Marine Ecosystems
Research Programme

Programme Outline

Revised from original Case for Support, September 2014

Marine Ecosystems Research Programme is jointly funded by the Natural Environment Research Council (NERC) and the Department for Environment, Food and Rural Affairs (Defra)

Contents

MERP: PART A: Previous Track Record

Partners

Plymouth Marine Laboratory (PML) conducts interdisciplinary marine science to increase understanding of the interactions between the marine environment and society in estuarine, coastal and shelf waters, as well as the upper layers of the global ocean. PML is a NERC National Capability delivery partner, responsible for long-term datasets and developing ecosystem models. Capabilities include data collection and analysis, field and laboratory experiments, environmental impact assessments, satellite observation, ecosystem modelling, method and tool development, socio-economic evaluation, programme co-ordination, policy advice and capacity building.

Paul Somerfield is a Principal Investigator with >25 years' experience in studying interactions between marine organisms and their environment across scales of space, time and biological organisation using a range of approaches.

Professor J. Icarus Allen (NERC band 4) is Head of Science for Modelling and Observing Systems at PML, leader of PML's ecosystem modelling NC and is an honorary visiting professor at the University of Exeter. He has been involved in and acted as PI for over 35 national and EC projects, including coordinating the FP7 MEECE and OpEc integrated projects. He is the PI for the modelling activities in the Shelf Seas Biogeochemistry program, the Ocean Carbon theme of the National Centre for Ocean Forecasting (NCEO), Integrated Marine Biogeochemical Modelling Network (i-MarNet). His primary expertise is in marine ecosystem modelling and ecosystem response to climate change. He has 78 ISI publications.

Angus Atkinson has >25 years of experience in studying distribution and rate processes in zooplankton and micronekton, particularly the diversity of feeding and trophic level interactions. **Steve Widdicombe** has >20 years' experience in using field observations and manipulative experiments to study the impact of benthic organism behaviour and diversity on biogeochemical processes and ecosystem function focused on the impacts warming and acidification.

Melanie Austen leads a broad spectrum of interdisciplinary research with >25 years' experience originally in marine ecology and for >10 years in ecosystem services interfacing between natural and social science research.

Nicola Beaumont is a marine environmental economist with >14 years' experience in the assessment and valuation of ecosystem services in the marine environment. The PML Communications Group is experienced in running large KE offices including that of NERC's UK OA Programme. They have also had significant input into other KE offices such as VECTORS and EPOCA and have produced a number of successful science communication media, e.g the Other CO2 Problem animation, (20,000 hits on You Tube, won the Bill Bryson Prize for Science Communication).

Jerry Blackford (NERC band 4) is a Merit scientist at PML. His principle interests are the impact of Climate Change and Ocean Acidification on marine systems (OA) and environmental impact assessments for Carbon Capture and Storage (CCS). He leads a NERC consortium on CCS impacts and a NERC-Defra funded project on regional climate /OA modelling.

Jorn Bruggeman in trait based modelling and **Dr Sevrine Sailley** expertise on zooplankton and trophic interactions**, Dr Yuri Artioli** provides expertise in modelling marine plankton diversity. **Dr Luca Polimene,** has expertise in pelagic process modelling and **Dr Nick Stephens** in benthic modelling and nutrient cycling.

Momme Butenschön has >10 years of experience in ecosystem modelling leading the development of the marine ecosystem model ERSEM. He with a particular focus on ecosystem trends, natural variability and climate change impacts.

Ana Queirós is a benthic ecologist with expertise in studying complex animal- environment relationships focusing on benthic responses to acute and chronic anthropogenic disturbance and climate related impacts.

Pennie Lindeque is a molecular ecologist with >18 years research experience in a wide range of molecular techniques; most relevant to this project is studying feeding interactions and the use of Next Generation Sequencing.

The School of Biological Sciences at **Queen's University Belfast** undertakes environmental research spanning fundamental through to applied, empirical through to theoretical work. Strengths include a focus on the drivers of biodiversity change, conservation biology and food web ecology, and ecosystem service delivery at a hierarchy of scales.

Mark Emmerson's work focuses on relationships between biodiversity and ecosystem functioning using marine, terrestrial and freshwater systems to explore the consequences of biodiversity change using food webs. He has published >40 papers on biodiversity and ecosystem functioning and food web dynamics.

Nessa O'Connor is an early career researcher and lecturer. Her work focuses on the loss of primary consumers and predators in coastal systems and, more recently, the effects of multi-trophic species loss, and how they interact with perturbations on marine intertidal assemblages. She has published 17 papers and a book chapter.

The Department of Animal & Plant Sciences of the **University of Sheffield** is one of the UK's leading departments for whole-organism biology, . It has a thriving research programme which includes macroecology, population and community modelling and ecology, and ecosystem services, with expertise in terrestrial and marine ecosystems and in both theoretical and empirical approaches. The School of Maths and Statistics has an international reputation for its methodological research in Bayesian statistics and the handling of uncertainty in complex models, and applied research in ecology and environmental science, among other areas.

Tom Webb, a Royal Society University Research Fellow since 2008, is a macroecologist with particular expertise in cross-domain (marine—terrestrial) approaches to ecology and use of global biodiversity databases.

Julia Blanchard is a Lecturer in Ecology and quantitative marine ecologist with expertise in macroecological and food web models and indicators for understanding and predicting responses of marine ecosystems to human and environmental pressures.

Paul Blackwell is a Bayesian statistician and modeller with expertise in stochastic processes, spatio-temporal modelling and computer-intensive methodology, with particular interest in applications in ecology and environmental science.

Centre for Environment, Fisheries & Aquaculture Science (Cefas)' marine ecosystem and biodiversity-related science focuses on assessing, modelling and predicting the effects of fisheries or environmental change on ecosystems and biodiversity. Expertise is in interpreting survey results, defining the relevance to legislation and determining the implications for marine planning and management. Our applied science has been influential nationally and internationally in providing scientific evidence to support decisions on marine biodiversity conservation, marine spatial planning and implementation of the MSFD. We collaborate internationally with leading universities and research institutes, and a full range of other stakeholders. We direct and influence world-class research to ensure scientific advice is underpinned by the best available evidence: eg, partners in many EU FP7 projects. Resources include RV Cefas Endeavour, two specialist laboratories, comprehensive IT facilities, controlled environment aquaria and fish-rearing facilities. Cefas bring to IMMERSE unique data archives, and specialist systems for interrogating and modelling.

Michaela Schratzberger: 14 years' post-doc; 35 peer-reviewed publications (PRP). Senior Benthic Ecologist, specialising in changes in benthic community structure in response to environmental change; Science Leader providing science leadership/direction within Cefas' Environment & Ecosystem Division.

Axel Rossberg: 14 years' post-doc; 53 PRP. Senior Ecosystem Scientist, expert in developing highly simplified descriptions of complex systems; past10 years specialising in food webs and marine ecology.

Steven Mackinson: 13 years' post-doc;52 PRP. Senior Fisheries Scientist, specialising in developing ecosystem models and applying acoustic methods to study behavioural ecology.

Jeroen van der Kooij: 15 PRP. Pelagic Fisheries Ecologist with 11 years' experience in modelling temporal and spatial dynamics of populations; application of acoustic technologies to fisheries assessment.

John Pinnegar: 13 years' post-doc;50 PRP. Programme Director for Marine Climate Change, providing leadership and strategic planning of CC research, stable isotope analysis, multispecies and food web modelling.

Dr Johan van der Molen (Cefas Pay Band 7) is a principal ecosystem modeller. He is Secretary for Coastal and Shelf Seas in the Oceans Division of the European Geosciences Union, and a convener in its annual assemblies. He has over 20 years of experience in numerical modelling of hydrodynamics, sediment transport, morphodynamics, transport of fish eggs and larvae, and biogeochemistry.

Dr Sonja van Leeuwen (Cefas pay band 6) is a senior ecosystem modeller with experience in primary production, eutrophication, coupling ERSEM to size-based higher trophic level models, and river runoff and nutrient loads.

Dr John Aldridge (Cefas pay band 6) is a senior mathematical modeller with broad experience in physical and biological marine systems, and specialising in benthic processes and phytoplankton and macroalgal productivity. Other Cefas staff may contribute to the project where appropriate.

The School of Ocean Sciences of **Bangor University** conducts interdisciplinary research to provide the science required to underpin the conservation and sustainability of natural resources. Bangor University has internationally recognised expertise in interpretation and quantification of threats to ecosystems.

Jan Geert Hiddink is a benthic ecologist with >10 years' experience in studying the effects of fishing gears on the state and functioning of seabed ecosystems. He has published 46 peer-reviewed papers and grant capture since 2006 exceeds £3.5M.

Peter G.H. Evans is a marine vertebrate ecologist with >35 years' experience in studies of marine mammals and birds; he has c. 200 peer-reviewed publications and is author or editor of 12 books. He is Scientific Director of the marine environmental research organisation, Sea Watch Foundation and Honorary Senior Lecturer.

The **Centre for Ecology & Hydrology (CEH)** is the UK's Centre of Excellence for integrated research in terrestrial and freshwater ecosystems and their interaction with the atmosphere. The organisation provides National Capability based on innovative and interdisciplinary science and long-term monitoring. CEH has an international reputation for long-term population and dietary studies of seabirds in UK shelf seas. The CEH staff involved in IMMERSE all have extensive experience of multi-disciplinary research and will contribute in-depth knowledge of avian predators, modelling and empirical skills.

Sarah Wanless has > 30 years research experience of climate and fishery effects on birds. She has published > 200 peer-reviewed papers (PRP) including several on bottom-up and top-down processes as causes of seabird breeding failures.

Francis Daunt is a population ecologist with 15 years' experience of research into drivers of seabird populations, in particular climate change, marine renewables and fisheries. He has published > 60 PRP and coordinates CEH's long term seabird study on the Isle of May.

Kate Searle is an ecological modeller specialising in the estimation and modelling of population processes and dynamics, particularly the role played by extrinsic and intrinsic processes and spatial and temporal heterogeneity.

The Institute of Biodiversity, Animal Health and Comparative Medicine of the **University of Glasgow** is a multi-disciplinary research organisation carrying out a wide range of pure and applied work at levels from viruses to natural ecosystems. One research focus of the institute comprises the effects of environmental change operating at all levels of biological organisationlinked to studies of how individuals cope with environmental fluctuations, and how in turn this influences population dynamics and species interactions (including those between predator and prey). The contribution to the project will be investigating seabird diets. The institute has a strong group (**Nager, Monaghan, Furness**) studying seabird ecology and the analysis of their diets using a range of approaches.

Scottish Association for Marine Science (SAMS) is an independent marine research institute and state-of-the art facility on the west coast of Scotland.

Mike Burrows is Head of Ecology & Principal Investigator in Ecological Processes.

Sheila Heymans has extensive experience in food web and ecosystem modelling using Ecopath with Ecosim and ecological network analysis. She has co-authored 35 peer-reviewed publications on food web models of both marine and fresh water ecosystems.

Sir Alister Hardy Foundation of Ocean Science (SAHFOS) operates the Continuous Plankton Recorder (CPR) Survey. The CPR survey is recognised as the longest sustained and geographically most extensive marine biological survey in the world. The dataset comprises a uniquely large record of marine biodiversity. The CPR survey is of global importance for understanding natural variability and human-induced change and it is used by scientists, policy makers and environmental managers across the world.

Martin Edwards is a macroecologist with >15 years' experience studying environmental change on marine ecosystems. He has written >60 peer reviewed papers and >50 policy related reports and assessments.

Pierre Helaouët is a numerical ecologist specialising in large-scale spatial and temporal statistical models.

Through two very successful rounds of SRIF funding, the **Queen Mary University London** School of Biological and Chemical Sciences' laboratories have been refurbished and re-equipped, with a total of £1.5 million having been invested in the last 5 years. Facilities include a specialist marine plankton laboratory, sea water aquaria, controlled temperature rooms, and phytoplankton and zooplankton culture facilities. All of these are available to support this project.

Andrew Hirst has produced some of the first global accounts of growth, mortality and fecundity in zooplankton. He has co-authored ~50 publications. Most recently this has included developing new models and making new measurements to explain the Temperature-Size Rule. Hirst has had grants totaling ~£3.5 million funded and as PI on 4 grants e has a track record in managing NERC grants to their successful completion .

The marine research group in the Department of Mathematics and Statistics from **University of Strathclyde** was established in 2010 as part of the Scottish marine pooling (MASTS) initiative. The group focuses on mathematical modelling of aquatic populations and ecosystems, hydrodynamic modelling, and statistical analysis of large data sets, with unique capability in fish stock assessment and fisheries modelling, multi-species food web modelling and ecosystem modelling. The group has produced two modelling products which are available as packages for the R statistical environment and form the basis for a range of UKRC and EU funded projects. The team is led by **Mike Heath** (Prof) and **Douglas C. Speirs** (Lecturer), and comprises1 technical support staff, 5 post doctoral researchers including 1 senior researcher, and 8 post graduate students supported by a range of internal, CASE and MASTS funding sources. Heath and Speirs have jointly generated £1.255million of research income since 2008.

The National Oceanography Centre (NOC) is a NERC Research centre that maintains world class oceanographic research, consisting of Liverpool (**NOC-L** formerly the Proudman Oceanographic Laboratory; POL) and Southampton (**NOC-S**) sites. This work sits within the Marine Systems Modelling (MSM) group, which has world-class expertise in high resolution ocean and Shelf Sea modelling of hydrodynamics, waves and biogeochemistry, and uncertainty. At MSM at NOC-L has a substantial international reputation and contributing to the development of operational shelf sea forecast services at the UKMO (based on NEMO) and marine impact climate projections for UKCP09 and MCCIP.

NOC Principal investigator: Dr Jason Holt (NERC band 4) is associate head of the MSM. He specialises in the synthesis of model and observations to develop our understanding of shelf-sea physical and coupled physical-biological systems. He leads the modelling component in the NERC FASTNet (ocean-shelf exchange) programme and the Next Generation Ocean Dynamical Roadmap Project. He has published 50+ peer reviewed papers primarily on the modelling of hydrodynamics and ecosystems in shelf seas and ocean margins. **Co-**

Investigators: **Dr. Hedong Liu** (NERC Band 5) works on the development and applications of 3-D unstructured and structured grid ocean models. He is currently a member of NEMO developer's committee and specialises in state-of-the-art numerical methods.

Dr Sarah Wakelin (NERC Band 6) specialises in the modelling of physical and coupled physics-ecosystem processes in shelf seas, including the impacts of climate change and the combine impacts of climate and anthropogenic drivers.

Marine Ecosystem Research Programme (MERP)

Formerly Integrating Macroecology and Modelling to Elucidate Regulation of Services from Ecosystems (IMMERSE) and the WP2 Developing a model based understanding of ecosystem service regulation grants.

MERP was created when two grants were combined to make an overarching programme.
Full original WP2 Case for support is available as appendix 1.

PART B. DESCRIPTION OF PROPOSED RESEARCH

1. Summary

IMMERSE is a highly integrated project designed to develop new understanding of the processes governing the dynamics of marine ecosystems, and how changes in them affect delivery of ecosystem services, from a whole ecosystem perspective. It will make step-changes in:

- marine macroecology, through applying the latest ecological theory coupled to novel integration of existing data using ecoinformatic approaches
- targeted field sampling and experimental studies of key features that are currently understudied
- ecosystem modelling through state of the art application of an ensemble of ecosystem models
- ecosystem services science through use of macroecology and models to hindcast and forecast ecosystem states, indicators, and estimates of goods and services.

2. Introduction and Rationale

Marine ecosystems provide a range of services to humanity. These are highly dependent on biodiversity and ecological functioning (Austen et al 2011). Most widely recognised are the provisioning services, particularly wild-capture fisheries. Others range from those supporting human life (e.g. climate regulation) to those enhancing the lives of individuals (e.g. leisure, recreation, tourism). Marine ecosystems are experiencing on-going environmental change (e.g. Halpern et al 2008), ecosystem restructuring generated by fisheries (e.g. Smith et al 2011), eutrophication, pollution and other environmental degradation (e.g. Diaz & Rosenberg 2008) climate-driven changes (e.g. Beaugrand et al 2009, Dulvy et al, 2008, Hoegh-Guldberg & Bruno 2010) and growing human consumption and pressures (e.g. marine renewables). Understanding the consequences of these changes, and designing, testing and refining potential management solutions to address them, is important for the long-term delivery of services from marine ecosystems (Pinsky et al 2009). It is becoming increasingly clear that human activities and environmental change that affect parts of the ecosystem (e.g. fisheries management) can have much wider consequences for biodiversity and ecosystem services than previously thought, due to interactions through food webs.

