The case for marine ecosystem models of intermediate complexity

Charles Hannah[a, *], Alain Vezina[a] and Mike St. John[b]

[a] Bedford Institute of Oceanography, Fisheries and Oceans Canada, Dartmouth, NS, Canada
[b] University of Hamburg, Hamburg, Germany

* Corresponding author : Charles Hannah, Tel.: +1 902 426 5961, email address : charles.hannah@dfo-mpo.gc.ca

Abstract:

Marine ecosystem models are reasonably proficient at simulating physically-driven features such as spring blooms. However, the demands on these models are shifting to complex biological issues such as functional diversity, and changes in ecosystems and their services such as exploited fish stocks and carbon sequestration. Current ecosystem models generally use a food web structure reduced to its bare essentials. A consequence of the simplified structure is that they are specialized to a particular time, place and ecosystem state and thereby have limited ability to evolve into a substantially different state as a result of internal dynamics or changes in external forcing. We use food web theory and the ideas from complexity theory to argue that an improved representation of the structure of marine food webs is essential for the next generation of marine ecosystem models. Here we propose that a useful guiding principle for model design is provided by earth system models of intermediate complexity; a willingness to sacrifice process detail in order to increase the number of interacting components in the system and simulate the web of feedback loops.

1. Introduction

Coupled physical-biological models of marine ecosystems have become reasonably proficient at simulating physically-driven features such as spring blooms (Doney et al. 2001; Findlay et al. 2006; Sharples et al. 2006). However, demands on marine ecosystem models are shifting to predicting functional diversity, ecosystem change and changes in ecosystem services such as carbon sequestration and production of exploited resources (IMBER 2005; Rothstein et al 2006). These demands clearly identify the need to develop ecosystem models that can deal with such questions without getting bogged down in unmanageable complexity.

The purpose of this paper was to provide a vision for the future of marine ecosystem models for the 'Symposium on Parameterization of Trophic Interactions in Ecosystem Modelling.' The model structures and applications covered by the phrase 'marine ecosystem models' are very diverse and we recognize that 'beautiful conceptual frameworks integrating all of the modelling applications break down in the face of the realities of modelling site specific problems for particular practical applications' (Hannah 2007). The goal of this paper is more limited. We ignore the details of any particular model or application and search for general principles that may be useful in guiding the development of the next generation of marine ecosystem models. We will review the notion that making models more complicated makes them less accurate and then look to complexity theory, climate modelling and food web research for insight on modelling principles.

The models discussed herein are biogeochemical-ecological in the sense defined by Tett and Wilson (2000). That is they are biogeochemical in that they conserve at least one element (e.g. nitrogen, carbon, phosphorus) and they are ecological in that they 'include at least one degree of freedom amongst a set of state variables with a common conserved quantity' (Tett and Wilson 2000). The models are also assumed to be spatially explicit since the physical environment sets the stage for the ecosystem dynamics (Longhurst 2006).

2. Accuracy and effectiveness

A recent review of aquatic biogeochemical models (Arhonditsis and Brett, 2004) supports the commonly held notion that adding complexity to an ecosystem model does not improve the simulation; they found no systematic improvement in accuracy or predictive capability. In the context of nutrient-phytoplankton-zooplankton (NPZ) models in the open ocean, Friedrichs et al (2006) show that in many cases a carefully tuned simple model can perform as well as a more complex model. On the other hand, a pragmatic review of ecosystem models by Fulton et al. (2003) concluded that 'The simplified webs, especially those reduced to less than 25% of the size of the original model web, are not able to represent enough of the processes and interactions in the system to faithfully reproduce system dynamics, particularly when the strength of environmental or anthropogenic pressures change.' As well, Blackford et al. (2004) and

Friedrichs et al. (2007) provide examples where the generality provided by a complex model structure allows a single parameter set to provide useful skill in different environments (i.e. the models are portable).

The idea that increasing model complexity decreases model accuracy was addressed by Costanza and Sklar (1985) in their analysis of freshwater wetlands models. They showed that the maximum model accuracy (fidelity to the observations) decreased monotonically as a function of model complexity (Fig. 1a); their word was articulation, a function of spatial resolution, temporal resolution and number of state variables. In other words, at the extreme of low complexity the models 'said much about little' and at the extreme of high complexity the models 'said little about much.' It is important to note that simplicity was not a guarantee of accuracy, most of the models did not achieve the accuracy frontier (Fig. 1a).

Costanza and Sklar (1985) then devised a metric that reflected the need for both accuracy and a comprehensive description of the system. They called the metric 'effectiveness' (a combination of articulation and accuracy) and showed that the maximum effectiveness was for models of intermediate complexity (Fig. 1b). Fulton (2001) extended the analysis to about 1800 models in a wide range of fields and found the same result; maximum effectiveness was for models of intermediate complexity

The concept of effectiveness provides a framework for reconciling two ideas: 1) that when compared against common data, a highly tuned simple model generally out performs a more complex one; and 2) a more complex model can provide information about the system that is not available from the simple model (e.g. greater trophic or spatial resolution). Effectiveness is an attempt to quantify the trade off between the two and answer the question 'Given the current state of modelling technology, how much complexity is useful?' The answer will change over time; as the models improve the accuracy frontier will move towards the upper right in Fig. 1a and the effectiveness peak will move to the right in Fig. 1b.

3. Insights from complexity theory

The dominant scientific metaphor is Newton's Third Law: for every action there is an equal and opposite reaction. This law, developed in the context of simple physical systems, when taken as a metaphor, gives rise to a mechanistic view of the world with linear chains of cause and effect. This world view implies that given the correct laws and good initial conditions one can confidently predict the time evolution of the system of interest. While this view has been extremely useful and powerful, the advent of quantum mechanics and turbulence theory in the late 1800's and early 1900s showed that the mechanistic view had limitations.

