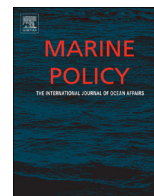




ELSEVIER

Contents lists available at ScienceDirect

Marine Policy

journal homepage: www.elsevier.com/locate/marpol

Making modelling count - increasing the contribution of shelf-seas community and ecosystem models to policy development and management



Kieran Hyder^{a,*}, Axel G. Rossberg^a, J. Icarus Allen^b, Melanie C. Austen^b, Rosa M. Barciela^c, Hayley J. Bannister^d, Paul G. Blackwell^e, Julia L. Blanchard^{d,f}, Michael T. Burrows^g, Emma Defriez^h, Tarquin Dorringtonⁱ, Karen P. Edwards^j, Bernardo Garcia-Carreras^{a,h}, Michael R. Heath^k, Deborah J. Hemburyⁱ, Johanna J. Heymans^g, Jason Holt^l, Jennifer E. Houle^m, Simon Jennings^a, Steve Mackinson^a, Stephen J. Malcolm^a, Ruairaidh McPike^k, Laurence Mee^g, David K. Mills^a, Caron Montgomeryⁱ, Dean Pearsonⁱ, John K. Pinnegar^a, Marilena Pollicinoⁱ, Ekaterina E. Popovaⁿ, Louise Rae^o, Stuart I. Rogers^a, Douglas Speirs^k, Michael A. Spence^{d,e}, Robert Thorpe^a, R. Kerry Turner^p, Johan van der Molen^a, Andrew Yoolⁿ, David M. Paterson^q

^a Centre for Environment, Fisheries & Aquaculture Science, Lowestoft Laboratory, Pakefield Road, Lowestoft, NR330HT, UK

^b Plymouth Marine Laboratory, Prospect Place, The Hoe, Plymouth PL1 3DH, UK

^c Hadley Centre & National Centre for Ocean Forecasting, Met Office, Fitzroy Road, Exeter EX1 3PB, UK

^d Animal & Plant Sciences, University of Sheffield, Alfred Denny Building, Western Bank, Sheffield S10 2TN, UK

^e School of Mathematics & Statistics, University of Sheffield, Hicks Building, Hounsfield Road, Sheffield S3 7RH, UK

^f Institute for Marine and Antarctic Studies, University of Tasmania, 20 Castray Esplanade, Battery Point, Tasmania 7004, Australia

^g Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll PA37 1QA, UK

^h Imperial College London, Silwood Park Campus, Buckhurst Road, Ascot, Berkshire SL5 7PY, UK

ⁱ Department for Environment, Food & Rural Affairs, Nobel House, 17 Smith Square, London SW1P 3JR, UK

^j Estuarine & Coastal Monitoring & Assessment Service, Environment Agency, Manley House, Kestrel Way, Exeter EX2 7LQ, UK

^k Department of Mathematics and Statistics, University of Strathclyde, Livingstone Tower, 26 Richmond Street, Glasgow G1 1XH, Scotland

^l National Oceanography Centre, Joseph Proudman Building, 6 Brownlow Street, Liverpool L3 5DA, UK

^m School of Biological Sciences, Queen's University Belfast, Medical Biology Centre, 97 Lisburn Road, Belfast BT9 7BL, Northern Ireland, UK

ⁿ National Oceanography Centre, University of Southampton Waterfront Campus, European Way, Southampton SO14 3ZH, UK

^o Centre for Environment, Fisheries and Aquaculture Science, Weymouth Laboratory, Barrack Road, Weymouth, Dorset DT4 8UB, UK

^p School of Environmental Sciences, University of East Anglia, Norwich Research Park, Norwich NR4 7TJ, UK

^q University of St Andrews, School of Biology, Scottish Oceans Institute, East Sands, St Andrews KY16 8LB, UK

ARTICLE INFO

Article history:

Received 25 February 2015

Received in revised form

10 July 2015

Accepted 11 July 2015

Available online 5 September 2015

This paper is in memory of Professor Laurence Mee who sadly passed away during the publication of this work.

Keywords:

Ecosystem models
Marine policy and management
UK environmental assessment,
management, and monitoring

ABSTRACT

Marine legislation is becoming more complex and marine ecosystem-based management is specified in national and regional legislative frameworks. Shelf-seas community and ecosystem models (hereafter termed ecosystem models) are central to the delivery of ecosystem-based management, but there is limited uptake and use of model products by decision makers in Europe and the UK in comparison with other countries. In this study, the challenges to the uptake and use of ecosystem models in support of marine environmental management are assessed using the UK capability as an example. The UK has a broad capability in marine ecosystem modelling, with at least 14 different models that support management, but few examples exist of ecosystem modelling that underpin policy or management decisions. To improve understanding of policy and management issues that can be addressed using ecosystem models, a workshop was convened that brought together advisors, assessors, biologists, social scientists, economists, modellers, statisticians, policy makers, and funders. Some policy requirements were identified that can be addressed without further model development including: attribution of environmental change to underlying drivers, integration of models and observations to develop more efficient monitoring programmes, assessment of indicator performance for different management goals, and the costs and benefit of legislation. Multi-model ensembles are being developed in cases where many models

* Corresponding author.

E-mail address: kieran.hyder@cefas.co.uk (K. Hyder).

exist, but model structures are very diverse making a standardised approach of combining outputs a significant challenge, and there is a need for new methodologies for describing, analysing, and visualising uncertainties. A stronger link to social and economic systems is needed to increase the range of policy-related questions that can be addressed. It is also important to improve communication between policy and modelling communities so that there is a shared understanding of the strengths and limitations of ecosystem models.

Crown Copyright © 2015 Published by Elsevier Ltd. All rights reserved.

1. Introduction

Marine legislation is becoming more complex as a consequence of increasing and more diverse use of the sea [1]. Commitments to marine ecosystem-based management that influence the UK are specified in national and regional legislative frameworks including the Marine Strategy Framework Directive (MSFD) [2], Common Fisheries Policy (CFP) [3], and the Water Framework Directive (WFD) [4]. However, the funding to provide the empirical evidence base that underpins monitoring, assessment, and management in support of these policies is decreasing in relative terms, requiring increasingly cost-effective decision tools for operational management and scenario planning. The key requirements for decision-makers are to understand links between human and environmental pressures and the state of the environment, to determine suitable management measures to meet objectives, to track progress in relation to those objectives, and to assess the performance of management options based on their environmental, social and economic consequences [5–7]. Shelf-seas community and ecosystem models (hereafter termed ecosystem models) can help to meet these requirements. Specific examples of contributions could include testing the sensitivity of indicators, increasing the cost-effectiveness of monitoring programmes, and supporting practical application of theoretical concepts like maximum sustainable yield (MSY).

Ecosystem models often differ fundamentally from models of physical systems because ecosystem dynamics are rarely directly governed by physical laws alone, but result from complex biological feedbacks requiring some form of approximation. Thus, it is usually important to embrace model diversity to account for uncertainty about the most appropriate model structure [8]. Consequently, multi-model ensemble approaches similar to that used by the Intergovernmental Panel on Climate Change (IPCC) for climate projections [9] can be used to convey uncertainty that results from differences in structure; an approach that is starting to be applied to advice on the management of fisheries [8,10].

Ecosystem models could make a much greater contribution to the evidence base that underpins policy development and decision-making, because they allow a priori testing of policies and management scenarios and quantification of the risk and uncertainty. In most cases, it is impossible to assess the performance of policies and potential management measures without models. For models to fulfil a greater role in policy development and decision-making, and for the associated advice to be treated as credible, salient and legitimate, the modelling approaches used need to be more transparent, verifiable, and repeatable than they are at present.

Ecosystem models are increasingly used in support of marine environmental assessment, management, and policy development in other parts of the world including the USA and Australia (e.g. [11,12]), but are not routinely used in the UK and Europe. In this paper, the prospects for increasing the contribution of community and ecosystem models to the evidence base that underpins assessment, management and policy support is assessed. Focussing on the UK shelf-seas community and ecosystem modelling

capability, the range of models available are reviewed, actions expected to increase the uptake and use of these models in environmental management are identified, and priorities for model development, application and presentation are highlighted.

