On the Emergent Properties of
Marine Ecosystem Models

Dissertation

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Abstract

In the context of marine ecosystem modelling an emergent property occurs when patterns or properties arise from the interaction of lower level properties, none of which exhibit it. This thesis takes a retrospective view of a series model studies to demonstrate the ability of the European Regional Seas Ecosystem Model (ERSEM) to produce emergent properties. The studies chosen fall into three main categories: emergent community structure in response to environmental forcing, community response the anthropogenic perturbation and whether the ecosystem can amplify a weak atmospheric signal. The model is found to demonstrate weak emergence in the sense of generating patterns at a higher lever of organisation (e.g. community structure, phytoplankton succession) generated by the underlying agents. However there is little evidence that intrinsic emergence is produced. The adequacy ERSEM and other current modelling approaches for creating emergence is discussed and suggestions made for new directions in which may better capture the emergent properties of marine ecosystems. It is suggested that more emphasise is placed on underlying mechanism of cell physiology and foodweb interactions and less on empirical or numerical parameter fitting. Ultimately there is a need to think differently and more creatively about how marine ecosystems are modelled

1. **Introduction**

Complex patterns are evident throughout nature, from the flocking of birds and colonies of insects through to phytoplankton succession and global biogeochemical cycles. Ecosystems, and indeed the global biosphere, are archetypal examples of complex adaptive systems, in which macroscopic system properties such as trophic structure, diversity–productivity relationships, and patterns of nutrient flux emerge from interactions among components, and may feed back to influence the subsequent development of those interactions. Elucidating these interactions across scales is fundamental to resolving the issue of biodiversity and ecosystem functioning, and requires a blending of insights both from population biology and from ecosystems science. A fundamental problem for the natural scientist in general is the explanation of how complexity emerges and its subsequent prediction. A further question is how do macroscopic patterns emerge and how are they sustained against evolutionary innovation in these 'complex adaptive systems? Understanding the factors which allow competing species to coexist remains a key question for theoretical biology.

A great challenge of our age is how will global change, the result of natural and anthropogenically induced climate change impact upon the structure and function of marine ecosystems through both abiotic and biotic drivers. Climate modelling studies (e.g. Bopp et al., 2005) indicate that large scale changes in climate patterns, ocean circulation and climate (i.e. structure, temperature and light) will impact platonic communities, while enhanced atmospheric CO_2 levels will lead to acidification of the oceans with significant impacts on ocean biogeochemistry (Bellerby, et al., 2005), calcareous organisms (Riebesel et al., 2001) and potentially the reproductive success of higher trophic levels (e.g. changing survival rates of early life history stages of metazoans and fish; Pörtner et al., 2004). These changes, may all impact on the overall trophodynamic structure and functioning of marine ecosystems. Simultaneously combinations of direct anthropogenic drivers such as fishing, eutrophication and pollution impact at both an organismal and population level thereby influencing the competitive ability and dominance of key species and thus the structure of marine ecosystems.

In recent years computational models have been proposed as a way to help assist us in understanding emergent properties. 'Computational models play and increasingly explanatory important role in cases where we are trying investigate systems or problems which exceed our native epistemic capacities' (Symons 2008). They are

only tools we have which can address non linear combinations of driver impacts in a dynamic environment including dynamic feedbacks. Our knowledge of driver impacts is currently limited to the climate envelope over which measurements have been made; the use of dynamic simulation models with feedbacks will allow us to assess driver impacts outside of the observed envelope.

This work takes a retrospective look at a complex model, the European Regional Sea Ecosystem Model (ERSEM, Baretta et al., 1995; Blackford et al., 2004) and references within) to assess its ability to generate emergent properties. Some definitions of emergence will be discussed shortly but in general we are referring to something 'new' or 'unexpected' appearing in the simulations which is not 'hard coded' into the model.

ERSEM was conceived in the early nineteen nineties and focused on the major issues of the day; the impacts of direct anthropogenic drivers (most notably eutrophication) on the structure and function of marine ecosystems. In recent years issue of global change impacts on marine systems has come to the fore and we must now consider a more holistic multi-driver approach. Underpinning ERSEM and many other models of its type is the ecosystem concept. The ecosystem is considered 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). It is a standard paradigm which underpins biological models. It cuts though 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 great advantage is that it can identify emergent properties such an energy flow and nutrient cycling and study the stability of function of this abstract structure. The major 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). A consequence of the ecosystem concept has been a systems analysis approach to ecology, where by it is viewed as being analogous to a machine, because it offers a pragmatic approach to understanding the complexity of natural systems (O'Neill, 2001).

2. Complex Adaptive Systems

Ecosystem services such as nutrient cycling, energy flow and community structure are the emergent properties of ecosystems (Levin, 1998). Ecosystems an example of a complex adaptive system, in which patterns at higher levels emerge from localized interactions and selection processes acting at lower levels. The study of complex adaptive systems is a study of how complicated structures and patterns of interaction can arise from disorder through simple but powerful rules that guide the change (Levin 1998).
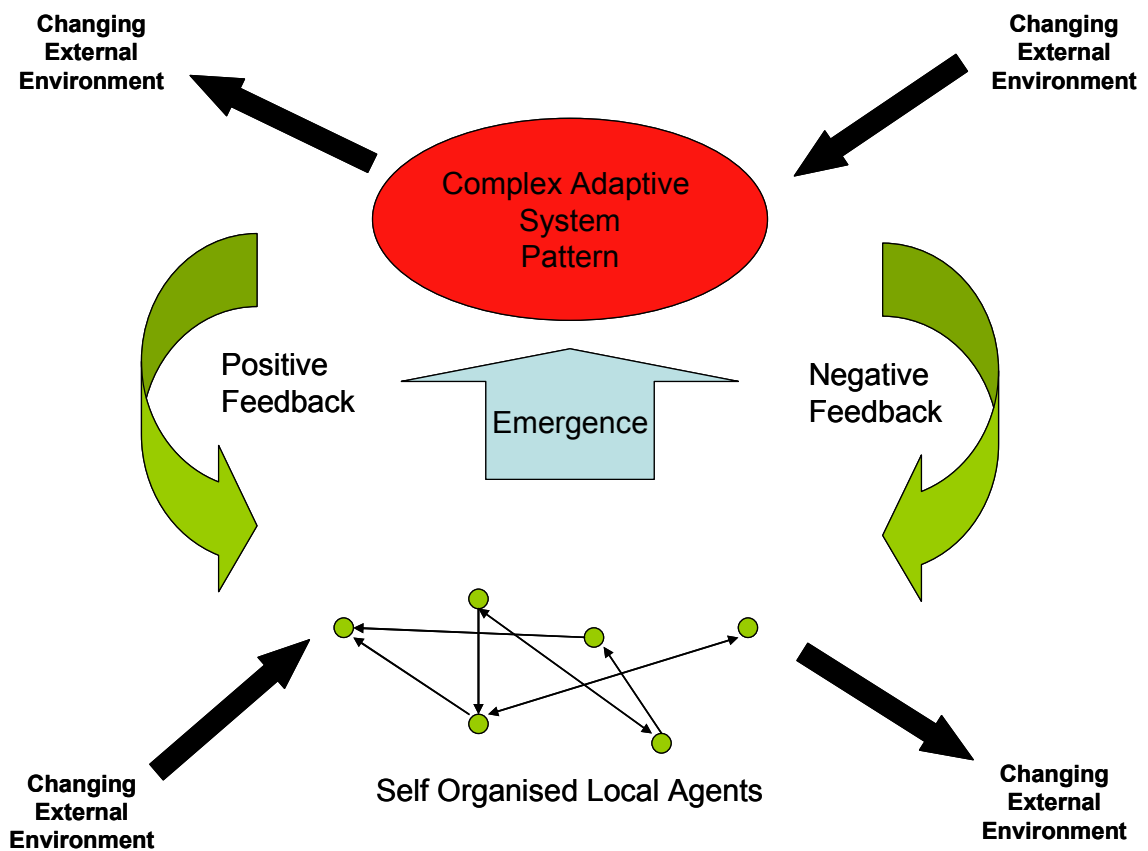
Figure 1: The agents in the system are all the components of that system for example the flora and fauna in an ecosystem. These agents interact and connect with each other in unpredictable and unplanned ways. From this mass of interactions regularities emerge and start to form a pattern which feeds back on the system and informs the interactions of the agents. These are in turn impacted by or impact on the external environment.

A schematic of a complex adaptive system is given in figure 1. At the lowest level agents interact in such a way that patterns emerge at a higher level of organisation. An

essential aspect of such interactions is non linear responses, leading to historical dependency and multiple possible outcomes of dynamics. The complex adaptive patterns which emerge then feed back on the original system of agents, which in turn are driven by and impact the external environmental forcing of the system. To fully understand this it is essential to determine the degree to which system features are determined by environmental conditions, and the degree to which they are the result of self-organization.