As an alternative metaphor, consider the classic thought experiment of complexity theory, a sand pile (Bak et al 1987). A pile of sand has a critical slope where for shallower slopes the pile is stable and for steeper slopes the pile is unstable (subject to

avalanches). Consider a sand pile near the critical slope. Then drop individual grains of sand onto the pile one at a time. Each grain introduces a small, and apparently identical, perturbation to the pile (the action). The most common reaction is that nothing happens, however sometimes there is a small avalanche and occasionally there is a catastrophic avalanche. The reaction of the system is not proportional to the action. It turns out that there is a power law relationship between the magnitude of the events and the frequency that they occur (Fig. 2). Similar relationships are observed for earthquakes (Bak and Tang, 1989; Sornette and Sornette, 1989), mass extinctions (Sneppen et al. 1995) and business failures (Cook and Ormerod 2003).

One interpretation of the sand pile result is called sensitive dependence on initial conditions; for each drop of a grain, small differences in the details of the initial state control whether an avalanche happens. This interpretation is also called the 'butterfly effect'; the image whereby a butterfly flapping its wings may influence a chain of atmospheric events that leads to a tornado (Lorenz 1963; see Wikepedia 2007 for an overview). This interpretation has been important for advances in numerical weather prediction. Over the last 40 years there has been an enormous effort to improve the initial conditions for the numerical simulation from a combination of better observations and data assimilation. As a result, the limits of deterministic predictability, a few days, have largely been achieved.

Another interpretation of the sand pile is self organized criticality, the idea that complex systems naturally evolve to a state where they are near a critical point (i.e. they are stable most of the time but subject to dramatic changes such as avalanches). This seems sensible in the context of a pile of sand. The key insight from complexity theory is that systems that exhibit self organized criticality have achieved a balance between stability and chaos, or between positive feedbacks and negative feedbacks (Waldrop, 1992). They are stable enough to have persistent patterns and fluid enough to be able to transmit information: they are always changing. In the case of the sand pile the positive feedback is the acceleration due to gravity and the negative feedback is friction. Even though Newton's Third Law holds at the microscopic scale, the interactions between the many grains of sand gives rise to unexpected behaviour (avalanches).

While self organized criticality is a theoretical model it can also be used as a metaphor: the key elements are listed in Table 1. For example, Ormerod (2006) interprets a power law relationship in the statistics of business failures in the United States (Cook and Ormerod 2003) as evidence of self organized criticality in the economy and claims that it is a manifestation of the 'Law of Unintended Consequences.' He argues that in an economic system with an enormous number of interacting entities, no individual or corporate strategy group can anticipate all of the consequences of a particular business decision. As a result, occasionally a decision gets made that leads to the failure of the company, through an unexpected chain of events.

Self organized criticality is a special case of the more general idea of critical behaviour or criticality. Criticality can be loosely defined as follows. A phase transition is the movement of the system from one (mostly) stable state to another (an avalanche is a transition from one state of the sandpile to another). Criticality is the behaviour of the system near a phase transition. Criticality arguments are now being used in theoretical

investigations in evolutionary ecology (Solé et al. 1999), food web dynamics and stability (Solé and Montoya 2001), and landscape ecology (Pascual and Guichard 2005).

The importance of chaos and criticality for understanding and modelling marine ecosystems is not widely accepted in the oceanographic modelling community. However the existence of regime shifts (Hare and Mantau 2000; Sheffer and Carpenter 2003; Choi et al. 2005) raises the distinct possibility that physics and chemistry are not sufficient to explain all the changes in marine ecosystems. The limitations of the Newtonian metaphor for ecological systems were revealed empirically by Hsieh et al. (2005). They found strikingly different dynamical behaviour in long time series of physical and ecological variables in the North Pacific. The time variation in physical variables could be modelled as the sum of a large number of linear modes whereas the variation in the ecological variables was best described by a few strongly nonlinear modes. The 'avalanche' metaphor seemed more apt in describing the pattern in ecological variability and their response to physical variability than the 'action-reaction' metaphor. A recently published analysis of an 8-year mesocosm study run under constant environmental conditions comes closest to demonstrating chaotic dynamics in a plankton community (Beninca et al. 2008). The study showed that the time variability of any particular plankton group could not be predicted beyond 15 days, a temporal window related to the generation time. These studies illustrate that nonlinear complexity theory cannot just be considered academic; it should be taken seriously in approaching the development of marine ecosystem models.

Despite the inherent difficulties in modelling systems that exhibit criticality, useful modelling and prediction is done in fields such as weather, climate, earthquakes, avalanches, and the economy. A reasonable set of guidelines for how one approaches such systems is provided by Waldrop (1992)
There is a need for extensive observations and ongoing monitoring;
Deterministic prediction of future states is not possible, one can only predict the likelihood of certain events;
There needs to be an ongoing search for nonlinear interactions and feedback loops.
Whether or not marine ecosystems exhibit criticality, these seem like reasonable guidelines. The next section of this paper focuses on feedback loops.

4. Models and feedback loops

Consider two broad categories of models: weather prediction and climate prediction. In atmospheric weather prediction, observations are used to prescribe the initial state and then the model predicts the state of the atmosphere over the next few days (the wiggles; Fig. 3). Whereas in climate modelling the goal is to compute the mean state of the earth system (atmosphere, ocean, ice, land surface, hydrology) without recourse to observations and then predict changes in the mean state (e.g. climate change prediction).

From the perspective of the atmospheric model the fundamental equations are the same for both the weather and the climate models; what differ are the feedback loops that are

included. Weather prediction models tend to include feedbacks that operate on the time scales relevant to predicting the weather 24 to 48 hours in advance, whereas climate models include feedback loops that operate on longer timescales. For example, in traditional weather forecast models the sea surface temperature (SST) is held constant as the impact of the changes in SST over a day or so have been thought to be small, whereas in climate modelling the ocean is an important component as the changes in SST play a major role in the evolution of the atmosphere.

