



Food for Thought

Projecting the future state of marine ecosystems, “la grande illusion”?

Benjamin Planque*

Institute of Marine Research and Hjordt Centre for Marine Ecosystem Dynamics, 9294 Tromsø, Norway

*Corresponding author: tel: +47 48 89 30 43; e-mail: benjamin.planque@imr.no

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Using numerical models to project the state of marine ecosystems several decades into the future is commonly advocated, in particular for investigating the possible effects of climate change. Numerical models are useful to explore how ocean climate and other drivers may regulate the dynamics of marine ecosystems and constitute indispensable tools to test our conceptual representations of how marine systems function. However, I argue here that these models might be of limited use to project the future state of marine ecosystems decades into the future because several factors limit predictability. These include stochasticity, deterministic chaos, enablement vs. entailment, non-ergodicity, ecological surprises, irreducibility, and limits to upscaling. Many simulations of ecosystem states in the distant future may be no more than a “grande illusion” until explicit evaluations of how uncertainties increase with the time horizon of projection are performed.

Keywords: climate change, marine ecosystems, numerical models, predictability.

Projecting the future

In the book *the value of science* published in 1905, the mathematician Henri Poincaré describes the role of science as follows: “*la science prévoit et c’est parce qu’elle prévoit qu’elle peut être utile et servir de règle d’action*”. [Science foresees, and it is because it foresees, that it can be useful and serve as rule of action (translation by George Bruce Halsted).] Prediction is identified as central to the role of science, a point of view somehow apparently contradicted in Niels Bohr famous quote that “*prediction is very difficult, especially about the future*”.

Whatever the degree of complexity of a model, the developers of numerical models of ecological systems are generally trapped between these two perspectives: justifying the existence of a model by its predictive capabilities while recognizing that predictions of future states of ecological systems may not be reliable.

Low predictive performances in marine ecosystem models are usually attributed to the absence—or the poor representation—of important ecological processes in numerical formulations. This has often served as justification to construct models of ever increasing complexity, in which large numbers of detailed processes can be represented simultaneously. Since the early simple marine ecosystem models (Steele, 1974), increasing numerical capabilities have supported the

development of models of ever growing complexity, which can combine ocean dynamics, biogeochemistry, biology of unicellular organisms, animal behaviour, trophic interactions, human effects through exploitation, pollution, or habitat modification, economical dynamics, and even governance and policy (e.g. Holt *et al.*, 2014).

I argue here that regardless of model complexity and refinement of model components, there are limits to the degree of predictability of marine ecosystems states into the future. I present below several theoretical arguments that justify why predicting future ecosystem states may not be achievable with reasonable levels of certainty at time horizons of several decades, as commonly required for climate change projections. By ecosystem state, I mean the “state variables” in a particular ecosystem model and refer more generally to an ensemble of ecosystem properties of interest to researchers and managers alike, such as nutrient levels, primary production, abundance, spatial distribution, phenology, age/size structure of particular species or species groups, biodiversity, etc.

Stochasticity

Chance, randomness, or stochasticity express the unpredictability of some events. Whether chance is a true feature in nature, as suggested

by Prigogine (1996), or simply the result of our inability to accurately observe and model natural phenomena is a matter of debate. However, the existence of *apparent* stochastic phenomena is undisputed. Throwing a dice or playing roulette are ways to produce a random outcome, although these processes are primarily ruled by the deterministic laws of Newtonian physics. Stochastic phenomena are not just *statistical nuisance* that results in increased uncertainty in ecological model projections, but rather structuring processes in the evolution of life and dynamics of ecosystems. For example, the two pillars of the theory of evolution are selection and variation, with the latter being based on the randomness of DNA mutations and recombination. In the—debated—ecological neutral theory, many patterns of biological diversity are shown to emerge from stochastic processes combined with specific constraints (Rosindell *et al.*, 2012). In marine fish populations, non-deterministic variations in migration routes have been shown to be essential to colonization of new habitats or recolonization of lost habitats (Petitgas *et al.*, 2006, 2010). These examples illustrate how stochastic events constitute an essential, but by definition unpredictable, component of the dynamics of ecosystems.