Marine food webs play a key role in regulating these ecosystem services but there are important gaps in our knowledge and understanding of the way they might respond to environmental change. Although there is evidence that marine food webs are affected by both ‘bottom-up’ (e.g. biophysical factors affecting primary productivity) and ‘top down’ (e.g. top predators modifying the biomass of lower trophic levels) processes (e.g. Ware & Thompson 2005, Baum & Worm 2011), existing knowledge is much greater for lower trophic levels and associated biophysical factors. This is reflected in current ecosystem models such as the European Regional Seas Ecosystem Model (ERSEM) that are limited in their ability to model ecosystem components larger than small zooplankton. This means it is currently difficult to understand the relative roles of these processes and hence the extent to which environmental change cascades through marine food webs and affects ecosystem services. These processes are also scale-dependent. For example large-scale removal of top predators (through fishing or other activities) can have a range of impacts across scales. However, scale-dependence is poorly understood, making it difficult to quantify the large- scale impacts on ecosystem services of changes at small spatial scales (e.g. marine conservation zones); and vice versa. Ecological patterns of most interest (e.g. variation in biodiversity, fish production or nutrient cycling) are often generated by processes operating at different spatial and temporal scales from those at which they are usually observed (Chave 2013). In particular, policy decisions regarding the conservation of biodiversity and sustainable ecosystem service provision typically require large-scale thinking (Kerr et al. 2007, Keith et al. 2012). To say anything meaningful about the potential consequences of future ecosystem change for ecosystem services we need ecosystem models. While ERSEM is currently limited to modelling lower trophic levels there are a number of models of higher-trophic levels which can be coupled to ERSEM. Improving our understanding in the areas above will aid in the development of more realistic marine ecosystem models and holistic modelling systems, which in turn will provide important tools for exploring the impacts of potential future changes on marine ecosystems, and testing their response to potential management solutions.

Although there is considerable activity and associated data in the North-East Atlantic region, from a whole ecosystem perspective it tends to be fragmented, focused on limited descriptors of foodwebs (e.g. a single tracer of trophic level and not others) or components of the system (e.g. a specific habitat or component of the biota) or issues (e.g. fishery management or renewables), largely reflecting the interests and responsibilities of individuals and organisations doing the work. There is widespread recognition among the research and policy communities that a **whole- ecosystem perspective** is now required. The step-change envisaged by the **Marine Ecosystem Research Programme (MERP)** is to integrate existing data, targeted new data, and state-of-the-art ecosystem models, all within a common framework built around the latest and most appropriate ecological theories, and to use these to improve our understanding of the whole marine ecosystem rather than just parts of it, how it responds to changes in pressures, and the consequences of those changes in terms of ecosystem services.

Modelling challenges: Macroecology is the study of the relationships between organisms and their environment at large spatial scales to characterise and explain statistical patterns of abundance, distribution and diversity (Brown and Maurer 1989). Scaling relationships are common at higher levels of biological organization, (e.g. Brown, 1995). Body size is an important determinant of many ecological properties, ranging from abundance and biomass to physiological and ecological rates and provides useful underpinning concept for characterizing and modelling marine ecosystems. The widely observed macro-ecological patterns in log abundance vs. log body mass of organisms can be explained by simple scaling theory based on food (energy) availability across a spectrum of body sizes. For example quarter-power scaling with body mass applies to virtually all organisms (West, Brown & Enquist, 1999) and for marine animals, metabolic rate and production scales at three-quarters power (e.g. Brey, 1990; Warwick & Price, 1979). Allometric equations have been derived for respiration, ingestion, excretion and photosynthesis for a variety of organisms of different sizes (e.g. Verdy et al 2009, Moloney and Field 1989). Finally, the temperature dependence of gross primary production and community respiration is consistent among the major types of ecosystems on the planet, suggesting that the fundamental biochemical kinetics of respiratory metabolism are highly conserved and can be scaled from organism to ecosystem levels (Yvon Durcher 2012).

Understanding the interactions of the various system controls, the consequences of change, and designing, testing and refining potential management solutions, is important for the long-term delivery of services from marine ecosystems. Dynamic models that link the physical, chemical and biological processes through food web interactions provide a means of understanding how human impacts on different parts of the ecosystem interact and of predicting the consequences of management actions.The traditional approach to modelling marine plankton has generally been to build modelling frameworks by coupling bulk biomass functional type (FT) models to 1D and 3D hydrodynamic models; The European Regional Seas Ecosystem Model (ERSEM*)* is one such model. The ecosystem can be divided into four sections, the pelagic cellular ecosystem, the pelagic mid trophic levels (zooplankton), the benthic ecosystem (bacteria, meiofauna, zoobenthos) and the higher trophic levels (fish, birds, mammals); ERSEM describes the first three.

The cellular ecosystem is represented as a biogeochemical flux model where the cell is a black box whereby the fluxes of carbon or nutrients are transferred across the cell walls via first order rate equations. Most often defined in terms of biogeochemical functions (e.g. diatom, non-diatom, calcifiers, grazers etc.), the functional groups are treated as passive tracers and are very sensitive to the biophysical environment they are placed in.

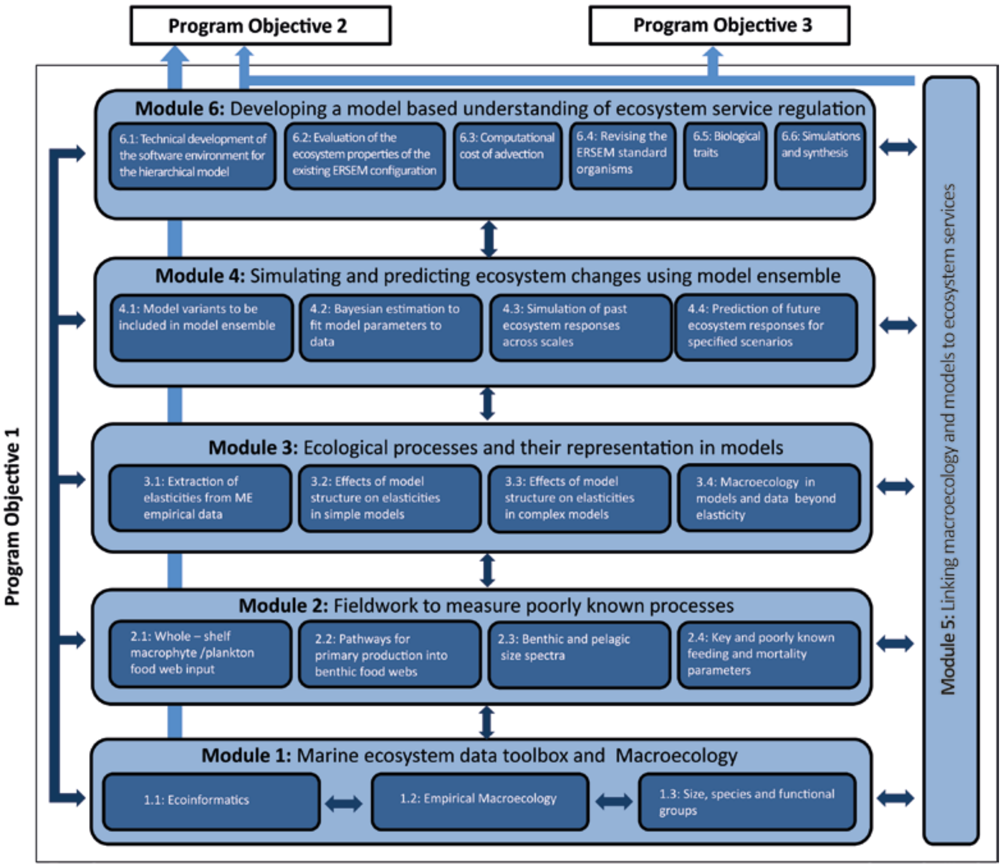
The pelagic mid trophic levels are particularly important yet are a weak component of all models. They are particularly important because they provide both the top closure for the planktonic ecosystem and the link to the higher trophic levels. This part of the foodweb is poorly represented in biogeochemical flux type models because the Eularian continuum approach becomes inadequate as behaviour and individual history becomes important. Grazers do not eat biomass; they eat individuals and the process is the sum of the interactions between large numbers of organisms. These interactions are potentially dependent on combinations of prey density (function of the number of potential prey), prey quality (nutritional status), prey type (species) and behaviour (e.g. vertical migration, foraging strategies and defence mechanisms). The challenge is to represent both biomass and population dynamics model in size / trait based foodwebs, coupled to biogeochemical cycles. The benthic system is strongly influenced by the physical sediment structure, environmental conditions and organic fluxes to the sediments. Benthic size spectra are more complex than their pelagic counterparts (Schwinghamer 2011); three biomass peaks, are observed corresponding to bacteria, interstitial meiofauna, and macrofauna, separated by low biomasses. Once again the requirement is to develop a size/trait based foodweb model from bacteria to top predators. Only by viewing the water column and benthos as a whole that will enable a more complete simulation and understanding of fish predating on benthic invertebrates, macroalgae contributions and benthic ecosystem resilience through the modelling of larval and reproductive abilities. Finally the Higher trophic levels are not a part of ERSEM, however the new model will be designed to provide data products to facilitate 1 way coupling to a range of different models ranging from dynamic size spectra and Ecopath with Ecosim to individual based models to further investigate the different model ecosystem structures and the ecosystem dynamics represented.

3. Project overview and relationship to the Programme objectives

3.1 Project overview

MERP is structured around six work **modules** that will enable novel integrated marine ecosystem science to propagate through to understanding of the dynamics of ecosystem services provided by marine ecosystems, leading in turn to a mechanism for providing advice on the likelihood of changes in ecosystem services in response to future changes in drivers.

A key characteristic of the project is **integration**. Findings and data from modules 1 and 2 will be used to improve models in modules 3 and 4. Outputs from modules 3 and 4 will be fed back into modules 1 and 2 to generate new hypotheses and to validate models, and outputs from modules 1, 2, 3 and 4 will feed into module 5. To facilitate integration regular integration workshops will be held.



Module 1. Marine ecosystem data toolbox & application of macroecology

We shall re- organise existing data records on aspects of marine ecosystems from a wide range of sources according to species traits (body size, habitat, feeding mode). We shall use this resource to conduct regional macroecological analyses. Macroecology seeks to identify relationships between taxa and their environment by statistical analysis of the emergent (observed) regional properties of the ecosystem.

Module 1 specifically addresses improving understanding of how the marine ecosystem as a whole responds to specific ‘bottom up’ and ‘top-down’ perturbations through the novel combination of existing data with recent theoretical advances from marine and terrestrial ecology.

Module 2. Fieldwork to measure poorly known processes

We have identified key components and properties of marine ecosystems which are currently under-sampled and not adequately represented in existing ecosystem models. We shall conduct a programme of field surveys and experiments to generate new understanding of these features and organise the information for inclusion in models.

Module 2 specifically addresses improving understanding of marine ecosystem responses to specific ‘bottom up’ and ‘top-down’ perturbations through the novel combination of existing long-term data, new field-based and experimental observations with recent theoretical advances from marine and terrestrial ecology

Module 3. Ecological processes and their representation in models

In contrast to macroecology, simulation models seek to assemble ‘from the ground up’ representations of relationships between taxa, so as to reproduce the observed properties of the ecosystem as a whole under known driving conditions. We shall identify the implications differences in model structure have on macroecological patterns and reduce structural model uncertainty.

Module 3 specifically addresses integrating improved understanding into marine ecosystem models using concepts and expertise derived from non-marine models.

Module 4. Simulating and predicting ecosystem changes using a model ensemble

The predictive engine of the project will be an ensemble comprising well documented, contrasting, whole or partial simulation models of marine ecosystems together with statistical models emerging from macroecological analyses. Following the ensemble modelling principles defined by the IPCC for forecasting the consequences of greenhouse gas emissions, we will apply parameter optimisation methods to fit each of the models to historic time series of observations under known driving conditions, and then forecast ecosystem states under scenarios of future conditions. The aim is to quantify the uncertainty in future predictions.

Module 4 specifically addresses integrating improved understanding of how the marine ecosystem as a whole responds to specific ‘bottom up’ and ‘top-down’ perturbations into marine ecosystem models using concepts and expertise derived from non-marine models, and the generation of predictions about the fate of marine ecosystems and their services under different past and future scenarios, at local and regional spatial scales.

Module 5. Linking macroecology and models to ecosystem services

We shall map the outputs from the model ensemble onto an inventory of ecosystem services developed by the National Ecosystem Assessment and the EU VECTORS programme (www.marine-vectors.eu). We shall translate outputs from modules 1, 2, 3 and 4 into quantitative measures of goods and services and relevant indicators of ecosystem status, in particular indicators that are defined in the MSFD. We will create an integrated system capable of making forecasts of ecosystem status, goods and services for various scenarios of future environmental conditions.

Module 5 specifically addresses translating improved understanding of the dynamics of marine ecological communities into the currency of ecosystem services.

Module 6. Developing a model-based understanding of ecosystem service regulation

This work will our capacity to assess the structure of marine ecosystems by improving the way that biodiversity and ecosystem function are represented in the European Regional Seas Ecosystem Model (ERSEM). Cornerstone of this development is the transition of ERSEM from a one-size-fits-all model of fixed complexity to a hierarchy of models that selectively inserts detail (e.g., species diversity) where demanded by applications. The enhanced model will be used to explore the impacts of human-induced stresses and natural variability on the structure of marine ecosystems (e.g., their species composition and size structure), and develop links to project ecosystem services in order to meet future science and policy needs.

Module 6. Developing a model-based understanding of ecosystem service regulation

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3.2 Relation to Programme Objectives

Modules 1, 2 and 3 directly support **Objective 1** of the broader NERC Marine Ecosystems Research Programme, which is to improve understanding of how the regulation of key ecosystem services such as food production, macronutrient cycling and cultural values by marine food webs are affected by ‘top down’ and ‘bottom up’ driven cascades, scale- dependence in the underlying processes and functional diversity at different trophic levels. This will be achieved by macroecological analysis of existing data, gathering of new data on key missing elements, and analytical study of the consequences for cascades of alternative model structures and mathematical formulations for representing key processes.

Modules 3, 4 and 5 support **Objective 2**, which is to integrate improved knowledge and understanding into existing ecosystem models, and to explore the impact of environmental change on the structure, function and services associated with marine food webs across scales. These modules will achieve this by analysis and extension of a suite of 5 existing ecosystem models linked to, or driven by, outputs from ERSEM. The suite will then be treated as an ensemble, driven by common drivers, optimised to hindcast past changes in west of UK shelf ecosystems, and run forwards to quantify the uncertainty in future states under scenarios of climate change and human activity .

Modules 4 and 5 provide a forward link to **Objective 3**, which is to apply models to test the impact of potential management solutions, such as marine conservation zones, on the structure and function of marine food webs, and explore the efficacy of specific indicators of Good Environmental Status (GES). Although the Programme specification specifically excludes the conduct of Objective 3 in this project, the work proposed is an essential precursor for it.

3.3 Geographical focus

This project will focus on the shelf seas off the western seaboard of the

British Isles (Fig. 1).

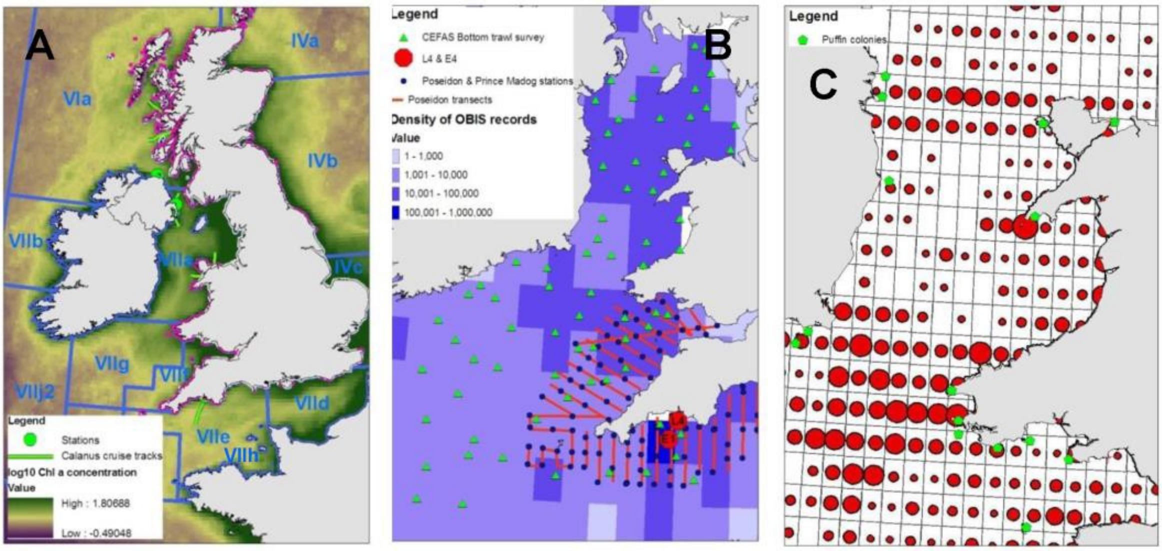

Figure 1. ***A*** *(left), background=sea surface algal chlorophyll; pink coastline=rocky substrate likely to support kelp; green symbols and lines=IMMERSE macrophyte study sites; blue area outlines and lettering=ICES regions.* ***B*** *(centre) background=OBIS record density; red track blue & red symbols=planned Cefas Endeavour and Prince Madog surveys and L4/E1 stations; green symbols=locations of exiting data for size spectrum analysis.* ***C*** *(right) green symbols=puffin colony locations; red symbols scaled to cetacean species richness.*

This region is characterised by highly-diverse foodwebs and supports important commercial fisheries. This geographic focus enables us to capitalise on an exceptional archive of existing data. For instance, the UK waters have more records in the Ocean Biogeographic Information System (OBIS, www.iobis.org) than any other region (Tyler et al. 2012) reflecting the long history of marine biological exploration of the UK's seas, and the operation of a number of significant, long-term and/or spatially extensive monitoring efforts of all major components of the ecosystem including fish (e.g. International Bottom Trawl Surveys, Cefas' DAPSTOM database of fish stomach content records and stable isotope analyses), plankton (e.g. Continuous Plankton Recorder Survey), predators (e.g. Seabird Monitoring Programme, European Seabirds at Sea), Cefas benthos surveys, and a network of comprehensive monitoring sites (e.g. Western Channel Observatory, L4 (Plymouth Marine Laboratory), Cefas CSEMP (Clean Seas Environmental Monitoring Programme) stations in the Celtic Sea, Irish Sea and Bristol Channel and Loch Ewe (Marine Scotland). Past (Tyler et al. 2012) and ongoing (EMODnet biological attributes) data compilation on the biological traits of key components of these systems, again mean that our project draws upon an exceptional base of existing data of international significance. The region is accessible using available inshore and medium-range vessels with appropriate capabilities. Finally, the focus on the western seas allows us to capitalise on the Cefas Poseidon project cruises in SW UK waters, Cefas groundfish surveys and the field work planned in the NERC Shelf Seas Biogeochemistry Programme, to provide an innovative characterisation of the whole system from biophysical ecosystem models through to top predator dynamics. Such a complete picture would be impossible for less well- studied regions.