Hannah et al. (2010) 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.

Furthermore, given the multiple levels at which dynamics become apparent and at which selection can act, central issues relate to how evolution shapes ecosystems properties, and whether ecosystems become buffered to changes (more resilient) over their ecological and evolutionary development. If we are to model and understand complex adaptive systems the focus should be on non linear interactions and feedback loops. A lack such interactions and feedbacks limits the ability of the current ecosystem models to evolve into a state substantially different from their original state.

3. Emergent Properties

Emergence is a term used to describe the appearance of new properties which arise when a system exceeds a certain level of size or complexity, properties that are absent from the constituents of the system. This is a key concept of complexity science (Davies, 2004). Bedau (1997) highlights two "vague but useful hallmarks of emergent phenomena"; that emergent phenomena are somehow constituted by and generated from underlying processes and that these processes are some how autonomous from these underlying processes. Colloquially this can be expressed as the whole is greater than the sum of the parts.

Philosophers like to distinguish between strong and weak emergence. A system exhibiting strong emergence is one where the truths concerning the high level phenomena arises from the underlying processes, but are not deducible from the truths concerning the underlying processes. That is the whole system exhibits properties and principles that cannot be reduced even in principle to the cumulative effect of the properties and laws of the components (Davies, 2004).

In contrast a weakly emergent system is one where the truths concerning the high level phenomena are unexpected given the principles governing the low-level domain. The causal dynamics of the whole are completely determined by the causal dynamics of its parts (together with boundary conditions and the external disturbances) for which complete and detailed behaviour could not be predicted without a one to one simulation (Davies, 2004). Weak emergence is the notion most common in recent scientific literature and is most commonly invoked by emergence in complex systems theory. Strong emergence is a much more contentious topic as Bedau (1997) observes: "Although strong emergence is logically possible, it is uncomfortably like magic. How does an irreducible but supervenient downward causal power arise, since by definition it cannot be due to the aggregation of the micro-level potentialities? Such causal powers would be quite unlike anything within our scientific ken. This not only indicates how they will discomfort reasonable forms of materialism. Their mysteriousness will only heighten the traditional worry that emergence entails illegitimately getting something from nothing."

For the purpose of discussion one might argue that emergence occurs when the whole is greater than the sum of the parts, i.e. the lower level components of a system interact to produce a response which cannot be inferred from the cumulative effects of the underlying processes (e.g. Holland, 1998). Alternatively we can frame emergence in terms of our model producing an unexpected high level response given the principles governing the lower level of model organisations. For the purpose of the discussions that follow Crutchfield (1994) gives a pragmatically useful definition which I will adopt. He describes emergence as a process that leads to the appearance of structure not directly described by the defining constraints and instantaneous forces that control a system. Over time "something new" should appear at scales not directly specified by the underlying equations. Crutchfield also notes that an emergent feature cannot be explicitly represented in the initial and boundary conditions. These definitions are further expanded on as follows (Crutchfield 1994).

1. The intuitive definition of emergence: is that "something new appears";

2. Pattern formation: an observer identifies "organization" in a dynamical system; and

3. Intrinsic emergence: referring to the cases in which the occurrence of patterns, even if compatible with the laws and the constraints in use, cannot in principle be foreseen in advance only relying on these latter, i.e. the model evolves to a new state.

One of the main features of intrinsic emergence is that it produces effects detectable on a macroscopic observational scale; a phenomenon is emergent when it cannot be confused with a fluctuation and whence its occurrence persists on all observational scales.

Finally an important concept is that of concept of "downward causation". Roughly, speaking a feature is emergent if it has some sort of causal power on lower level entities". Essentially this refers to 2-way causal relation between upper and lower level entities. As an example, we can imagine individuals organising into a community. Their actions affect how the community develops (upward causality) and the development of the community itself affects the behaviour and interaction of the individuals (downward causality).

When trying to decide if a system demonstrates emergence we need to be able to detect it. One approach to detecting emergence makes use of the idea that the complex behaviour of interacting components results in some form of coordination: a persistent multi-agent relationship distinct from both chaotic and completely ordered dynamics. Essentially, a departure from randomness, and correlations between components, may be an indicator of emergent properties. Consequently dimensionality-reduction tools such as Self-Organising Maps (SOM), Principle Component Analysis (PCA) and non parameteric multivariate analysis are potentially powerful analytical tools. The purpose of such tools is to identify low dimensional pattern in higher dimensional data sets and all have been used to analyse ERSEM simulations demonstrating distinct higher order patterns (Allen et al., 2002; Allen et al., 2006; Allen and Somerfield, 2009; Lewis and Allen, 2009).
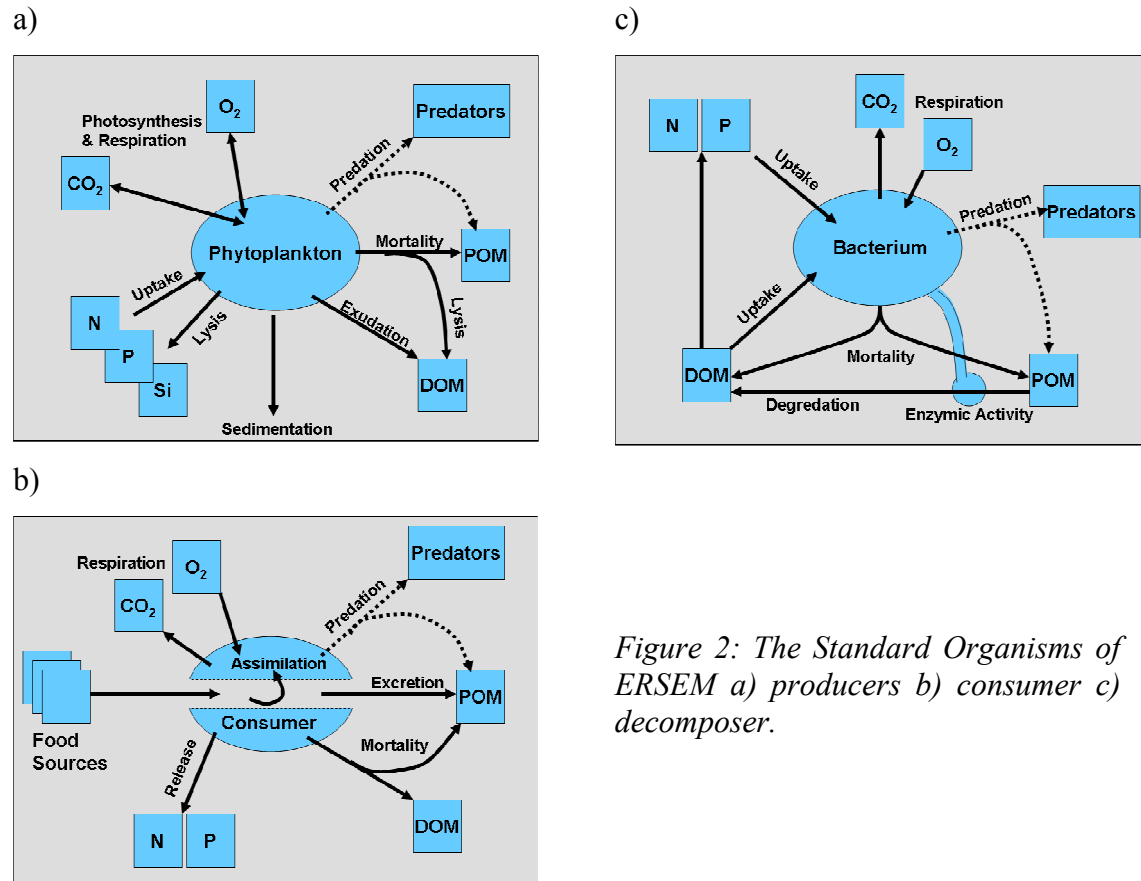
a)

b)

c)

Figure 2: The Standard Organisms of ERSEM a) producers b) consumer c) decomposer.

4. European regional Seas Ecosystem Model (ERSEM)

ERSEM is a generic model which represents the ecosystem as a network of physical, chemical and biological processes that together exhibit coherent system behaviour. ERSEM was originally developed and applied in the context of the North Sea (e.g. Baretta et al., 1995, Allen et al., 2001). It has also been successfully applied in the Mediterranean Sea (Allen et al., 2002, Siddorn & Allen, 2003), the Adriatic Sea (Allen et al., 1998, Vichi et al., 1998) and the Arabian Sea (Blackford & Burkill, 2002). ERSEM has undergone extensive validation with a focus on the North Sea and is perhaps the most rigorously evaluated marine model currently in use. Numerous approaches have been adopted making use of uni-variate methods (e.g. Holt et al., 2006; Allen et al., 2007), qualitative trend analysis (Lewis et al., 2006) and multivariate analysis (Allen et al., 2006; Allen and Somerfield, 2009).