Deterministic chaos

Deterministic chaos happens when the dynamics of a deterministic (i.e. non-stochastic) system do not converge towards equilibrium points or cycles but instead towards a succession of many possible states, in a non-repeatable fashion. Deterministic chaos has been formalized for living systems since the mid-1970s (May, 1976). Specific features of deterministic chaos include sensitivity to initial conditions and limited predictability beyond certain time horizon. The ability to predict system state at a certain time horizon depends on the sensitivity to initial conditions and on how accurate the initial state of the system can be measured. The initial states of marine ecosystems, as required by complex ecosystem models, are generally known with poor accuracy because of the inherent difficulties in observing life underwater. Hsieh *et al.* (2005) have shown that in the North Pacific Ocean, non-linear processes that display chaotic behaviour best represent variations in the biological states. If complex non-linear dynamics operate in marine ecosystems, as suggested by empirical studies (Hsieh *et al.*, 2005; Glaser *et al.*, 2014), this implies that decadal predictions of the future state of the system may be highly uncertain even when the underlying deterministic processes are known exactly, which is usually not the case in ecology. Predictions with acceptable levels of accuracy may only be achieved for short time horizons, while in the longer term, uncertainties may be as large as the chaotic attractor of the modelled system.

Enablement, not entailment

Numerical modelling approaches employed to simulate ecosystem dynamics are predominantly inspired from, and built on, principles developed for Newtonian physics. These include sets of differential equations, knowledge on initial and boundary conditions, and the division of a complex system into an ensemble of simpler constitutive elements, i.e. reductionism. The engine of such model construct is a set of deterministic relationships, each relating a cause to its effects, i.e. *entailment*. A precondition for Newtonian models is that the state space, i.e. the space describing the possible states of the system, can be defined and that its dimensions remain unchanged, or at least predictable. Longo *et al.* (2012) and Kauffman (2014) have argued that this precondition cannot be met by living systems because changes in the ecosystem configuration lead to changes in the ensemble of adjacent possible opportunities for

further evolution (the state space), so the temporal evolution of a system constantly leads to new sets of possibilities. The formation of new dimensions in the state space cannot be stated in advance, i.e. it is *unprestable*. The result is that no law entails the evolution of living systems and that instead this is driven by the emergence—i.e. *enablement*—of novel opportunities as life constantly adjusts to its environment while modifying it. In marine ecosystems, enablement can be exemplified by the introduction of new species, accidentally or not. This creates new opportunities for potential prey, predators, parasites, or diseases to develop, thereby creating new opportunities for prey, predators, and parasites of the latter, etc. Species introduction can thereby enable a new, but *unprestable*, set of adjacent possible opportunities for ecosystem dynamics.

Non-ergodicity

Ecosystem models that use past observations as the basis for predictions rely on system ergodicity, i.e. that the space of possible system states has been appropriately explored in past situations. At least several repetitions of an event are necessary to compute its probability, but unfortunately, unique events are prevalent in ecosystem dynamics. Following the reasoning of Ulanowicz (2009), it only requires 75 distinguishable events to co-occur by chance to generate a combinatorial statistics of $75! \approx 10^{106}$, a number greater than that of all simple events that have occurred in the universe since its beginning 13–15 billion years ago (Elsasser, 1969). Thus, past ecosystem states only cover a minute fraction of the gigantic number of possible ecosystem configurations. In other words, the future states of marine ecosystems are likely not contained in the set of their past configurations. Process-based models can apparently circumvent this problem by focusing on system processes rather than historical correlations. They do not depend directly on the exploration of past ecosystem states but nevertheless rely on the ergodicity of biological processes, i.e. they require that the ensemble of possible ecological processes has been observed in the past. But, living systems are characterized by their ability to evolve, that is the ability to restructure themselves and to develop new ways of functioning. As a consequence, processes that drive their dynamics are continually altered and the range of processes observed in the past cannot be expected to cover those that will operate in the future. The lack of ergodicity is problematic for ecosystem models, because it implies that their performance in reproducing past dynamics says little about their ability to simulate future ones. For example, current ocean acidification is driving marine ecosystems towards environments and configurations that have not been experienced before and the processes associated with bio-calcification, that were ignored in ecosystem modelling efforts few decades ago, may be central to future models. While it may be possible to achieve ergodic sampling of physiological or behavioural characteristics, by studying many individuals in the same population, ergodicity is not achievable for ecosystems since the historical trajectory of an ecosystem is unique, time limited, and cannot be assumed to have explored the ensemble of its possible trajectories. This is even true at the scale of marine communities or populations for which there are no available replicates to ensure a full exploration of possible states. The earth system is an extreme case in which the historical trajectory is evidently unique and can only inform on an infinitesimal fraction of the possible earth system states.