4. Policy relevance and impact goals

MERP will link services to variables within ecological models to assess how ecosystem services will change in the future (incorporating IPCC climate scenarios), contributing to the objectives of the EU Biodiversity Strategy and the Natural Environment White Paper. We anticipate that IMMERSE understanding, models and outputs will support decision making (e.g. marine planning, licencing and conservation) of regulators under the Marine and Coastal Access and the Marine (Scotland) Acts.

The UK and other European states are investing heavily in monitoring and consultations designed to quantify descriptors of Good Environmental Status (GES) defined in the MSFD. Current specification of descriptors is largely driven by the availability of data. We expect that our research will indicate new and different measurements and assessments that could be implemented to provide more insightful and sensitive indicators of GES. The MERP framework can be used strategically to project relative changes of descriptors of GES (e.g. biodiversity, fish stocks, foodwebs, and seabed integrity) (Lassen et al 2013) under different management scenarios (within programme Objectives 3). Outputs from this project will help inform future revisions of the EU Data Collection Regulations (DCR) on the management and use of fisheries data, and support the revised EU Common Fisheries Policy. Our impact goal is to have a decisive influence on the next generation of marine monitoring programmes deployed in the UK and across Europe, and to provide a holistic framework to support decision making in the marine environment.

5. Collaborations with NERC, LWEC and other research programmes

MERP builds on several recent marine research programmes, including Quest-fish (www.quest-fish.org.uk) (ended 2010), (GLOBEC (www.globec.org) (ended 2010) and Oceans 2025 (www.oceans2025.org) (ended 2012). Several of the partners in MERP were leading participants in these programmes. The project also complements ongoing work in international programmes where the UK has a significant (often leading) role: VECTORS (www.marine-vectors.eu), DEVOTES (www.devotes-project.eu), Euro-Basin (www.euro-basin.eu), GreenSeas (www.greenseas.eu), MEECE (www.meece.eu) IMBER (www.imber.info/index.html), ICED (www.iced.ac.uk), EMECO (www.emecogroup.org/), EuroSITES (www.eurosites.info), ESONET (www.esonet-emso.org), MarBEF+ (www.marbef.org), EuroMarine (www.euromarineconsortium.eu), EMODNet (http://bio.emodnet.eu/) and EUR-Oceans (http://vds1719.sivit.org/eoc/). Again, IMMERSE scientists are involved in these programmes.

The project has close working ties with the UK National Capability in ecosystem modelling, which is based on the European Regional Seas Ecosystem Model (ERSEM). Outputs from ERSEM (50 yr hindcast) will inform macroecological analyses and model development. Several of the models which will be used in the project have been interfaced with ERSEM or actively use output ERSEM as input driving data. ERSEM is a biogeochemical model that largely ignores the macroecology of larger bodied organisms which provide a substantial part of ecosystem goods and provisions. IMMERSE will provide an understanding of the wider, "end-to-end" food web to be elaborated and integrated into ERSEM in subsequent funding rounds. Data from all modules will feed back into ERSEM validation and development. **Momme Butenschön**, a key member of the ERSEM development team, is a member of the consortium to facilitate this integration. IMMERSE draws heavily on NERC National Capability investment in observational systems around the UK, especially the Continuous Plankton Recorder Survey and the Western Channel Observatory. The project will also capitalise on the heavy UK investment in trawl surveys for fish and benthos (Cefas, MSS and AFBI). The project will also interface closely with ongoing NERC Programmes (in particular Shelf Seas Biogeochemistry (SSB), and Biodiversity and Ecosystem Services (BESS)). Members of the MERP consortium are involved in both these programmes, and the former in particular is conducting field work in the same geographical region. The MERP and SSB project will work closely together to share data and resources.

6. Work module descriptions

6.1 Module 1: Marine ecosystem data toolbox & application of macroecology

Co-Is: Webb (Sheffield), Burrows (SAMS), Daunt, Searle, Wanless (CEH), Edwards (SAHFOS), Emmerson (QUB), Evans (Bangor), Hirst (QMUL), Nager (Glasgow), Pinnegar, Schratzberger, Van Der Kooij (Cefas), Somerfield (PML)

Macroecology investigates patterns of ecological systems that emerge at large spatial or temporal scales, as well as the interactions between these scales (Beck *et al.* 2012; Keith *et al.* 2012). By focusing on properties of ecosystems that emerge at large scales from the complex interactions of many fine-scale processes, macroecology complements the mechanistic ecosystem models described in Modules 3 and 4. Macroecological scaling rules linking body mass with characteristics such as population abundance, individual space use and foraging rate (Brown *et al.* 2004; Jetz *et al.* 2004; Pawar *et al.* 2012) can be used to parameterise mechanistic ecosystem models, whereas model outputs can be tested against alternative, independent macroecological patterns such as community size spectra and species-abundance distributions (SADs) which have robust empirical support (Webb 2012).

Comprehensive macroecological analyses of the Western Seas are rare, and whole-system quantification of key descriptors of food webs, size spectra, and SADs are lacking. Although this region is data rich (Fig 1), the data are disparate, scattered, and contain gaps and biases. Creating Big Data by combining these outputs from past projects provides significant opportunities (Hampton *et al.* 2013). We will synthesise existing data using an **ecoinformatics** approach (Peterson *et al.* 2010; Michener & Jones 2012; Hardisty & Roberts 2013), repurposing available data (see Outline Data Management Plan) to support our theoretical and empirical modelling framework, developing tools to efficiently and transparently access and quality screen the data, and identifying major gaps that will be addressed by compiling data from the literature and via the field sampling described in Module 2. This data synthesis will feed directly into work to quantify major macroecological patterns across functional groups, including how they vary in space and time in response to changing environmental and anthropogenic pressures, and how patterns covary across trophic levels – in particular, the top-down role of the spatial and temporal dynamics of vertebrate predators (seabirds, marine mammals, and fish) on lower trophic levels. This provides both a means to test outputs of the models developed in Modules 3 and 4, and a route (task 1.3) to translating size-based model outputs into the species-based indicators of Ecosystem Service provision (Module 5).

6.1.1 Module Tasks

T1.1 Ecoinformatics

The Western UK focus of this project enables us to capitalise on exceptional coverage of existing **biodiversity**, **ecological**, **environmental**, and **socio-economic data**. The major large-scale, long-term surveys and atlases of species distributions are listed in our Outline Research Data Management plan, together with the organisations responsible for their management, and fixed-location monitoring time series, extensive environmental records (e.g. temperature, ChlA, bathymetry, substrate) and information on human pressures and ecosystem service provision (e.g. fisheries landings, nutrient cycling). Task 1.1 is designed to collate and provide access to these data such that key macroecological patterns (T1.2, T1.3) can be directly compared with the predictions of our model ensemble (Modules 3, 4). Our **key innovation** is to link these well-established marine biological databases to facilitate such analyses. Together, the taxonomic name of an organism and its location in space and time provide unique 'access keys' (Hardisty & Roberts 2013) as the basis for a suite of data enrichments. Taxonomic names link directly to other resources including biological and physiological traits, habitat affinities, and ecological function and a comprehensive UK list is already available in the World Register of Marine Species. Where and when a biodiversity record was collected enables links to physical environmental observations made *in situ*, obtained from remote sensing, or inferred from models (e.g. ERSEM). These enrichments allow us to leverage existing biodiversity data into the development and testing of the ecosystem models described in Module 3, including delimiting the spatial distributions of taxa of contrasting mobilities (e.g. Isojunno et al. 2012; Wakefield et al. 2013), and quantifying macroecological patterns, relationships and dynamics at various spatio-temporal scales (Task 1.2). They also identify priorities for new data collection from the literature (e.g. predator life histories; Evans & Raga 2001) and from the sampling programmes in Module 2 to fill key gaps. Important information relevant to the ecosystem models and not included in existing data compilations are spatially- and temporally-resolved quantitative data on resource utilisation for top predators and focused data collection from the literature will fill this gap across the major foraging guilds, correcting for known biases of different methods of diet identification (Barrett et al. 2007). Throughout the focus is on developing open, lasting ecoinformatics tools, primarily in R, as this is both more useful and more sustainable than developing new user interfaces which may not outlive the duration of the funded project.

T1.2 Empirical Macroecology

We will develop, test and apply whole-system macroecological analyses (specifically based around the fundamental parameters body size and temperature). Because organisms from different habitats and of different sizes interact and are influenced by their environment in fundamentally different ways (Chave 2013) we hypothesise that ***patterns at a single scale will differ between size classes, functional groups, and habitats in gross and predictable ways.*** For instance, Pawar *et al*. (2012) derive the scaling implications of differences between trophic interactions in 2D (benthic) versus 3D (pelagic) systems, while different organisational levels – and predators versus prey – have different thermal dependence to their ecological rates (Dell *et al.* 2011; Frederiksen et al. 2013). Our approach will be extended to consider differences between habitats *within* systems, including comparing benthic systems with and without macrophytes, predators with their prey, and the role of spatial and temporal heterogeneity in environmental conditions applying the framework developed by Searle et al. (2010). We will examine the consequences of changes in abundance of top predators on scaling relationships lower in the food chain, and the role of functional diversity and spatio-temporal heterogeneity in lower trophic levels and climate on predator abundance, richness, and population dynamics. There is a comprehensive understanding of scaling of feeding, growth and metabolic rates for many terrestrial and aquatic organisms (Brose *et al.* 2008, Kiørboe & Hirst submitted), we will test the generality of such scaling for benthic species (Emmerson & Raffaelli 2004, Twomey *et al.* 2013), and organisms which move, or have trophic dependence, between these domains (e.g. benthic species with planktonic larvae, seabirds that breed on land but forage at sea).

Comparisons will be based on meta-analyses and estimation of parameters from simple quantitative macroecological summaries will include vital rates, life history, size spectra (slope, non-linearity estimated using Generalized Additive Models (GAMs)), SADs (mean and variance of log-normal fits; Saether *et al.* 2013), and species-area relationships (SAR, slope). Combined they will produce novel *trivariate* food web data descriptions combining abundance, body mass and food web structure (Cohen et al. 2003). We will quantify these relationships in different functional groups, e.g. benthos, zooplankton, demersal fish, seabirds and cetaceans, and test weighting factors (e.g. typical distributional extent; Storch et al. 2012) to examine scale independence across groups.

T1.3 Size, species and functional groups

To relate model outputs from Module 3 (e.g. biomass within functional groups (EwE), community size spectra (Size spectrum models, fishSUMS)) to empirical descriptions of these same phenomena, we will undertake an extensive comparison of different metrics for summarising community structure, focusing on comparing size structure (slope and linearity of size spectrum, diversity and evenness across size classes) with characteristics of the SAD (mean, variance) over space in contrasting environments, through time, and across major functional groups, and building on recent efforts to reconcile size spectra with taxon-based trophic pyramids (Trebilco *et al.* 2013) and species richness (Rossberg 2013). We will focus on datasets which include both species identity and individual size (or where the latter can be accurately estimated) over extensive spatial scales (e.g. IBTS, Cefas fish stomach content database) or at very fine temporal resolution (e.g. L4) to empirically resolve patterns of covariation between different metrics, and to develop a simple conversion between the currencies of modelling (mostly size-based), macroecology (size- or species-based), and ecosystem services (mostly species- based). We will also examine how species-level variation in seabird and marine mammal populations influences size-based properties of the system at lower trophic levels. We will explore material flux through size-structured food webs, and test predictions of the Metabolic Theory of Ecology (Brown *et al*. 2004) using biomass- and density-size distributions and our empirical descriptions of size dependence of rate processes. Integrating with modules 2 & 3, we will quantify density-dependent aspects of population size using the slope, shape and variation of density-size spectra.

Dependencies: T2.2

6.1.2 Milestones

No.	Milestone	Date completion	Lead Partner
M1.1	Identify, compile, format and initial quality control long-term datasets for major functional groups, for use in model development and testing	(M12)	Sheffield
M1.2	Build R package to access data via web services	(M12)	Sheffield
M1.3	Produce a map of raw data availability across taxa and through time to identify major gaps	(M24)	Sheffield
M1.4	Compile Species Abundance Distributions from diverse sampling programmes across multiple taxa	(M24)	Sheffield
M1.5	Develop Shiny web applications to enable simple visualisations of biodiversity data for non- academic users	(M36)	Sheffield
M1.6	Develop and test methods (including GAMs, GAMMs, Random Forests) for the spatial interpolation of survey data	(M36)	Sheffield
M1.7	Produce synthetic data products in useable open formats satisfying EU and UK drivers towards open science	(M48)	Sheffield

6.1.3 Deliverables

No.	Deliverable	Date completion	Dependencies	Lead partner
D1.1	Inventory of large-scale, long-term datasets for major functional groups in the Western Seas, including known sampling issues and biases	(M12)	None	Sheffield (Webb)

D1.2	Submit R package for accessing marine taxonomy to CRAN	(M12)	None	Sheffield (Webb)
D1.3	Joint meeting with British Ecological Society Macroecology Special Interest Group & National Biodiversity Network on frontiers in marine macroecology and data	(M18)		Sheffield (Webb)
D1.4	Paper on macroecology of major functional groups in the Western Seas: scale dependence and the role of environmental covariates	(M24)	D1.1, D1.2, work contributing to D1.5	Sheffield (Webb)
D1.5	Submit additional R packages for accessing marine macroecological data to CRAN	(M24)	D1.1, D1.2	Sheffield (Webb)
D1.6	Report on methods for interpolating sampled distribution and abundance data across taxa, and advice on best practice	(M36)	D1.1	Sheffield (Webb)
D1.7	Report empirical relationships between size spectra and species-level macroecological patterns, and scale-dependence of species abundance distributions across functional groups	(M36)	D1.1, D1.2, D1.5	Sheffield (Webb)
D1.8	Report on environmental and biological correlates of regional differences and temporal variation in top-predator communities	(M48)	D1.1, D1.5	CEH (Searle)
D1.9	Deliver synthetic data products and tools to BODC in accordance with Research Data Management Plan	(M48-60)	D1.1, D1.2, D1.5, D1.6, D1.7	Sheffield (Webb)

Links to other Modules

Module 1 provides the empirical data underpinning the modelling in M3-4, and gaps identified will feed into the survey designs in M2. The data management and ecoinformatics tools will provide immediate access to the new data collected in M2. Task 1.3 is designed to enable transitions between the currencies of models (M3-4) and Ecosystem Services (M5).

6.2 Module 2: Fieldwork to measure poorly known processes

Co-Is Atkinson, Queirós, Lindeque (PML), Burrows (SAMS) Emmerson, O'Connor (QUB), Hiddink (Bangor), Van Der Kooij, Pinnegar (Cefas), Hirst (QMUL)

While the ecology of NW European shelf is generally well quantified (Module 1), for the purposes of modelling and understanding services some key gaps remain. These gaps represent components and processes not sufficiently understood to be resolved in ERSEM or the models studied in Modules 3 and 4, and form the basis of the Module 2 Tasks.

Given what is known about area-specific production rates (Mann 1973) and relative habitat areas for production (8000km^2 kelp (Walker 1953), 133000km^2 phytoplankton <20km UK coastline), intertidal and subtidal macrophytes (mainly kelp) may contribute 45% of total primary production in UK coastal waters, supporting the shellfish fishery worth £282M in 2011, greater than demersal and pelagic landings. Despite its potential importance, macrophyte detritus is not included directly in any ecosystem model, including ERSEM. The contribution of kelp forests in supporting culturally and commercially valuable inshore fisheries is not yet known and will be a key outcome of this project.