The marine ecosystem is modelled using the concept of the standard organism (Baretta et al., 1995). Universal biological processes both physiological (ingestion,

respiration, excretion and egestion) and population (growth, and mortality) processes are defined. The differences lie mainly in the rate constants which are mostly derived from experiment or allometric consideration and foodweb interactions. The ecosystem is subdivided into three standard organisms: primary producers, consumers and decomposers (Figure 2), and subdivided on the basis of trophic links and/or size to create a functional group foodweb (Figure 3). The state variables are chosen to keep the model relatively simple without omitting any component that has a significant influence on the energy balance of the system. These dynamics are described by fluxes of carbon and nutrients between functional groups. Each functional group is defined by a number of components, namely carbon, nitrogen, and phosphorus and, in the case of diatoms silicon, each of which is explicitly modelled.
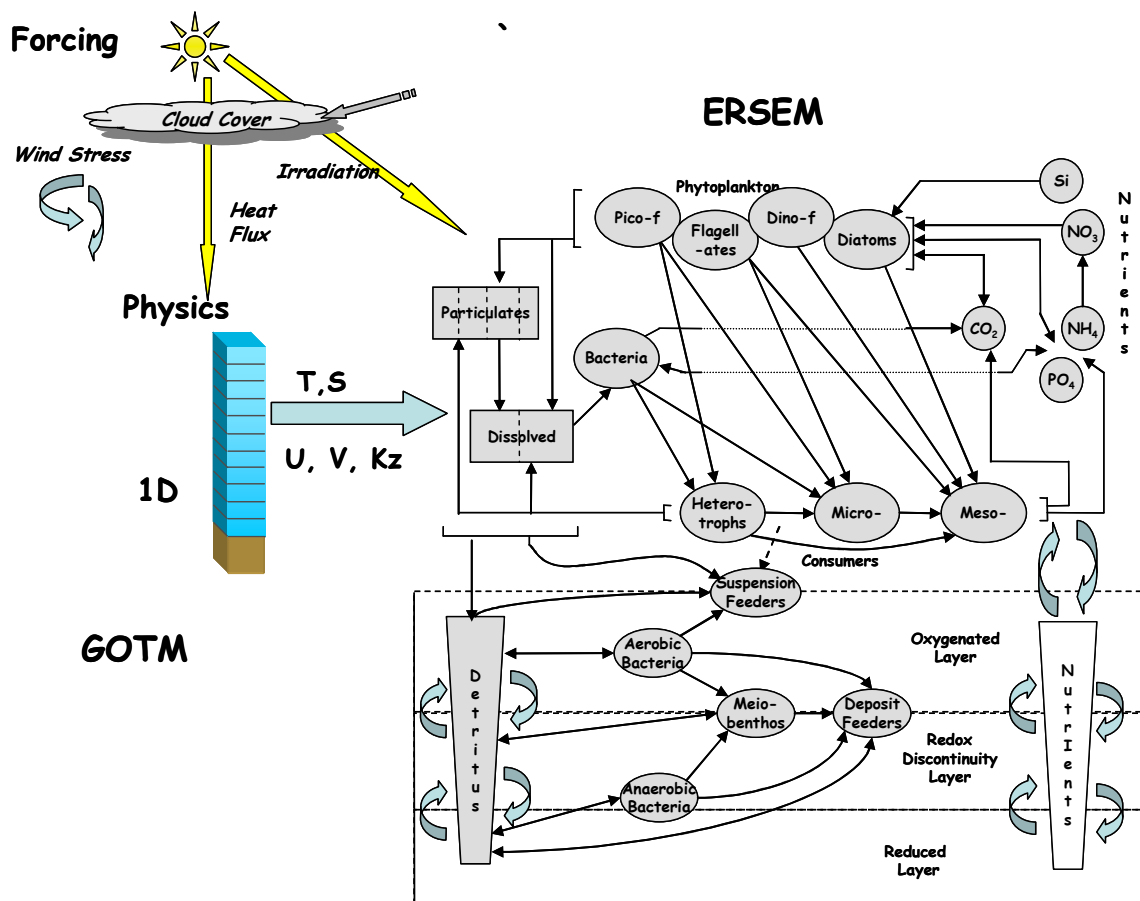
Fig. 3. *The model system, including atmospheric forcing, the hydrodynamic model and the benthic and pelagic foodwebs of ERSEM. T = temperature, S = salinity, U = current velocity (east +ve), V = current velocity (north +ve), Kz = vertical diffusion coefficient.*

The phytoplankton community is described by four functional types; picophytoplankton (0.2–2 μm), small autothrophic flagellates (2–20 μm), large autotrophic flagellates (20–200 μm) and diatoms (20–200 μm). The phytoplankton populations' adaptation to ambient light is described by the variable carbon to chlorophyll photosynthesis model of Geider et al. (1997). Light in the water column is modelled from astronomical values, corrected by cloud cover, to give PAR at the sea surface. Photosynthetic production is a function of temperature, availability of and adaptation to light and phytoplankton biomass. In the case of diatoms silicon availability is also considered. Nutrient limitation is a function of the internal C: N and C: P ratios of the phytoplankton. Nutrient stressed lysis (partitioned between particulate and dissolved detritus), excretion (activity excretion and nutrient stress excretion) to the dissolved phase and respiration (activity respiration and basal metabolism, related to ambient temperature) are the loss processes for the phytoplankton groups. Sedimentation of phytoplankton is assumed to occur if they are nutrient stressed. Three zooplankton functional groups are described: mesozooplankton, microzooplankton and heterotrophic nanoflagellates. Grazing uptake is a function of a maximal assimilation rate, temperature, food availability and the zooplankton biomass. Respiration loss consists of two terms, a temperature dependent rest respiration and an activity respiration. Excretion is a function of assimilation efficiency and excreted fraction of uptake and is split between particulate detritus and dissolved organic carbon. Mortality loss consists of two terms, one triggered by low oxygen conditions and a constant term. As with excretion, mortality loss is split between the dissolved and particulate fraction. The zooplankton itself may also be preyed upon. The mesozooplankton is assumed to become sedentary when (depth-integrated) food supply falls below a given threshold. In this 'over-wintering state' biomass is only affected by a minimal mortality and respiration rate. An increase in food availability over the threshold in spring provides the cue for the mesozooplankton to resume its normal physiological and ecological role. There is one pelagic decomposer functional group, bacteria. Bacterial uptake is a function of potential assimilation rate, temperature, oxygen availability and the concentration and nutrient quality of the food source (dissolved organic matter). Respiration loss consists of two terms, a temperature-dependent rest respiration and an activity respiration which contains a variable component dependent on the ambient oxygen

saturation. Mortality is given by a temperature-dependent rate. Additionally bacteria are considered to mediate the breakdown of particulate organic matter to dissolved organic matter according to the nutritional content of the particulate fraction. The particulate carbon model has been subdivided into three classes with differing sink rates whose sources are related to the size of functional groups as follows: >200 μ faecal material from mesozooplankton, sink rate 10 m d^{-1}; >20μ faecal material and grazing by microzooplankton, diatoms, dinoflagellates, sink rate 1.0 m d^{-1}; 20 μ picoplankton, autotrophic flagellates, excretion and grazing by heterotrophic nanoflagellates, sink rate 0.1 m d^{-1}. The ERSEM pelagic foodweb is described in Fig 2. Detailed descriptions of the pelagic submodels and parameters of the version of ERSEM used can be found in Blackford et al. (2004) and references within.

The benthic model (Figure 3) describes 3 layers, an oxic layer, a denitrifying layer and an anaerobic layer. The benthic foodweb consists of aerobic and anaerobic bacteria, meio-benthos (all heterotrophs between protzoa and 1mm), suspension feeders (feeding directly on the pelagic system) and deposit feeders (feeding on benthic detritus and other benthic organisms). It should be noted that individual species may behave as both deposit and suspension feeders thus straddling more than one functional group, consequently functional groups describe particular types of behaviour rather than species lists. The benthic system is driven by the settling of overlying detritus and filter-feeding by suspension feeders. Detritus is remineralised by bacteria releasing phosphate and ammonia into the sediment pore-waters. Other chemical processes include nitrification of ammonia, phosphate sediment interactions and the dissolution of silicate. Nutrients are released from the pore-waters into the overlying water column. These flux rates are enhanced by biomass dependent parameterisations of bio-irrigation; a Monod function is used to describe the increase in bio-irrigation rate as macro-benthic biomass increases. Detailed descriptions of both the equations and parameters can be found in Blackford (1997), Ruardij and van Raaphorst, (1995) and Ebenhöh et al. (1995).