2. UK ecosystem modelling capability and its impact on policy

Many different global marine ecosystem models have been developed [13] and extensive intercomparisons have been made [14], but here the focus is on regional models (e.g. shelf-wide, regional sea) as these have the most direct relevance for application to UK marine environmental policy and management including regulation. UK institutes and universities already use many classes of models that represent different components of the ecosystem (Fig. 1). These range from models of biogeochemistry and low trophic levels (e.g. [15]) to size-based approaches (e.g. [16–19]) and models of the whole food web (e.g. [20,21]). Some ecosystem models have been coupled to physical models and aim to represent the entire system from physics to fishers [22]. Models vary in structure and parameterisation since they have been developed to address different questions by researchers with different philosophies and approaches. For example, ERSEM was originally developed as an end-to-end ecosystem model to study nutrient cycling and planktonic ecosystem dynamics [15], the Population-Dynamical Matching Model (PDMM) (e.g. [23,24]) was constructed to develop theoretical understanding of food-web patterns and biodiversity [25,26], and Ecopath with Ecosim (EwE) to assess the impacts of fisheries on food webs and consequences for fisheries (e.g. [27]).

At least fourteen different marine ecosystem models are being used in the UK (Table 1 and model summaries provided at <http://www.masts.ac.uk/research/marine-ecosystem-modelling/>). Few of these models have directly influenced or routinely supported management and policy development, but many are likely to have influenced societal and scientific perceptions about the state of the marine environment. This has had an indirect influence on the emphasis given to ecosystem considerations in contemporary policy (e.g. [28–31]). As policy-making is normative and reflects societal values, alongside the evidence base [32], it is often difficult to ascribe direct links between models and decisions. However, there are some good examples including predicting harmful algal blooms, eutrophication, and comparisons between targets for environmental legislation as explained below.

Operational forecasting and monitoring of water quality enables timely interventions by both stakeholders and the agencies responsible for public health. The AlgaRisk monitoring tool is a prototype that provided warnings of algal blooms to support the statutory obligations of the Environment Agency [33,34]. This tool combines data from an operational physical-biological coastal model with satellite observations, and the results are available through an internet portal where users can visualise both model output and observations (<http://www.neodaas.ac.uk/multiview/pa/>). A demonstration AlgaRisk service was implemented in 2008 to support the European Union Bathing Waters Directive.

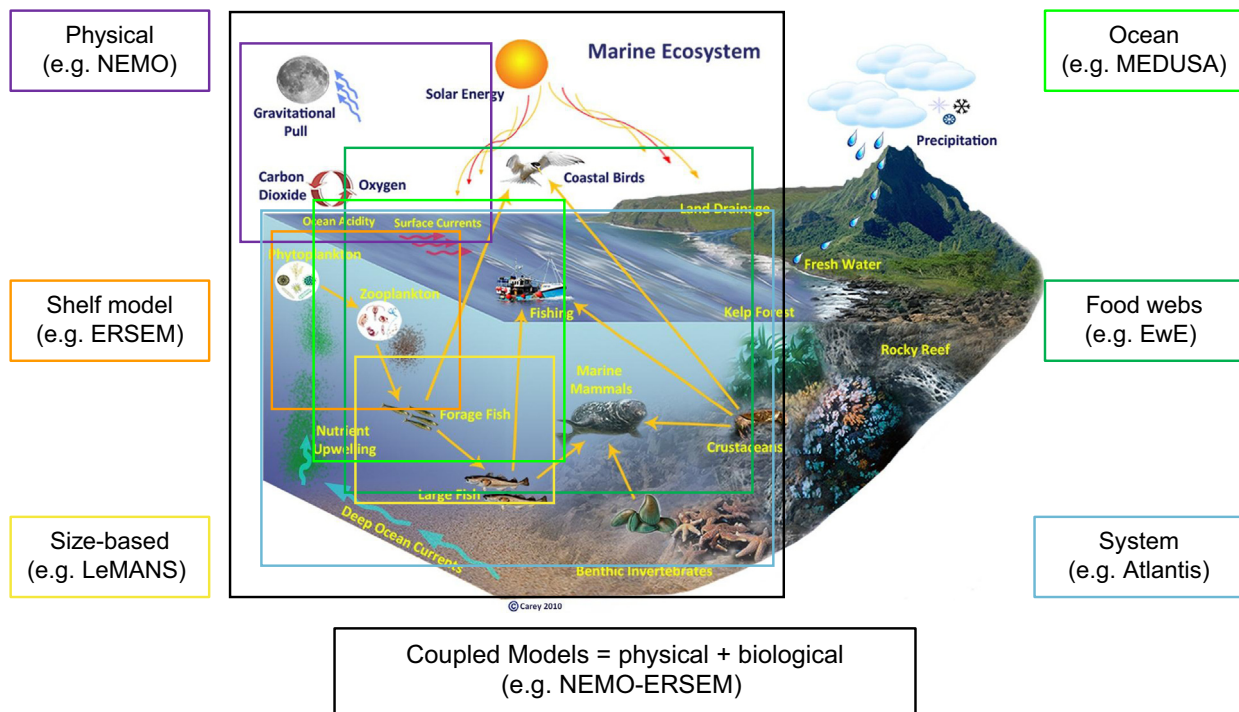


Fig. 1. Categories of ecosystem models and the parts of the ecosystem that they include.

Detection and diagnosis of eutrophication is required for a range of EU legislation (e.g. MSFD [2], WFD [4]) and by the OSPAR Convention [35]. Following the first assessment of eutrophication for OSPAR, the Netherlands and Germany identified eutrophication problem areas in their marine waters and alleged that inputs of nitrogen from the UK made a significant contribution. The OSPAR Eutrophication Committee tasked the Intersessional Correspondence Group for Eutrophication Modelling (ICG-EMO) to undertake modelling based on OSPAR riverine nutrient reduction scenarios and trans-boundary nutrient transport [36,37]. This work involved the application of seven ecosystem models by different institutes for pre-defined scenarios, using the same forcing, validation data, methods, and post-processing procedures. The resulting multi-model ensemble was used to assess uncertainty, which substantially enhanced the overall credibility of the results reported to the OSPAR Eutrophication Committee. Their subsequent influence on OSPAR decision making was far greater than would have been achieved by one national source. This modelling work was also used as supporting evidence in a case where the UK successfully defended against the European Commission in the European Court of Justice (Case C-390/07).

Advice on fisheries management is routinely supported by single-species modelling through the UK contribution to the work of ICES assessment groups. Ecosystem models are less widely used, but have been adopted to provide advice on the prospects for meeting single-species management targets simultaneously, and assessing the trade-offs between meeting targets for fisheries management and conservation. For example, three different models have been used to support advice on whether meeting MSY targets for fish in the North Sea under CFP [3] would be sufficient to meet a proposed target for the Large Fish Indicator (LFI) under Descriptor 4 of the MSFD [2,38]. It was found that, even though the rationale underlying the two targets is very different, they were indeed compatible with each other within the uncertainty of the combined model data (Axel Rossberg, pers. comm.).

3. Challenges for the uptake of ecosystem modelling by policy makers

3.1. Producing the right information from ecosystem models to inform policy

Policy questions are generally formulated much more broadly than scientific hypotheses [7], so there can be a mismatch between policy needs and the specific outputs produced by models. For example, the Defra Marine and Fisheries Evidence Plan [6] has the high level policy goal “to secure healthy food supplies delivered by a more sustainable fishing industry” that comprises of many different evidence needs including “reducing the adverse impact of commercial fishing”. This particular evidence need is subdivided into research needs including “developing an ecosystem approach to fisheries management through evaluating the impacts of different management scenarios”. To maximise the utility of models, high level policy goals need to be translated into evidence needs and matched against scientific questions that can be addressed using models.