Understanding how matter and energy flows between benthic and pelagic systems is vital to modelling marine ecosystems, and thus how such processes (and the valuable ecosystem services they underpin) will be impacted by future climate scenarios. While the ERSEM model and NERC's Shelf Sea Biogeochemistry programme emphasise physical/geochemical processes, many biological processes contribute to the incorporation of primary production into benthic foodwebs (e.g. contact of live versus dead material with the seafloor, trophic assimilation, bioturbation), and their relative importance is poorly known (Evrard et al. 2012).

The strength of benthic-pelagic coupling and asymmetry between detrital and primary producer energy pathways is important for stability and resilience in simple consumer-resource and coupled size spectrum models (Rooney & McCann, 2006, Blanchard et al. 2011). Within benthic-pelagic coupled systems, body size dictates the pace of life (physiology, feeding and reproduction) and forms an underlying structuring element across the >18 orders of magnitude of body mass (White et al. 2007). While this is well grounded in both the terrestrial and aquatic literature (O'Gorman & Emmerson 2011), complete biomass spectra are not available at whole system scales and very little is understood about the details of various types of coupling across all trophic levels.

Similar size/trophic level organisms can have fundamentally different roles for ecosystem services. For example, under the MSFD, the relative abundance of gelatinous zooplankton and fish larvae is proposed as an indicator of Good Environmental Status. The suggestion that jellies are increasing due to degraded ecosystem states, displacing fish larvae (Richardson et al. 2008), is debated. Our 4th objective is thus to quantify variation in feeding and mortality as a function of species traits, e.g. as a function of body mass and feeding mode.

Central to IMMERSE is scale dependency and the sampling is orientated to encompass a continuum of time and space scales. The Plymouth L4 shelf monitoring site has 25 years of weekly sampling across the whole planktonic food web and seasonal benthic monitoring. This will form part of a UK-wide group of shore-to-30 km offshore transects quantifying the macrophyte derived subsidy to the food web (Fig. 1), embedded in regional scale Cefas-Poseidon and NERC-Prince Madog cruises, and using data synthesised in Module 1. Our approach will extend scales of space and time to shelf wide processes such as top predator foraging ambits.

6.2.1 Tasks

T2.1 Quantify the macrophyte versus phytoplankton contribution to the food web in relation to distance offshore and at whole-shelf scales

This task will be approached at two scales. First we will estimate kelp production and compare with overall primary production by phytoplankton at whole UK scales. Secondly we will measure the onshore-offshore gradient in kelp subsidy to the benthic food web by following the assimilation of natural markers for kelp versus phytoplankton up into the foodweb along five transects. Biomass and production of kelp will be estimated on a UK scale by synthesising existing data on distributions (JNCC, NHM, Channel Coastal Observatory), and production rates (Krumhansl and Scheibling, 2012). We will measure habitat extent for kelp species using satellite data that show kelp beds (Casal et al. 2011, Byrnes et al. 2011) and use synoptic data on primary drivers of distribution, ocean colour, wave fetch and temperature (Burrows 2012, Bekkby et al. 2009), to drive measurements and collated abundance data into models of species distribution and production. At local scales (1-20km) near Oban and Belfast, novel data from new technology (RPAs, ROVs, and AUVs from developing SAMS capabilities and facilitated by AFBI) on the incidence of kelp along high resolution environmental gradients will improve the performance of the distribution models.

We propose four primary sites across a latitudinal gradient with different kelp species and environmental conditions (Fig. 1) where (1) Primary production will be estimated by: (a) *in situ* production and rates of loss of fronds and whole plants, (b) *in situ* PAM fluorometry, and (c) floating mesocosms enclosing whole plants in sheltered areas. (2) Direction and distance of detritus transport will be tracked with labeled fragments and thalli using diver surveys and towed video. (3) Kelp bed monitoring will include estimations of blade damage (to estimate detrital inputs from small particles to whole thalli) and rates of dislodgement and erosion (particles). UK-wide estimates of total kelp production will be compared to those for phytoplankton primary production based on current best spatially resolved ecosystem models (primarily ERSEM) and satellite observations.

At the finer scale we will sample along gradients from the shore to ~30 km offshore using inshore boats of AFBI (see letters of support), SAMS, PML and *Prince Madog.* This work, along a variety of habitats right across the UK (Fig. 1) will quantify the relative roles of phytoplankton- and macrophyte-derived material in supporting the food-web. We will conduct full depth CTD profiles to collect suspended POC with concurrent dredge, sledge and core sampling sampling of kelp detritus, sediment POC and DOC, infauna, up to commercial species such as *Nephrops*. Given the methodological challenges (e.g. Dethier et al. 2013) we will use a combination of dietary approaches, namely mixing models based on contrasting kelp/phytoplankton $\delta^{13}C$ signatures, lipid/fatty acid markers and molecular approaches (18S RNA). The transport of coastal detritus will be modelled with FVCOM, POLCOMS/NEMO. In combination these approaches will reveal the spatial scale of kelp subsidy over 10s m to 100 kms in coastal areas, and provide an understanding of the role of macrophyte-derived material in supporting the commercially valuable inshore food web.

T2.2. Quantify pathways by which sources of primary production enter benthic food webs

We will conduct a **seasonal** (4 times per year for 2 years) **sampling programme** extending the mechanistic insights obtained in Task 2.1 and adding trophic information to the biomass spectrum sampling in Task 2.3, by tracing trophic and non-trophic flows of macrophyto-detritus/phytoplankon through the benthic food-web. We will use a combination of tracing techniques including stable isotope and phospholipid derived fatty acid analysis (PLFA, Hardison et al. 2010, Evrard et al. 2012). Using an epibenthic sledge, the natural food source in the bottom few cm of the water column will be sampled throughout the tidal cycle and compared with the overlying water column derived from isotopic and FlowCAM analyses (Task 2.4). These same techniques will be used to provide seasonal coverage of the quality and origin of detritus, e.g. phytoplankton versus macrophyte, that supplies the benthic food web. Using sediment cores we will undertake seasonal tracer experiments to 1) determine seasonal variation in the uptake of detritus material in to the benthic foodweb (water, sediment, bacteria, meio- and macrofauna) by determination of $\delta^{13}C$- backgound signatures; 2) Seasonally resolve changes in food-web structure with and without the experimental addition of ^{13}C enriched macrophyte material, illustrating the potential for bottom-up control of coastal food webs at a fine spatial scale; and 3) measure bioturbation in parallel to clarify the relative importance of this non-trophic pathway in the overall uptake of macrophyte detritus by the benthic ecosystem.This work will inform the trophic and non-trophic characterization of **functional groups** and their influence on ecosystem processes in large-scale models like ERSEM (Module 3). All fauna will be measured to help generate biomass trophic spectra (Tasks 1.3, 2.3). The range of oceanographic data available from the L4 site helps to provide a mechanistic understanding, and placement of this work in the wider context within the onshore-offshore network of transects (Task 2.1).

Dependencies: T1.3, T2.1, T2.3, T2.4

T2.3 Determine the complete biomass-size spectrum in the benthic and pelagic food web

We will capitalise on *Poseidon*, an annual pelagic sampling cruise undertaken aboard *Cefas Endeavour* (Fig. 1) spanning the autumn bloom in 2015, using RV *Prince Madog* to take additional samples at a subset of the stations. These stations will be selected to fit a hierarchical sampling design, where a range of distances between sampling stations allow the analysis of the role of scale in the food web. Stations will also be harmonised with those sampled the previous year on the NERC Shelf Sea Biogeochemistry Programme. Together, the 2-ship cruise will quantify food webs and size-spectra over crossed gradients of primary production: i.e. for *Prince Madog* (4 levels, as a bottom up driver) and fishing activities (4 levels, as an anthropogenic top-down driver) resulting in 16 sampled benthic stations, c.f. ~70 pelagic stations for *Endeavour*. Substantial gradients in primary production and fishing effort exist in the study area in the Celtic Sea and past work (Hiddink et al. 2011) shows that this design allows estimation of large-scale effects of fisheries.

Using these platforms we will **quantify size-spectra for pelagic and benthic ecosystems** using a wide variety of sampling gears to capture the full size spectrum quantitatively. Water bottle profiles, an array of 4 net sizes (80 µm up to pelagic trawls) and acoustic records will be processed respectively by flow cytometry, flowCAM, zooscan and Echoview acoustics software. During the cruises, marine bird and mammal densities will be determined using distance sampling line- transect methods (Thomas *et al*., 2010). At select food patches where aggregations of top predators occur, sampling will take place at all trophic levels, and their persistence determined over the short-term to establish spatio-temporal variation across the food chain, in relation to measured or estimated (task 1.1) consumption rates (cf. Benoit-Bird & McManus, 2012).

Observations of higher predators including seabirds and seals and cetaceans are integral to these cruises, and the complete biomass spectrum for larger, more mobile organisms will be supplemented by the array of existing data compiled within Module 1. Benthic sampling will focus on important but hard-to-sample groups (e.g. large bivalves and mobile hyper benthos) using targeted dredges and sledges. A second *Prince Madog* cruise, during the spring bloom of 2016, will repeat this sampling coverage.

These regional cruises cover spring and autumn blooms only. We recognise that there are fundamental seasonal shifts from putative export systems (large producers) to regenerating type systems (small producers), and to capture the dynamics of the full seasonal size spectrum for the pelagic environment we will sample the Plymouth L4 site monthly throughout 2015. This will use equivalent gears and analysis methods as above to enable effective integration of the data. The advantage of the L4 site is that it has 25 years of weekly planktonic sampling with partial size spectra data collected under NERC National Capability, forming a longer-term context for the 2015 intensive study season. Using data gathered in the NERC Oceans 2025 programme, supplemented by cores obtained in Task 2.2, we will construct a benthic biomass spectrum for the L4 site that resolves seasonal variability. In conjunction with the tracer work in Task 2.2 this will allow construction of feeding guilds.

Dependencies: T1.1, T2.2

T2.4 Quantify key, but poorly known, feeding and mortality parameters

Within MERP we have particular expertise in the measurement of diets, feeding and mortality using a wide range of classic and state-of-the-art techniques (Atkinson 1996, Pinnegar et al. 2002 Hirst et al. 2004, Emmerson & Raffaelli 2004, McLaughlin et al. 2010, O'Gorman & Emmerson 2010, Twomey et al. 2013).

Quantification of diets is non-trivial, and consequently we will target key species that require better appraisal. Much diet/trophic level data are already available for fish (Module 1) but we know less about feeding and diet at lower trophic levels. Smaller consumers can have multiple feeding modes (e.g. Kiørboe 2010), large ranges in predator-prey mass ratios (Wirtz 2011) and rapid isotopic turnover (Schmidt et al. 2003), hampering some methods applied to larger consumers. Likewise mortality is notoriously hard to estimate, and the density-dependent terms often used to close ecosystem models (Module 3), including ERSEM, are poorly grounded in evidence.

To address these issues we will:

1) employ trait-based approaches to experimentally estimate parameter values such as feeding- and mortality rates as a functions of body mass. We will test these approaches for estimating parameter values across benthic and pelagic food webs and validate size based feeding relationships that have been documented extensively elsewhere (Brose et al. 2008, Rall et al. 2010).

2) Given constraints on size-based approaches at lower trophic levels we will use a model food web motif of key species ubiquitous in UK waters to estimate the strength of predator-prey and competitive interactions. This pelagic food web motif will comprise *Oithona similis* (tiny but numerically dominant ambush feeder), *Calanus helgolandicus* CV/adults (biomass dominant, mainly suspension feeder and key dietary item), fish larvae (larger raptorial, visually-feeding carnivores supporting recruitment to commercial fisheries), and Ctenophores and Cnidarians (largest, often non-visual, passive ambush predators). Benthic species will include amongst others *Nephrops norvegicus*, *Necora puber*, *Buccinum undatum*, and *Asterias rubens*, reflecting dominant benthic species and those of commercial importance.

We will sample these across scales, namely across the diel cycle, across the seasonal cycle (during 12 visits of L4 during 2015) and regionally (*Poseidon* cruises aboard CEFAS *Endeavour* in autumn 2015). For the MSFD life-form pair of jellies and fish larvae we will combine approaches to their diet. We will apply stable isotopes (bulk ^{13}C and ^{15}N) to estimate food resource base and trophic level, comparing this with a novel molecular diet approach using Next Generation Sequencing (NGS) technology. At PML we have shown that high throughput 454 pyrosequencing of nuclear small subunit 18S rRNA gene amplicons is a powerful tool for estimating diversity and species richness of mixed zooplankton communities. NGS of 18S amplicons will be used to assess gut content (see O'Rorke et al. 2012). The third diet method will be classic stomach content analysis. For taxon-and size-specific information on the crustacean part of the diet, prey mandible size will be converted to prey size (Atkinson et al. 2002). Laboratory feeding incubations at PML will compare functional responses of *O. similis*, *C. helgolandicus* and *Ctenophores* based in experiments using the ambient seasonal food assemblages with their naturally varying food types and sizes, providing estimates of consumer satiation as input to Module 3. The PML flowCAM, which quickly and automatically counts, measures and classifies thousands of food items will also enable us to better measure prey switching and the clearance rates on items when in low abundance. Mortality of *O similis* and *C. helgolandicus* will be estimated by the vertical life table approach, based on the weekly samples collected routinely at the L4 monitoring site (Hirst et al. 2004). We will construct empirical models to tease out the effects of mortality, including predator abundance, size, temperature as well as density-dependent effects. Likewise, functional responses of the benthic species will be measured in the mesocosm facilities at QUB under the supervision of Co-I Emmerson.

6.2.2 Milestones

No.	Milestone	Date completion	Lead partner
M2.1	Field programme to estimate scale and extent of macrophyte subsidy to UK marine ecosystems	(M24)	PML
M2.2	Experimental programme to determine rates and pathways of incorporation of primary production at the base of marine food-web	(M36)	PML
M2.3	Field programme to quantify seasonal variation in body-size spectra	(M36)	PML

M2.4	Combined Poseidon/Prince Madog large-scale field programme to characterise whole-ecosystem size spectra and spatial scaling	(M36)	PML

6.2.3 Deliverables

No.	Deliverable	Date completion	Dependencies	Lead partner
D2.1	Report on the quantification of trophic and non-trophic benthic-pelagic coupling pathways for macroalgae-derived carbon sources	(M36)		SAMS (Burrows)
D2.2	Report on the dynamics of interactions between gelatinous zooplankton and fish larvae	(M36)		PML (Lindeque)
D2.3	Report on "end to end" pelagic and benthic biomass spectra across regional gradients and seasons	(M42)	M1 for provision of data on larger organisms to construct full "end to end" biomass spectra.	Bangor (Hiddink)
D2.4	Report on the parameterisation of functional responses of feeding and mortality related to traits	(M42)		QMUL – benthic (Emmerson) PML - pelagic (Atkinson)
D2.5	Parameterization of trophic and non-trophic pathways of carbon assimilation in coastal benthic-pelagic systems in ecosystem models	(M42)		PML (Quierós)

Links to other Modules M2 provides empirical data underpinning the modelling in M3-4, and data will feed into the macroecological analyses in M1. The data management and ecoinformatics tools will provide immediate access to the new data collected in M2. Data and information (in terms of appropriate measures and indices) will inform spatio-temporal assessment of ecosystem services (M5).

6.3 Module 3: Ecological processes and their representation in models

Co-I Rossberg (Cefas), Blanchard, Webb (Sheffield), Heath, Speirs (Strathclyde)

Simulation models seek to capture the essence of relationships between taxa to reproduce properties of complex ecosystems and thus to enable predictions of ecosystem responses to perturbations. Because ecosystems are complex, this requires simplification, and the simplifying assumptions of a particular model inevitably lead to imperfect predictions of true dynamics due to 'structural uncertainty' (Hosack et al. 2008). Simplifications include the combination of taxa into 'functional groups' which occupy similar habitats, feed in similar ways, or have similar body size; and assumptions regarding the functional responses governing intake rates by predators in response to prey densities. Alternative formulations are used to reflect variation in underlying biology and can have very different effects on trophic cascade propagation (Herendeen 1995, 2004; McCann *et al.* 1998). Most models include density dependent (self-limiting) terms applied to either mortality or intake rates which confer numerical stability with highly significant consequences for both top-down and bottom-up propagation (Herendeen 1995; Heath et al. submitted; McCann *et al*. 1998), but although meta-analyses have revealed some generalisations (Borer et al. 2005; Shurin et al. 2002) the basis for different model formulations remains uncertain. Module 3 will characterise the relationship between formulations of density-dependent population control mechanisms and the resulting properties of trophic cascades to identify which response forms are appropriate in different circumstances. Our primary tool to compare empirical macroecological data with simple analytic and complex numerical models will be elasticity indices (Hill et al. 2008), defined as ratios of the form (% change in *Y*)/(% change in *X*) to quantify the strength of the effect that a variable *X* (e.g. primary production) has on another variable *Y* (e.g. fish production). The strengths of trophic cascades can be quantified by the elasticities of the effects that changes at one trophic level have on other trophic levels. Observations and models (Ware & Thomson 2005; Rossberg 2012) suggest that the elasticity indices for bottom-up effects are usually >1, whereas top-down cascades in models are usually damped (elasticity < 1, Andersen & Pedersen 2010), but not always (Rossberg 2012).