5. Rationale

The purpose of this work is to assess the ability of a marine ecosystem model (ERSEM) to demonstrate weak emergence, which in general terms will be defined as interacting functional types producing a response at the higher level (community

structure) which is not just the sum of the individual components. The structure of ERSEM is such that it is a potential candidate for showing complex adaptive behaviour and emergent properties. The functional groups are agents, and these interact with each other via competition for food resource and foodweb interactions. The interactions between the functional groups produce patterns at a higher level of organisation (community structure). Feedbacks between functional groups are described, primarily via the recycling of nutrients and these may modify the simulated community structure. Also there is some capacity for phytoplankton to adapt to changes in the environment (light and nutrients) and modify their environment through self shading. Consequently a retrospective look is taken at a series of papers where the simulations produced properties which could be viewed as emergent. The reader should bear in mind that the original studies were not designed to address these issues and the primary focus is on particular outcomes and properties of the chosen simulations and not always on the published conclusions of the work. The chosen papers fall into three main categories: emergent community structure in response to environmental forcing, community response to anthropogenic perturbation and investigation of whether the ecosystem can amplify a weak atmospheric signal. The papers included demonstrate a variety of responses which could be described as emergent but as Crutchfield 1994 points out detecting the emergence of complexity in nature is an inherently subjective activity. The emergent properties demonstrated by these simulations are discussed along the adequacy ERSEM and other current modelling approaches for creating emergence. Suggestions for new directions in marine ecosystem modelling are proposed.

6.1 Ecosystem dynamics at six contrasting sites: a generic modelling study

Blackford JC, Allen JI, Gilbert FJ

Journal of Marine Systems 52, 191-215, 2004.

Abstract: A pelagic marine ecosystem simulation model ERSEM-2004, developed from the European Regional Seas Ecosystem Model (ERSEM II), is presented along with a parameter set applicable to six highly contrasting sites, ranging from a temperate mixed shelf station to a permanently stratified tropical deep-ocean station. The physical characteristics are simulated by direct coupling to a ID vertically resolved turbulence model, parameterised for each site. A mathematical description of the pelagic ecosystem model is presented. Additions to ERSEM II's well resolved community and decoupling of gross production and ambient nutrient concentration include variable carbon to chlorophyll ratios, coupling of bacterial production to nutrient availability, improved resolution of the organic particulate and dissolved fractions and developments to the mesozooplankton description. Comparison of seasonally depth resolved and integrated properties illustrates that the model produces a wide range of community dynamics and structures that can be plausibly related to variations in mixing, temperature, irradiance and nutrient supply. The spatial-temporal variability in key environmental indicators only partially correlates with the spatial-temporal variability in community structure ($p < 0.5$). Thus we infer that the complexity of the model's trophic structure and hence that of the marine system is important in defining the ecological response to the environment. A physical description of a marine domain may not be an adequate indicator of marine community structure or function. Particularly, lysis and grazer response are identified as important processes that define ecosystem dynamics and community structure. There is a closer correlation ($p > 0.75$) between spatial-temporal variability in community structure (biomass) and function (production). ERSEM-2004 is shown to be a robust model that is capable of representing a range of systems commonly described in the marine system. Consequently, the model is proposed as a potential basis for an ecosystem-based management toot that may, with appropriate physical representation, be applied over large geographic and temporal scales with utility to both heuristic and predictive studies of the marine lower trophic levels.

6.2 Primary and bacterial production in the Mediterranean Sea: a modelling study

Allen JI, Somerfield PJ, Siddorn J

Abstract: Relationships between bacterial and primary production in the eastern and western basins of the Mediterranean Sea are different. In this study, a ID coupled ecosystem model is used to simulate primary and bacterial production along the west-east trophic gradient and to ascertain the physical and biogeochemical controls that determine regional variations in production. Simulations demonstrate differences in ecosystem function between the western and eastern basins of the Mediterranean Sea at the level of bacterial and primary production. Vertical mixing processes (deep mixing and convection), particularly in late winter, are crucial in determining total annual production in both basins, and the dissolved organic carbon pool, from which bacteria obtain their carbon, is derived from autotrophic rather than heterotrophic activity. Bacterial production is nutrient limited in the cast, and may be grazer controlled in the west. The dissolved organic nutrient pools are derived from heterotrophic rather than autotrophic activity. The eastern basin is characterised by strong competition between phytoplankton and bacteria for nutrients whereas the western basin is characterised by relatively high levels of heterotrophic activity. Nitrogen and phosphate uptake by phytoplankton is biologically important in both basins, whereas bacterial uptake of these is only important in the eastern basin. A generic model parameterisation produces simulation results which concur with recent observations although simulated production rates are very sensitive to the initial conditions upon which those simulations are based.

6.3 Validation of a hydrodynamic-ecosystem model simulation with time-series data collected in the western English Channel

K. Lewis, J.I. Allen

J. Mar. Sys. 77, 296–311,2009.

Evaluation is essential if ecosystem models are to be used to simulate short-term and climate scale forecasts. A three-dimensional hydrodynamic-ecosystem model (ERSEM-POLCOMS) simulation of the western English Channel for the period 2003–2005 has been validated with a series of univariate and multivariate tests using physical, biological and chemical data collected routinely at time-series station L4 (50° 15′N, 04° 13′W). Our assessment indicates a varying confidence in model ability to simulate different variables: In terms of high frequency variability there is a high level of confidence in temperature, some confidence in nutrients, especially nitrate, but much development needs to be done before there will be confidence in the model ability to simulate phytoplankton, zooplankton and bacteria at sub weekly timescales. In terms of seasonal timescales, the model captures the phytoplankton succession when diatoms and flagellates dominate the system, but performs less well when dinoflagellate blooms are dominant. The evaluation provides a benchmark for future model development, and highlights the importance of data collection for model validation and the need to expand the range of biological variables sampled. The potential for coastal observatories to play a key role in the future development of marine ecosystem models is discussed.

6.4 Effects of demersal trawling on ecosystem functioning in the North Sea: a modelling study

Allen JI, Clarke KR

Marine Ecology-Progress Series, 336, 63-75, 2007

Abstract: Demersal trawling causes chronic and widespread disturbance to the seabed in shallow shelf seas potentially leading to changes in function and trophic structure of benthic communities and with important implications for the processing of primary production and the wider functioning of the marine ecosystem. We used a coupled physical-ecological model (the European Regional Seas Ecosystem Model (ERSEM) with the General Ocean Turbulence Model (GOTM)) to investigate the impact of demersal trawling on the benthic and pelagic ecosystems of generic stratified and unstratified water columns in the central North Sea. Perturbation experiments were used to simulate trawling events using estimates of mortality of benthic fauna caused by different fishing gears in different habitats, derived from a meta-analysis of over 100 trawling disturbance experiments reported in the literature. The results suggest that the biogeochemical impact of demersal trawling is most significant in regions where gear type, trawl frequency and bed type cause high levels of filter feeder mortality. This results in substantially increased oxygen content of the benthic system and significant changes in its biogeochemistry (increased phosphorus absorption, increased nitrification of ammonia, reduced silicate cycling). The impacts of these changes on the overlying pelagic ecosystem are, however, buffered by the physical environment and the ability of phytoplankton to vary their internal cell nutrient contents. Analysis of recovery of the benthic system on complete cessation of demersal trawling suggests that the system will return to its original state within 5 yr, except in extreme cases where the deposit or filter feeder function is effectively removed, when a permanent change in the function of the benthic ecosystem may result.

6.5 Extraction of a weak climatic signal by an ecosystem

Taylor AH, Allen JI, Clark PA

Nature, 416, 629-632, 2002

Abstract: The complexity of ecosystems can cause subtle and chaotic responses to changes in external forcing. Although ecosystems may not normally behave chaotically, sensitivity to external influences associated with nonlinearity can lead to amplification of climatic signals. Strong correlations between an El Nino index and rainfall and maize yield in Zimbabwe have been demonstrated; the correlation with maize yield was stronger than that with rainfall. A second example is the 100,000-year ice-age cycle, which may arise from a weak cycle in radiation through its influence on the concentration of atmospheric CO_2. Such integration of a weak climatic signal has yet to be demonstrated in a realistic theoretical system. Here we use a particular climatic phenomenon-the observed association between plankton populations around the UK and the position of the Gulf Stream - as a probe to demonstrate how a detailed marine ecosystem model extracts a weak signal that is spread across different meteorological variables. Biological systems may therefore respond to climatic signals other than those that dominate the driving variables.

6.6 Changes in DMS production and flux in relation to decadal shifts in ocean circulation

Allen JI Archer SD, Blackford JC, Gilbert FJ, Taylor AH.