Model outputs also need to be expressed in a form that is meaningful to policy makers. Knowledge of science, evidence, and policy is required to achieve this, so it is important that policy makers work closely with modellers to ensure a common understanding of, and to maximise the benefits from models. For example, policy questions are often framed in terms of socio-economic consequences, but there is often no simple way to express ecosystem model outputs in this way. Modification or development of models to allow assessment of the impact of different management measures on ecosystems in biological, social and economic value will increase the prospects for use (e.g. [39]).

3.2. Confidence in ecosystem model products

Lack of confidence in ecosystem model products may reduce their uptake by decision-makers. In contrast, managers routinely

Table 1
UK ecosystem modelling capability and impact (existing and potential). EM1–EM3 are biogeochemical formulations, EM4–EM7 are food-web formulations. EM8–EM14 are size-based formulations

Name	Description	Impact
EM1 European Regional Seas Ecosystem Model (ERSEM)	ERSEM is a lower-trophic level model designed to represent the biogeochemical cycling of carbon and nutrients (N, P, Si, O ₂ , Fe) as an emergent property of ecosystem interaction [15,78]. It is coupled to a number of hydrodynamic models for the north-east Atlantic. It has been validated against in situ data (e.g. [79]) and satellite ocean colour. In general predictions are reasonable for temperature, salinity, nutrients, oxygen, nutrients, but less good for chlorophyll and plankton, with predictions becoming less accurate at higher trophic levels [79]. Models capture seasonality well and can predict at spatial scales of order > 50 km ² .	ERSEM has been used to assess shelf seas water quality and climate impact, ocean acidification, eutrophication, trophic amplification, and to assess potential climate impacts on harmful algal blooms, fisheries, fisheries economics and food security. For future use, the model is being developed to quantify 'blue carbon', assess nutrient budgets, and simulate changes in ecosystem function and the consequences of such changes in the context of ecosystem services.
EM2 GETM-ERSEM-BFM	This is a coupled hydrodynamic and biogeochemical model that is based on the cycling of carbon and nutrients. It represents phytoplankton, zooplankton, bacteria, macroalgae and filter feeder larvae, and has a coupled benthic system. It is available in a North Sea setup and a north-west European shelf setup that have been validated using chlorophyll, SPM, temperature, and ship-based benthic data [80].	The model has been used to investigate eutrophication and riverine nutrient transport, potential impacts of large-scale macroalgae farms, potential impact of climate change and trawling, ecosystem indicators, deep chlorophyll maximum production, <i>Phaeocystis</i> blooms, and potential impact of large-scale wind farms. In future it could be used to attribute causes of change, optimise monitoring programme, assess impacts of wind farms, tidal farms, macroalgae farms, nutrient reduction scenarios, trawling, and thermal plumes, within the context of a changing environment.
EM3 Model of Ecosystem Dynamics, carbon Utilisation, Sequestration and Acidification (MEDUSA)	MEDUSA is intermediate complexity model of lower-trophic level plankton ecosystems that is typically run within a global earth system model context to address the biogeochemical response to anthropogenic driven changes (including ocean acidification) in the oceans [81]. It has been evaluated at the global scale using observational nutrient, chlorophyll and carbon cycle fields. In general, simulations of nutrients, carbon and primary production are reasonable, though less accurate for chlorophyll. MEDUSA was selected from a UK-wide group of models to be the marine biogeochemical component of the UK Earth System Model (UKESM1) that will be used in IPCC AR6 [14].	The model is currently used at a range of resolutions (up to 1/12 th -degree) to study global-scale ocean biogeochemistry and marine productivity. It is also used to make future projections of ocean biogeochemistry and acidification at the global-scale. In future, the model will provide regional predictions addressing policy issues relating to vulnerability, resilience, and adaptation to climate change. It will also be used (within UKESM1) across the suite of UK simulations submitted to IPCC AR6.
EM4 Population-Dynamical Matching Model (PDMM)	The PDMM is a simple theoretical ecosystem model that can represent typical temperate marine shelf communities, covering species of all sizes from phytoplankton to large fish. The model constructs complex and population-dynamically stable ecological model communities by mimicking the community assembly process of successive invasion. The model can reproduce size-abundance relations, distributions of species richness, species-size distributions, and key patterns in food-web [25].	The model has been used to understand mechanisms controlling size-abundance relationships, verify the theory of food-web structure, assess the Large Fish Indicator (LFI), and study biodiversity-production relationships for fish. In future, the model could be used to assess the relationship between biodiversity and ecosystem function, and the long-term implications of fisheries management strategies to reach MSY for multiple interacting stocks.
EM5 Strathclyde end-to-end ecosystem model (StrathE2E)	StrathE2E models the dynamics of nitrogen in ecosystem components including detritus, inorganic nitrogen in solution, plankton, benthos, fish, birds and mammals. Key physical, geochemical and biological processes which occur in the sea and seabed sediments are included [82]. Parameters were computationally fitted for a model of the North Sea to minimise the discrepancy between observed and modelled annual cycles and averaged abundances, production rates, and feeding fluxes [82].	StrathE2E has been used to simulate fishery yields in relation to harvesting rates, trophic cascades, sensitivity of MSY to changes in the environment, and implementation of a discard ban. In future, it could be used to assess sensitivity of fisheries to ocean acidification, disaggregate the effects of environment and fishing, compare observed fishery yields and MSY, project cumulative effects of harvesting and environmental change, and the ecological effects of the discard ban measures.
EM6 Ecopath with Ecosim (EwE)	EwE is an ecosystem modelling framework that quantifies food-web and fishery interactions. Biological components and fishing fleets can be described, and information on landings, discards and economics can be included. The 'core' of the model is determined by specifying who eats (or catches) who and how much. Models have been developed for many regions and there is a strong research community with quality standards being established. Models exist for North Sea, Celtic Sea, Western English Channel, Eastern English Channel, English channel, West Coast of Scotland, Deep West Coast of Scotland, Clyde Sea and Irish Sea, some of which have been calibrated against 20–30 years of data.	EwE has been used to evaluate the trade-offs among fishing strategies in relation to sustainable fishing and mixed fisheries, assess relative impact of fisheries and climate, investigate closed area management, evaluate impact of aggregate dredging, model dynamics of gadoid and demersal fish, and assess ecosystem based management. In future it could be used to assess the spatial impacts of fisheries and climate on the structure and function of ecosystems; quantify the performance of different management strategies; and evaluate the benefits of spatial management policies (e.g. MPA) and impacts of pressures (e.g. oil and gas) on ecosystems.
EM7 Atlantis	Atlantis is a modelling framework that contains a biophysical model that tracks nutrient flows and models consumption, production, migration, predation, recruitment, habitat dependency, and mortality. The physical environment is represented by the major geographical and bioregional	Atlantis models are being developed for the North Sea and English Channel that could be used to examine interactions between fisheries, wind farms, MPAs and climate change. The Atlantis framework has been used more extensively in other parts of the world for ecosystem based management (see

Table 1 (continued)

