

---

## **Top-down, bottom-up or middle-out? Avoiding extraneous detail and over-generality in marine ecosystem models**

J.I. Allen<sup>a,\*</sup> and E.A. Fulton<sup>b</sup>

<sup>a</sup> Plymouth Marine Laboratory, The Hoe, Plymouth PL1 3DH, United Kingdom

<sup>b</sup> CSIRO Marine Res., GPO Box 1538, Hobart, Tasmania 7001, Australia

\* Corresponding author : J.I. Allen, Tel.: +44 (0) 1752 633441; fax: +44 (0) 1752 633101, email address : [JIA@pml.ac.uk](mailto:JIA@pml.ac.uk)

---

### **Abstract:**

The paper by Hannah et al. (this volume) invokes foodweb theory and the ideas of complexity theory to guide the construction of models of intermediate complexity, which sacrifice explicit process detail to increase the number of interacting components of the system and simulate the web of feedback loops. This approach has its merits, if best practice modelling guidelines are followed and the method is used well. However, if this is not the case then the fundamental weakness of the intermediate model approach is that it may end up producing models that are over general and therefore not useful. To make the most of the intermediate complexity approach it is essential to keep the tenets of the middle-out approach in mind. Under the middle-out approach computational models are constructed and tested at the levels where we have the most detailed information, building on our existing knowledge and data and coupling a hierarchy of models rather than being swamped in a morass of detail or missing key feedbacks through over-generality.

# 1. Introduction

---

The paper by Charles Hannah and co-authors examines the current states of marine ecosystem modelling (Hannah et al. this volume). They make the observation that while existing models do a reasonable job of predicting physical driven features such as spring blooms, the foodwebs are overly simplified and incapable of predicting functional diversity, ecosystem change and changes in ecosystem services. They argue that as the demand for such predictions increases the challenge is to develop ecosystem models which can encapsulate such processes. To do this they invoke foodweb theory and the ideas of complexity theory to guide the construction of models of intermediate complexity which sacrifice explicit process detail to increase the number of interacting components of the system and simulate the web of feedback loops.

## 1.1. The state that the art is in

Before addressing the specific points and questions addressed by Hannah et al. (this volume), firstly we take a look at some of the current constraints on our thinking. The standard paradigm which underpins biological models (including marine ones) is the ecosystem concept; i.e. the ecosystem as a natural system whereby the biotic and abiotic components interact to produce a stable system in which the exchange of materials between the living and non living parts follows circular paths (Odum, 1953). This has led to a systems analysis approach to ecology, where by it is viewed as being analogous to a machine, because it offered a pragmatic approach to understanding the complexity of natural systems (O'Neill, 2001). The ecosystem concept cuts through the myriad of complex interactions at a species level by focusing on a small subset of average or integrated properties of all the populations within the area of study. Its big advantage is that it can identify emergent properties such as energy flow and nutrient cycling and study the stability of function of this abstract structure. The weakness lies in its ability to explain the relative stability of ecological systems in a changing environment; the focus on a self regulating system leading to a focus on local and short term stability (i.e. recovery from disturbance) rather than flexibility in the sense of maintaining variability in space and time as conditions change (O'Neill, 2001). The result of the ecosystem approach has been the development of the current generation of coupled biophysical models, with a limited ability to respond to environmental change. Marine systems modellers are increasingly aware of these limitations; the paper by Hannah is one such response, the Dynamic Green Ocean Model (Le Quéré et al., 2005) and the emergent biogeography model of Follows et al., (2007) are others.

There are very few if any true models of the whole marine ecosystem, most of them focus on one of three aspects, cellular plankton, zooplankton or fisheries; this is largely a consequence of the interests of the researchers and the information available to construct them. Even those models which adopt a whole ecosystem approach e.g. ECOPATH (Christensen and Pauly 1992), ERSEM (Baretta et al., 1995) or SEAPODYM (Lehodey et al., 1998, Lehodey, 2001, Lehodey et al., 2003) tend to be focused by their users on specific trophic level(s). However there is a requirement to understand the impact of multiple climatic and anthropogenic drivers (Fig 1) on the whole ecosystem, which requires the development of a new generation of end to end models.