6.3.1 Tasks

T3.1 Extraction of relevant elasticities from the empirical macroecological data

The statistical methodology to conduct empirical elasticity analyses is well developed (Qian and Giles, 2007). The relevant macroecological data – spatially- and temporally resolved size spectra distributions across major functional groups and top-predator density dependencies, including effects of resource heterogeneity – will be obtained in Module 1 and Module 2 (T2.3, T2.4),. The focus will be on top- down and bottom-up cascades. Approaches to take spatial and temporal correlations into account will be informed by analyses of scale dependence in Modules 1 and 2.

Dependencies: T1.3, T2.3, T2.4

T3.2 Mathematical analyses of the effects differences in model structure have on elasticities in simple models

Mathematical elasticity analysis for simple models is facilitated by the fact that elasticity is determined by the linear response of the system to pressures, enabling the use of Generalized Modelling (Gross et al. 2004) to derive elasticity indices. This method measures the dependence of the elasticity coefficients for system-level responses on the elasticity coefficients for the direct density-dependent interactions among species or functional groups. Large classes of conceivable functional forms for these interactions can therefore be covered by a few analytic calculations. For example, the analysis of a simple, infinitely long food chain (Rossberg 2013) reveals a strong dependence of elasticities for top-down cascades on consumer satiation, i.e., on the elasticity of the dependence of consumer intake on resource abundance. Quantitative data on functional response types, satiation, and density-dependent mortality determined in Task 2.4 is used to constrain the parameter ranges relevant for the study area. Analyses will be extended to incorporate phenomena such as benthic-pelagic coupling of food chains (Module 2).

Dependencies: T2.2, T2.4

T3.3 Numerical analyses of the effects of model structure on elasticities in complex models and comparison with data

The numerical experiments required to probe the elasticities of macroecological responses of complex ecosystem models to pressures are straightforward with fast model software and the knowledgeable model operators. This task will therefore be conducted in one of the project's integrative workshop that brings together experts on a representative yet easily simulated sub-set of the candidate models to be included in the model ensemble of Module 4, as well as empiricists with a good understanding of the macroecological data used (Module 1). The workshop will evaluate the standard implementations of models as well as variants with different representations of density dependencies, informed by Task 3.2. The resulting enhanced understanding of the implications of model structure will be used to adapt models as required by comparisons with data such as that obtained in Task 3.1, while leaving variations in model structure that are not constrained by this comparison intact. General recommendations for representations of density-dependencies in models will inform the model ensemble in Module 4.

Dependencies: T1.2, T3.1, T3.2

T3.4 Comparison of macroecology in models and data beyond elasticity

The conceptual simplicity of elasticity analysis allows its broad application to various data and models, but it cannot cover all macroecological patterns and processes of interest. Some models make much richer predictions. Such model outputs will be confronted with the detailed macroecological pictures obtained in Module 1, including relationships between food-web structure, size spectra, and SAD. This will lead to both improvements in model structure and mechanistic interpretations of observations. Recent theory (e.g. Rossberg 2013) will guide this comparison. Among the hypotheses we examine will be that modulations of size spectra can generate modulations of richness along size such as wasp-waist food-web topologies (Cury et al. 2000).

Dependencies: T1.2, T1.3,

6.3.2 Milestones

No.	Milestone	Date completion	Lead partner
M3.1	Numerical experiments to probe the elasticities of macroecological responses of complex ecosystem models	(M24)	Cefas
M3.2	Improvements in models and mechanistic interpretations of observations	(M36)	Cefas

6.3.3 Deliverables

No.	Deliverable	Date completion	Related Milestone	Lead partner
D3.1	Report empirical values of relevant elasticity indices confronted with analytic results	(M18)	Spatially or temporally resolved size spectrum data available from Modules 1 and 2	Cefas/UoS
D3.2	Joint module 3/4 workshop	(M24)	D3.1	Cefas/SU
D3.3	Manuscript on in-depth comparison between models and macroecological data	(M36)	Detailed macroecological data from Module 1	Cefas, SU

Links to other Modules Data provided by M1 will be used to calculate empirical elasticity indices. Observations in M2 will support choices for variants of model structure. Constraints on model structure derived in M3 inform construction of the model ensemble in M4.

6.4 Module 4: Simulating and predicting ecosystem changes using a model ensemble

Co-Is: Blanchard, Blackwell (Sheffield), Heath (Strathclyde), Heymans (SAMS), Rossberg, Mackinson (Cefas), Wanless (CEH)

In this module we build the capacity in modelling to support predictions of ecosystem states and services. There are many different ways in which complex ecosystems are conceptualised for empirical analyses and development into models. By combining the ecoinformatics toolbox and new data collected (Module 1,2) at different scales with these existing ecosystem models and their variants (Module 3) we will assemble a **whole ecosystem model ensemble**. We will advance the predictive capacity of marine ecosystem models beyond the state-of-the-art by developing a system for utilising the ensemble of models to deliver assessments of the uncertainty in ecosystem forecasts (and hindcasts) analogous to the ensemble approach employed by the IPCC to make prognoses of future climate change. We will objectively select models and sub-models based on structural uncertainty analyses, their performance from elasticity analyses and capacity to predict macroecological patterns, reducing key uncertainties of existing models and their predictions, invigorating models with new process-based understanding and evaluating the appropriateness and utility of specific models at different temporal and spatial scales.

Statistical inference methods will be used to establish an ensemble of ecosystem models and quantify the uncertainty in predictions arising from structural differences within and among models (Gardmark et al. 2013, Purves et al. 2013). These methods are widely and routinely used in climate and environmental modelling (e.g. Chandler 2013; Perkins et al. 2013, Hoeglind et al. 2013). Using the ensemble approach, this Module will provide a systematic account of the uncertainty in predictions of ecosystem states under given forcing, arising from the inherent structural uncertainty in models. Crucially, we will also provide tools to link ecosystem properties and dynamical processes to ecosystem services.

6.4.1 Tasks

T4.1 Whole ecosystem model ensemble

Ecosystem ecology, food web ecology and macroecology have all influenced the modelling tools that are currently being developed and applied to marine ecosystems around the UK. Our models (**Box 1**) have been selected on the basis of representing state-of-the-art in ecosystem modelling, their computational efficiency, their application to real ecosystems, our expertise, and their availability as open source code. **EwE, StrathE2E and size spectrum models** already **have already been interfaced with ERSEM** and work is ongoing.

Box 1: Model ensemble members

1) **Ecopath with Ecosim (EwE)** (Christensen &Walters 2004) incorporate diet and biomass data from fisheries and oceanographic datasets and the literature to carry out a mass-balance network analysis (Ecopath), to simulate dynamical changes in biomass of functional groups or species through time (Ecosim) and space (Ecospace) at a regional scale. Models available include West of Scotland (Bailey et al. 2011), Celtic Sea (Lauria 2012) and Irish Sea (Lees & Mackinson 2007).

2) StrathE2E (Heath, 2012) simulates the fluxes of nutrients (nitrogen) through ecosystems from dissolved inorganic (nitrate and ammonia), through plankton, benthos and fish, to birds and mammals, regeneration through excretion and mineralization of detritus in the water column and sediment and physical exchanges across geographic boundaries. Models available include the North Sea, English Channel, Celtic Sea, Irish Sea and west of Scotland (EU-FP7 project BASIN).

3) The Population-Dynamical Matching Model (**PDMM**, Rossberg et al. 2008) combines community assembly and species biomass dynamics via body mass foraging/vulnerability traits and relative adult body masses. Recent model applications include the Celtic Sea and the North Sea to study the Large Fish Indicator (Fung et al. 2013).

4) Size-spectrum models for pelagic (Law et al. 2009), coupled benthic-pelagic (Blanchard et al., 2009, 2011, 2012) and trait-based (Hartvig et al. 2011, Rossberg 2012)) communities predict changes in abundance across a continuum of body masses through time and space (Castle et al. 2011). Models available include the North Sea, Celtic Sea, deep waters off the West of Scotland (EU-FP7 Deepfishman) and global shelf seas (Blanchard et al. 2012, NERC Quest-Fish).

5) **FishSUMS** is a size-structured model that includes a suite of species and functional groups (Speirs et al. 2012). Populations of 10-15 species are represented by a series of discrete length classes from egg to adult as well as benthic and zooplankton resources. FishSUMS has been parameterised for the North Sea with an implementation for the west of Scotland in progress.

6) **Simple consumer resource models**(e.g. Murdoch et al.2003) that follow energy pathways through focal groups of species rather than whole webs will also be employed (particularly for studying top predators and through development in Module 3).

Outputs of all models include time series of biomass, changes in mortality, food consumption and diets, estimated for each functional group/species and catch for each group fished. Existing **links to Marine Strategy Framework Directive** include the capacity of the models to output existing and proposed indicators for GES. The models can all output macroecological abundance-body mass patterns, either as size spectra, species abundance/biomass-mean body mass or trophic level directly or through conversion of relationships between mean and variance of species body mass and/or trophic levels. Building on work in Modules 1 and 3 we will develop a standardised suite of model variants to investigate and quantitatively assess structural uncertainty within and across these models (see also tasks 4.2, 4.3). We will combine model code with data and develop data assimilation methods as part of the ecoinformatics toolbox (Module 1). We will also engage with the international community and provide opportunities for inclusion of other models into the ensemble (see letters of support).

Dependencies: T1.1, T1.2

T4.2 Bayesian data assimilation for ecosystem models

Although a subset of the models (StrathE2E, EwE and size spectrum models) have been formally subjected to parameter optimisation to fit them to a suite of observational data, only maximum likelihood or least squares estimation has been used and the nature of the model fitting algorithms has not been formally evaluated. We will extend statistical parameter estimation to other models in our ensemble within a Bayesian framework.

These methods require very high repetition of model simulations to explore multi-dimensional parameter space, so computational efficiency is of paramount importance. The different models represent the system differently, e.g. only as particular species or only as bulk biomass of groups or size classes. Hence the observational data (Module 1) will need to be aggregated in different ways to compare with the different models. Then, we will use a simulation-based algorithm such as Markov Chain Monte Carlo, particle filtering, or a hybrid of both (Dowd 2007; Golightly & Wilkinson, 2011; Mortier, 2013; Weir et al., 2013), Approximate Bayesian Computation (Sunnaker et al, 2013), or a combination of these. This will give us fully Bayesian multi-model inference, while allowing us to take into account suitable prior information where available and appropriate.

Dependencies: T1.2, T1.3,

T4.3 Simulations of past ecosystem responses at different spatial and temporal scales

Using information on parameter sets from the empirical work (Modules 1,2) we will ensure priors are developed using biological realism (within metabolic and physiological constraints). Traits-based analyses will benefit species/groups for which parameters are not available (Modules1,2). **We will test the performance of models at different spatial and temporal scales.** Each model and their selected variants will be fitted to data at one spatial/temporal scale (e.g. whole Celtic Sea and/or annual production rates) and cross-validated using data from another spatial/temporal scale (e.g. L4 and/or seasonal production rates). This will enable us to evaluate and rank the performance of the models and their variants across spatial scales. This will allow further model testing and selection of the type of future scenario projections to be made with each respective model. Model variants will incorporate alternative formulations based on new information derived from MERP Modules 1, 2, and 3. We will specifically use data on macrophyte-derived subsidies to the food web (EwE, Strathe2E, size spectrum models), detrital and predator bentho-pelagic coupling (all models), complete regional and seasonal biomass structure (all, especially size spectrum models), trophic level information (all models), role of functional diversity such as gelatinous zooplankton versus fish larvae (all models), density-dependence and top predator foraging traits (all models), system-level responses to pressures (all models). The ecoinfomatics and macroecology (Module 1) will synthesise these data with existing understanding to provide fundamental scaling considerations, for example on functional feeding relationships, growth and mortality with temperature and body size, and provide data in the form required here. Specific variants to include in the ensemble will be determined by linking Modules 1-4.

Dependencies: T1.1, T1.2,T1.3, T2.1, T2.2, T2.3, T3.1, T3.1, T3.3

4.4 Predictions of future ecosystem responses and services

We expect that models will respond differently to top-down and bottom-up perturbation scenarios due to their different structures and processes. We will test this via a series of carefully constructed model experiments utilising well-established, simple but well specified scenarios. These will capture a **range of both bottom-up and top-down pressures** and we will do full factorial experiments to examine responses to single and multiple drivers of change. They will include but not be limited to: (i) ocean warming, (ii) multispecies fishing (synergies with the EU-FP7 MYFISH and BASIN), (iii) changes in nutrients from runoff (iv) changes in the species, size and abundance of primary producers, (v) key species replacement at mid trophic levels, for example increases in gelatinous zooplankton, (vi) temperature-related reductions in body sizes (vii) spatial closures for example by Marine Protected Areas or fisheries management. Warming and nutrient scenarios will use forecasts carried out under IPCC scenarios from POLCOMS-ERSEM (EU-FP7 BASIN). Predictive model outputs will include those specified in Module 5 to quantify uncertainty in ecosystem services.

6.4.2 Milestones

No.	Milestone	Date completion	Lead partner
M4.1	Specification of the alternative models and their driving and fitting data that will form the ensemble and the baseline runs	(M10)	Sheffield
M4.2	Comparative assessment of the baseline outputs from the model ensemble as the basis for quantifying uncertainty	(M20)	Sheffield
M4.3	Predictions of the response of ecosystem states and services in response to climate and anthropogenic drivers	(M30)	Sheffield

6.4.3 Deliverables

No.	Deliverable	Date completion	Dependencies	Lead partner
D4.1	Report on model fitting methodology and results	(M18)	M4.1, M4.3	Sheffield
D4.2	Paper on model skill specifying the selected model ensemble	(M24)	M4.2, M4.4	Sheffield
D4.3	Report on ensemble predictions of ecosystem responses and services across scenarios.	(M36)	M4.5	Sheffield/PML
D4.4	Policy report on ecosystem service predictions and uncertainty.	(M42)	M4.5	PML/Sheffield

Links to other Modules This module will rely on inputs from M1, 2 and 3, and provide outputs to M5. Sub-processes and structures to include into models will be identified through empirical macroecological and food web analyses (M1), dedicated experiments and observations (M2) and elasticity analyses (M3). Methods for translation of model outputs into ecosystem services will be developed for M5 and integrated into the models.

6.5 Module 5: Linking macroecology and models to ecosystem services.

Co-Is: Austen, Beaumont (PML) and all MERP Co-Is

The inclusion of ecosystem services within marine management and regulatory frameworks is limited by a lack of understanding of the relationships between ecosystem structure and processes and how they integrate to provide ecosystem services, and of the spatial and temporal scales that are key to these relationships (Mace et al 2011, Austen et al 2011). As lead authors in the National Ecosystem Assessment and lead researchers in projects such as EU VECTORS and UKERC we have already made significant progress in identifying and understanding what services are delivered by marine ecosystems, the underlying functions and processes and, in particular, ecologically-based indicators for provisioning and regulating services (e.g. Austen et al 2011, Hattam et al submitted). Improved mechanistic understanding gained in MERP (Modules 1-4) will be used to improve understanding of the processes and structures that are relevant to ecosystem services. This will enable us to translate outputs from macroecological analysis (Module 1) and predictions derived from the model ensembles (Module 4) indicative of changes in these processes and structures into the currency of ecosystem services. Bringing together natural scientists together with interdisciplinary ecosystem service researchers working between and among natural and social science disciplines, we will develop a framework to generate predictions about the fate of marine ecosystem services under different past and future scenarios, at local and regional spatial scales, allowing exploration of the implications of different management scenarios for ecosystem services and their socio-economic benefits (Programme Objective 3.)

6.5.1 Tasks

T5.1 Translate understanding and predictions derived from macroecological and empirical approaches and model ensembles into the currency of ecosystem services.

Ecosystem services that will be addressed are climate regulation (carbon flows and stocks); wild species biodiversity; food provision (support for fish and shellfish stock and structure); and bioremediation and detoxification of waste, as well as some elements of disturbance prevention or moderation, regulation of water flows and coastal erosion prevention (marine aspects of hazard regulation). It is clear that both higher trophic level organisms (e.g. seabirds and mammals) as well as large megafauna at lower trophic levels (basking sharks) are important for the cultural services of leisure, recreation, tourism and aesthetic experience which also provide health benefits (White et al 2010, 2012; Wheeler et al 2012) and MERP will also address these aspects of cultural service provision.

Module 5 will utilise the MERP Stakeholder Panel to ensure that the research outputs are relevant. An Integrating Workshop at the Kick-Off Meeting will be used to explain our approaches, including their limitations and uncertainties, and refine them to ensure that they will have utility. A second workshop at the end of the project will explain the outcomes and then explore their implications for current policy and management.