Name	Description	Impact
	features, and the biological model components are replicated at each depth. Atlantis also includes a detailed exploitation sub-model that is focused on the dynamics of fishing fleets and can address the impact of pollution, coastal development and broad-scale environmental change, in terms of economics, compliance decisions, and exploratory fishing and other complicated real world concerns such as quota trading.	[12] for a general review).
EM8 Strathclyde spatial population dynamics model (StrathSPACE)	StrathSPACE simulates the spatial and temporal dynamics of a single-species population in terms of birth, death, growth and movement of fish [83]. It has been calibrated by tuning a small number of key parameters to minimise error. In each case, the tuned model has then been compared with other independent data that were not involved in the tuning to check for compatibility.	The model has been used to address hypotheses about the mechanisms governing dynamics of copepods [84], and various fish species including cod [85] and haddock [86]. Model outputs contributed to development of the Cod Recovery Plan in the North Sea [87]. In future, it could be used for blue whiting, copepods, sand eels, and scallops
EM9 Coupled Community Size-Spectrum Model (CCSSM)	CCSSM represents the size and abundance of organisms in two coupled size-structured food chains, one based on predation and supported by primary production, and one based on energy sharing and supported by detritus [16]. Species are not represented explicitly. Predictions of size-spectrum were validated in the North Sea by comparing model predictions with empirical data on the size structure of pelagic predators and benthic detritivores [16].	Applications of this model have included the assessment of fishing impacts on community size structure and abundance in the North Sea [16], the effects of coupling pelagic and benthic food webs on responses to fishing, and prediction of the medium- and long-term effects of climate change on fish production at regional and global scales [18].
EM10 Species Size-Spectrum Model (SSSM)	SSSM is a highly simplified size-based description of the dynamics of marine species, and is unique in the fact that no assumptions about stock-recruitment relationships are made [88]. The SSSM has been shown to reproduce known classical effects at size-spectrum level [88].	After a more comprehensive validation, it could be used to inform policy makers about high-level ecosystem responses to anthropogenic pressures.
EM11 Multispecies size spectrum ecological modelling in R (MIZER)	MIZER was developed to represent the size and abundance of all organisms from zooplankton to large fish predators in a size-structured food web. An R package has been developed for application of the multi-species size spectrum model to a wide range of systems, which also contains documentation on the model equations and processes. The model provides predictions of the abundance of each species at size, and has been validated for the North Sea [17].	The model has been used to assess ecosystem responses to fishing and to determine whether meeting management targets for exploited North Sea populations will be sufficient to meet proposed Marine Strategy Framework Directive targets for biodiversity and food web functioning [17]. This modelling framework is being developed for use in management strategy evaluation and in a risk assessment framework.
EM12 Strathclyde length-structured partial ecosystem model (FishSUMS)	FishSUMS represents the population dynamics of a set of predator and prey species. For each species, the model predicts biomass by length class and includes growth, reproduction, density-dependent mortality, and losses due fishing and predation. The model produces biomass, length distributions, annual recruitment, catch, and landings. The cod-focused North Sea model has been validated against ICES stock assessment biomass, recruitment, and landings, and by comparing length distributions with IBTS survey data [89].	The model has been used to simulate cod yields and MSY in relation to harvesting rates on other species, particularly herring [89], the historical North Sea LFI and its response to changes in fishing, and changes in fish diet and biomass fluxes in the North Sea. In future, the model could be used as a length-based multispecies stock assessment tool, to make comparisons of fishery yields and MSY, to compare top-down and bottom up processes, and effects of alternative discard ban measures.
EM13 Fish community size-resolved model (FCSRM)	FCSRM represents an ecosystem including fish populations resolved by species and body size, fishing mortality, and zooplankton is included as a food source. The model predicts the types of fish communities that might coexist. This is a dynamic ecosystem size-based model [23] and a representation of the North Sea fish community has been calibrated and validated [17].	The model has been used broadly to advance ecological theory and to understand how and why ecosystems respond to fishing pressure. The model will continue to be used to address questions about the ecosystem response to different types of fishing, and competing management measures.
EM14 Length-based Multispecies Analysis by Numerical Simulation for the North Sea (LeMANS)	LeMANS is a size-structured multi-species model of a fish community with a realistic distribution of life-history attributes [19]. This approach differs from other size-based models as it maintains both the species identity and the individual population size structure. The model was validated by using fish community properties, biomass estimates from surveys North Sea, and comparisons with six assessed stocks [90]. An ensemble approach has been implemented that are screened against ICES abundance data to produce models that are consistent with data [57].	The model has been used to assess whether fishing preserves biodiversity [90]. In future it could be used in risk-based decision support including the trade-off between yield and risk of different harvest strategies in a multi-species fish community. Other potential uses include assessment of uncertainty in multi-species reference point estimates, trade-offs in fleet management, multi-species harvest control rule evaluation, and assessment of signal to noise ratios for fish community indicators.

accept results from single-species fish stock assessment models, despite uncertainties. The contrast may exist because stock assessment models are embedded in a well-established process, and there is international political acceptance of their use as the basis of advice, a good understanding of the models, and confidence in the outputs and their interpretation through quality assurance by scientific experts (e.g. ICES). In many cases, expert judgement is required to interpret the range of model outputs and these procedures can appear opaque to policy makers and lack legitimacy. Expert groups are needed that provide impartial advice on the use of ecosystem models, maintain quality standards for models, publish key validation runs, and provide clear output that can be used by decision makers (e.g. ICES Working Group on Multispecies Assessment Methods [40]). The UK Earth System Model 1 project builds on the iMARNET experience [14] to provide a common framework for marine biogeochemistry models to sit within and, as such, provides an example of how a community can be united around a common framework with common standards.

3.3. Visibility and access to ecosystem model products

Models are often developed by the research community to answer scientific questions and are then used by modelling experts to help decision-makers [11,12,41]. For ecosystem models, this process is generally neither robust nor transparent due to the lack of visibility of existing models, difficulties accessing model products, and the absence of documentation of model metadata. This contrasts with the current initiatives on data management and data standards that provide public access to metadata catalogues and databases in order to maximise the use of existing data, and may be due to the volume and complexity of model products. However, this lack of visibility can lead to the false impression that models are not suitable for decision making.

Policy makers have often called for a “*decision support toolbox*” comprising models that can be used interactively to explore different options when negotiating and formulating policies [42,43]. Complex ecosystem models can be impractical in this context, as they generally have long runtimes, require trained operators, and produce ‘big data’. It is therefore an important aim to increase transparency, and make model products available through web portals (e.g. Copernicus Prototype Marine Core Service – <http://www.myocean.eu/>, Marine OPEC – <http://www.portaldev/marineopec.eu>) and include model products in tools designed for use by evidence and decision-making communities (e.g. EMECO – <http://www.emecodata.net/>).

3.4. Development of ecosystem models and methods for understanding uncertainty

The quantification of uncertainty has clear importance in policy [44] yet uncertainty assessments are open to a range of interpretations that may lead to a different outcome (e.g. [45]) and communication of uncertainty can have a large impact on the decision making process (e.g. [46]). Being able to communicate uncertainties presupposes knowing what they are and this is no simple matter: ecosystem models are often extremely complex and associated with many different uncertainties. There are many different classifications of uncertainty, but a simple example relevant to marine ecosystem modelling that has been used in the context of climate change climate includes: ontological (related to underlying processes); epistemological (related to observations and model predictions); methodological (related to model structure); and axiological (related to the world view of the research) [47]. Ontological uncertainties are often accounted for through expert knowledge, and epistemological uncertainties are generally incorporated through assessment of model predictions and

knowledge of the observing system.

In the context of methodological uncertainty, there are complex sets of challenges surrounding parameterisation, validation, data sets, uncertainty, visualisation, and ecosystem modelling methods that require further development. These challenges are significant, and a contrast to the physical components of earth system models that are based on well-understood physical laws and scalable processes (e.g. global predictions can be downscaled to regional seas), where the focus of development has shifted towards smaller scales, resolution, speed and numerical implementations. There is also a mismatch between the timescales associated with production of advice (weeks to months) and model development required where models do not produce the outputs needed (years to decades). Hence, there is need to anticipate how models might be used in future in order to produce advice on the timescales required.

New statistical methods are needed to analyse uncertainty in ecosystem (multi-)model ensembles that can be presented to decision-makers in order to understand the risk associated with a particular decision. The successful communication of uncertainties to decision-makers is important for transparency and robust decision-making, thus ensuring management efforts are not misplaced [48]. New visualisation methods are therefore needed to build trust and effectively communicate the outputs and associated uncertainty of ecosystem models to decision-makers and would increase the uptake of ecosystem models.