The quest for improved simulation has led both modelling communities to include feedbacks from other (non-atmospheric) components of the earth system such as air-sea interactions (Chen et al. 2007; Zhang et al. 2006), land-atmosphere interactions (Dai et al. 2003; Brochu and Laprise 2007) and ice-ocean-atmosphere interactions (Pellerin et al. 2004). In addition there has been a move towards ensemble prediction (prediction of statistics; Zhu 2005; Buizza et al. 2005) to deal with sensitive dependence on initial conditions and critical behaviour. In a recent assessment of global climate models, Reichler and Kim (2008) found that the multi-model ensemble mean performed much better than any of the individual models. This reinforces the importance of considering not only different initial conditions and parameter values but different model formulations (e.g. Gentleman et al 2003).

For the purposes of this discussion the important conceptual difference between the weather prediction and the climate prediction models is that the weather prediction models are much more strongly constrained by observations. A key feature of weather prediction over the last 40 years has been the development of the global observation network and the data assimilation technology to enable the models to take advantage of the observations in order to improve the initial conditions in order to combat the butterfly effect.

Another way to think about the use of the observations is that key feedback loops have been cut and replaced by observations. For example in a model based on an NPZ structure, the community composition is embedded in the model's rate parameters. If the rate parameters are fixed then the implied community structure cannot change even if the natural response to the external forcing would be a change in community structure. Allowing the community composition (or the rate constants) to be determined by the model allows the model solutions more freedom to adjust to changing conditions but also provides the opportunity for the solution to wander off into states that differ greatly from the observed state.

Although comparisons between physical and ecosystem models must be approached with caution, we suggest that the current generation of ecosystem (or NPZ type) models with typically 3-10 state variables share some characteristics with the weather prediction models (as defined above). For any given application, the choice of the number of state variables, the parameterizations, the biological rate constants and the selection of which feedback loops to simulate, means that the model has been specialized for a particular time, place and state of the ecosystem. This allows one to understand the current state of the system and to make short term predictions. But most of the feedback loops have been cut and this limits the ability of the system to evolve into a state substantially different from the original state. As such the models are not able to simulate large

changes in community composition that might be expected to occur due to climate change or anthropogenic impacts (e.g. eutrophication or removal of large predators).

5. Insights from food web theory

So far, we have argued that systems that exhibit critical behaviour are poised between stability and rapid transitions to alternative states and that critical feedback loops must be included in models to reproduce these transitions. The interplay between complexity, stability and feedbacks has pre-occupied theoretical ecologists for decades. A major line of inquiry started with May's (1972) seminal finding that community models (based on Lotka-Volterra equations) become increasingly unstable as they become more complex, in opposition to a large body of field and experimental observations which pointed to ecosystem complexity (biodiversity) as a positive influence on ecosystem resilience and stability. Many person-years of research have been expended in resolving this conundrum and, although the answers are not in by any means, some of the findings from that body of work link back to the ideas we raised above and can provide guidance in the development of marine ecosystem models.

One general finding is that the structure of the food web matters, independently of the details of how each compartment in the model functions. For example, randomly connected webs do not result in stable, functioning ecosystems (Martinez et al. 2006) and they are not found in nature anyway (Lawlor 1978). Apparently, there is no neutral model of food web structure comparable to the neutral model of community assembly. There is continuing research for theories that explain observed food web structures with the least number of assumptions (maximum parsimony). A model popular in the late 1980s-early 90s was the cascade hypothesis (Pimm et al. 1991). This model assigned food web links randomly subject to two constraints: (1) all feeding relations are hierarchical (e.g. the large eat the small) and (2) species only feed lower in the hierarchy. This model enjoyed some initial success when synthetic food webs generated from it seemed to compare well with empirical food webs. However, this early success turned out to be due in good measure to limitations of the data. As better and more detailed data on food web structure came in, the cascade model was shown to be inadequate (Williams and Martinez 2000) and tends to be dynamically unstable (Martinez et al. 2006). This has implications for the strict feeding hierarchy that is a common feature of marine ecosystem models (Armstrong 1999).

An alternative to the cascade model is the niche model proposed by Williams and Martinez (2000). The niche model retains the feeding hierarchy, but randomly assigns each consumer (or predator) a niche value (where they fall on the hierarchy) and a feeding range whose mid-point is less than the consumer with a higher niche value. A consumer then eats from all the species that fall in its assigned range. This model leads to synthetic food webs with cannibalism, omnivory (feeding on more than trophic or niche level) and trophic overlap (consumers share resources). All these features have been found in empirical food webs, including marine food webs (Link 2002). They have also long been proposed as stabilizing features of food web dynamics (Kuijper et al. 2003; Emmerson and Yearsley 2004). As a result, the niche model is having good success in reproducing empirical patterns (Jordàn and Scheuring 2004) as well as in producing food web models with good stability properties (Martinez et al. 2006). In particular, a

niche structure improves persistence of species in model food webs, i.e. it minimizes the risk of extinction. Marine ecosystem models that explicitly model omnivory (Armstrong 2003, Pahlow et al 2008) may find additional justification here.

Marine ecosystem models however are not only about connections but also about flows of matter and energy among compartments. From a theoretical ecological perspective, this brings in the concept of interaction strength. Interaction strengths are derived from the well-known Lotka-Volterra equations (Jordan and Scheuring 2004). They quantify how much changes in the abundance of one species directly affect the abundance of another species (there are also indirect effects that are not included). They are phenomenological and are independent of any specific mechanistic interaction between pairs of species.   They are exceedingly difficult to measure in practice (Berlow et al. 2004), and only in experimental settings or in well defined ecosystems that can be followed over extended periods of time. Nevertheless, the study of interaction strengths in models and in the real ecosystems has been a central feature of community ecology for a long time.

Early food web models assumed that interaction strengths are randomly distributed (May 1972, 1973). Empirical research however established that most interaction strengths are weak, that is, most species really have very little influence on others, with only a few strong interactions (Paine 1980, Berlow 1999). Therefore, the distribution of interaction strengths in a complex food web is not random but skewed towards weak interactions. Theoretical research has also shown that models that are built on weak interactions are more stable than models built on strong interactions (McCann et al. 1998, Kokkoris et al. 1999). Most importantly, models skewed towards weak interactions can grow in complexity without loosing stability; thus apparently resolving the conundrum raised by May's (1972, 1973) work. However, what is more important is the pattern of interaction strengths, i.e. how the few strong interactions are coupled to the many weak ones (De Ruiter et al. 1995, Neutel et al. 2002). Recent research suggests that the stability of complex food webs may depend on long feedback loops that involve multiple trophic levels (at least 3) and coupling of weak and strong chains of interactions (Rooney et al. 2006, Neutel et al, 2007). These results support the finding from Fulton et al. (2003) that excessive truncation of food webs in models leads to unrealistic results.