Building on e.g. Austen et al (2011), Hattam et al (submitted) and Worm et al (2006) preliminary conceptual models will be developed that link different aspects of biodiversity and ecosystem processes to each of the ecosystem services. Such models are already being developed via UKERC and BESS support for carbon elements of climate regulation based on coastal shelf carbon flows in ERSEM, and for bioremediation of waste and greenhouse gas sequestration in estuaries. The understanding derived from macroecological, empirical and model ensemble approaches (Modules 1-4) as well as their outputs (for parameterisation) will be used to further develop these conceptual models. A variety of processes will be addressed for each service. For food provision, for example, these include primary production, maintenance of food web dynamics, nutrient cycling to maintain food web dynamics for target species, supply of larvae and gametes of target species and rovision of suitable habitats. For climate regulation, processes include pelagic and benthic fixation of carbon through photosynthesis, C storage over time in living biomass (e.g. kelp, fish, mammals, benthic organisms, microbiota etc.), deposition and burial of carbon in seabed sediments through bioturbation.

Through statistical analysis of model parameters we will define the key processes and biodiversity elements that are essential to ecosystem service delivery and good indicators of changes in delivery of the different ecosystem services, and at which spatial and temporal scales. We will also identify which current indicators of GES can indicate change in ecosystem services. We recognize that neither the empirical results of Modules 1 and 2, nor the theoretical and modelling results of Modules 3 and 4, can directly represent all structures and processes relevant for major ecosystem services. This will necessitate a triage of all marine ecosystem services, identifying those directly represented by models (such as harvestable fish production), those for which proxy indices can be defined that can be computed from the model data (e.g. for climate regulation and for waste treatment and assimilation) or extracted through ecoinformatics approaches (e.g. wild species diversity), and those that are inaccessible to our methodology (e.g. some cultural services). We will thus first identify which are the key model and data outcomes of MERP that can be used to indicate changes in ecosystem services. We will then use the model and data outputs (from Modules 1-4) to identify how ecosystem services change in response to changes in food web structure, and generate predictions of change in marine ecosystem services at local and regional spatial scales under different past and future scenarios.

Dependencies: Module 5 will rely on the outputs for all modules to feed into their work.

6.5.2 Milestones

No.	Milestone	Date completion	Lead partner
M5.1	Integrating workshop with consortium and stakeholders	(M6)	PML
M5.2	Develop conceptual models for different ecosystem services	(M24)	PML
M5.3	Macroecological and ecosystem models linked to services	(M36)	PML
M5.4	Final workshop	(M48)	PML

6.5.3 Deliverables

No.	Deliverable	Date completion	Related Milestone	Lead partner
D5.1	Paper on conceptual models relating ecosystem structure and processes to ecosystem services	(M30)	M5.2	PML
D5.2	Paper on analysis of changes in ecosystem services at different spatial and temporal scales	(M42)	M5.3	PML

Links to other modules M5 will use data from M1 and M2 at different scales, mechanistic understanding of processes from M1-3 and simulations of past and future ecosystem responses across spatial and temporal scales from M4.

6.6. Module 6

6.6.1 Tasks

T6.1. *Technical development of the software environment for the hierarchical model.* We will establish a version controlled development trunk for DivERSEM. Using a modular approach based on the standard organism the code will be designed to provide a scalable model system, with a traceable hierarchy whereby more complex foodweb structure can by systematically and coherently related to simple foodweb structures. *Funded though NC* (PML)**.**

T6.2. *Evaluation of the ecosystem properties of the existing ERSEM configuration.* To inform both the model development and WP1 we will evaluate and existing hindcast of the NW European Shelf, in terms of the model reproduction of observed size spectra, metabolic scaling, observed ecosystem variability and shifts in trophic control. The focus will be on data rich regions (PML, Cefas).

T6.3. *Computational cost of advection.* The horizontal advection of biological variables is a substantial computational cost. This task involves improving the capacity of the model to scale and capability to work with 10's to 100's state variables. Firstly we will optimise, for 10s-100s state variables, existing schemes in NEMO (TVD and PPM) that are accurate, monotonic and non-diffusive. Then we will explore the implications (on efficiency/accuracy) of combining these schemes with substantially cheaper but lower fidelity methods (e.g. upwind and centred), using a master variable/subsidiary variable approach and test these approaches in a frontal resolving NEMO model (~1.8km). Finally we will review and assess other advanced transport methods, such as those used in multi-tracer atmospheric simulations (e.g. Lauritzen et al 2010) (NOC).

T6.4. *Revising the ERSEM standard organisms*. The purpose of this task is to improve the trophic structure in terms of organism size and function through revisiting the definitions of the standard organisms combining pelagic and benthic approaches as appropriate, improving the individual process descriptions based on, allometric scaling and metabolic theory where possible to define a baseline set of size scalable core parameters. This will allow us to address whether size and function based relationships can describe macroecological relationships and explain the flow of energy though the ecosystem. The performance of this model will be evaluated against the standard SSB ERSEM model in 1D water column models.

- *Autotroph's*: Analysis of nutrient-dependent growth and uptake in phytoplankton, reveals physiological trade-offs in species abilities to acquire and utilize resources (Litchman et al 2007). Such trade-offs, arise from fundamental relations such as cellular scaling laws and enzyme kinetics and define contrasting ecological strategies of nutrient acquisition and the subsequent modulation of cellular stoichiometry with size (Finkel et al., 2010). Cellular stoichiometry provides a link between bottom up control (availability of light and nutrient) and top down control in the planktonic food web (zooplankton stoichiometric modulation of predation). Starting with the standard phytoplankton organism from the SSB ERSEM model and drawing on the published analysis of size based traits (e.g. Litchman et al 2007, Finkel et al 2010, Edwards et al 2012) the parameterisation of the standard autotrophic organism will be refined to better represent these tradeoffs. The applicability of the standard autotroph to the benthic system (as developed in Blackford, 2002) will be further developed and evaluated. (PML).

- *Heterotrophic Consumers*: We will refine the pelagic and benthic foodweb, focusing on the allometeric scaling of growth, ingestion and respiration to better resolve the observed size structures. (Cefas, PML).
- *Decomposers (Heterotrophic prokaryotes)* Heterotrophic prokaryotes (bacteria and archaea) play a crucial role in both the benthic (Lloyd et al., 2013) and pelagic systems (Carlson et al. 2007). ERSEM is being developed by including (and further refining) the formulation proposed by Polimene et al. (2006). This describes the release of excess of carbon (overflow metabolism) which decouples the uptake of carbon from cell growth (i.e. “net” production), thus making the variability of Bacterial Growth Efficiency as a function of the environmental conditions. We shall draw on this work to develop the basic standard decomposers for both the benthic and pelagic systems. Further work will be undertaken to improve the parameterisations of aerobic and anaerobic bacteria in the benthic system.
- We will explore the top closure of both the pelagic and benthic models starting with a simple quadratic term, but also considering the external closure from and offline HTL model. In addition we will make data available for 1 way coupling to drive external HTL models being applied in WP1. Depending on the nature work proposed by the modelling activities in WP1 we will explore the collaborative development of 2 way couplers with WP1 if required. (Cefas, PML).

T6.5 *Biological traits*. To further improve our capability to reproduce the observed spatial and temporal heterogeneity in ecosystem structure this task focuses on improving the description of size / functional class diversity, and within trait diversity. Although size is the major driver for many physiological and behavioural parameters, other traits are not size-dependent and they can significantly contribute in determining the fitness of the organisms and therefore potentially contribute to the general ecosystem structure. We shall focus on expanding the biological trait diversity of autotrophs, zooplankton and zoobenthos, and explore how these groups drive the energy supply into the ecosystem and its transfer to higher trophic levels.

- *Autotrophs*: Diatoms play a crucial role in determining the ecosystem properties of both pelagic and benthic ecosystems, the latter through the supply of fast sinking detritus in the spring. The current version of ERSEM describes one category of diatoms (defined as silicate consumers). We will focus on differentiating the size classes of diatoms. In addition we will parameterise traits in benthic autotrophs (e.g. benthic diatoms and macroalgae). (PML, Cefas).
- *Zooplankton* For the heterotrophic grazers, the strength of the predator–prey interactions, are driven by the choice of parameters and more specifically the food preferences (Sailley et al 2013). This illustrates the importance of equation and parameter choice as they define interactions between FTs and overall food web dynamics (competition, bottom-up or top-down effects). Related to this is the issue of the relationships between key processes such as prey selectivity, ingestion and digestion to the amount of prey, its quality and its type (Mitra and Flynn, 2005). Drawing on work being undertaken in the SSB program, the description of zooplankton grazing activity will be refined by including processes such as the stoichiometric modulation of predation (Mitra, 2006; Mitra and Flynn, 2005) and prey palatability (i.e. production of toxins), which may heavily contribute to promote algal blooms in coastal eutrophic areas (Mitra and Flynn, 2006). In addition they

exhibit a number of foraging behaviours ranging from ambush feeding (waiting for random prey encounters), to cruise feeding (increasing prey encounters by swimming) and current feeding (increasing prey encounters by generating a feeding current). Each strategy has a different set of penalty costs, trading prey availability against metabolic costs of movement and increased risk of predation. The current version of ERSEM describes zooplankton by size (e.g. micro, meso) but does not take account of foraging behaviours. We will focus on differentiating the different feeding strategies by initially differentiating between ambush feeders and filter feeders (PML).

- *Zoobenthos:* In an analogous manner to the zooplankton above, we shall focus on refining the benthic foodweb, primarily by defining the macro fauna in terms of feeding and burrowing strategies. (PML, Cefas).
- *Adding species diversity*: To fully explore the impact of changes in diversity on the resistance and resilience of ecosystems requires representation of intra trait diversity. This trait variability will be included in the model by randomly varying the value of some of the parameters of the modelled organism (e.g. growth rate, carbon: nutrients ratio, food preference, clearance rate) based on the variability of the allometric relationships observed in the literature. The variability of ecosystem properties depending on these parameters will be compared to that one depending on size in order to assess how much of the observed patterns can be explained by the size, and how much the other traits contribute (PML)**.**

T6.6. *Simulations and synthesis*: The DivERSEM model will be used to explore the importance of biological traits in defining major ecosystem properties like diversity, primary and secondary production, energy transfer efficiency and their temporal and spatial patterns.

- GOTM water columns with be set up for data rich sites (e.g. L4, Stonehaven, Cefas Oyster Grounds) and validated. Sensitivity analysis will be performed to explore natural variability, trophic controls and diversity/function relationships (PML, Cefas).
- A 40 year hindcast of the NW European Shelf will be made, exploiting the common model forcing data base setup by the SSB project. This hindcast will be assessed in terms of its skill in reproducing macro-ecological properties (PML, NOC).
- We will also explore the effects of refining model resolution (from ~7km to ~1-2km), so as to better represent the structure and dynamics of shelf sea fronts and investigate the consequences for ecosystem structure and function (e.g. Holt et al 2004). For this we will exploit developments of fine resolution NEMO models in FASTNet (NERC ocean –shelf exchange RP), but on a reduced area nested domain covering the Celtic Sea, English Channel and Irish Sea (see Holt and James, 2006). The 3D simulations will be evaluated using large spatial data sets e.g. Satellite Ocean Colour (NEODASS) and the CPR. (NOC)

6.5.2 Milestones

No.	Milestone	Date completion	Lead partner
M6.1	Delivery of new model code with improved representation of biodiversity	(M30)	PML
M6.2	Finalized hindcast and re-analysis simulations	(M36)	PML

6.5.3 Deliverables

No.	Deliverable	Date completion	Related Milestone	Lead partner
D6.1	Published version of the model code – submitted manuscript	(M24)	M6.1	PML
D6.2	Community modelling tools available on the web	(M30)	M6.1	PML
D6.3	Paper(s) on new trait based models - submitted manuscripts	(M30)		PML

D6.4	Paper on advanced advective methods - submitted manuscripts	(M30)		NOC
D6.5	Hindcast simulations and re-analysis simulations, sub sets of the data deposited with appropriate BODC data centre	(M36)	M6.2	PML
D6.6	Scientific paper(s) on the sensitivity and resilience of shelf seas marine ecosystems, to climate change and other anthropogenic drivers – submitted manuscripts	(M42)	M6.2	PML

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Appendix 1 Original Case for Support for WP2 Developing a model based understanding of ecosystem service regulation

Part 1: Previous Track Record: See individual CVs for further details and relevant publications

Plymouth Marine Laboratory (PML) is an International Centre of Excellence in Marine Science & Technology and a Collaborative Centre of NERC that carries out innovative and timely fundamental, strategic and applied research in the marine environment from the uppermost reaches of estuaries to the open ocean. The research at PML contributes to the issues of global change, sustainability and pollution delivering solutions for national and international marine and coastal programmes. PML is an independent, impartial provider of scientific research in the marine environment with a focus on understanding biodiversity and ecosystem function, biogeochemical cycling, pollution and health, and forecasting the role of the oceans in the Earth System. PML has an outstanding reputation at a national and international level for its capabilities in the modelling of regional marine ecosystems. **PML Principal Investigator: Professor J. Icarus Allen** (NERC band 4) is Head of Science for Modelling and Observing Systems at PML, leader of PML's ecosystem modelling NC and is an honorary visiting professor at the University of Exeter. He has been involved in and acted as PI for over 35 national and EC projects, including coordinating the FP7 MEECE and OpEc integrated projects. He is the PI for the modelling activities in the Shelf Seas Biogeochemistry program, the Ocean Carbon theme of the National Centre for Ocean Forecasting (NCEO), Integrated Marine Biogeochemical Modelling Network (i-MarNet). His primary expertise is in marine ecosystem modelling and ecosystem response to climate change. He has 78 ISI publications. **Co-Investigator: Jerry Blackford** (NERC band 4) is a Merit scientist at PML. His principle interests are the impact of Climate Change and Ocean Acidification on marine systems (OA) and environmental impact assessments for Carbon Capture and Storage (CCS). He leads a NERC consortium on CCS impacts and a NERC-Defra funded project on regional climate /OA modelling. **Research Co-Investigators** (PML scientists): **Dr Jorn Bruggeman** in trait based modelling and **Dr Sevrine Sailley** expertise on zooplankton and trophic interactions**, Dr Yuri Artioli** provides expertise in modelling marine plankton diversity. **Dr Luca Polimene,** has expertise in pelagic process modelling and **Dr Nick Stephens** in benthic modelling and nutrient cycling.

Cefas (Centre for Environment, Fisheries and Aquaculture Science) is a multi-disciplinary research centre providing services in fisheries management, environmental monitoring and assessment, and aquaculture to Defra and a large number of clients worldwide. Cefas has an ocean-going research vessel and a monitoring buoy network. Cefas has published 755 peer- reviewed scientific papers in the past five years in the fields of marine ecology, fisheries science, climate change, impacts of marine policy and ecotoxicology. Cefas scientists hold senior advisory positions in organisations such as ICES and the EU, and honorary positions in universities in the UK. Cefas staff have significant experience in developing empirical and numerical models to study environmental and fisheries effects of management scenarios. Cefas has a long history in R&D and providing scientific advice to a range of UK Government Bodies ensuring the sustainable use of natural resources. Cefas currently participates in joint NERC-Defra funded projects (Shelf Seas Biogeochemistry Programme and EBAO). **Cefas Principal Investigator**: **Dr Johan van der Molen** (Cefas Pay Band 7) is a principal ecosystem modeller. He is Secretary for Coastal and Shelf Seas in the Oceans Division of the European Geosciences Union, and a convener in its annual assemblies. He has over 20 years of experience in numerical modelling of hydrodynamics, sediment transport, morphodynamics, transport of fish eggs and larvae, and biogeochemistry. **Co-I's Dr Sonja van Leeuwen** (Cefas pay band 6) is a senior ecosystem modeller with experience in primary production, eutrophication, coupling ERSEM to size-based higher trophic level models, and river runoff and nutrient loads. **Dr John Aldridge** (Cefas pay band 6) is a senior mathematical modeller with broad experience in physical and biological marine systems, and specialising in benthic processes and phytoplankton and macroalgal productivity. Other Cefas staff may contribute to the project where appropriate.

The National Oceanography Centre (NOC) is a NERC Research centre that maintains world class oceanographic research, consisting of Liverpool (**NOC-L** formerly the Proudman Oceanographic Laboratory; POL) and Southampton (**NOC-S**) sites. This work sits within the Marine Systems Modelling (MSM) group, which has world-class expertise in high resolution ocean and Shelf Sea modelling of hydrodynamics, waves and biogeochemistry, and uncertainty. At MSM at NOC-L has a substantial international reputation and contributing to the development of operational shelf sea forecast services at the UKMO (based on NEMO) and marine impact climate projections for UKCP09 and MCCIP. **NOC**

Principal investigator: Dr Jason Holt (NERC band 4) is associate head of the MSM. He specialises in the synthesis of model and observations to develop our understanding of shelf-sea physical and coupled physical-biological systems. He leads the modelling component in the NERC FASTNet (ocean-shelf exchange) programme and the Next Generation Ocean Dynamical Roadmap Project. He has published 50+ peer reviewed papers primarily on the modelling of hydrodynamics and ecosystems in shelf seas and ocean margins. **Co-Investigators**: **Dr. Hedong Liu** (NERC Band 5) works on the development and applications of 3-D unstructured and structured grid ocean models. He is currently a member of NEMO developer's committee and specialises in state-of-the-art numerical methods. **Dr Sarah Wakelin** (NERC Band 6) specialises in the modelling of physical and coupled physics-ecosystem processes in shelf seas, including the impacts of climate change and the combine impacts of climate and anthropogenic drivers.