Abstract: A fundamental question is are the biological processes regulating dimethylsulphide (DMS) production by the marine ecosystem interconnected and responding to atmospheric or ocean signals at decadal timescales? Related to this is a need to quantify how climate change affects these interconnections and understand the expected levels of natural variability on decadal timescales. To explore this we have used indicators of climate variability [the Gulf Stream North Wall (GSNW) and the North Atlantic Oscillation (NAO) indices] as probes to demonstrate that a marine ecosystem model, incorporating DMS production, can extract and amplify a climatic signal, which is spread across a variety of meteorological variables. The GSNW signal is imparted through the wind and cloud forcing, despite the fact there was not significant relationship observed between the GSNW index and the meteorological forcing data. The model simulations appear to reproduce observed decadal variability in phytoplankton community structure in the eastern North Atlantic and imply that DMS(P) biogeochemistry may vary on decadal timescales as a consequence of changes in community structure. The GSNW index is a potential indicator of such changes and there may have been a regime shift in DMSP production in the eastern North Atlantic coincident with that observed for plankton. Sensitivity analysis indicates that the impact of climate variability on DMS biogeochemistry may potentially be damped by the ability of microbial communities to adapt physiologically to the effects of changes in light and nutrients.

7. Discussion

The first example (Blackford et al., 2004) considers an evaluation of ERSEM as a generic model. In this case the same equations and parameter set are used to simulate community structure in six highly contrasting marine environments. The environments simulated range from temperature shelf seas (tidally well mixed and seasonally stratified North Sea), the seasonally stratified Mediterranean Sea (nitrogen limited Western Basin, and phosphorus limited oligotrophic Eastern Basin) and the Indian Ocean (Arabian monsoonal upwelling and stratified oligotrophic). In each case the only differences between simulation set-ups are the initial conditions and meteorological forcing, all other aspects being identical. The models produce distinct and plausible community structures for each station (Figs 5 & 11 tables 7 & 8 Blackford et al., 2004) and these patterns can be explained by the variations in environmental variable (light, temperature, stratification, nutrient supply). This can be regarded at a qualitative level as subjective validation of the basic model structure. However whether these simulations demonstrate emergence is a moot point. Multivariate analysis of the simulations demonstrates that the spatio-temporal variation in model environmental variables is only weakly correlated with model community structure and function (Blackford et al., 2004 table 9). If we use the criteria of Bedau (1994), 'that emergent phenomena are somehow constituted by and generated from underlying processes and that these processes are some how autonomous from these underlying processes' we can argue that the simulated community structures are emergent as the only differences between the six simulations is the physical forcing. However none of these simulations produce unexpected results.

A study simulating seven different regions along an east west transect across the Mediterranean Sea (Allen et al., 2002) draws similar conclusions about the role of environmental forcing and initial conditions in determining the emergent community structure. However there is another potential example of emergence contained within this paper. Turley et al. (2000) found highly significant relationships between primary production and bacterial production in the western and eastern basins on the Mediterranean Sea, indicating that primary production is a significant source of .dissolved organic carbon (DOC) for bacterial production in both areas. The Turley et al. (2000) paper was published after the reported simulations had been made. Analysis of the simulations demonstrated that the model was capable of reproducing the same

relationships (Allen et al., 2002 Fig 6) both quantitatively and qualitatively. At the very least this is a genuine independent validation of the model, but could also be viewed as an unexpected outcome in the sense that we are interrogating the model to see if it reproduces observed behaviour which was not anticipated when the model was constructed.

A 3D modelling study of the western English Channel demonstrates the ability of the model to simulate phytoplankton succession (Lewis and Allen, 2009). The analysis focuses on the L4 stations of the Plymouth time-series which in its current form has been sampled for phytoplankton and zooplankton weekly since 1988. We analysed the phytoplankton succession by sampling the simulation in space and time to recreate the observed data set and the analysing it using principal component analysis. Correlative comparison of model and data suggests the model has little skill in simulating phytoplankton functional types. After applying Principal Component Analysis (PCA) independently to both model and data, comparison of the 1st PCA component (Lewis & Allen, 2009 Fig 10) reveals the model reproduces the major mode of variability in 2003 when the observed system is diatom and flagellate dominated, but fails to do so in 2004 when the observed system is dino-flagellate dominated. Once again we have a successfully simulated community structure under certain conditions. This study highlights two key points. The nature of emergence is subjective and it requires the right analysis tools in order to be seen. Secondly the model community structure fails to adapt to the changing environment, implying a lack of adaptive capability in ERSEM.

The impacts of direct anthropogenic drivers on benthic ecosystem structure and function are considered in Allen and Clarke (2007), in this case the mortality of benthic fauna from demersal trawling. The numerical experiments once again focus on a North Sea water column. Demersal fishing induced mortality of benthic fauna was parameterised based on meta-analysis of the response and recovery of benthic biota to fishing (Kaiser et al., 2006). The results demonstrate that biogeochemical impact of demersal trawling is most significant in areas where the combinations of gear type, substrate and trawling frequency cause high levels of filter feeder mortality. Once again changes in community structure and biogeochemical function are the emergent properties from the model; in this case the unanticipated (with reference to the model when it was constructed) simulation of observed properties. The removal of model filter feeders leading to increased oxygen content of the benthos and enhanced

phosphate absorption as has been observed (Warwick et al., 1997, Widdecombe and Austen 1997). Analysis of the recovery of the system on the cessation of trawling suggests the model ecosystem system will return to its initial state within five years except in extreme cases where the deposit or filter feeder function has effectively been removed. This gives a tantalising suggestion that the model may have moved to a different state where a permanent change in the function of the ecosystem has occurred (Allen and Clarke 2007 fig 8). However as the model is a closed system with a repeating forcing it is likely that the system has not been run for long enough for the previous state to have been restored.

Perhaps the best examples of emergence from ERSEM simulations are associated with the model investigation of the observed statistical relationships between the position of the North Wall of the Gulf Stream (GSNW) and biological populations in Northern Europe. A statistical association has been found between the GSNW index and Continuous Plankton Recorder data in and around the North Sea (Taylor et al., 1992; Taylor, 1995), coastal North Sea data (Frid and Huliselan, 1996), jellyfish data (Lyman et al., 2005) and young fish (Lindley et al., 2003). The relationship is also found in freshwater data (George & Taylor, 1995; George, 2000) and in terrestrial data from a roadside verge in the UK (Willis et al., 1995) from which it can be inferred that the association must be transferred via the atmosphere. Relationships between long-term biological/planktonic time-series and the North Atlantic Oscillation (NAO) have also been found (e.g. Fromentin and Planque, 1996; Reid et al., 1998). The NAO is the dominant atmospheric pattern over the North Atlantic and Western Europe and is associated with changes in the winter surface westerly winds. It is important to note that there is no statistical relationship between the meteorological forcing and the biological response implying that the ecosystem is amplifying the atmospheric signal and is hence an emergent property of the observed system. This has been simulated using 1D ERSEM model system (Taylor 2002, Allen et al., 2006) demonstrating that the model can reproduce the observed GNSW biological variable relationships along with observed shifts in plankton community structure. Once again we were looking for an observed relationship rather than observing an emergent property in the simulations as a pre cursor to observing it in nature.

The final example is from Allen et al. (2006) which hints at the ability of the model to simulate a regime shift. The North Atlantic and NW European shelf displays strong

decadal changes in planktonic biomass (e.g. Reid et al., 1998) as evidenced by long term plankton monitoring (e.g. CPR www.sahfos.ac.uk) which shows strong decadal changes in the Plankton Colour Index (PCI), and the abundance of diatoms and dinoflagellates (Leterme et al., 2005); PCI and dinoflagellate abundance increase over time while diatom abundance decreases. In a qualitative sense the model can capture the observed variability of some diatoms species, dinoflagellates and the PCI (Allen et al 2006 Table 1). Simulations (Allen et al 2006 Fig. 5a) also show clear decadal variability in gross production of DMSP, with a significant change in sign occurring in the mid eighties (decreasing before 1985, increasing after) coincident with the observed regime shift in plankton in the North Sea (Reid et al., 1998). This implies the model may be able to capture at least some aspects of the observed regime shift in a quantitative sense and hence the model demonstrates weak emergence.