4. Increasing the use of ecosystem models in decision making

The question of how to increase the uptake and use of community and ecosystem models to support marine environmental management in the UK and Europe is addressed in this section. The conclusions are based on discussions which took place at a two day workshop that brought together 55 people from 23 organisations across the UK that included advisors, assessors, biologists, social scientists, economists, modellers, statisticians, policy makers, and funders. To understand how to increase the contribution of the models to support policy, it was important to identify policy needs and match them against models that might support these needs. The outcomes included identification of potential quick wins and gaps in existing ecosystem modelling capability in the context of biological sustainability, social benefits, and economic value.

4.1. Understanding the policy and management drivers that can be addressed using ecosystem modelling

Climate change, biodiversity, and marine evidence needs have been identified by the UK Government [5,6,49,50] and were translated into tractable modelling questions. These were categorised into the following headings: natural variability and monitoring, management measures, ecosystem goods and services, Good Environmental Status (GES) targets under MSFD [2] and pollution, and environmental change and climate adaptation (Table 2). Since it is often unclear how models have and could be used to support policy, examples of the impact of models on policy and management were identified (Table 1). A simple mapping exercise was then used to understand the potential contribution of ecosystem modelling in the policy and management arena through comparing available models against evidence needs. The utility (ranked qualitatively as “High”, “Medium”, or “Low”) and time-scale for development (1 year, 5 years, 10 years) of each type of model to deliver policy relevant goals were then used to identify:

- Gaps – new models or long-term development required.

Table 2

Policy questions derived from evidence plans [5,6,49,50] split into 5 topics and reformulated for modellers.

Policy area	Modelling questions
1. Natural variability and monitoring	<p>A. What are the spatial and temporal scales that a particular model can address and do these match the policy requirements?</p> <p>B. How long would it take to quantify the uncertainty of model predictions?</p> <p>C. Can the model distinguish between relative performances of candidate environmental indicators?</p> <p>D. Can the model identify high risk areas?</p> <p>E. Can the model contribute to assessing the potential efficiency gains from redesigning monitoring programmes?</p> <p>F. Does the model have a capacity to blend models and data to get best estimate of state of system e.g. data assimilation, parameter fitting, tuning?</p> <p>G. Can the model be used to inform engineering the ecosystem to reach the state that you require?</p>
2. Management measures	<p>A. What are the expected changes in habitat extent and condition resulting from environmental change for a given network of Marine Protected Areas (MPAs)?</p> <p>B. How effective are given networks of MPAs in achieving their management objectives?</p> <p>C. How will the network of MPAs deliver objectives and outcomes in relation to environmental impacts, ecosystem structure and function?</p> <p>D. What are efficient programmes of measures to achieve Marine Strategy Framework Directive (MSFD) targets?</p> <p>E. Can the effects of changes (pressure and response) be attributed to individual and cumulative effects, and the risk (uncertainty) associated with this?</p> <p>F. What are the management strategies for exploitation of mixed fisheries to achieve Maximum Sustainable Yield (MSY)?</p> <p>G. What are the impacts of landing obligations on MSY objectives through e.g. food web interactions?</p> <p>H. What are the effects of changes in fisheries management on the environment, in particular through food-web effects?</p> <p>I. What is the risk of population decline or regional extinction of valuable, endangered or vulnerable species from CFP reform?</p>
3. Ecosystem goods and services	<p>A. What are the socio-economic impacts of given networks of MPAs?</p> <p>B. What are the costs and benefits of MSFD/Water Framework Directive (WFD)/Marine Spatial Planning (MSP) implementation?</p> <p>C. What are the interactions between different sectors and ecosystem services?</p> <p>D. What are the marginal costs/values of changes in ecosystem services?</p> <p>E. How are different ecosystem functions and services dynamically coupled?</p> <p>F. How are different ecosystem services and benefits coupled in a socio-economic system?</p>
4. Good Environmental Status (GES) target and pollution	<p>A. Can the model contribute to the ecosystem approach through interactions with other models?</p> <p>B. What is the responses of indicators to specific management measures for MSFD descriptors?</p> <p>C. Are there more effective MSFD indicators than those currently proposed/in use?</p> <p>D. What are the impacts of pollutant dispersants in the marine environment, their impacts on marine ecosystems?</p> <p>E. How can effectiveness of pollutant dispersants be maximised?</p> <p>F. What are the effects of pollution on the marine environment?</p> <p>G. What are the interactions between biodiversity (Descriptor 1) and other descriptors of GES Status under MSFD?</p> <p>H. What are the interactions between commercial fish (Descriptor 3) and other descriptors of GES under MSFD?</p> <p>I. What are the interactions between food web structure (Descriptor 4) and other descriptors of GES under MSFD?</p> <p>J. What are the interactions between sea floor integrity (Descriptor 6) and other descriptors of GES under MSFD?</p> <p>K. Are there alternative useful indicators that can be derived from models but not from direct observation?</p>
5. Environmental change and climate adaptation	<p>A. What are the impacts of regional scale climate patterns on ecosystem state (GES), and can these be valued?</p> <p>B. Can a change in environmental status be attributed to a combination of drivers?</p> <p>C. Which aspects of environmental status are sensitive to climate change?</p> <p>D. What are the impacts of non-native species on ecosystem state (GES)?</p> <p>E. What are the impacts of harmful species on human and animal health?</p> <p>F. How are detailed local effects of local pressures captured?</p> <p>G. What are the impacts of ocean acidification on ecosystem state (GES)?</p> <p>H. What are the impacts of changes in shelf seas biogeochemistry on ecosystem state (GES)?</p> <p>I. What is the impact on land/sea transition zone?</p> <p>J. Can the risk or impact from artificially introduced non-native species be modelled?</p> <p>K. What are the impacts of wind farms and other offshore structures?</p>

- Quick wins – short development time and high utility.
- Ensembles – many models and short development times.

A matrix of future ecosystem model impact was developed for the UK (Table 3). This highlighted that there were a number of areas where we have many models that can be quickly developed to address questions (e.g. 3B – “What are the costs and benefits of MSFD/WFD/Marine Spatial Planning (MSP) implementation?”), some areas that few models can address (e.g. 5D – “What are the impacts of non-native species on ecosystem state from changes in the

environment or transport opportunity?”), and some areas where it was difficult to assess if ecosystem models have any potential (e.g. 3F – “How are different ecosystem services and benefits coupled in a socio-economic system?”).

4.2. Identifying potential quick wins, ensembles and gaps for ecosystem modelling

The quick wins, potential ensembles and gaps were identified for each theme, with the management measures and ecosystem

Table 3
Scoring of ecosystem models (model names as in Table 1) and their ability to address policy questions (defined in Table 2). Scoring system: 0=not possible, 1= within ten years, 2=within five years, 3=within one year (darker grey indicates higher score), and diagonal hashing is not possible to assess here.

