncertainty into the forecasting procedure from the outset, in order to deliver probabilistic rather than deterministic projections that, although less precise, are more accurate.

There are various possible approaches to incorporating uncertainty into simulation projections. The Intergovernmental Panel on Climate Change forecasts of global temperatures under different carbon dioxide emission scenarios take the form of a range of possible outcomes based on results from an ensemble of independent models, each having different numerical implementations of essentially a common set of processes (*30*). Meteorologists now use ensemble forecasts to improve their predictive skill particularly for medium-range (3- to 15-day) forecasts (*31*). The International Whaling Commission also uses an ensemble approach to identify management procedures that are least sensitive to uncertainties (*32*). In contrast, medium-term (5- to 10-year) projections of the state of various fish stocks are presented as probability distributions of future spawning stock biomass for different exploitation scenarios (*25*). In this case, iterative simulations are performed with interannual variability in recruitment to the stock represented as a stochastic process with a statistical distribution parameterized from historical data. Although there have been some attempts at incorporating probabilistic processes into ocean basin–scale physical and biological simulations (*33*), the ensemble approach is difficult to apply to ecological systems,
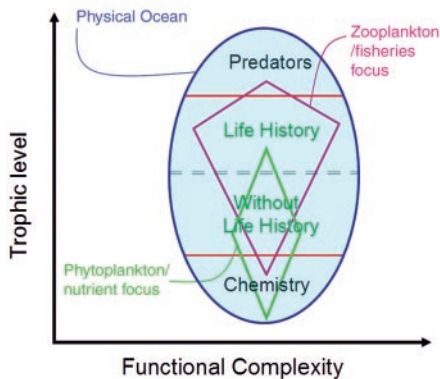
Fig. 3. Schematic illustrating the relation between trophic level (vertical axis) and functional complexity (horizontal axis) within marine ecosystem models. The rhomboids indicate the conceptual characteristics for models with different species and differing areas of primary focus. The rhomboid is broadest, i.e., has its greatest functional complexity, at the level of the target organism of the model. The line separating organisms with and without life history is dashed to indicate that this boundary is not fixed. The same organism could be on either side of this boundary, depending on the target species and the problem to be addressed. The magenta rhomboid applies to a model with a primary focus on zooplankton that go through complex life-history development, thus requiring greater fidelity to ontogenetic development. The green rhomboid applies to a model with a primary focus on phytoplankton and biogeochemical cycles, but which also includes zooplankton with lower life-history resolution. The blue oval represents the physical ocean. Few models represent much of the functional complexity of predators; hence, the rhomboids only touch upon the uppermost trophic level.

because results from models that incorporate different processes and variables are not easily comparable (*34*). Similarly, the iterative stochastic approach is difficult to conceive for a large, computationally intensive simulation model. Nevertheless, ocean modeling is clearly at the point where the issue of uncertainty must be explicitly addressed, with new initiatives likely involving a combination of ensemble and stochastic approaches.

Future Challenges

Building models of marine ecosystems that integrate processes ranging from the biogeochemical, through the multiple stages of secondary producers, to the life cycles of fish cannot proceed by simply including more variables. Some of the main issues follow:

1) Modeling the higher trophic levels requires different approaches than modeling phytoplankton and microbes. Individual variability and life-history details become increasingly important with distance up the food web, necessitating structured-population and even individual-based models to produce meaningful simulations of population dynamics.

2) The challenge for marine ecosystem modeling is to integrate models of different types, that is, to couple models across trophic levels. Even with powerful computers, it is necessary to simplify the problem so that parameter richness and biological relevance are balanced. Rather than model the entire ecosystem, we should focus on key target species and develop species-centric models.

3) We can build on deterministic models, recognizing the growing requirement to develop probabilistic simulations. There is a pressing need to incorporate uncertainty into models, because simulations lacking probability analysis are of rather limited value.

4) For many marine ecosystem forecasting problems, the key issues relate to decadal variability of taxa that have ocean basin–scale distributions. Our models must explicitly span the relevant spatial and temporal scales of the target organisms.

5) Forecasting decadal variability will require more accurate physical models, of both the atmosphere and the ocean. Although physical modeling has made great advances, there remains much to be done to improve our ability to forecast at decadal periods.

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