Expected surprises

Whether they are called ecological surprises, unexpected events, unforeseeable catastrophes of black swans, ecological systems are

always open for dramatic events that numerical models are not designed to forecast (Duarte, 2014). While these may come as surprises from a modelling perspective, these are so common in real ecological systems that they can hardly come as a shock. Regime shifts have been reported repeatedly in marine systems worldwide (Blenckner and Niiranen, 2013), and so have major changes in species dominance, such as outburst of the alien comb jelly *Mnemiopsis leidyi* in the Black Sea (Daskalov *et al.*, 2007), rapid expansion of the red king crab and snow crab in the Barents Sea (Alvsvåg *et al.*, 2009; Windsland *et al.*, 2014), or decadal booms and burst of small pelagic fish populations over millennium time-scales (Baumgartner *et al.*, 1992). Observations, theory, and simulation models can be, and have been, used to reconstruct the history of catastrophic events in marine ecosystems, but this has provided little additional capacity to predict similar events in the future, so it is most predictable that marine ecosystems will continue to take modellers by surprise.

Irreducibility

Introduced by Wolfram (2002), irreducibility refers to the impossibility of constructing a simplified version of a computational system and still reproduce its dynamics. In Wolfram's *New Kind of Science*, living systems are assimilated to complex computational systems. Ecosystems display extremely large dimensionality driven by a large number of variables operating at a large number of scales, a situation often referred to as the "curse of dimensionality" (Yodzis and Innes, 1992). Beckage *et al.* (2011) have argued that the dynamics of these complex systems are computationally irreducible and that the only way to "compute" the future state of an irreducible ecological system is to allow the system itself to compute it. In practice, only simplified representations can be constructed to simulate ecosystem's future and numerical models of ecosystem dynamics, as complicated as they may be, are gross simplifications of real-world ecosystems. Under the hypothesis of irreducibility, these simplified representations cannot compute the future states of ecosystems. While there exists theory and methodological approaches to evaluate optimal degrees of complexity for statistical models of simple systems (Burnham and Anderson, 2002), there is yet no theory that establish a relationship between model complexity and prediction accuracy for dynamical models of complex ecological systems. The rhomboid approach suggested by de Young *et al.* (2004) and following suggestions for models of intermediate complexity (e.g. Collie *et al.*, 2014; Plagányi *et al.*, 2014) have attempted to define strategies for modelling populations in the wild and still incorporate ecosystem features that get simpler as they are situated further away from the main focus of the model. For models that focus on the dynamics of the whole ecosystem, however, it is not obvious where simplifications should be operated and what degree of model simplification is acceptable to ensure suitable reproduction of the dynamics of real ecosystems.

Limits to upscaling

Upscaling occurs when a deterministic process defined at a *low* level of organization in a system (e.g. an individual organism) is used to model the dynamics at a *higher* level of organization (e.g. a population). For example, the effect of temperature on individual growth or the effect of prey density on individual feeding rates can be quantified experimentally and then used to parameterize growth functions and trophic functional relationships. Typically, experimental measures of growth and feeding rates consider isolated systems with few *state variables* (e.g. species) and under few controlled

pressures (e.g. temperature, food density). Marine ecosystems, on the other hand, are open systems made up of a particularly large number of components and under many possible pressures. In these systems, the response of an individual species to temperature or prey density may turn rather different from that observed under controlled conditions, because the presence of other preys, ocean currents, turbulence, variations in light or salinity, mating behaviour, parasitic infestation, etc., usually interact with, and can often override, those of temperature and prey density alone. In a recent review, Cahill *et al.* (2012) showed that the impact of warming on population extinctions is predominantly driven by changes in species interactions rather than by direct physiological effects of temperature on individual populations. In other words, what are considered externalities at a small experimental scale become integral parts of the picture at a larger scale. As a result, many deterministic processes operating at low level cannot easily be translated to ecosystem level in a simple and useful way, even when they are theoretically well grounded and empirically parameterized with precision.

La grande illusion?

The above arguments are not new but are often not well recognized when constructing marine ecosystem models. The result is that when complex numerical simulation models are used to make projections of ecosystem states several decades into the future (e.g. Ellingsen *et al.*, 2008; Wisz *et al.*, 2015), these projections are often met with a high degree of scepticism by end-users (Ruiz and Kuikka, 2012).