Recent Related Work

As a component of the NERC-Defra Shelf Seas Biogeochemistry program, PML, Cefas and NOC in collaboration with the UKMO are developing the ERSEM model system to address the overarching scientific goal of enhancing our capacity to assess the physical, chemical and biological controls on biogeochemical cycling, with a focus on the NW European Shelf. This will allow quantification with uncertainties the budgets of C, N, P, Si including their response to climate, natural variability and anthropogenic stress. The work undertaken in the SSB project focuses on merging the existing versions of ERSEM used by the UK community into a single code. The process developments will focus on extending biogeochemical function in the plankton foodweb (e.g. calcifiers, Phaeocystis), including plasticity of response in zooplankton grazing due to food quality, extending the description of benthic and pelagic nitrogen chemistry to include denitrification and N_2O production, and extending the description of the benthic model to describe non-cohesive advective sediments as well as cohesive sediments. The program will develop, two core modelling tools based on ERSEM as community model system. These will be made freely available for academic use. The first is a relocatable biogeochemical water column model based on GOTM-ERSEM. This system can by run on a PC and provides an entry level modelling tool for non-specialist modellers to engage in process modelling. This system will be made available to all SSB scientists. We see developing better synergy between modelling and experimental studies as key to progress over the next decade. The second tool is the high resolution coupled 3D hydrodynamic biogeochemical model based ERSEM-NEMO-shelf, providing the basis of a community modelling approach for looking at spatially resolved system response. In addition we will provide a library of model skill assessment tools. Model data sets provide an important resource across the spectrum of oceanographic science. Examples include use in habitat identification, planning field work effort, the provision of boundary and environmental conditions for local studies and lab based experiments.

Part 2 – Case for Support

Background: Biodiversity refers to the variability among living organisms at all scales of organisation and includes the diversity within species, between species, and of ecosystems. Marine ecosystems are extremely diverse and the functional role this diversity provides underpins major ecosystem services for example: food production, climate regulation through the cycling of carbon and other macronutrients, and a range of cultural values (e.g. recreation and tourism). In many regions marine ecosystems are in serious decline, primarily as a result of over-harvesting, pollution, and the direct and indirect impacts of climate change. Combinations of direct anthropogenic stresses and natural variability have in some locations been associated with dramatic shifts in species composition, known as phase or regime shifts, which maybe long lasting and difficult to reverse (e.g. Lindegran et al 2012; Mollman et al 2009, Mackas and Beaugrand 2009). Changes in species composition affect fundamental ecosystem properties including biodiversity and size structure. For example changes in the physical and chemical environment (temperature, circulation, light availability, nutrients) mainly affect primary production and thus impact the foodweb through bottom up control, whilst impacts such as harvesting act on top predators thus altering top down grazing control (e.g. Frank et al 2006). However the relative roles and interactions of these processes and hence the extent to which environmental change cascades through marine food webs and affects ecosystem services is still poorly understood. In addition secondary impacts on key system determinants such as reproductive success, benthic- pelagic coupling and phenology must be considered in order to get a full picture of ecosystem resilience or vulnerability.

These bottom up, top down and internal processes are inherently scale-dependent. For example, the physical structure of the water column (e.g. stratification, fronts) and the distribution of benthic habitats affect the spatial distribution and abundance of all trophic levels. The large-scale removal of top predators through fishing or other activities can have a range of impacts across scales. In the benthic system the sediments are also dynamic and heterogeneous with differences in particle composition, size and shape. These initial physical variations are diverse leading to large spatial heterogeneity on relatively small sub-metre scales. Subsequent variations observed in the biology are even greater and result in a relatively complex and diverse community structure.

Scale-dependence is poorly understood, making it difficult to quantify the large-scale impacts on ecosystem services of changes at small spatial scales (e.g. marine conservation zones); and *vice versa*.

Finally there is growing evidence that the loss of biodiversity from marine ecosystems can adversely impact ecosystem function and hence the way marine food webs regulate ecosystem services. Studies suggested that species loss decreases the productivity of communities and how efficiently they capture and consume limited resources (e.g. Cardinale et al 2006). The interpretation of these studies has and continues to provoke considerable debate, and subsequent work produced several counter examples that questioned the generality of these biodiversity effects. Consequences of biodiversity loss are likely to be idiosyncratic, differing quantitatively and qualitatively between trophic groups and ecosystems (Cornell and Lawton. 1992). Changes in diversity though the arrival of non-indigenous species (taxa ranging from phytoplankton to fish) introduced by both natural and human vectors also impact on biodiversity, communities, habitats and ecosystem functioning and hence economic impacts. Their increasing spread is a major concern for many world and European seas (Costello et al 2010, Coll et al2010).

Modelling challenges: Macroecology is the study of the relationships between organisms and their environment at large spatial scales to characterise and explain statistical patterns of abundance, distribution and diversity (Brown and Maurer 1989). Scaling relationships are common at higher levels of biological organization, (e.g. Brown, 1995). Body size is an important determinant of many ecological properties, ranging from abundance and biomass to physiological and ecological rates and provides useful underpinning concept for characterizing and modelling marine ecosystems. The widely observed macro-ecological patterns in log abundance vs. log body mass of organisms can be explained by simple scaling theory based on food (energy) availability across a spectrum of body sizes. For example quarter-power scaling with body mass applies to virtually all organisms (West, Brown & Enquist, 1999) and for marine animals, metabolic rate and production scales at three-quarters power (e.g. Brey, 1990; Warwick & Price, 1979). Allometric equations have been derived for respiration, ingestion, excretion and photosynthesis for a variety of organisms of different sizes (e.g. Verdy et al 2009, Moloney and Field 1989). Finally, the temperature dependence of gross primary production and community respiration is consistent among the major types of ecosystems on the planet, suggesting that the fundamental biochemical kinetics of respiratory metabolism are highly conserved and can be scaled from organism to ecosystem levels (Yvon Durcher 2012).

Understanding the interactions of the various system controls, the consequences of change, and designing, testing and refining potential management solutions, is important for the long-term delivery of services from marine ecosystems. Dynamic models that link the physical, chemical and biological processes through food web interactions provide a means of understanding how human impacts on different parts of the ecosystem interact and of predicting the consequences of management actions.The

traditional approach to modelling marine plankton has generally been to build modelling frameworks by coupling bulk biomass functional type (FT) models to 1D and 3D hydrodynamic models; The European Regional Seas Ecosystem Model (ERSEM*)* is one such model. The ecosystem can be divided into four sections, the pelagic cellular ecosystem, the pelagic mid trophic levels (zooplankton), the benthic ecosystem (bacteria, meiofauna, zoobenthos) and the higher trophic levels (fish, birds, mammals); ERSEM describes the first three.
The cellular ecosystem is represented as a biogeochemical flux model where the cell is a black box whereby the fluxes of carbon or nutrients are transferred across the cell walls via first order rate equations. Most often defined in terms of biogeochemical functions (e.g. diatom, non-diatom, calcifiers, grazers etc.), the functional groups are treated as passive tracers and are very sensitive to the biophysical environment they are placed in. The pelagic mid trophic levels are particularly important yet are a weak component of all models. They are particularly important because they provide both the top closure for the planktonic ecosystem and the link to the higher trophic levels. This part of the foodweb is poorly represented in biogeochemical flux type models because the Eularian continuum approach becomes inadequate as behaviour and individual history becomes important. Grazers do not eat biomass; they eat individuals and the process is the sum of the interactions between large numbers of organisms. These interactions are potentially dependent on combinations of prey density (function of the number of potential prey), prey quality (nutritional status), prey type (species) and behaviour (e.g. vertical migration, foraging strategies and defence mechanisms). The challenge is to represent both biomass and population dynamics model in size / trait based foodwebs, coupled to biogeochemical cycles. The benthic system is strongly influenced by the physical sediment structure, environmental conditions and organic fluxes to the sediments. Benthic size spectra are more complex than their pelagic counterparts (Schwinghamer 2011); three biomass peaks, are observed corresponding to bacteria, interstitial meiofauna, and macrofauna, separated by low biomasses. Once again the requirement is to develop a size/trait based foodweb model from bacteria to top predators. Only by viewing the water column and benthos as a whole that will enable a more complete simulation and understanding of fish predating on benthic invertebrates, macroalgae contributions and benthic ecosystem resilience through the modelling of larval and reproductive abilities. Finally the Higher trophic levels are not a part of ERSEM, however the new model will be designed to provide data products to facilitate 1 way coupling to a range of different models ranging from dynamic size spectra and Ecopath with Ecosim to individual based models to further investigate the different model ecosystem structures and the ecosystem dynamics represented.

Aims and Objectives
The overarching scientific goal is to enhance our capacity to assess trophic and spatial controls on the structure of marine ecosystems through improving the representation of biodiversity and ecosystem function in ERSEM. This enhanced model will be used to explore the impact of anthropogenic stress and natural variability on the structure of marine ecosystems and its consequences for ecosystem services, in order to better meet future science and policy needs. To achieve this we will develop a traceable hierarchy of models of different complexity based on ERSEM using a modular approach with consistent process descriptions based on size, function (autotrophy, heterotrophy, decomposition), and biological traits (e.g. feeding strategy, motility, physiology). Through species-neutral process descriptions, the approach will allow scalable representation of diversity within and between functionally similar “guilds” of species. Building on the ERSEM model developments being undertaken in the Shelf Seas Biogeochemistry Program we will establish an ecosystem focused version of ERSEM called ‘DivERSEM’. This will form the basis of a new community model system which will be made freely available to the UK and international research communities.

The project will be delivered through 2 phases of model development, testing and application: Phase I (M1-36), will develop and test v1 of DivERSEM while Phase II (M36-54) will iterate and develop a second version v2 of DivERSEM exploiting the new data and knowledge from the program. Both phases will be underpinned by activities to develop and maintain core model infrastructure, funded through National Capability at PML and NOC. The proposed activities in Phase I are described in this document; Phase II is outlined and will be detailed towards the end of phase1 in response to progress within WP1 and the needs of stakeholders.

Scientific questions: Underpinning this is a suite of key scientific questions, which provide a framework for model development, simulation experiments and analysis.

- Can the model reproduce the observed emergent macroecological relationships (e.g. body size relationships with biomass and rates) and help to explain how these relationships emerge?
- To what extent and at which spatial and temporal scales can size and function based relationships describe and explain the flow of energy though the ecosystem.
- Does the introduction of selected biological traits other than size (e.g. feeding, reproduction, physiology, motility) improve our capability to reproduce the observed spatial and temporal heterogeneity (e.g. seasonality, inter-annual and inter-decadal variability and biogeography) in ecosystem structure?
- Can changes in control on the ecosystem (top down and bottom up) explain observed spatial and temporal heterogeneity (e.g. seasonality, inter-annual and inter-decadal variability and biogeography)?
- How do the spatial scales of pelagic and benthic habitats of lower trophic levels (phytoplankton) relate to those of mid (zooplankton) and higher trophic levels (zoobenthos and fish) and vice versa?
- How do changes in inter and intra guild diversity (including invasion and extinction) impact on the resistance and resilience of ecosystems and hence biogeochemical function.

Technical objectives: Alongside the scientific goals there are technical objectives, which are required to deliver the model system.

- To construct a version controlled software environment for a traceable hierarchy based on size and function – this will allow scaling for a simple size based plankton / zooplankton model to one with stochastic functional variability.
- To provide model outputs to facilitate the 1 way coupling of ERSEM to other ecosystem model, e.g. those of higher trophic levels used in WP1.
- To explore differing approaches to the transport schemes to balance the computational cost of the model with the accuracy of the simulation of various components.

Models will be developed within the Framework for Aquatic Biogeochemical Models (FABM[1]), produced within FP7 project MEECE, to enable the rapid, run-time combination of any number of stochastically initialized models into a coupled ecosystem. This coupler will enable the software to scale from a classic ERSEM configuration to stochastic multi-species setups using a single, unified code base.

Existing Modelling tools

ERSEM was originally conceived as a generic model, which when coupled to a qualitatively correct physical model, is able to simulate the principle dynamics of the marine system across eutrophic to oligotrophic gradients of the range of marine environments from the global ocean to coast shelf seas (e.g. Blackford et al 2004, Blanchard et al 2012). ERSEM simultaneously describes pelagic and benthic ecosystems in terms of phytoplankton, bacteria, zooplankton, zoobenthos, and the biogeochemical cycling of C, N, P, Si (e.g. Baretta et al., 1995, Ruardij et al.,1995, Baretta-Bekker et al., 1997, Blackford 1997, Blackford et al., 2004). The ecosystem as described by ERSEM is considered to be a series of interacting physical, chemical and biological processes which together exhibit coherent system behaviour where state variables have been chosen in order to keep the model relatively simple without omitting any component that exerts a significant influence upon the energy balance of the system. ERSEM uses a functional group approach to describe the ecosystem whereby biota are grouped together according to their trophic level (subdivided according to first size, then trophic role and finally feeding method). All biological functional groups in ERSEM are modelled according to the concept of the 'standard organism' (Baretta et al 1995). There are three classes of standard organisms: autotrophs, heterotrophic consumers and decomposers. The dynamics of biological functional groups are described by both physiological (ingestion, respiration, excretion and egestion) and population processes (growth, migration and mortality). The differences between the functional groups mainly lay in the rate constants, which are derived experimentally from the literature or from allometric considerations (e.g. Moloney and Field 1989), and in the food components on the uptake side. This concept works well for those groups where data are usually derived from population or even community studies.

Physical models: Underpinning, any ecosystem, model is the ability to accurately represent the physical environment at appropriate time/space scales and adequate process descriptions. Here we build on the UK's involvement in the NEMO[2] consortium. Originally a global ocean model

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[1] FABM (http://www.meece.eu/documents/deliverables/WP2/D2.14.pdf)
[2] Nucleus for European Modelling of the Ocean (www.nemo-ocean.eu/)

NEMO has now been developed as a coastal-ocean model that includes (e.g.) tides and sophisticated vertical coordinates (O'Dea et al 2012) and direct coupling to ERSEM (Edwards et al, 2012). These papers describe the 7km resolution Atlantic Margin Model (AMM7) which is the chosen baseline 3D configuration for this work. The sensitivity of the system to different processes/process descriptions and parameterisations will be tested in 1D (GOTM[3]-ERSEM) where thousands of different test runs are tractable. The integrated impact of the processes on seasonal and inter-annual variability of the shelf will be evaluated using the 3D AMM7 model (NEMO-ERSEM). We will explore the implications of moving to DivERSEM on computational capability and ways of facilitating this, while retaining accuracy.

Darwinian ERSEM[4]: A version of ERSEM has been modified to include phytoplankton diversity; each of the four phytoplankton groups have been substituted with 10 different sub type or 'species' whose characteristics are selected to simulate diversity, using an approach analogous to that used by Follows et al (2007). The community is then allowed to develop in response to its environment through intraspecific competition for the same resources. The model was used in the FP7 MEECE project to explore the consequences of the disruption of the local phytoplankton community by invasive species.

Model Development

In order to meet the challenges of the programme we require a scalable model system, with a traceable hierarchy whereby more complex foodweb structures can be systematically and coherently related to simple foodweb structures. Building on the concepts of the standard ERSEM organisms and the SSB ERSEM size structured foodweb as a baseline we will establish and test a hierarchical framework which describes three levels of organisation of the foodweb

1. Trophic structure in terms of organism size and function (here we refer to high level ecosystem function, i.e. autotrophy, heterotrophy, decomposition).
2. Within size / functional class diversity, by subdividing by biological traits (e.g. feeding strategy, motility, physiology).
3. Within trait diversity whereby intra- and inter-specific competition is described by defining a set of species within each trait type, stochastically drawing parameters from a rule based parameter space.

The capabilities of ERSEM will be expanded in two ways. First, distinctions within functional type (FT) size classes (e.g., phytoplankton, zooplankton, bacteria, zoobenthos) that are currently present in the model will be reduced by introducing unified models, suitable for broad classes of organism types. These will be able to replicate the behaviour of the various original FTs if configured with appropriate parameter values. This unification will enable div-ERSEM's stochastic approach to cross FT boundaries, thus reducing the emphasis on traditional, subjective, hard- coded subdivision of FTs. Second, the parameter space spanned by the stochastic approach will be reduced by identifying a low number of principal traits (e.g., size, feeding strategy) that determine other functional traits through trade-offs. Identification of principal traits and trade-offs will be based upon trait value compilations published in existing literature (e.g., Bruggeman 2011, Edwards et al. 2013, Wirtz 2013). By breaking down model barriers between types and by focusing on a low number of principal traits that characterize interspecific variability, div-ERSEM will be able to generate ecosystem models of varying degrees of complexity, merely by varying the number of stochastically created model species. This approach will be used to assess the relationship between diversity (number of species) and ecosystem functioning, and to identify the optimal level of complexity required to describe ecosystems at the sites of study. It is anticipated that aspects of DivERSEM (e.g. parameterisations of scale and diversity/function relationships) would be fed back to improve the core biogeochemical model developed under the SSB programme.