We have argued here that we need to include all the necessary feedbacks in order to predict ecosystem dynamics beyond the near term. Food web ecologists have been pioneers in the analysis of complex networks. Many decades of research have provided strong evidence that the structure of the ecosystem is central to its function, as is the case with other types of complex networks (Strogatz 2001). The theoretical focus on ecosystem stability and persistence is increasingly relevant to marine ecosystem modelling as we move towards models with multiple functional groups (Le Quéré 2005, Hood 2006). There are still very significant challenges in modelling the regional and global distribution of functional types (Anderson 2005), in particular preventing the simulation of "kingdoms" where one functional type dominates and others become extinct or near extinct (Gregg et al. 2003; Le Quéré et al. 2005). Drawing on food web theory might help design models that are more robust and where functional groups are more persistent.

One major difference between the class of models investigated in food web theory and the models commonly developed and applied in marine biogeochemistry and ecology is the greater importance of environmental forcing in the latter. Marine models assume that biogeochemical and ecological variability is largely determined by the physical environment (Friedrichs et al. 2006). Ecosystem models coupled to physical models are closer to linear webs that are controlled largely by external inputs (e.g. nutrients), and such webs tend to be globally stable or persistent (McCann 2000, Woods et al. 2005). The lessons from food web theory therefore may be less applicable than portrayed here. On the other hand, the importance of external forcing in controlling ecosystem dynamics in the ocean may be overstated. Apart from the evidence of different dynamics in physical and ecological time series (e.g. Hsieh et al 2005) and of ecological variability independent of physics (Beninca et al. 2008), f-ratios (the ratio of allochthonous to recycled nutrients in fuelling marine food webs) are low over most of the oceans and over non-bloom periods (Laws et al 2000).   Under these conditions, questions of structure and stability similar to those asked of community (Lotka-Volterra) models become relevant (e.g. Lima et al. 2002).

6. The way forward

A major issue in designing an ecosystem model is how to provide a reasonable representation of the overall structure of the food-web without drowning in a sea of state variables and unconstrained parameters. This issue is often characterized as a choice between adding more state variables to explicitly represent more of the components of the ecosystem and using a small number of state variables with sophisticated parameterizations that allow the internal dynamics to evolve in response to the state of the system (e.g. Denman 2003). In short a choice between 'lots of dumb boxes' and 'a few smart boxes.'

An approach developed by some members of the climate modelling community is called Earth System Models of Intermediate Complexity (EMICS; Claussen et al. 2004). The driving force was the need to have computationally tractable models while acknowledging the need to include more components of the earth system in a spatially explicit framework. The overall philosophy is a willingness to sacrifice process detail in order to increase the number of interacting components (e.g. atmosphere, ocean, ice, hydrological cycle, land surface). The approach is a philosophy not a prescription; a range of different approaches have been tried.

The primary assumption of the intermediate complexity approach is that the entire system needs to be modelled in order to simulate the large scale features and the response to external forcing. This approach accepts that sacrificing process detail and spatial and temporal resolution will result in an increasing disconnect (or misfit) between local data and model predictions as one move up the trophic-size scale. In some cases, the connection to local (species specific) data may have to be provided by detailed models for specific applications which are driven by the intermediate complexity model. A similar approach was proposed by Kareiva et al. (2005) following an extensive review of ecosystem models for all parts of the biosphere.

The differences between the intermediate complexity approach and the rhomboid approach of de Young et al. (2004) are largely a matter of emphasis. The approach advocated here emphasizes the need to model the entire system in order to provide the proper virtual environment for the detailed species models. The rhomboid emphasizes the increased trophic resolution at the level of interest and presupposes the existence of a model of the entire system. The proposed approach also contrasts with the incremental approach where additional components are added to a truncated food web only when they can be justified by improved agreement with observations (e.g. Anderson 2005).

Incorporating more complete representations of food web structure into marine ecosystem models will inevitably push them towards increased complexity. Anderson (2005) and Hood et al. (2006) among others rightly point out that model performance is likely to fall with increasing complexity because of the effect of the large number of unconstrained parameters. We argue that the decline in accuracy is not a sufficient reason to reject a more complex model structure. The effectiveness metric (Constanza and Sklar 1985) attempts to quantify the trade-off between model accuracy and a more comprehensive description of the system. The community needs such a framework to guide us to the complexity level that is justified by our current understanding of processes and our ability to constrain them with data. Friedrichs et al. (2007) by looking at both accuracy and portability of the models have made a useful start in that direction. The potential links between effectiveness and portability remain to be explored.

Two recent attempts to model complete aquatic ecosystems contain aspects of the intermediate complexity approach. The Bay Model 2 (BM2) of Fulton et al. (2004) and the Lakeweb model of Håkanson and Gyllenhammer (2005) used coarse spatial, temporal, and trophic resolution in order to include many of the interacting components. In the context of global biogeochemistry, Le Quéré et al (2005) developed a more complex version of an NPZ model to better capture the variability in plankton and biogeochemical properties. They sacrificed biological process detail by using simple internal dynamics in order to include 10 plankton functional types embedded in a global ocean model.

Model validation is crucial for weeding out weak approaches and keeping the models and modellers on track. This is admittedly more difficult as the models become more complex. In that context, the validation has to go beyond the comparison of point data towards testing whether the models capture the main features and statistics of ecosystem structure. Output could be compared to findings from macro ecology, which describes broad scale patterns in the terrestrial and more recently oceanographic ecosystems (Li 2002). The self-organizing maps of Allen et al. (2007) provide a novel approach to validation based on broad patterns across multiple variables. Validation on statistics rather than point data meshes well with the theoretical and empirical evidence that ecosystems display nonlinear and even chaotic dynamics that place fundamental limits on the predictability of the system.