Obviously, the development of simulation models is an ongoing process and one can expect that modelling capabilities are constantly improving. The continuous increase in computing power has nurtured great hope that complex ecosystems could be simulated by equally complex numerical models, with a high degree of realism. Fifty years after Holling's aspiration to use computers as the ideal tool to handle the conceptual problems faced in ecological analysis (Holling, 1966), we are seeing the emergence of complex simulation models of marine ecosystems at scales ranging from few kilometres to regional seas, ocean basins, or even the entire globe (e.g. Ellingsen *et al.*, 2008; Huse and Ellingsen, 2008; Link *et al.*, 2010; Chust *et al.*, 2014; Harfoot *et al.*, 2014; Cressey, 2015). Interestingly, in his seminal article on ecosystem resilience, Holling (1973) identified important limits to numerical modelling of living systems and emphasized that the conclusions derived from existing models did not hold when (i) systems are composed of many components, (ii) processes are complex (e.g. include feedback mechanisms), (iii) spatial and temporal processes interact, and (iv) there is a high degree of stochasticity; four situations that are the rule rather than the exception in marine ecosystems. These limits can unfortunately not be passed by brute force and predictive modelling capability cannot expect to improve by the sole increase in computing power. In fact, rather the reverse may happen. When super complex models are built by assembling multi-scale and multi-purpose modelling bricks, the many assumptions and model parameter uncertainties render the sensitivity of the models intractable, which tend to increase, rather than reduce, projection uncertainties. This is not to say that uncertainties are ignored in ecosystem models and model projections. Rather, quantifying uncertainties has become a central issue and it is now essential that model projections be presented with associated uncertainty estimates. Unfortunately, these estimates are usually limited to parameter uncertainty and do not account for other sources of uncertainties that

can have a more dramatic impact on projections (e.g. Planque *et al.*, 2011; Gregr and Chan, 2014).

The ongoing movement to promote predictive ecology (Evans *et al.*, 2012) is accompanied by confusion between “prediction” as the necessary ingredient of science, *à la* Poincaré, and “prediction” about the future. Prediction is critical in science to produce strong inference *sensu* Platt (1964), i.e. to test model predictions against empirical observations, but this does not equate to forecasting the state of extremely complex natural systems decades into the future. Physical events such as earthquakes or storms, which are fairly well understood and described by theory that is supported by testable predictions, cannot be predicted into the future beyond relatively short time horizons. Model-based predictions, decades into the future, are already performed, but nearly none of these predictions are used directly for management purpose (although many of these models get financial support under the promises of being applicable to management, Ruiz and Kuikka, 2012). When complex whole-of-ecosystem models such as Atlantis have been used in management, the purpose has generally been to investigate the trade-offs of various management options rather than to make predictions about the future, and the intention has been to provide insight into ecosystem dynamics rather than operational tools for day-to-day management decisions (Fulton *et al.*, 2011).

Whole-of-ecosystem (or end-to-end) models of marine ecosystems support the reconciliation of reductionist and holistic approach, they offer a platform for multi-disciplinary collaborations and provide the potential to match the demands and expectations of many end-users. Output from these models can inform on the directions in which various ecosystem components may respond to specific pressures and provide useful description of the trade-offs that results from physical, biological, economical, or historical constraints. However, their use as computational platforms to simulate what ecosystems will look like decades into the future is questionable (Figure 1). The ever-increasing list of environmental model prediction failures (Pilkey and Pilkey-Jarvis, 2006) should act as a strong warning against decadal or multi-decadal projections.



Figure 1. Was the pet included in the pet ecosystem model? (drawing: Juliette Planque).

There is a clear need to recognize the limits of numerical models when projecting the states of marine ecosystems at time horizons of decades and beyond, and to refrain from computing and disseminating projections when the uncertainties around these have not been evaluated adequately. Without clear identification and quantification of model projection uncertainties, simulations may simply be faith-based constructions disguised behind complex computations. It is equally critical to recognize that the building of more complicated simulation models, even when supported with more empirical data, may not resolve this issue. This does not undermine the value of numerical modelling of marine ecosystem as an essential tool to test our conceptual representations of how marine systems function and to provide insight into the possible states and dynamics of these systems. There is however a need to evaluate how these models may contribute to the advancement of marine ecological understanding and when they can be used or may be misused for projections. Among others, two advances may improve marine ecosystem model developments in the future. The first is to explicitly assess how model prediction uncertainties increase with the time horizon of projection (as done, for example, in Glaser *et al.*, 2014). In other words, it is necessary to determine the forecast horizon of ecological predictions (Petchey *et al.*, 2015). In this way, it will be possible to provide reliable simulations of future ecosystem trajectories within “reasonable” time frames. The second approach is to construct models supported by few simple assumptions on the limits of ecosystem configurations or rates of change rather than on (often hypothetical) laws that regulate ecosystem trajectories. In this way, it is possible to investigate what can happen in the future rather than to predict precisely future ecosystem states. This approach, related to the mathematical theory of viability (Aubin *et al.*, 2011), is slowly emerging in marine ecosystem modelling (Mullon *et al.*, 2009; Planque *et al.*, 2014).

For the reasons highlighted above, predictions of the state of marine ecosystems into the distant future will likely remain highly uncertain, but as stated by Tukey (1962) “*Far better an approximate answer to the right question, which is often vague, than an exact answer to the wrong question, which can always be made precise*”.

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