In conclusion ERSEM clearly demonstrates an ability to produce plausible patterns and organisation of model ecosystem community structured and biogeochemical function (Allen et al., 2002, Blackford et al., 2004; Allen and Clark, 2007). These patterns are influenced by the external forcing and while the responses are non linear in many cases mechanisms can be inferred or postulated. The high order patterns reorganise in response to changes in external forcing which then drive feedbacks through nutrient recycling, self shading and grazing. The dominant switch in ERSEM is competition between phytoplankton and bacteria for nutrients, when competition occurs we have a microbial loop ecosystem, otherwise its closer to the classical phytoplankton –zooplankton type of foodweb. There is also evidence that some of these results could be defined as emergent on the basis that known patterns are reproduced. Other examples can be construed as emergent in terms of an unexpected response, for example the relationship between ecosystem variables and climate indicators (GSNW index and NAO; Taylor et al., 2002) and the regime shift in the North Sea (Allen et al., 2006). In these cases we are getting emergence which was unanticipated when the original model was constructed. What's very clear is that these properties are useful and give insight into ecosystem processes. However intrinsic emergence is absent from all our examples; the model lacks the ability to evolve new model states from the existing model. ERSEM contains model processes (e.g. variable C:Chl, variable C:N) which allow acclimation of model in response to environmental changes with in certain pre-defined parameter limits. However it lacks parameterisations which allow organisms to evolve to new states in response to

environmental changes. This lack of evolutionary adaptability suggests that of this type have limited functionally when simulating ecosystem response to climate once the current climate envelope has been pushed.

8. Towards the next generation of plankton models.

The examples from the papers presented in this thesis clearly demonstrate that bulk biomass functional type models are capable of producing weakly emergent properties. In general existing models of marine plankton do a reasonable job of predicting physical driven features such as spring blooms and clearly have many useful applications particularly when trying to quantify and understand biogeochemical cycles and their response to environmental change. However we must acknowledge that the foodwebs are overly simplified and incapable of predicting functional diversity, ecosystem change and changes in ecosystem services (e.g. Hannah et al., 2010). However as the demand for such predictions increases the challenge is to develop ecosystem models which can encapsulate such processes.

The cell as a chemical factory

Currency – elemental concentrations C, N, P ,Si etc…

What is the correct level of detail Required to capture this in a model?

A_N

X_{CN}

Physiological Processes

B_C

Y_{CN}

Environment

Challenge to scale from the cell to the globe and seconds to eons.
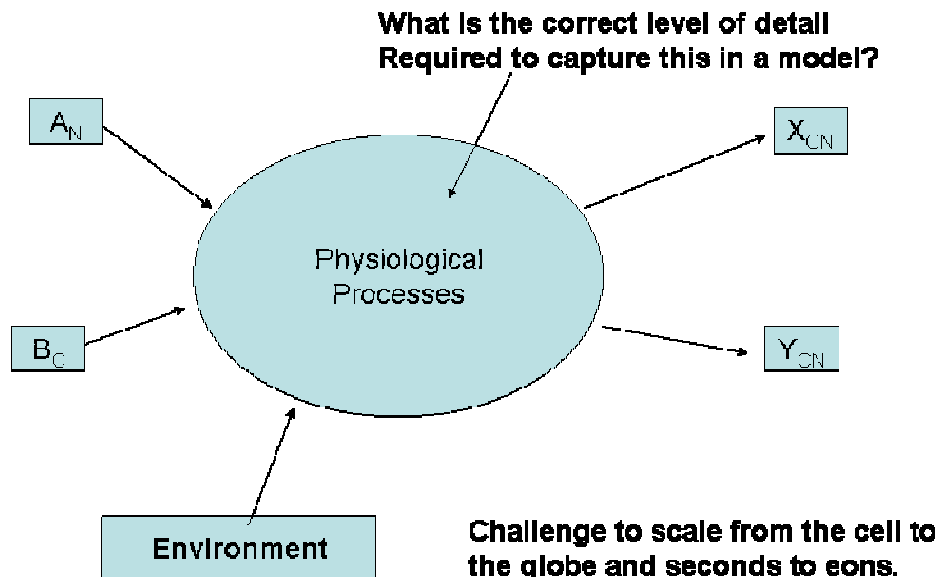
Figure 3. The cell as a chemical factory.

In the context of biogeochemistry the cell can be considered to act as a chemical factory (Figure 3). The big question is how much detail is required to capture the key

processes in a model. Existing plankton functional type models are often black boxes which fail to describe the physiological processes taking place in the cell which impact on ecosystem structure and function, which limits their ability to develop emergent properties. Current plankton models exist in a Newtonian framework essentially describing the bulk transfer of energy (e.g. carbon, nitrogen, heat, momentum) whereby physiological processes and population dynamics are parameterised by fluxes of carbon or nutrients between functional groups, rather than by describing the processes mechanistically. It is assumed that whatever compositional changes occur within each pool over time, they are not large enough to cause substantial and persistent errors in the prediction of pool scale rate processes. The result is that the ecosystem is essentially described as a chemical engineering process model. Transfers between model states are parameterised in terms of simple 1st order rate equations parameterised from experimental or allometric considerations without reference to intracellular processes. Broadly speaking photosynthesis is described as a product of light, temperature and nutrient limitation. For example Tian (2006) identifies 13 different parameterisations of the relationship between growth rate and light, all of which are basically different mathematical expressions of empirical relationships. Nutrient limitation of phytoplankton growth is described by two basic functions the Michaelis–Menten function and the Droop function. More complex models such as ERSEM invoke variable carbon to chlorophyll (e.g. Gieder et al., 1996 or cell quota nutrient models e.g. Ebenhoh et al., 1997). Parameterizations of zooplankton feeding are even more confusing, for example Tian (2006) identified 20 equations for feeding on a single type of prey and 15 for feeding on multiple types of prey. Inspite of the fact that trophic dynamics are complex at the secondary production level zooplankton are often represented by aggregated state variables, e.g. zooplankton, mesozooplankton and microzooplankton and these various equations have been used to describe, trophic linkages and energy flow from low to high trophic levels. Major loss processes such as respiration, mortality, excretion, lysis are mostly represented as either linear or quadratic loss terms. For example Tian (2006) identifies eight functions describing zooplankton mortality and six functions describing respiration.

Anderson (2005) identifies a number of problems with the bulk biomass plankton functional type approach including, poorly understood ecology, the difficultly of aggregating diversity within functional groups into meaningful state variables, the

sensitivity of outputs to parameter choice and the external physical and chemical environment. Furthermore Anderson (2005) states that "while the continuing articulation of detail in ecosystem models is the way forward, I argue that this can only be so with due care and attention to the formulation and a healthy does of scepticism about the outcomes". Flynn (2005) argues that representations of biological behaviour should not be omitted form a model unless it is demonstrated that it is safe to do so either empirically and or mathematically. Flynn (2005) also states that "the performance of each part of the model should be demonstrated as being fit for purpose and not dysfunctional". Flynn (2005) further suggests that for each organism type simulated we should ask a series of questions; is the form of each model component dysfunctional? When run alone do model organisms always exhibit sensible behaviour? What components of physiology have been omitted and why? Is it safe for all realistic scenarios?

The important point to note is that the real ecological or physiological processes underlying the observed correlation are not explicit; these various functions are mostly based on empirical relationships that express correlation between measurable variables. In addition there is little sound statistical or physiological basis with which parameter choices can be made to but it is clear that choice can be critical in determining model functionality (Gentleman et al., 2003).

9. Establishing the rules of the game

To build cellular ecosystem model capable of demonstrating a range of emergent properties it is important to think very carefully about the level of organisation required in the model. 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 simples set of rules (Holland, 1998).

The crux of the issue is that a model should be constructed at an appropriate level of complexity to address the hypothesis being tested and the data available to support it. 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). To construct the next generation of plankton models what is required is the establishment of a set of generic rules. These rules should be both simple yet capture the essence of key processes and interactions i.e. be mechanistic rather than empirical. If the 'rules' are established correctly then

properties such as adaption and plasticity of response should become the emergent properties of our models.
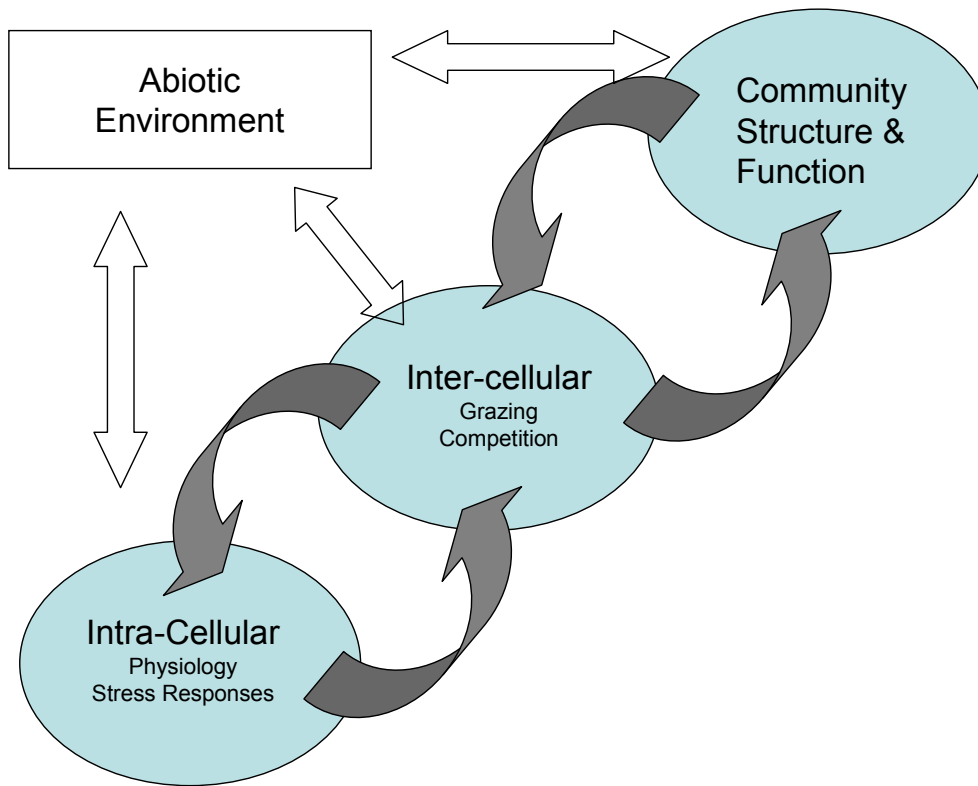
Figure 4: Conceptual model of the complex adaptive ecosystem.