Question	EM1	EM2	EM3	EM4	EM5	EM6	EM7	EM8	EM9	EM10	EM11	EM12	EM13	EM14
1A	3	3	3	3	3	3	2	3	3	3	3	3	3	3
1B	2	2	2	2	3	3	1	3	3	3	3	3	3	3
1C	3	3	3	3	3	3	3	3	3	3	3	3	3	3
1D	3	3	3	1	3	3	2	3	1	1	1	1	1	1
1E	3	3	2	2	2	2	2	2	2	2	2	2	2	2
1F	3	2	2	0	3	3	3	3	3	2	3	3	2	2
1G	3	3	3	3	3	3	3	2	3	3	3	3	3	3
2A	3	3	2	1	1	3	2	1	1	1	1	1	1	1
2B	3	3	2	1	1	3	2	1	1	1	1	1	1	1
2C	3	3	2	1	1	3	2	1	1	1	1	1	1	1
2D	3	3	2	2	3	3	2	2	2	2	3	2	2	3
2E	2	2	2	2	3	3	2	2	3	2	3	2	2	3
2F	0	0	0	3	3	3	2	0	3	3	3	3	3	3
2G	0	0	0	3	3	3	2	3	3	3	3	3	3	3
2H	3	3	0	3	3	3	2	0	3	3	3	3	3	3
2I	0	0	0	0	0	2	2	0	0	0	0	2	2	2
3A	3	3	2	0	0	2	2	3	0	0	0	0	0	0
3B	3	3	2	3	3	3	2	3	3	3	3	3	3	3
3C	3	3	2	3	3	3	2	0	3	3	3	3	3	3
3D	3	3	3	3	3	3	2	0	3	3	3	3	3	3
3E	3	3	3	3	3	3	2	0	3	3	3	3	3	3
3F	3	3	3	3	3	3	2	0	3	3	3	3	3	3
4A	3	3	3	2	3	3	2	2	3	2	2	2	2	2
4B	3	3	3	3	3	3	2	3	3	3	3	3	3	3
4C	3	3	3	3	3	3	2	2	3	2	2	2	2	2
4D	2	2	2	2	3	3	1	1	0	0	0	0	0	0
4E	2	2	2	0	0	0	0	0	0	0	0	0	0	0
4F	3	3	3	3	3	3	3	1	0	0	0	0	0	0
4G	3	3	3	3	3	3	3	3	1	1	1	1	1	1
4H	0	0	0	3	3	3	2	2	2	3	2	2	2	2
4I	3	3	3	3	3	3	3	2	2	2	2	2	2	2
4J	3	3	0	3	3	3	2	2	0	0	0	0	0	0
4K	3	3	3	3	3	3	3	3	3	3	3	3	3	3
5A	3	3	2	3	3	3	2	3	3	2	2	3	2	2
5B	3	3	2	3	3	3	2	3	3	2	2	3	2	2
5C	3	3	2	3	3	3	2	3	3	2	2	3	2	2
5D	0	0	0	0	0	3	1	0	0	0	0	1	0	0
5E	2	2	0	0	0	1	2	0	0	0	0	0	0	0
5F	2	3	1	0	0	3	2	3	0	0	0	0	0	0
5G	3	3	3	0	3	3	3	0	0	0	0	0	0	0
5H	3	3	2	0	3	1	2	0	2	2	2	2	0	0
5I	2	3	1	0	0	3	2	3	0	0	0	0	0	0
5J	0	0	0	2	0	1	1	2	0	0	2	2	0	0
5K	2	3	1	0	0	3	2	3	0	0	0	0	0	0

goods and services themes combined for this purpose (Table 4). A number of policy and management issues can be addressed immediately and are brought together under the following general headings: (1) attribution of change to underlying drivers; (2) integration of models and monitoring to develop more efficient monitoring programmes; (3) assessment of indicators and the interactions between legislative descriptors; and (4) cost-benefit of legislation (Table 4).

It was clear that multi-model ensembles could be used in some areas (Table 4), but the methods for delivering multi-model ensembles for ecosystems still need to be developed. The general methods for multi-model ensembles exist in the climate area [9], but ecosystem model structures are very diverse (e.g. food-web, size-based, nutrient cycling) making a standardised approach of combining outputs difficult. This is because it is difficult to relate the variables from different models (e.g. relating functional types to size-based groups) and this challenge increases at higher trophic levels. There are programmes underway to develop these methods (e.g. Marine Ecosystem Research Programme – <http://www.marine-ecosystems.org.uk/>) and includes the creation of a multi-model ensemble that builds on the ideas of Chandler [51]. The outputs are modelled using a hierarchical structure which separates individual and shared model discrepancies. This approach allows models with different outputs to inform one another through correlations and gives estimates of the true output as well as robust measurements of uncertainty. Additionally, it is possible to introduce a level to the hierarchical structure that groups models that have similar discrepancies, e.g. size-based models. Some examples of model intercomparison also exist (e.g. ocean biogeochemistry [14], nutrient transfer [36], fisheries [8]), but more work is required before multi-model ensembles can be used routinely to support policy development and management.

Potential gaps in existing ecosystem modelling capability were also identified including those relating to non-native species, disease transmission, ocean acidification, coastal zone management, marine protected areas, cumulative effects, socio-economics, and pollution and oil spills (Table 4). However, this assessment was done in the context of existing ecosystem modelling capability in the UK, and other methods exist internationally (e.g. MARXAN – <http://www.uq.edu.au/marxan/> – for marine protected areas, OSCAR – <http://www.sintef.no/home/SINTEF-Materials-and-Chemistry/About-us/Departments/Environmental-Monitoring-and-Modelling/OSCAR-Oil-Spill-Contingency-and-Response/> – for oil spills).

4.3. Developing the link between biological, social, and economic drivers for ecosystem management

Policy questions are often framed in terms of socio-economic value (e.g. Policy Area 3 in Table 2), but few ecosystem models express the outputs in these terms. Moreover, there are significant challenges in valuation of the marine environment and there is often a mismatch between the complexity of biological and economic models. The workshop identified a need to develop methods that use the outputs from ecosystem models to drive the valuation of ecosystem services dynamically.

Ecosystem services are the direct and indirect contributions of ecosystems to human well-being, and are made up of tangible goods (e.g. food and raw materials) and less direct and often more intangible services (e.g. the regulation of our climate and the remediation of waste) [52]. The changes in an ecosystem and how this affects value are important for policy development, with changes in ecosystem services determined from empirical data or using models. Often it is the trade-offs among the different services under alternate policies or management strategies that

Table 4

Potential for use of ecosystem model-derived products in addressing policy needs in terms of quick wins, possible multi-model ensembles (italics), and gaps that cannot currently be addressed.

Theme	Quick Wins	Gaps
Natural variability and monitoring	<ul style="list-style-type: none"> • <i>Distinguishing between the sensitivity and utility of different indicators.</i> • <i>Quantifying uncertainty.</i> • Integration of models with monitoring to increase efficiency. • Identifying current system state. 	<ul style="list-style-type: none"> • Improve the ability of models to capture inter-annual variability and long term trends.
Management measures, goods and services	<ul style="list-style-type: none"> • <i>Efficient programme of measures for achieving Good Environmental Status (GES).</i> • Impacts of landing obligations on Maximum Sustainable Yield (MSY) through food webs interactions. • <i>Management strategies for achieving MSY in a mixed fishery.</i> • <i>Effects of fishery management on food webs.</i> • <i>Cost-benefit of implementation of legislation (e.g. MSFD, Water Framework Directive – WFD, Common Fisheries Policy-CFP).</i> • <i>Marginal costs / values of changes in ecosystem services.</i> • <i>Links between ecosystem function and services.</i> 	<ul style="list-style-type: none"> • Assessing networks of Marine Protected Areas (MPAs) in terms of connectivity, achieving management objectives and socio-economics. • Cumulative effects. • Risk of decline of endangered species from CFP reform. • Coupling between ecosystem services and benefits in socioecological systems.
Good Environmental Status (GES) target and pollution	<ul style="list-style-type: none"> • <i>Sensitivity of indicators to management measures and identification of better indicators.</i> • <i>Effects of pollution on the marine environment.</i> • <i>Interdependencies between MSFD descriptors.</i> 	<ul style="list-style-type: none"> • Impacts of pollutant dispersants. • Interdependencies between different descriptors within MSFD. • Model interoperability – modular approaches.
Environmental change and climate adaptation	<ul style="list-style-type: none"> • <i>Regional scale climate impacts and their value.</i> • <i>Attributing change in ecosystems to environmental drivers and the systems response.</i> • <i>Impacts of changes in shelf-seas biogeochemistry on ecosystem state, function and services.</i> 	<ul style="list-style-type: none"> • Introductions and impacts of non-native species. • Animal and human disease. • Local effects of pressures. • Impacts of ocean acidification. • Impacts on the land-sea transition zone. • Impacts of geo-engineering. • Impacts of offshore structures.

determine the economic and social importance. The simplest way to use ecosystem models to help understand the changes in ecosystem services is to develop linkages between changes in ecosystem function and service. This has been done for Dogger Bank where indicators have been developed of changes in ecosystem services and the changes in the underlying ecological function [53].