A major driver of marine ecosystem model development over the last decade has been the orders of magnitude increase in computation capacity. This has arguably been a double edged sword. On the plus side there has been a massive increase in

our ability to simulate biology coupled to high resolution physics at both global, (e.g. Moore et al., 2004) and regional scales (e.g. Allen et al., 2001) and increasingly decadal timescales (e.g. Werner et al., 2007). This has led to a better understanding of the spatial and temporal scales of biophysical interactions. Sub-grid scale processes (including habitat and finer scale trophic or technical interactions with fishing gear) are important at all trophic levels and highly resolved bio-physical models contribute towards the parameterisation of such effects. A downside is that this has led to a focus on improving internal process descriptions (the machine model) rather than on interactions; particularly where plankton models are concerned. A compounding factor is that increasingly large volumes of simulation data are harder to analyse. This exacerbates the reluctance of the marine modelling community to validate its models. Part of the reason for this is that larger volumes of output make it harder to find the equivalent volumes of observations for validation. Arhonditsis et al. (2006) reported no relationship between the level of skill assessment presented or the accuracy of planktonic models, and the subsequent citation rate of the published paper. Both complex model structures and large simulation data volumes also limit the opportunities for sensitivity analysis potentially leading to less understanding of model dynamics. The analysis of Arhonditsis et al. (2006) is symptomatic of this.

Another driver in model development has been the increase in knowledge of new processes e.g. the microbial loop (e.g. Azam et al., 1983), iron limitation (e.g. Martin and Fitzwater 1988) and ocean acidification (e.g. Raven et al., 2005). This has led to increasing model complexity, but often at a rate where the speed with which processes are included in models outstrips the modelling community's ability to realistically parameterise them (Anderson 2005). This is despite the increased availability of integrated data sets, such as the World Ocean Atlas ([http://www.nodc.noaa.gov/OC5/WOA05/pr\\_woa05.html](http://www.nodc.noaa.gov/OC5/WOA05/pr_woa05.html)). Even with easier and broader access to such datasets, rigorous model evaluation is not yet a universally common practice.

Finally model development is often inhibited by the very existence of established ecosystem models. Over time many model systems have a tendency to ossify through a combination of dogma and pragmatism. For example the plankton functional type/model complexity issue (e.g. Le Quéré et al., 2005; Anderson 2005) is a debate in danger of being trapped in the dogma surrounding NPZD versus PFT modelling approaches. One could argue that they are identical approaches, the only difference being the degree of aggregation, and the focus should be on evaluating their usefulness. Ecosystem models require substantial amounts of time and resources in order to develop and run them. Consequently the pragmatic approach is often to try and answer questions using existing tools rather than building specifically designed new ones. There is nothing wrong with using established model systems as long as they are either actually useful as is (in their old state) or like a living document kept alive by growth and revision. There is also immense value to having multiple models/tools; so when constructing new models/tools they should be new and not just another implementation of exactly the same equations.

## **2. Foodwebs and Complexity**

---

### **2.1. Is foodweb theory useful when building models?**

A central theme of ecology is that ecosystem dynamics are profoundly influenced by the complex web of trophic interactions, which links all species together. Hannah et al (this volume) rightly point out the importance of food webs because the structure of the foodweb (who is connected to who) and the strength of its interactions are critical

to the stability and persistence of ecosystems (Dunne, 2006; McCann, 2000) and that the structure and dynamics feedback on each other. We don't dispute that these aspects should be included in marine ecosystem models, they are crucial, but pragmatically much care is needed when using foodwebs so that they are being usefully applied. The biggest issue is that the marine foodweb is poorly defined, the studies often being limited to a low number of species with a tendency to focus on higher trophic levels, high levels of aggregation and often of limited spatio-temporal extent (Link, 2002). Consequently we don't have a detailed understanding of the structure of some (if not many) parts of the marine ecosystem and even less understanding of their interactions. Ultimately lack of knowledge is the limiting factor in model construction. To apply foodweb theory to marine models the first challenge is to get a better description of the structure and dynamics of the whole foodweb including plankton at appropriate spatial and temporal scales. Clearly including all interactions at a species level is intractable so the second challenge is how to aggregate the foodweb in such a way that it captures the important ecosystem dynamics and feedbacks. While some guidelines exist (Fulton et al., 2003), this is work in progress and debate is ongoing (e.g. Anderson, 2005). An obvious issue is the tension between resolving biogeochemical function and resolving ecological function which often don't logically map onto each other. This is particularly true of many planktonic models whose primary focus is on biogeochemical cycles of carbon and nutrients. As we go up the food chain the focus moves towards ecological interactions. Here we need to understand how the network structure of the foodweb influences what happens when species are added or removed (May, 2006); generally speaking removing the most highly connected species has more impact than random removal. A further issue related to interaction strengths is capturing plasticity in the realised diets of organisms.