Experience in other fields suggests that the way to deal with limits on predictability is to abandon the reliance on deterministic prediction and explore the suite of possible outcomes from many model runs with different initial conditions and model formulations. We need to move towards ensemble prediction that makes probabilistic statements and

assesses the likelihood of events rather than focussing on the mean trajectory of the system. In that sense, more complex models may be more effective than the simpler models in revealing the full range of dynamic behaviour that is consistent with our current understanding.

Findings from food web theory clearly support a more comprehensive coverage of the food web than is common in marine ecosystem models. The stability properties of food webs appear linked to long feedback loops that integrate structure and dynamics across all trophic levels. Truncated food webs may not be able to reproduce the dynamics of these systems and their responses to environmental change. But food web theory may also help in the design and parameterization of more complex marine ecosystem models. High level rules such as "some food web structures are better than others at producing stable and persistent food webs" and "Interaction strengths are patterned to maximize stability" can help constrain structure and parameters. When coupled to the growing field of metabolic ecology which sets constraints on organism activity, abundance, and trophic structure, based on body size and temperature (Brown et al. 2004; Woodward 2005), the parameterization of more complex models may be more tractable than is sometimes allowed.

The concepts of unpredictable behaviour and system stability may seem contradictory. However, the definition of stability that underpins much of the recent work on ecosystem structure and dynamics is not an equilibrium view. Many of the results are based on non-equilibrium definitions of stability, considering the variance of fluctuating populations, rather than the speed of return to equilibrium. In that context, non-equilibrium dynamics and structural properties that confer stability are actually complementary facets of the same view of ecosystems as continuously changing, yet persistent, systems. The idea of community, rather than population, stability (Tilman 1996) is broadly consistent with the idea of dynamic stability.

While encouraging the development of complex models, we do not discount the importance of simpler models that provide both insights into processes and prediction models for specific questions (Harte 2002; Peters 1991). The proposal here is for a system view (or simulation model in the sense of Harry, 2003) that integrates the separate processes and feedback loops into a framework for assessing possible state changes (e.g. regime shifts) and the occurrence of extreme events.

We have argued that including a comprehensive description of the structure of marine food webs is central to the design of the next generational of marine ecosystem models; it is not simply a desirable feature. This would represent a transition from biogeochemical to ecological models (Tett and Wilson 2000). We propose that a useful guiding principle is provided by the earth system models of intermediate complexity, a willingness to sacrifice process detail in order to increase the number of interacting components in the system and simulate the web of feedback loops.

Acknowledgements

References

Allen, J.I., P.J. Somerfield, F.J. Gilbert. 2007. Quantifying uncertainty in high-resolution coupled hydrodynamic-ecosystem models. Journal of Marine Systems 64:3-14.

Anderson, T.R. 2005. Plankton functional type modeling: running before we walk? Journal of Plankton Research 27:1073-1081.

Arhonditsis, G.B., M. T. Brett. 2004. Evaluation of the current state of mechanistic aquatic biogeochemical modeling. Marine Ecology Progress Series 271:13–26.

Armstrong, R.A. 1999. Stable model structures for representing biogeochemical diversity and size spectra in plankton communities. Journal of Plankton Research 21:445-464.

Armstrong, R.A. 2003. A hybrid spectral representation of phytoplankton growth and zooplankton response: The ''control rod'' model of plankton interaction. Deep-Sea Research 50:2895-2916.

Bak, P., Tang, C. and Wiesenfeld, K. 1987. Self-organized criticality: an explanation of 1/f noise. Physical Review Letters 59:381–384. DOI:10.1103/PhysRevLett.59.381.

Bak, P., C. Tang, Earthquakes as a self-organized critical phenomena, Journal of Geophysical Research 94:15635-15637, 10.1029/89JB01265, 1989.

Beninca, E. , J. Huisman, R. Heerkloss, K.D. Jöhnk, P. Branco, E. H. Van Nes, M. Scheffer and S.P. Ellner. 2008. Chaos in a long-term experiment with a plankton community. Nature 451:822-825.

Berlow, E.L. 1999. Strong effects of weak interactions in ecological communities. Nature 398: 330-334.

Berlow, E. L., A-M. Neutel, J. E. Cohen, P. De Ruiter, B. Ebenman, M. Emmerson, J. W. Fox, V. A. A. Jansen, J. I. Jones, G. D. Kokkoris, D. O. Logofet, A. J. McKane, J. Montoya, and O. L. Petchey. 2004. Interaction strengths in food webs: issues and opportunities. Journal of Animal Ecology 73:585-598.

Blackford, J.C., J.I. Allen, F.J. Gilbert. 2004. Ecosystem dynamics at six contrasting sites: a generic modelling study. Journal of Marine Systems 52:191-215.

Brochu, R., R. Laprise. 2007. Surface water and energy budgets over the Mississippi and the Columbia River basins as simulated by two generations of the Canadian regional climate model. ATMOSPHERE-OCEAN 45:19-35.

Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage and G.B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771-1789.

Buizza, R., P.L. Houtekamer, Z. Toth, G. Pellerin, M. Wei, and Y. Zhu. 2005. A comparison of the ECMWF, MSC, and NCEP global ensemble prediction systems. Monthly Weather Review 133:1076-1097.

Chen, S.S., J.F. Price, W. Zhao, M.A. Donelan, E.J. Walsh. 2007. The CBLAST-Hurricane Program and the Next-Generation Fully Coupled Atmosphere–Wave–Ocean

Models for Hurricane Research and Prediction. Bulletin of the American Meteorological Society 88: 311-317. DOI: 10.1175/BAMS-88-3-311

Choi, J.S., Frank, K.T., Petrie, B.D., and Leggett, W.C. 2005. Integrated assessment of a large marine ecosystem: a case study of the devolution of the Eastern Scotian Shelf, Canada. Oceanography and Marine Biology: An Annual Review 43:47-67.