There are a number of more complex ecosystem service frameworks, with one good example being the UK National Ecosystem Assessment Follow On (UKNEAFO [54]). UKNEAFO describes a set of strategic principles based on the adaptive management approach together with practical tools including models to inform the sustainable management of coastal and marine ecosystem services. A decision support system (DSS) was developed that adapted the Drivers–Pressures–State–Impact–Response (DPSIR) approach to assess changes in ecosystem services and their impact on human well-being, as coastal zones are increasingly affected by environmental change drivers and pressures [55]. This has highlighted key policy issues, and was adapted to include state changes and impacts specifically tailored to ecosystem services and their human welfare effects. Four main marine based scenarios which deviated from a baseline condition were explored and exposed to changes in selected environmental change (e.g. climate, socio-economic development, political, social and cultural drivers). A set of ecosystem change indicators consistent with the implementation of the MSFD were derived covering processes, intermediate and final ecosystem service delivery, in stock and flow terms [56]. The data needed for these indicators were drawn from national level observations and models. Given the uncertainty surrounding ecosystem functioning and the impact on overall biodiversity of some ecosystem changes, a number of modelling approaches were applied and tested. The UKNEAFO assessed formal models to

quantify changes in ecosystem service stocks and flows, and in particular the practicality of coupling land use change, estuarine and coastal and marine models.

The incorporation of feedback between biological, social, and economic systems can be difficult in an ecosystem services framework. This is an issue because feedback loops are important for making accurate predictions of the response of systems to management measures and are inherent in the DPSIR approach. Systems dynamics is an alternative approach that is gaining support in environmental economics and is used to model complex non-linear systems including the design and analysis of policy. Current knowledge of how the ‘system’ functions has been used to develop a number of simple conceptual models that may not always encapsulate the entirety of the system, but include significant components (e.g. key habitats, sub-systems, human uses for fishing or renewable energy). These simple conceptual models can help to define information needs to build more information-rich system models that may be quantitative (stochastic or deterministic) or qualitative (narrative-rich models). These enable exploration of the consequences of current or proposed policy for the delivery of ecosystem services and for maintaining the integrity of the system as a whole, where different models can be employed together and the approach is not prescriptive. Promising ‘wide spectrum models’ that can work across the natural–social science boundary include extended Ecopath with Ecosim models [31], End-to-End models, and Atlantis [11].

4.4. Methods for analysis and visualisation of model products

The requirement for uncertainty quantification has led to a move from optimising parameter sets that fit observations [17] to finding a range of possible solutions [57,58]. However, standard

methods of uncertainty analysis are difficult to conduct due to the complexity of ecosystem models and the computational power required to evaluate them (e.g. Markov Chain Monte Carlo [59]). These problems are not unique to marine ecosystem models and lessons can be learned from other disciplines including: fitting models to observations (e.g. [60]), examining structural uncertainty in decision models (e.g. [61]) and ensemble modelling (e.g. [62]).

There is an abundance of scientific literature assessing the methods used to resolve the linguistic uncertainties in communicating model output [63–65], but there is little guidance about visualising the outputs and uncertainty from complex models [66]. Many of the techniques used for data visualisation ignore the presence of uncertainties or are only able to depict one source of uncertainty at a time [67,68]. More recently methods have been developed to depict multiple uncertainties within a single visualisation, although efforts have been hindered by the presence of deep uncertainties and the challenges associated with disentangling various sources of uncertainty [66].

5. Future challenges for ecosystem modelling that encompass natural, social, and economic systems

A clear limitation to the development of policy-relevant ecosystem models is the maturity of the underlying science. The link between biodiversity, ecosystem function and the flow of ecosystem services is being addressed, but is not yet well enough understood or described to fulfil the requirements for management and policy advice [69]. Concepts that are underpinned by strong evidence are regularly questioned (e.g. global warming) and others accepted before the science is fully resolved. For example, biodiversity is often “protected” because of the assumed link between biodiversity and ecosystem function and services (MSFD) although in reality this link is complex, widely debated and often recognised as context dependant [69]. There is no absolute point at which a model is sufficiently advanced to support management and policy advice, as this depends on many political and societal factors as well as the development and presentation of the science. Consequently, clear communications between scientists, modellers, statisticians, managers and policy makers is important to build understanding of the capabilities of models and the associated uncertainties.

Ecosystem functions are believed to be reliant on the organisms that inhabit the ecosystem, but predicting the functionality and how it changes with different pressures is a significant challenge. However, these uncertainties do not prevent the development of models that include biodiversity or functionality based on knowledge of the species assemblages, but this does require understanding of the limitations of scientific knowledge of the drivers of these relationships. The relative uncertainty varies depending on the ecosystem service under consideration; for example, primary production is easier to address than detoxification of xenobiotics, for which we have less specific knowledge. Progress is being made and mapping of biodiversity, habitat type and related functions and service provisions is becoming more common in terrestrial systems [70], with more information on coastal and marine systems emerging. The valuation of service in marine systems is also more problematic since the benefits of marine ecosystem services provision are less tangible than in terrestrial systems and methods of valuation (both monetary and non-monetary valuations) are more difficult to apply [71]. Hence, providing a common (comparable) currency across terrestrial and marine system can be difficult. However, the application of ecosystem models will help to focus on the most urgent issues to be addressed.

Much environmental decision-making assumes smooth cause-effect relationships, but there is increasing evidence of regime shifts

at a number of different scales in both tropical and temperate marine ecosystems (e.g. [72–75]). Knowledge of ‘tipping points’ is empirical and conjectural, so their prediction is a huge challenge. Changes in global circulation will also affect shelf-models and represent another challenge over the next decade (e.g. [76]). Most models have to be constrained within defined spatial and temporal boundaries, and for natural systems focus on, for example, habitats, populations, or ecosystems. Social-ecological systems scales are more complex, partly because people who interact with marine systems live on the land, so operate on different scales to the natural systems they exploit. This scale mismatch presents a further challenge for modelling.

Coupled social-ecological systems suffer from ‘locked-in’ processes that have a profound effect on the potential options for their management. These factors can be modelled when they are properly understood but many feedback processes have not been identified as yet and can only be suspected from non-linear cause-effect behaviour, making them very difficult to model. All systems have rate limiting steps or choke points that can simplify modelling. Complex social-ecological system modelling has an added dimension, the ‘on-off’ behaviour of the decision-making process. This provides a challenge for ‘stock and flow’ models for example. Modelling the factors affecting human decisions is complex and culturally dependent, making predictions using models a significant challenge (e.g. fisher behaviour [77]).

6. Conclusions

These conclusions have been developed from this assessment of UK ecosystem modelling, but some of the challenges and solutions apply internationally. While some countries may at present be more comfortable with deploying ecosystem models to guide management and policy than others (e.g. Australia, USA), there is still a large gulf between modellers and decision-makers, and the full utility of ecosystem models has not yet been realised.

To increase the uptake and use of ecosystem models and better support marine environmental management and policy, it is important to

- Ensure that decision-makers know where and how ecosystem models can be used in the context of the limited resources for evidence generation.
- Build multidisciplinary communities of policy makers, data collectors, modellers, statisticians, and socio-economists that speak a common language and work together to develop, apply, review and compare ecosystem models.
- Define and employ rigorous quality standards to satisfy legal challenge in policy and management decisions that ensure model-derived products are available and robust.
- Put in place programmes to fill existing knowledge gaps that can only be addressed using contributions from models (e.g. linking biological sustainability, social benefits, and economic values, address the challenges of modelling dynamic systems).
- Maximise the pull-through of new modelling techniques to ensure that the latest science is being used to underpin decision-making.
- Encourage the development and use of new statistical methodologies and visualisation techniques, for inference from model ensembles and for the propagation, management and communication of uncertainty in general.