A further challenge maybe to include the role of biodiversity. Ecological theories predict that biodiversity is one of several significant factors governing the stability, productivity, nutrient availability and invasibility of ecosystems (Tilman, 1999). For example these theories predict that greater biodiversity should increase productivity, decrease amount of unconsumed limiting resource and increases ecosystem stores of limiting nutrients (Tilman, 1999). This is not to argue that diversity is the strongest force, other drivers such as climate maybe more influential, but we should take a broad perspective of all the drivers affecting ecosystem functional and stability and weight them accordingly in our models.

## **2.2. Is complexity theory a useful metaphor?**

Hannah et al. (this volume) offer the metaphor that complex systems naturally evolve towards critical states and that in the context of ecology a system is critical if poised at a transition phase (Pascaul and Guirard 2005). There are three types of criticality: classical which leads to sharp phase transitions based on wide spread disturbance; self organized criticality where disturbance is must faster than recovery; and robust criticality where temporal scales of disturbance and recovery are similar (Pascaul and Guirard 2005). Essentially the hypothesis is that a system may evolve to a state (near phase transition) whereby local interactions and feedback loops can lead to large scale events and that it is not necessarily an action-reaction response. They argue that we should focus on non linear interactions and feedback loops and that a lack of them limits the ability of the system to evolve into a state substantially different from the original state.

The real questions are, is the metaphor relevant? and if so how do we extend it? While these arguments are being used theoretical in ecology (e.g. Pascaul and Guirard 2005) there is less information on critical processes occurring in the marine system. The inclusion of feedback loops and non linear interactions has been a long

standing goal of marine systems modellers for many years and there is some evidence that existing models (e.g. Allen et al., 2006) are capable of simulating observed shifts in ecosystem function (i.e. between functional groups but not within). However there is a danger that fixed parameterisations mean evolution and the shifting composition of functional groups is missed - this would impact on rate parameters, for instance, but also has the potential to impact on realised population and community dynamics (Pelletier et al., 2007). The problem is if you try to move towards time evolving parameters how do you calculate the shift? Structurally dynamic models are technically difficult, but also depend on what some judge as dubious objective function assumptions and we need a more concrete way of capturing this significant factor.

It is important to note that there is a fundamental difference between a complex process and a complex response, and that in many cases a complex response can be derived from a simple set of rules; this is sometimes referred to as 'Deep Simplicity' (Gribben 2004). The relevance of complexity ideas maybe more useful philosophically rather than mathematically and these general relationships may provide a broad context in which to interpret data and frame model systems. Ultimately the only answer is to have a go at using it and see whether or not it works.

### **3. Are models of intermediate complexity the solution?**

---

Hannah et al, (this volume) argue 'that in order for ecosystem models to be useful for dynamic simulation of the response to climate change and other human impacts they must include sufficient feedback loops to be climate models' (models that can predict changes in the mean state)' and 'that to achieve this, the models will need to represent the ecosystem from plankton through to higher trophic levels'. Essentially they suggest a transition from biochemical to ecological models.

In principle we agree with these sentiments, however the question which remains unresolved is how we achieve these goals. When constructing a model the heart of the procedure are the definition and evaluation of models of the system in question. Drawing analogies from system's biology, a model should be 'a simplified abstract reproduction that allows insight to the essence of a system that helps to identify gaps in biological knowledge' (e.g. Noble 2003). Conceptual models of biological systems are common, arise from the interpretation of biological data, they often exist in isolation from one another, and are frequently not formally or explicitly declared. For even the simplest conceptual models the results or outcomes are not always tractable or apparent. Numerical models rely on conceptual models to define equations, empirical studies to parameterise them, and statistics to evaluate them.

The crux of the issue is that models should be constructed at an appropriate level of complexity to address the hypothesis being tested and the data available to support it. In his paper 'putting Humpty-Dumpty together again' Noble, (2003) advocates this 'middle out' approach for modelling biological processes (Fig. 2), whereby computational models are constructed and tested at the levels where we have the most detailed information. The alternatives being the bottom-up approach (i.e. everything from first principles) and the top down approach which attempts to simply everything to basic principles. Examples of the bottom up approach are physiological process /mechanistic models of phytoplankton growth and grazing (e.g. Flynn 2001), which have the problem that we can only characterise a few species well enough experimentally to make such models; and that we need to know about higher levels of organisation to fully characterise the lower levels properly. The 'intermediate approach' advocated by Hannah et al (this volume) could be construed as a top down model in the nomenclature of Noble (2003). This means, unless its done with care, it can suffer from the fundamental weakness of some top-down theories, which

can be over general and therefore not completely useful for targeted questions (Ginzburg et al., 2007). For intermediate models to be effective process detail must be implicitly included in functions describing sub-scale processes rather than being explicitly spelt out at great length for all parts of the model. In this form the method has similarities with the ideas put forward under the middle out approach.