Noble (2003; 2006) advocates the 'middle out' approach for modelling biological processes, 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 would be building models from the level of genes and proteins, which have the problem that we can only characterise a few species and we are only just beginning to make the links between genes and biogeochemical function; and that we need to know about higher levels of organisation to fully characterise the lower levels properly. The bulk biomass PFT approach could be construed as a top down model in the nomenclature of Noble (2003) and its fundamental weakness is that we end up with theories that are over general and therefore not useful (Ginzburg et al., 2007). For such models to be effective process detail must implicitly included in functions describing sub-scale processes rather than being explicitly spelt out at great length.

The middle out approach leads inevitably to the concept of the hierarchy of models and the challenge then, becomes how to couple them together to ensure we capture the important interactions and feedbacks (Figure 4). This is where the quest for generic physiological building blocks resides.

There are three main aspects to consider. The first is the representation of physiological processes within cells focusing in establishing underlying equations for key processes based around those conserved in all eukaryotic cells, for example autophagy, respiration and oxidative stress responses. Essentially redefining the standard organism concept so to focus is on describing the key processes within the cell, rather than empirically derived rates of transfer across the cell wall. Secondly we need to consider the interactions between organisms; Predators eat individuals not bulk biomass i.e. recognising that grazing operates in a lagrangian rather than a eularian framework. Finally we need to consider how both physiological processes and organismal interactions may adapt as the environment changes. Underpinning this are two key concepts the standard organism and the middle out approach. When taking the middle out approach 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.

The application of new microbiological and genomic techniques in marine studies is creating an avalanche of new information (Hood et al., 2007). For example Venter et al 2004 report over 148 unknown bacterial phylotypes and over 1.2 million unknown genes but many questions remain. At the moment this is raising far more questions that it answers. We don't yet understand the role genes and proteins play in driving marine-ecosystem dynamics and biogeochemical cycles, nor do we have much idea about which are important and what role are they might play in the evolution of marine microbial communities? From the perspective of the ecosystem modeller, while recognising such information crucial to understanding both adaption and evolution the sheer volume of data potentially leads to information overload and is currently computationally intractable. Also from a systems level perspective, how genes are expressed is crucial, the same genes expressed in a different order can produce a completely different physiological response (Noble, 2006). We should also bear in mind that gene expression is controlled by feedback with organisation at the cellular level. To begin to make use of this information it is crucial that our models begin to capture the essence of the major physiological processes in the cell.

10. The Generic Cell.

As an example of the physiological approach consider the proposed anti oxidant function for DMPS in phytoplankton (Sunda et al., 2002), who reported results that, together with those in the literature, indicate that DMSP and its breakdown products (DMS, acrylate, dimethylsulphoxide, and methane sulphinic acid) readily scavenge hydroxyl radicals and other reactive oxygen species, and thus may serve as an antioxidant system, regulated in part by enzymatic cleavage of DMSP. The cellular content of DSMP being substantially increased when the cell is exposed to oxidative stressors as solar UV, carbon and iron limitation and exposure to copper. It can be postulated that most if not all phytoplankton produce DMSP, but some more than others, e.g. diatoms produce only small amounts while dinoflagellates and phaeocycstis produce larger amounts (e.g. Archer et al., 2004).
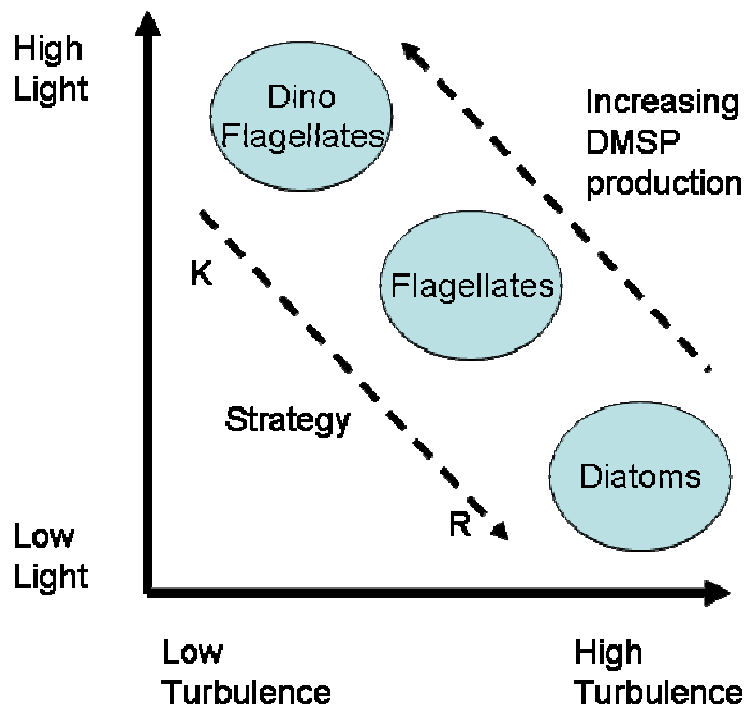

Figure 5: 'Mandala' type illustration of the relationship between light, turbulence, phytoplankton type and DMSP production. It is assumed at a first order that nutrient availability is tightly coupled to turbulence; i.e. low turbulence high nutrient stress.

The conventional way of dealing with such observations is a reductionist attempt to parameterise each process individually for each PFT. However Reactive Oxidative Stress (ROS) responses are ubiquitous in eukaryotic cells (e.g. Livingstone, 2001).

Perhaps what we are seeing when we see changes in DMSP production between phytoplankton functional types is not a reflection of the species but a reflection of the response of generic processes to the environment in which the plankton live (Figure 5).

One might then argue that the reason diatoms (and other R strategists) don't produce large amounts of DMSP is not because they can't but because the environmental niche they favour (high nutrient, high turbulence, well mixed water columns) doesn't require them to, particularly as they tend to sink when nutrient stressed. At the other extreme K strategists e.g. dinoflagellates favour low nutrient, low turbulence environments (e.g. stratified systems) meaning they are exposed to both light stress and nutrient stress and hence produce large amounts of DMSP. Therefore what we may be seeing is the emergent behaviour of the same ubiquitous process in differing environments, not a different mechanism for each plankton type.

The important point here is the concept of generic responses not the specific example. The debate as to the exact purpose of DMSP production by phytoplankton is ongoing, and it may yet turn out that it is not a stress response. The example serves to illustrate the concept of seeking generic process descriptions and parameterisations. This is essentially the middle out approach. We should endeavour to capture essence of key physiological processes such the photo-system, nutrient and endocytotic uptake, ingestion, respiration, oxyradical defence mechanisms (ROS) and augmented autophagy as a stress response. Recent evidence indicates that autophagy is much more than just a survival process in response to stress and is intimately involved in cell physiology (Figure 6). Augmented autophagy is induced by nutrient deprivation and hypoxia and autophagic removal of oxidatively damaged organelles and proteins may perhaps provide a second tier of defence against oxidative stress. (Moore et al 2006).