Claussen M., L. Mysak, A. Weaver, M. Crucifix, T. Fichefet, M.-F. Loutre, S. Weber, J. Alcamo, V. Alexeev, A. Berger, R. Calov, A. Ganopolski, H. Goosse, G. Lohmann, F. Lunkeit, I. Mokhov, V. Petoukhov, P. Stone, Z. Wang. 2004. Earth system models of intermediate complexity: closing the gap in the spectrum of climate system models. Climate Dynamics 18:579-586.

Cook W., P. Ormerod. 2003. Power law distribution of the frequency of demises of US firms. Physica A 324:207-212.

Costanza R, Sklar FH (1985) Articulation, accuracy and effectiveness of mathematical models: a review of freshwater wetland applications. Ecological Modeling 27:45-68.

Dai, Y., X. Zeng, R.E. Dickinson, I. Baker, G.B. Bonan, M.G. Bosilovich, A.S. Denning, P.A. Dirmeyer, P. R. Houser, G. Niu, K.W. Oleson, C.A. Schlosser, Z.-L. Yang. 2003. The Common Land Model. Bulletin of the American Meteorological Society 84:1013-1023. DOI: 10.1175/BAMS-84-8-1013.

Denman, K.L., 2003. Modelling planktonic ecosystems: parameterizing complexity. Progress in Oceanography 57:429-452.

De Ruiter, P.C., Neutel, A.-M. and Moore, J.C. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269:1257-1260.

deYoung B, Heath M, Werner F, Chai F, Megrey B, Monfray P. 2004. Challenges of modeling ocean basin ecosystems. Science 304:1463-6.

Doney, S., I. Lima, K. Lindsay, J.K. Moore, S. Dutkiewicz, M.A.M. Friedrichs and R.J. Matear. 2001. Marine biogeochemical modeling: recent advances and future challenges. Oceanography 14:93-107.

Emmerson, M. and J.M. Yearsley. 2004. Weak interactions, omnivory and emergent food web properties. Proceedings of the Royal Society of London B 271:397-405.

Findlay, H.S., A. Yool, M. Nodale and J.W. Pitchford. 2006. Modelling of autumn bloom dynamics. Journal of Plankton Research 28:209-220.

Friedrichs, M.A.M., R.R. Hood, J.D. Wiggert. 2006. Ecosystem model complexity versus physical forcing: Quantification of their relative impact with assimilated Arabian Sea data. Deep-Sea Research II 53:576-600.

Friedrichs, M.A.M, J.A. Dusenberry, L.A. Anderson, and 12 others. 2007. Assessment of skill and portability in regional marine biogeochemical models: Role of multiple planktonic groups. Journal of Geophysical Research 112, C08001, doi:10.1029/2006JC003852.

Fulton, E.A. 2001. The effects of model structure and complexity on the behaviour and performance of marine ecosystem models. PhD thesis, School of Zoology, University of Tasmania, Hobart, Australia.

Fulton, E.A., A.D.M. Smith and C.R. Johnson. 2003. Effect of complexity on marine ecosystem models. Marine Ecology Progress Series 253:1-16.

Fulton, E.A,. J.S. Parslow, A.D.M. Smith, C. R. Johnson 2004. Biogeochemical marine ecosystem models II: the effect of physiological detail on model performance. Ecological Modelling 173:371–406.

Gentleman, W., A. Leising, B. Frost, S. Strom and J. Murray. 2003. Functional response for zooplankton feeding on multiple resources: a review of assumptions and biological dynamics. Deep-Sea Research 50:2847-2875.

Gregg, W.W., P. Ginoux, P.S. Schopf, N.W. Casey. 2003. Phytoplankton and iron: validation of a global three-dimensional ocean biogeochemical model. Deep-Sea Research 50:3143-3169.

Hannah, C.G. 2007. Future directions in modelling physical-biological interactions. Marine Ecology Progress Series 347:301-306. doi: 10.3354/meps06987.

Håkanson, L., A. Gyllenhammar. 2005. Setting fish quotas based on holistic ecosystem modelling including environmental factors and foodweb interactions – a new approach. Aquatic Ecology 39:325-351. DOI 10.1007/s10452-005-3418-x.

Hare, S.R., and N.J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103-145.

Harry, D.L. 2003. Numerical Modelling Strategies Revisited. EOS Transactions 84:100-101.

Harte, J. 2002. Toward a synthesis of the Newtonian and Darwinian worldviews. Physics Today 55:29-35.

Hood, R.R., E.A. Laws, R.A. Armstrong, N.R. Bates, C.W. Browne, C.A. Carlson, F. Chai, S.C. Doney, P.G. Falkowski, R.A. Feely, M.A.M. Friedrichs, M.R. Landry, J. K. Moore, D.M. Nelson, T.L. Richardson, B. Salihoglu, M. Schartau, D. A. Toole, J.D. Wiggert,. 2006. Pelagic functional group modeling: Progress, challenges and prospects. Deep-Sea Research II 53:459-512.

Hsieh, C-h, S. M. Glaser, A. J. Lucas, G. Sugihara. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature 435:336-340. doi:10.1038/nature03553.

IMBER. 2005. Science Plan and Implementation Strategy. IGBP Report No. 52, IGBP Secretariat, Stockholm. 76 pp.

Jordan, F., I. Scheuring. 2004. Network ecology: topological constraints on ecosystem dynamics. Physics of Life Reviews 1:139-172.

Kareiva, P. State of the Art in Simulating Future Changes in Ecosystem Services. Millenium Ecosystem Assessment, Chapter 4, www.millenniumassessment.org

Kokkoris, G. D., A.Y. Troumbis, and J. H. Lawton. 1999. Patterns of species interaction strength in assembled theoretical competition communities. Ecological Letters 2:70-74.

Kuijper, L.D.J., Kooi, B.W., Zonneveld, C. and S.A.L.M. Kooijman. 2003. Omnivory and food web dynamics. Ecological Modeling 163:19-32.

Lawlor, L. R. 1978. A comment on randomly constructed model ecosystems. American Naturalist 112:445-447.