The middle out approach inevitably leads to the concept of the hierarchy of models. The challenge then becomes how to couple them together to ensure we capture the important interactions and feedbacks. This is analogous to the rhomboid approach (de Young et al., 2004) which involves the integration of detailed models of key species directly into the overall model in a two-way coupling so that the details influence the overall system. When taking the middle out approach (or when using the intermediate approach well) then it is vital that any critical processes outside that domain, which impinge on it, are captured in some empirical impact formulation, even if there is no process information available.

There is an essential requirement to be clear about the hypothesis being tested and crucially to have the data to test our hypotheses. Another way of expressing this is that we need to know what we are modelling; what are the characteristics of the system we are trying to model and what are the features a model must have to represent the observed nonlinearities or complexity? Ultimately there are no hard and fast rules other than clarity of thought and a realistic assessment of the adequacy of the underlying knowledge base. Therefore rather than slaving ourselves to a single approach, we should consider a balanced combination of all three (top-down, bottom-up and middle out) approaches and focus on the following criteria; a good model should be,

descriptive (represents the available data),  
integrative (demonstrate how elements interact),  
explanatory (provide biological insight).

Additionally we should bear in mind that a well constructed model which fails can be more informative than one that succeeds. This is particularly the case if alternative model structures have differing implications and if it is not clear if a model has succeeded for the correct reasons.

#### **4. Conclusions and recommendations**

---

Quoting Ginzburg et al. (2007) 'A good theory is focused without being blurred by extraneous detail or over-generality'. Yet ecological theories frequently fail to achieve this desirable middle ground'. This is the essence of the problem in marine ecology and points towards the value of keeping the middle out approach in mind even if taking a more top down or bottom up approach in any one instance. We have identified that lack of knowledge about the marine foodweb and how to encapsulate the essence of its dynamics and feedbacks is a factor limiting progress. Again the recommendation is to follow (or be guided by) the middle out approach, building on our existing knowledge and data and coupling a hierarchy of models rather than being swamped in a morass of detail or missing key feedbacks through over-generality. It follows that there is a pressing requirement to develop the software interfaces to create an end to end hierarchy of models capable of responding to multiple climatic and anthropogenic drivers. Coupling numerical models is a central issue in climate research and we should learn from their experiences.

Perhaps the biggest limiting factor in applying any of the modelling approaches is the cultural disconnect between, the modellers, laboratory experimentalists and in-situ observationalists, whereby the non modellers very often lack a sense of ownership of

numerical models even though their ideas and data have contributed to the development. Models come in many forms, conceptual and statistical as well as numerical and all good scientists should have at the very least a conceptual model of the system they are studying. The challenge is therefore to get the experimental/observational scientists to be stakeholders in the models and vice versa.

## Acknowledgements

---

JIA's and EAF would like to thank IGBP programs IMBER and GLOBEC as well as the Network of Excellence EUR-OCEANS of the European Union's 6th Framework Program for funding the symposium on "Parameterization of Trophic Interactions in Ecosystem Modelling", Cadiz, March 2007, and the meeting conveners for the invitation to participate. JIA was also funded by NERC Oceans2025 strategic research program and MARQUEST. Thanks go to everyone who contributed to the discussion session and Jerry Blackford (PML) for commenting on the manuscript.