Recognising that we don't understand the ecology very well (Anderson, 2005), the problems caused by the subjective nature of aggregation and the poor representation of physiology in current models (Flynn, 2005) the contention is that this is the way forward is to establish a new standard organism described by a set of underlying generic physiological process equations rather than empirical formulation that characterise the growth and loss terms of cells and the associated biogeochemical cycling. The generic cell approach has previously been used as a proxy for the whole organism to simulate the response of the blue mussel (*Mytlus Edulis*) to pollutants

(Moore and Allen, 2002; McVeigh et al., 2006) This is the building block of our ecosystem model and could be used to underpin both conventional plankton functional type approaches. In order to turn this into a complex adaptive system we need to consider the interactions between organisms.
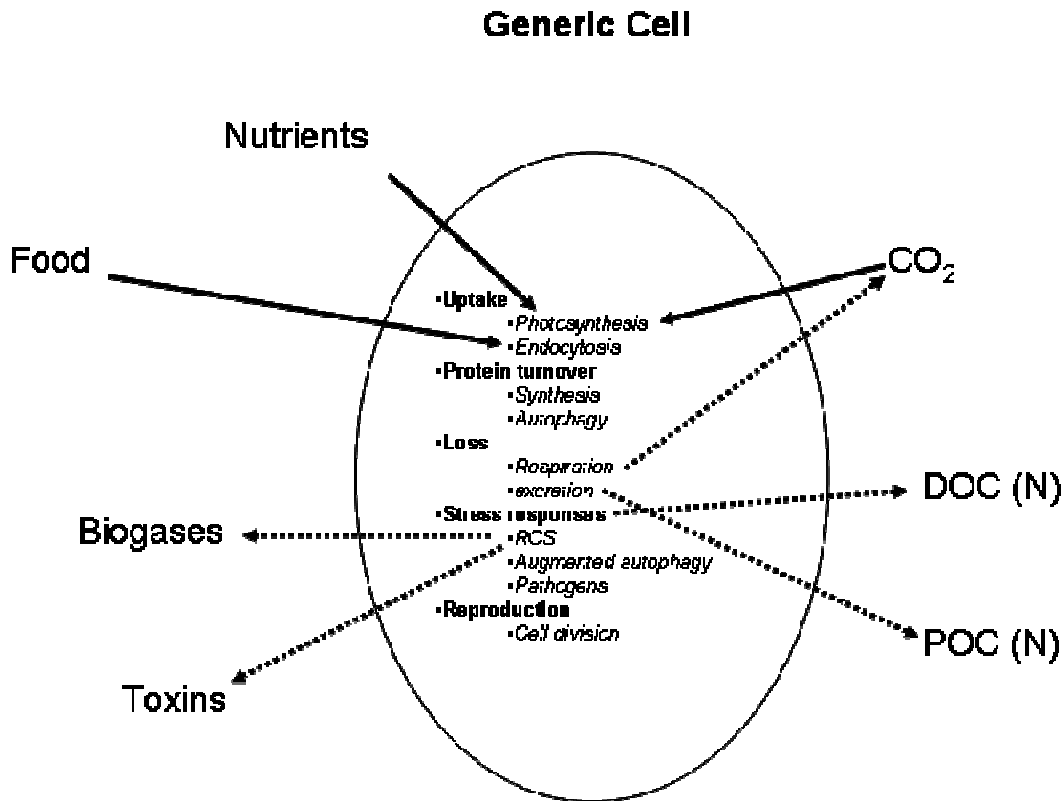
Figure 6 Schematic some of the processes that could be included in the generic cell.

11. Foodweb interactions and population dynamics

Ecosystem dynamics are profoundly influenced by the complex web of trophic interactions, which links all species together and feedback on each other. In the context of marine modelling, foodwebs are particularly important (Hannah et al. in press). In particular the structure of the foodweb and the strength of its interactions are critical to the stability and persistence of ecosystems (Dunne, 2006; McCann, 2000). A detailed understanding of the structure of some (if not many) parts of the marine ecosystem is currently lacking and we have even less understanding of their interactions. Studies are often limited to a low species numbers coupled with a tendency to focus on higher trophic levels (Link, 2002). In particular the interactions in the planktonic foodweb are poorly defined. A further issue related to interaction

strengths is capturing plasticity in the realised diets of organisms. These are all serious hurdles for modellers (Anderson, 2005) and ultimately, this lack of knowledge is the limiting factor in model construction.

The challenge is to get a better description of the structure and dynamics of the whole foodweb including plankton. At the heart of this lies a better mechanistic description of the processes of involving grazing. Rather than try to directly parameterise grazing rates from, we should focus of defining some generic rules of interaction and allow ecosystem properties to emerge from these interactions. In general plankton models treat grazing as a function of biomass in a eularian framework. However grazing is a lagrangian process. Grazers don't eat biomass they eat individuals and the process is the sum of they interactions between large numbers of organisms. These interactions are potentially both density (function of the number of potential prey) and behaviour (e.g. predator motility, food preferences/quality, ingestion time, prey defence mechanisms) dependent. Measured grazing rates are bulk measures of the interactions between species, or groups of species and could be considered as the emergent property of grazing interactions. A robust physiological understanding of processes such as ingestion and assimilation are required to underpin this approach, which the generic cell should provide along with individual based population dynamics. One way forward maybe to draw on the experience of higher trophic level modeller who use rule based descriptions of behaviour in their models (e.g. Humston et al., 2004). This would then need to be coupled with some representation of population dynamics either explicitly including population (number of organisms) as a model variable or adopting and agent based modelling approach describing groups of individuals such as the Lagrangian Ensemble (Woods, 2005) or 'super individuals' e.g. Travers et al, (2007).

12. Towards models with intrinsic emergence

Changes in community structure and ecosystem function in response to environmental change can be considered to be driven by three mechanisms (e.g. Bruggeman and Kooijman, 2007). These are;

> 1. Succession, i.e. the net balance between growth and death of the populations of the species involved,

2. Physiological acclimation, e.g. photo-acclimation.

3. Genetic evolution, i.e. when mutation and selection cause changes in phenotype.

Evolution results in organisms that are better adapted to their environment than their competitors. It is also known that, because of variability in the environment, there is not a single optimum state that every organism evolves towards (Armstrong, 2006). Models such as ERSEM are essentially models of selection and acclimation, having no capacity to evolve.

The final challenge is to get intrinsic emergence from ecosystem model in the sense of allowing model organisms to evolve and adapt to their environment rather than just occupy niches. Follows et al. (2007) used a novel approach towards generating biogeography; a marine ecosystem model was seeded with many phytoplankton types, whose physiological traits were randomly assigned from ranges defined by field and laboratory data. Global scale simulations generated an emergent community structure and biogeography consistent with observed global phytoplankton distributions; but once again this is a model of selection not adaption. The methodologies used by Follows et al. (2007) provide a conceptual framework within which we can create emergent ecosystems combining generic cells with foodweb interactions.

To address issues such as physiological adaption to ocean acidification or the plasticity of response in foodweb dynamics requires a theoretical framework which allows processes to adapt. The system of infinite diversity (SID) approach (Bruggeman and Kooijman, 2007) simulates biodiversity by describing the ecosystem with one generic population model and species characterising parameters and models phytoplankton succession as evolution of the parameter value distribution and may provide one starting point.

13. Time to put theory first

To develop planktonic ecosystem models capable of demonstrating intrinsic emergence a change in thinking about how models are constructed is required. While the existing modelling approaches have much merit, and demonstrate aspects of weak emergence they do not demonstrate an ability to adapt to environmental change and develop new states. Ultimately this limits their application. Marine ecosystem

modellers have been focusing on the middle out approach at an intermediate level of organisation, where they have the most empirical information. Unfortunately this information lies at an intermediate level of organisation lying between intra and inter cellular processes rather than at the levels at which emergence actually occurs i.e. at the intra cellular and inter cellular levels (Fig. 4). .

The proposition is to move away from parameterisation based on empirically derived functions and instead try the capture the fundamental underlying processes which are generic to all organisms. The focus should be on building theoretical models which capture the essence of the processes we are interested in and then designing the experiments to theoretically validate them. To fully capture ecosystem dynamics we need to capture both the physiology of the component organisms and the interactions between them. This required modelling at two levels of organisation (Figure 4) in order to capture all the feedbacks. To get to intrinsic emergence we then need to account for evolutionally element processes, which may then involve parameters changing in time and space, obeying pre defined rules and tradeoffs along with a stochastic element.

Model design should be question driven. If the focus is on biogeochemical cycling the priority is probably resolving the cellular processes, while if the questions are more focused on community structure and response or links to higher trophic levels. Neither the middle out approach nor the standard organism are new ideas, nor is the combination of the two, e.g. ERSEM. The important issue is identifying where in the system the 'middle is' in order to focus effort. Some of the information required already exists but much new knowledge and understanding will have to be acquired. This in turn will require new experimental techniques and better interaction between modellers and experimentalists. The computational cost of such an approach will be one or two orders of magnitude large than current model systems. Given the enormous increase in computing power over the last 20 years, this is likely to become tractable within a decade. At this stage lot of experimental work and synthesis will be required to develop the basic models and it will be a few years before such models can be run in 3D at high resolution. The reader may not agree with the details of what has been proposed but hopefully they will at least agree that there is a need to think differently about how marine ecosystems are modelled.

Acknowledgements

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