Laws, E.A., P.G. Falkowski, W.O. Smith, Jr., H. Ducklow and J.J. McCarthy. 2000. Temperature effects on export production in the open ocean. Global Biogeochemical Cycles, 14:1231-1246.

Le Quéré, C., S.P. Harrison, I. C. Prentice, E.T. Buitenhuis, O. Aumont, L. Bopp, H. Claustre, L. C. Da Cunha, R. Geider, X. Giraud , C. Klaas , K.E . Kohfeld, L. Legendre, M. Manizza, T. Platt, R.B. Rivkin, S. Sathyendranath, J. Uitz and A.J. Watson. 2005. Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. Global Change Biology, 11: 2016-2040.

Li, 2002. Macroecological patterns of phytoplankton in the northwestern North Atlantic Ocean, Nature, 419:154-157.

Lima, I.D., D.B. Olson and S.C. Doney. 2002. Intrinsic dynamics and stability properties of size-structured pelagic ecosystem models. Journal of Plankton Research 24: 533-556.

Link, J. 2002. Does food web theory work for marine ecosystems? Marine Ecology Progress Series 230:1-9.

Longhurst, A.R. 2006. Ecological Geography of the Sea. 2nd edition. Academic Press.

Lorenz, E.N. 1963. Deterministic Nonperiodic Flow. Journal of the Atmospheric Sciences 20: 130–141.

May, R. M. 1972. Will a Large Complex System be Stable? Nature 238:413-414.

May, R. M. 1973. Stability and Complexity in Model Ecosystems. Princeton, NJ: Princeton University Press.

Martinez, N.D., Williams R.J. and Dunne J.A. 2006. Diversity, complexity and persistence in large model ecosystems. In: M. Pascual and J.A. Dunne (eds), Ecological Networks: linking structure to dynamics in food webs. Oxford University Press. pp. 163-185.

McCann, K., A. Hastings, G.R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794-798.

McCann, K.S. 2000. The diversity-stability debate. Nature 405:228-233.

Neutel, A. M., J. A. P. Heesterbeek, P. C. de Ruiter. 2002. Stability in real food webs: weak links in long loops. Science 296: 1120–1123.

Neutel, A.-M., J.A.P. Heesterbeek, J. van de Koppel, G. Hoenderboom, A. Vos, C. Kaldeway, F. Berendse and P.C. de Ruiter. 2007. Reconciling complexity with stability in naturally assembling food webs. Nature 449: 599-602.

Ormerod, P. 2006. Why most things fail: and how to avoid it. Faber and Faber. London.

Paine, R. T. 1980. Food webs, linkage interaction strength, and community infrastructure. Journal of Animal Ecology 49:667–685.

Pahlow, M., A.F. Vézina, B. Casault, H. Maass, L. Malloch, D.G. Wright. Y Lu. 2008. Adaptive model of plankton dynamics for the North Atlantic. Progress in Oceanography 76:151-191.

Pascual, M. and F. Guichard. 2005. Criticality and disturbance in spatial ecological systems. Trends in Ecology and Evolution 20: 88-95.

Pellerin, P., H. Ritchie, F.J. Saucier, F. Roy, S. Desjardins, M. Valin, and V. Lee, 2004: Impact of a two-way coupling between an atmospheric and an ocean-ice model over the Gulf of St. Lawrence. Monthly Weather Review 132, 1379-1398.

Peters, R.H. 1991. A Critique for Ecology. Cambridge University Press. Cambridge. 366pp.

Pimm, S.L., Lawton, J.H., Cohen, J.E. 1991. Food web patterns and their consequences. Nature 350:669-674.

Reichler, T., J. Kim. 2008. How well do coupled models simulate today's climate? Bulletin of the American Meteorological Society 89:303-311. DOI:10.1175/BAMS-89-3-303.

Rooney, N., K. McCann, G. Gellner and J.C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442:265-269.

Rothstein, L., J. Cullen, M. Abbott, E. Chassignet, K. Denman, S. Doney, and 15 others. 2006. Modeling Ocean Ecosystems: The PARADIGM Program. Oceanography 19:22-51.

Scheffer, M., and S.R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends in Ecology and Evolution, 18:648-656.

Sharples, J., O.N. Ross, B.E. Scott, S.P.R. Greenstreet and H. Fraser. 2006. Inter-annual variability in the timing of stratification and the spring bloom in the North-western North Sea. Continental Shelf Research 26:733-751.

Sneppen, K., P. Bak, H. Flyvbjerg, M. H. Jensen. 1995. Evolution as a self-organized critical phenomenon. Proceedings of the National Academy of Science (USA) 92:5209-5213.

Solé, R.V., S.C. Manrubia, M. Benton, S. Kauffman and P. Bak. 1999. Criticality and scaling in evolutionary ecology. Trends in Ecology and Evolution 14:156-160.

Solé, R.V. and J.M. Montoya. 2001. Complexity and fragility in ecological networks. Proceedings of the Royal Society of London B 268: 2039-2045.

Sornette, A. D. Sornette. 1989. Self-organized criticality and earthquakes. Europhysics Letters, 9:197-202.

Strogatz, S.H. 2001. Exploring complex networks. Nature 410: 268-276.

Tett, P., H. Wilson. 2000. From biogeochemical to ecological models of marine microplankton. Journal of Marine Systems 25:431-446.

Tilman D. 1996. Biodiversity: population versus ecosystem stability. Ecology 77: 350-363.

Williams and Martinez. 2000. Simple rules yield complex food webs. Nature 404:180-183.

Waldrop, M.M. 1992. Complexity: The emerging science at the edge of order and chaos. Simon and Shuster. 1992. 363 pp.

Wikipedia contributors. 2007. Butterfly effect. Wikipedia, The Free Encyclopedia. Available at: http://en.wikipedia.org/w/index.php?title=Butterfly_effect&oldid=136437753. Accessed June 7, 2007.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, P. H. Warren. 2005. Body size in ecological networks. Trends in Ecology and Evolution 20: 402-409.

Woods, J.D., A. Perilli, W. Barkmann. 2005. Stability and predictability of a virtual plankton ecosystem created with an individual-based model. Progress in Oceanography 67:43-83

Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. Journal of Animal Ecology 67:635-658.