## References

---

- Anderson, TR. 2005. Plankton functional type modelling: running before we walk? *J. Plankton Research* 27: 1073-1081.
- Arhonditsis, G.B., B.A. Adams-VanHarn, L. Nielsen, C.A. Stow, and K.H. Reckhow. 2006. Evaluation of the current state of mechanistic aquatic biogeochemical models: citation analysis and future perspectives. *Environmental Science & Technology*, 40: 6547-6554
- Allen, J.I., Blackford, J.C., Holt, J.T., Proctor, R., Ashworth, M., Siddorn, J. 2001. A highly spatially resolved ecosystem model for the North West European Continental Shelf. *Sarsia* 86:423-440
- Allen, J.I., Archer, S.D., Blackford, J.C., Gilbert, F.J., Taylor, A.H. 2006. Changes in DMS production and flux in relation to decadal shifts in oceanic circulation. *Tellus B* 58:242-255.
- Azam F, Fenchel T, Field JG, Gray JS, Meyer-Reil LA, Thingstad F (1983) The ecological role of water-column microbes in the sea. *Marine Ecology-Progress Series* 10: 257-263
- Baretta, J.W., Ebenhoh, W., Ruardij, P., 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model. *Neth. J. Sea Res.*, 33: 233-246.
- Christensen, V. Pauly, D. 1992. ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological Modelling* 61, 169-185.
- deYoung B, Heath M, Werner F, Chai F, Megrey B, Monfray P. 2004. Challenges of modeling ocean basin ecosystems. *Science* 304:1463-6.
- Dunne, J.A. 2006. The network structure of food webs. Pp. 27-86 In: M. Pascual and J.A. Dunne (eds), *Ecological Networks: linking structure to dynamics in food webs*. Oxford University Press.
- Follows, M.J., S. Dutkiewicz, S. Grant, S.W. Chisholm. 2007. Emergent Biogeography of Microbial Communities in a Model Ocean. *Science*, 315:1843-1846. doi: 10.1126/science.1138544
- Flynn, K.J., 2001. A mechanistic model for describing dynamic multi-nutrient, light, temperature interactions in phytoplankton. *J. Plankton. Res.* 23, 977-979.