Adaptive dynamics: In ecology, "adaptive dynamics" approaches have been used to summarize the behaviour of multi-species models in terms of a few key statistics: total biomass, mean trait value, and trait variance (a measure of functional diversity) (Abrams 1992, Norberg et al. 2001, Merico et al. 2009). Critically, the dynamic behaviour of these statistics, rather than abundances of the species they describe, is evolved in time. This drastically reduces the number of modelled tracers. A similar approach has been used to describe the size distribution of the plankton community in terms of a dynamically evolving size spectrum slope (Kriest & Oschlies 2007). These methods are approximations that maintain a traceable link with multi-species models. It is therefore possible to evaluate their accuracy of approximation by directly comparing their results with that of species-explicit simulations (Norberg et al. 2001, Merico et al. 2009). Moreover, a key feature of adaptive dynamics approaches is that they explicitly represent functional biodiversity in the form of a single tracer, i.e., trait variance. This makes it possible to directly (analytically) assess the interaction between diversity and ecosystem functioning (e.g., bulk biogeochemical fluxes).

DivERSEM and similar approaches that offer refined representations of variability in size (Baird & Suthers 2007, Banas et al 2011, Ward et al 2012) and other functional traits (Follows et al. 2007; Bruggeman & Kooijman 2007) do so by explicitly simulating large numbers of species. This is computationally expensive, particularly in 3D models. Moreover, species-explicit approaches only allow empirical assessment of the link between biodiversity and ecosystem functioning, by experimentally varying the number of simulated species and observing the response in model behaviour. We will apply adaptive dynamics-type approximations to aggregate multi-species configurations of DivERSEM in terms of total biomass, and the mean and variance of a few principal traits (e.g. size). To embed these in spatially explicit hydrodynamic models, we will use and refine existing variable transformation methods developed for water columns (Bruggeman 2009). The performance of approximate methods will be assessed by comparing their results with those of species-explicit DivERSEM simulations.

Physical scales and advance approaches to advection: Advective transport is a key element of biophysical interaction that is often overlooked because our view of the seasonal cycle of plankton growth in shelf

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[3] General Ocean Turbulence Model www.gotm.com;
[4] Darwinian ERSEM (http://www.meece.eu/documents/deliverables/WP4/D4.3_P3_InvasiveSpecies.pdf)

seas has tended to focus on vertical mixing processes, for the good reason that these are largely the first order controls on seasonal timescales. Moreover a 'vertical only' view fits nicely with timeseries observations and computationally fast models such as GOTM-ERSEM. However, shelf sea production is also characterised by strong horizontal gradients (e.g. at fronts and coastal regions of freshwater influence), and in neglecting processes driven by these gradient we miss a crucial aspect of the system and its response to change e.g. enhanced frontal production (Richardson et al 2000) and in doing so possibly under-estimate the diversity of niches in the model. On longer (annual to decadal) timescales, horizontal transport sets the overall elemental budgets the ecosystems have to work with (e.g. Holt et al 2012). In addition the numerical treatment of advection is the primary limit for 3D models to exploit current increases in computer power, which now largely occur by increased parallelism rather than computational speed. Hence, the challenge is to provide a computationally efficient horizontal transport scheme that can accommodate a substantial increase in the number of state variables and maintain accuracy in the representation of the key biophysical interactions. In tidally active shelf seas advective transport generally dominates over horizontal diffusive transport and so is our focus here.

Data Requirements: data is the life blood of modelling and is required to both parameterise and verify models. Observations may also be used to formulate derived functions or function-related parameters that can be used to test or improve the functional representations in ERSEM. Assessing the skill of DivERSEM will require new approaches to model skill assessment beyond those commonly used in biogeochemical modelling. We will develop novel methods applying statistical techniques commonly used for analysing biodiversity data (e.g. non parametric multi- dimensional scaling). More specifically, to validate models we require information on the larger scale emergent patterns (time, space, and emergent ecosystem properties such as biogeography, size spectra, trophic levels, connectivity, diversity, and also key functions such as primary and secondary production, respiration and stability measures). The interactions with WP1 are crucial to this aspect of the project.

Workplan

Task 1. *Technical development of the software environment for the hierarchical model.* We will establish a version controlled development trunk for DivERSEM. Using a modular approach based on the standard organism the code will be designed to provide a scalable model system, with a traceable hierarchy whereby more complex foodweb structure can by systematically and coherently related to simple foodweb structures. *Funded though NC* (PML)**.**

Task 2. *Evaluation of the ecosystem properties of the existing ERSEM configuration.* To inform both the model development and WP1 we will evaluate and existing hindcast of the NW European Shelf, in terms of the model reproduction of observed size spectra, metabolic scaling, observed ecosystem variability and shifts in trophic control. The focus will be on data rich regions (PML, Cefas).

Task 3. *Computational cost of advection.* The horizontal advection of biological variables is a substantial computational cost. This task involves improving the capacity of the model to scale and capability to work with 10's to 100's state variables. Firstly we will optimise, for 10s-100s state variables, existing schemes in NEMO (TVD and PPM) that are accurate, monotonic and non-diffusive. Then we will explore the implications (on efficiency/accuracy) of combining these schemes with substantially cheaper but lower fidelity methods (e.g. upwind and centred), using a master variable/subsidiary variable approach and test these approaches in a frontal resolving NEMO model (~1.8km). Finally we will review and assess other advanced transport methods, such as those used in multi-tracer atmospheric simulations (e.g. Lauritzen et al 2010) (NOC).

Task 4. *Revising the ERSEM standard organisms*. The purpose of this task is to improve the trophic structure in terms of organism size and function through revisiting the definitions of the standard organisms combining pelagic and benthic approaches as appropriate, improving the individual process descriptions based on, allometric scaling and metabolic theory where possible to define a baseline set of size scalable core parameters. This will allow us to address whether size and function based relationships can describe macroecological relationships and explain the flow of energy though the ecosystem. The performance of this model will be evaluated against the standard SSB ERSEM model in 1D water column models.

- *Autotroph's*: Analysis of nutrient-dependent growth and uptake in phytoplankton, reveals physiological trade-offs in species abilities to acquire and utilize resources (Litchman et al

2007). Such trade-offs, arise from fundamental relations such as cellular scaling laws and enzyme kinetics and define contrasting ecological strategies of nutrient acquisition and the subsequent modulation of cellular stoichiometry with size (Finkel et al., 2010). Cellular stoichiometry provides a link between bottom up control (availability of light and nutrient) and top down control in the planktonic food web (zooplankton stoichiometric modulation of predation). Starting with the standard phytoplankton organism from the SSB ERSEM model and drawing on the published analysis of size based traits (e.g. Litchman et al 2007, Finkel et al 2010, Edwards et al 2012) the parameterisation of the standard autotrophic organism will be refined to better represent these tradeoffs. The applicability of the standard autotroph to
the benthic system (as developed in Blackford, 2002) will be further developed and evaluated. (PML).

- *Heterotrophic Consumers*: We will refine the pelagic and benthic foodweb, focusing on the allometeric scaling of growth, ingestion and respiration to better resolve the observed size structures. (Cefas, PML).
- *Decomposers (Heterotrophic prokaryotes)* Heterotrophic prokaryotes (bacteria and archaea) play a crucial role in both the benthic (Lloyd et al., 2013) and pelagic systems (Carlson et al. 2007). ERSEM is being developed by including (and further refining) the formulation proposed by Polimene et al. (2006). This describes the release of excess of carbon (overflow metabolism) which decouples the uptake of carbon from cell growth (i.e. "net" production), thus making the variability of Bacterial Growth Efficiency as a function of the environmental conditions. We shall draw on this work to develop the basic standard decomposers for both the benthic and pelagic systems. Further work will be undertaken to improve the parameterisations of aerobic and anaerobic bacteria in the benthic system.

- We will explore the top closure of both the pelagic and benthic models starting with a simple quadratic term, but also considering the external closure from and offline HTL model. In addition we will make data available for 1 way coupling to drive external HTL models being applied in WP1. Depending on the nature work proposed by the modelling activities in WP1 we will explore the collaborative development of 2 way couplers with WP1 if required. (Cefas, PML).

Task 5 *Biological traits*. To further improve our capability to reproduce the observed spatial and temporal heterogeneity in ecosystem structure this task focuses on improving the description of size / functional class diversity, and within trait diversity. Although size is the major driver for many physiological and behavioural parameters, other traits are not size-dependent and they can significantly contribute in determining the fitness of the organisms and therefore potentially contribute to the general ecosystem structure. We shall focus on expanding the biological trait diversity of autotrophs, zooplankton and zoobenthos, and explore how these groups drive the energy supply into the ecosystem and its transfer to higher trophic levels.

- *Autotrophs*: Diatoms play a crucial role in determining the ecosystem properties of both pelagic and benthic ecosystems, the latter through the supply of fast sinking detritus in the spring. The current version of ERSEM describes one category of diatoms (defined as silicate consumers). We will focus on differentiating the size classes of diatoms. In addition we will parameterise traits in benthic autotrophs (e.g. benthic diatoms and macroalgae). (PML, Cefas).
- *Zooplankton* For the heterotrophic grazers, the strength of the predator–prey interactions, are driven by the choice of parameters and more specifically the food preferences (Sailley et al 2013). This illustrates the importance of equation and parameter choice as they define interactions between FTs and overall food web dynamics (competition, bottom-up or top-down effects). Related to this is the issue of the relationships between key processes such as prey selectivity, ingestion and digestion to the amount of prey, its quality and its type (Mitra and Flynn, 2005). Drawing on work being undertaken in the SSB program, the description of zooplankton grazing activity will be refined by including processes such as the stoichiometric modulation of predation (Mitra, 2006; Mitra and Flynn, 2005) and prey palatability (i.e. production of toxins), which may heavily contribute to promote algal blooms in coastal eutrophic

areas (Mitra and Flynn, 2006). In addition they exhibit a number of foraging behaviours ranging from ambush feeding (waiting for random prey encounters), to cruise feeding (increasing prey encounters by swimming) and current feeding (increasing prey encounters by generating a feeding current). Each strategy has a different set of penalty costs, trading prey availability against metabolic costs of movement and increased risk of predation. The current version of ERSEM describes zooplankton by size (e.g. micro, meso) but does not take account of foraging behaviours. We will focus on differentiating the different feeding strategies by initially differentiating between ambush feeders and filter feeders (PML).

- *Zoobenthos:* In an analogous manner to the zooplankton above, we shall focus on refining the benthic foodweb, primarily by defining the macro fauna in terms of feeding and burrowing strategies. (PML, Cefas).
- *Adding species diversity*: To fully explore the impact of changes in diversity on the resistance and resilience of ecosystems requires representation of intra trait diversity. This trait variability will be included in the model by randomly varying the value of some of the parameters of the modelled organism (e.g. growth rate, carbon: nutrients ratio, food preference, clearance rate) based on the variability of the allometric relationships observed in the literature. The variability of ecosystem properties depending on these parameters will be compared to that one depending on size in order to assess how much of the observed patterns can be explained by the size, and how much the other traits contribute (PML)**.**

Task 6. *Simulations and synthesis*: The DivERSEM model will be used to explore the importance of biological traits in defining major ecosystem properties like diversity, primary and secondary production, energy transfer efficiency and their temporal and spatial patterns.

- GOTM water columns with be set up for data rich sites (e.g. L4, Stonehaven, Cefas Oyster Grounds) and validated. Sensitivity analysis will be performed to explore natural variability, trophic controls and diversity/function relationships (PML, Cefas).
- A 40 year hindcast of the NW European Shelf will be made, exploiting the common model forcing data base setup by the SSB project. This hindcast will be assessed in terms of its skill in reproducing macro-ecological properties (PML, NOC).
- We will also explore the effects of refining model resolution (from ~7km to ~1-2km), so as to better represent the structure and dynamics of shelf sea fronts and investigate the consequences for ecosystem structure and function (e.g. Holt et al 2004). For this we will exploit developments of fine resolution NEMO models in FASTNet (NERC ocean –shelf exchange RP), but on a reduced area nested domain covering the Celtic Sea, English Channel and Irish Sea (see Holt and James, 2006). The 3D simulations will be evaluated using large spatial data sets e.g. Satellite Ocean Colour (NEODASS) and the CPR. (NOC)

Outline workplan for Phase II (M37-M60) In the 2nd phase of the project we will introduce reproductive processes to represent one of the largest trophic shifts in the benthic ecosystem, namely the release of larval forms into the pelagic water column, a substantially large perturbation in organic material and a transfer of energy from sediment to water column. Such dispersal events often affect the phenology of various heterotrophic life cycles and in particular those of fish. We will also implement a dynamic top closure scheme based on a dynamic size spectrum model (e.g. Blanchard 2008). Finally we will undertake a set of hindcast and scenario experiments to further explore the sensitivity of the marine ecosystems of the NW European Shelf to natural and anthropogenic drivers. The exact details of these scenarios will be defined following consultation with WP1 and policy focused stakeholders.

National Capability: We assume the following additional support will be available to the project: PML 3 FTE NC, In addition model development will be underpinned by activities in the following NERC programs, NCEO, UKOA, SSB, and FastNet.

Linkages within the Marine Ecosystems program: Model development is most effective when the non-modelling scientists are stakeholders in the model development. To ensure full interaction with the wider community we propose to hold a modeller / stakeholder workshop at project meetings. We propose establishing explicit linkages by creating mini working groups whereby model developers and appropriate PI's or researchers, team up to focus on modelling key ecosystem properties.
Links with the wider international ERSEM community: We will use the inputs provided by the project to cross fertilise ideas with the wider community and share code, to ensure that both the Div-ERSEM model benefits from the international activity and vice versa (see letters of support).

Deliverables and legacy

- Published versions of the model code
- Community modelling tools available on the web; 1D Div-ERSEM-GOTM, 3D Atlantic Margin Model -(Div-ERSEM NEMO-Shelf), model evaluation tools.
- Hindcast simulations and re-analysis simulations, sub sets of the data deposited with appropriate NERC data centre.
- Publication of new trait based models
- Scientific publications on the sensitivity and resilience of shelf seas marine ecosystem, to climate change and other anthropogenic drivers

Project and resource management

The PI will provide overall leadership of the project and assume responsibility for reporting OPMs to NERC and the final report. The programme of research is described in the table 1. The project duration is five years (Phase I 3years, Phase II 2 years) and will begin in January 2014. To coordinate the different elements of the model development project meetings will be held in months 1, 6, 12, 18 and 24, 30 and 36. In addition the project teams will update each other on progress via monthly video conferences.

Table 1	**Year 1**		**Year 2**		**Year 3**		**Phase II**	
Supporting Activities								
T1 Setup and maintain hierarchical model tools	■	■	■	■	■	■	■	■
Phase I								
T2 Analysis of existing ERSEM hindcast	■	■						
T3 Advanced advective schemes		■	■	■				
T4 Refining the standard organism	■	■	■					
T5 Adding traits and trait diversity		■	■	■				
T6 1D GOTM scenarios				■	■	■		
T6 3D NEMO shelf scale hindcast					■	■		
Phase II								
Addition of reproductive processes							■	
Dynamic top closure							■	
Scenarios, reanalysis and synthesis								■

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Outline Data Management Plan

1. Data management procedures

All the data produced by this project will for numerical simulation outputs from the DiVERSEM – NEMO Shelf Model system.

The model code will be maintained using a version controlled core trunk for DivERSEM, linked to the NEMO Shelf trunk using the PUMA shared repository following JWCRP guidelines. All data outputs will be in a standard platform independent NETCD format, with a header which describes the layout of the rest of the file, in particular the data arrays, as well as arbitrary file metadata in the form of name/value attributes. The contents of this header and metadata will be agreed with the relevant NERC data centers at the beginning of the project.

The version controlled model codes, along with the parameter sets and external forcing will be archived at PML, with mirrored copies at NOC and Cefas. Large shelf scale simulation such as those proposed here produces TBytes of model output. It is not practical to store the complete runs on disk for long periods of time. Therefore the full model runs will be archived to tape at PML as soon as they are completed. A set of standard model validation metrics will be defined and applied to quantify the quality of the outputs. Research Co-I Y Artioli, who is a member of the PML data management committee, will act as data manager.

2. Existing datasets

We will make use of existing data sets held at BODC (e.g. Western Channel Observatory, shelf seas biogeochemistry) to validate models and atmospheric forcing data held by BADC to force hindcast simulations (e.g. ERA40). Satellite Ocean Colour data and SST will be requested from NEODAAS for model validation.

3. Datasets likely to be created

Data Centre	Data set description	Release to data centre	Reuse scenarios
BODC	40 year hindcast of NW European Shelf Ecosystem made with DivERSEM-NEMO. Outputs would include, T, S, biomass of all biological variables, production and grazing rates, nutrients and other biogeochemical information. The output frequency would need to be discuss to keep the data set tractable and usable	M36 of the project	Model data would be made available to support shelf seas marine ecosystem research and the development and implementation of marine environmental policy