Zhang, W., W. Perrie, W. Li. 2006. Impacts of waves and sea spray on midlatitude storm structure and intensity. Monthly Weather Review 134:2418-2442.

Zhu, Y. 2005. Ensemble forecast: a new approach to uncertainty and predictability. Advances in Atmospheric Sciences 22:781-788.

Tables

Table 1. The key elements of self-organized criticality (and the sand pile) as a metaphor

|	
1	The system naturally evolves towards a critical state, i.e. it is 'self organized';
2	The dominant feature is small scale interactions between a large number of entities (the grains of sand);
3	These interactions (or feedback loops) can lead to large scale events;
4	There is not necessarily an action-reaction relationship between the observed forcing and the observed response, in other words, unobserved changes in the system can lead to observable consequences (e.g. avalanches).
5	Prediction of the detailed evolution of the system is not possible, however, probabilistic prediction is.

Figures

a)

b)
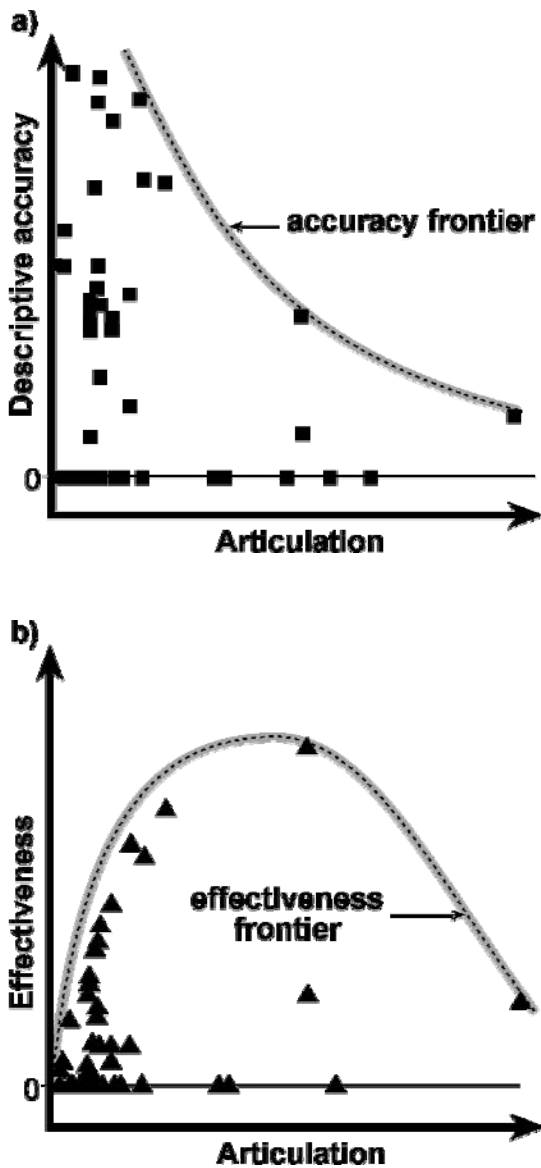
Fig. 1: a) Accuracy as a function of articulation from the review of wetlands models by Costanza and Sklar (1985), where articulation is a proxy for model complexity. The 'accuracy frontier' is an estimate of the maximum possible accuracy as a function of articulation for wetlands models at the time of the review. b) Model effectiveness as a function of articulation from Costanza and Sklar (1985). The effectiveness frontier is their estimate of the maximum possible effectiveness as a function of articulation for wetlands models at the time of the review. The panels are redrawn from Costanza and Sklar (1985).
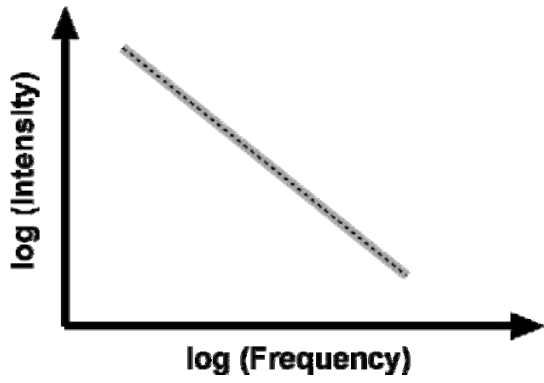
Fig. 2: A power law relationship between the frequency of occurrence and the intensity of the events.
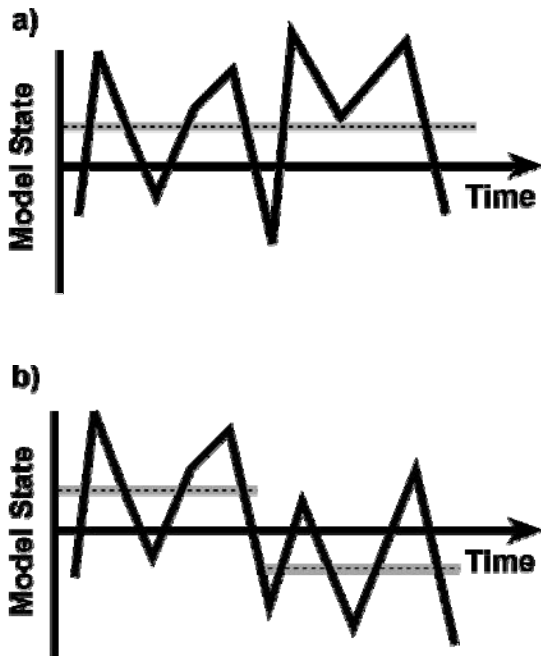
Fig. 3: Schematic of the difference between weather prediction models (a) and climate models (b) for the purposes of this paper. In each panel the black line represents the fluctuations (or wiggles) about the mean (or observed state) and the grey line represents the mean state which changes in panel b). In the weather prediction family the model predicts the fluctuations about an observed state whereas in climate prediction family the model must predict the changes in the mean state and the fluctuations (or at least the statistics of the fluctuations which often contribute to the maintenance and evolution of the mean state).