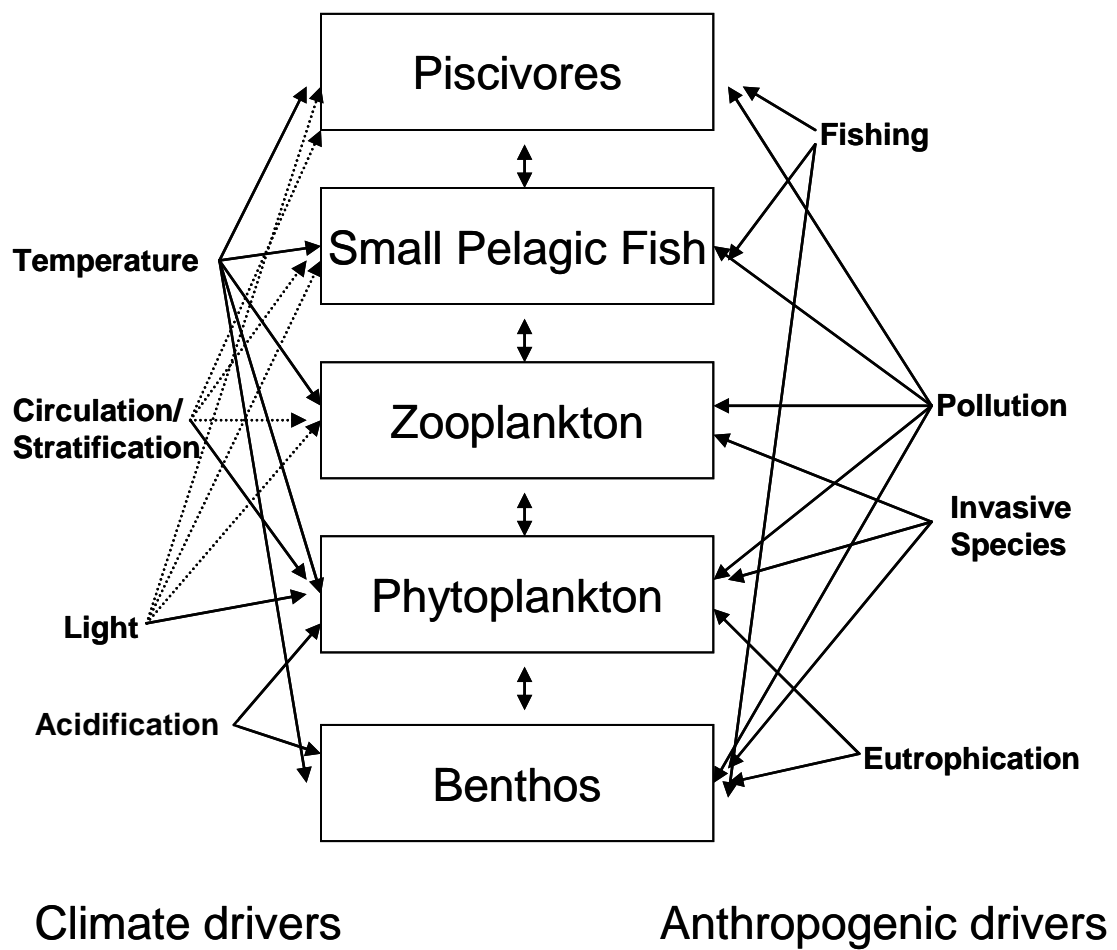
- Fulton, E.A., Smith, A.D.M. and Johnson C.R., 2003. Effect of complexity on marine ecosystem models. *Mar. Ecol. Prog. Ser.* 253, 1-16.
- Ginzburg, L.R., Jensen, C.X.J., Yule, J.V. 2007. Aiming the “unreasonable effectiveness of mathematics” at ecological theory. *Ecol. Mod.* 207, 356-362.
- Gribben, J., 2004. *Deep Simplicity*, Penguin London 251pp.
- Hannah. C., Vezina, A., St John, M., (this volume) The case for marine ecosystem models of intermediate complexity. *Progress in Oceanography*
- Lehodey, P. 2001. The pelagic ecosystem of the tropical Pacific Ocean: dynamic spatial modelling and biological consequences of ENSO. *Prog. Oceanogr.* 49: 439-468.
- Lehodey, P., André, J-M., Bertignac, M., Hampton, J., Stoens, A.C., Menkes, L. and G.N. Memery. 1998. Predicting skipjack forage distributions in the Equatorial Pacific: preliminary results using a coupled dynamical bio-geochemical model. *Fish. Oceanogr.* 7: 317-325.
- Lehodey, P., Chai, F. and J. Hampton. 2003. Modelling climate-related variability of tuna populations from a coupled ocean-biogeochemical-populations dynamics model. *Fish. Oceanogr.* 12: 483-494.
- 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 Biol.* 11: 2016-2040.
- Link, J., 2002. Does food web theory work for marine ecosystems? *Mar. Ecol. Prog. Ser.* 230: 1-9.
- Martin, J. H., and S. E. Fitzwater (1988), Iron deficiency limits phytoplankton growth in the northeast Pacific subarctic, *Nature*, 331, 341–343.
- May, R.M., 2006. Network structure and the biology of populations. *Trends in Ecol. Evolution.* 21, 394-398.
- McCann, K.S. 2000. The diversity-stability debate. *Nature* 405: 228-233.
- Moore, J.K., Doney, S.C., Lindsay, K., 2004. Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. *Glob. Biogeochem. Cycles* 18, 4028.
- Noble, D., 2003. The future: putting Humpty-Dumpty together again. *Biochemical Society Transactions* 31, 156-158.
- Odum, E.P., 1953. *Fundamentals of Ecology*. W.B., Saunders, Philadelphia, Pennsylvania, USA.
- O’Neill, R., 2001. Is it time to bury the ecosystem concept? (With full military honours of course!). *Ecology*, 82, 3275-3284. .
- Pascual, M., F. Guichard. 2005. Criticality and disturbance in spatial ecological systems. *Trends Ecol. Evol.* 20: 88-95.
- Pelletier, F., Clutton-Brock, T., Pemberton, J., Tuljapurkar, S., Coulson, T., 2007. The evolutionary demography of ecological change: Linking trait variation and population growth. *Science* 315: 1571-1574.
- Raven, J. A. *et al.* 2005. *Ocean acidification due to increasing atmospheric carbon dioxide*. Royal Society, London, UK
- Tilman, D., 1999. The ecological consequences of changes in biodiversity: a search for general principles. *Ecology* 80, 1455-1474.
- Werner, F.E., Ito, S.I., Megrey, B.A., Kishi, M.J., 2007. Synthesis of the NEMURO model studies and future directions of marine ecosystem modelling. *Ecol. Mod.* 202, 211-223.



## Figures

---

**Figure 1.** A schematic of an end to end ecosystem model, showing the links between trophic groups and some of the climatic and anthropogenic drivers which may influence them.



**Figure 2.** Strategies for modelling marine ecosystems; A bottom up approach involves starting with the physiology and behaviour of individual species and reconstructing higher level processes from them; the top down approach involves trying to simplify to high level function and then work downwards; and the middle out approach involves building models at the level where sufficient data exists. The diagram implicitly assumes the ecosystem sits within a physical environment. Figure based on the schematic of model structure presented in Noble (2003).