Acknowledgements

This initiative was led by Kieran Hyder (Cefas) and David Paterson (University of St Andrews) developed as a theme under the

Science Alignment Workgroup of the Marine Science Coordination Committee (MSCC – <https://www.gov.uk/government/groups/marine-science-co-ordination-committee>) in collaboration with the Marine Alliance for Science and Technology for Scotland (MASTS – <http://www.masts.ac.uk/>). MASTS is funded by the Scottish Funding Council (Grant reference HR09011) and contributing institutions. Kieran Hyder, Emma Defriez, Bernardo Garcia-Carreras, Ruairaidh McPike, John Pinnegar, Louise Rae, Stuart Rogers, Axel Rossberg and, Johan van der Molen were supported by the Defra project ME5428 (“Developing ecosystem modelling capability in the UK”) and Cefas Seedcorn funding under DP348. Icarus Allen, Paul Blackwell, Julia Blanchard, Michael Burrows, Johanna Heymans, Michael Heath, Douglas Speirs, and Michael Spence were supported by the Natural Environment Research Council and Department for Environment, Food and Rural Affairs (Grant number NE/L003279/1, Marine Ecosystems Research Programme). David Paterson received funding from MASTS and their support is gratefully acknowledged. Jennifer Houle was supported by a Beaufort Marine Research Award carried out under the Sea Change Strategy and the Strategy for Science Technology and Innovation (2006–2013), with the support of the Marine Institute, funded under the Marine Research Sub-Programme of the Irish National Development Plan 2007–2013. Robert Thorpe received financial aid from the European Commission (OCEAN-CERTAIN, FP7-ENV-2013-6.1-1; no: 603773). Steve Mackinson was supported by GAP2 (EU FP7 project, Grant agreement 266544) and the UK Department for Environment, Food and Rural Affairs (Defra) Project MF1228 “Linking Physics to Fisheries Management”. Simon Jennings was supported by the Department for Environment, Food and Rural Affairs (Defra) project “Integration of fisheries and environmental management” (MF1225). A special thanks to Louise Docherty for all her help with organisation of the workshop and to Claire Hedley for providing the underlying picture used in Fig. 1.

References

- [1] S.J. Boyes, M. Elliott, Marine legislation-The ultimate “horrendogram”: International law, European directives & national implementation, *Mar. Pollut. Bull.* 86 (2014) 39–47, <http://dx.doi.org/10.1016/j.marpolbul.2014.06.055>.
- [2] EU, Directive 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy (Marine Strategy Framework Directive), *European Parliament and Council of the European Union, Off. J. Eur. Union* 164 (2008) 19–40.
- [3] EU, Regulation (EU) No 1380/2013 of the European Parliament and of the Council of 11 December 2013 on the Common Fisheries Policy, amending council Regulations (EC) No 1954/2003 and (EC) No 1224/2009 and repealing Council regulations (EC) No 2371/2002; EC, *Off. J. Eur. Union* 354 (2013) 22–61.
- [4] EU, Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy, *European Parliament and Council of the European Union, Off. J. Eur. Commun.* 327 (2000) 1–72.
- [5] Defra, *Making the Most of our Evidence: A Strategy for Defra and its Network*, Department for Environment, Food & Rural Affairs, 2014.
- [6] Defra, *Marine programme evidence*, Department for Environment, Food & Rural Affairs (2013).
- [7] W.J. Sutherland, S. Armstrong-Brown, P.R. Armsworth, B. Tom, J. Brickland, C. D. Campbell, et al., The identification of 100 ecological questions of high policy relevance in the UK, *J. Appl. Ecol.* 43 (2006) 617–627, <http://dx.doi.org/10.1111/j.1365-2664.2006.01188.x>.
- [8] I.J. Stewart, S.J.D. Martell, Reconciling stock assessment paradigms to better inform fisheries management, *ICES J. Mar. Sci.* (2015), <http://dx.doi.org/10.1093/icesjms/fsv061>.
- [9] C. Tebaldi, R. Knutti, The use of the multi-model ensemble in probabilistic climate projections, *Philos. Trans. A Math. Phys. Eng. Sci.* 365 (2007) 2053–2075, <http://dx.doi.org/10.1098/rsta.2007.2076>.
- [10] A. Gardmark, M.L. Indegren, S.N. Euenfeldt, T.B. Lenckner, O. Eikinheim, B. Muller-Karulis, et al., Biological ensemble modeling to evaluate potential futures of living marine resources, *Ecol. Appl.* 23 (2013) 742–754, <http://dx.doi.org/10.1890/12-0267.1>.
- [11] E.A. Fulton, J.S. Link, Modeling approaches for marine ecosystem-based management, in: M.J. Fogarty, J.J. McCarthy (Eds.), *Marine Ecosystem Management: The Sea*, vol. 16, Harvard University Press, 2014, pp. 121–170.
- [12] E.A. Fulton, J.S. Link, I.C. Kaplan, M. Savina-Rolland, P. Johnson, C. Ainsworth, et al., Lessons in modelling and management of marine ecosystems: the Atlantis experience, *Fish. Fish.* 12 (2011) 171–188, <http://dx.doi.org/10.1111/j.1467-2979.2011.00412.x>.
- [13] J. Holt, J.I. Allen, T.R. Anderson, R. Brewin, M. Butenschön, J. Harle, et al., Challenges in integrative approaches to modelling the marine ecosystems of the North Atlantic: Physics to fish and coasts to ocean, *Prog. Oceanogr.* 129 (2014) 285–313, <http://dx.doi.org/10.1016/j.pocean.2014.04.024>.
- [14] L. Kwiatkowski, A. Yool, J.I. Allen, T.R. Anderson, R. Barciela, E.T. Buitenhuis, et al., iMarNet: an ocean biogeochemistry model inter-comparison project within a common physical ocean modelling framework, *Biogeosci. Discuss.* 11 (2014) 10537–10569, <http://dx.doi.org/10.5194/bgd-11-10537-2014>.
- [15] J.W. Baretta, W. Ebenhöf, P. Ruardij, The European regional seas ecosystem model, a complex marine ecosystem model, *Neth. J. Sea Res.* 33 (1995) 233–246, [http://dx.doi.org/10.1016/0077-7579\(95\)90047-0](http://dx.doi.org/10.1016/0077-7579(95)90047-0).
- [16] J.L. Blanchard, S. Jennings, R. Law, M.D. Castle, P. McCloghrie, M.-J. Rochet, et al., How does abundance scale with body size in coupled size-structured food webs? *J. Anim. Ecol.* 78 (2009) 270–280, <http://dx.doi.org/10.1111/j.1365-2656.2008.01466.x>.
- [17] J.L. Blanchard, K.H. Andersen, F. Scott, N.T. Hintzen, G. Piet, S. Jennings, Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model, *J. Appl. Ecol.* 51 (2014) 612–622, <http://dx.doi.org/10.1111/1365-2664.12238>.
- [18] J.L. Blanchard, S. Jennings, R. Holmes, J. Harle, G. Merino, J.I. Allen, et al., Potential consequences of climate change for primary production and fish production in large marine ecosystems, *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 367 (2012) 2979–2989, <http://dx.doi.org/10.1098/rstb.2012.0231>.
- [19] S.J. Hall, J.S. Collie, D.E. Duplisea, S. Jennings, M. Bravington, J. Link, A length-based multispecies model for evaluating community responses to fishing, *Can. J. Fish. Aquat. Sci.* 63 (2006) 1344–1359, <http://dx.doi.org/10.1139/f06-039>.
- [20] V. Christensen, C.J. Walters, Ecopath with Ecosim: methods, capabilities and limitations, *Ecol. Modell.* 172 (2004) 109–139, <http://dx.doi.org/10.1016/j.ecolmodel.2003.09.003>.
- [21] J.J. Heymans, M. Coll, S. Libralato, L. Morissette, V. Christensen, Global patterns in ecological indicators of marine food webs: a modelling approach, *PLoS One* 9 (2014) e95845, <http://dx.doi.org/10.1371/journal.pone.0095845>.
- [22] S. Libralato, C. Solidoro, Bridging biogeochemical and food web models for an End-to-End representation of marine ecosystem dynamics: the Venice lagoon case study, *Ecol. Modell.* 220 (2009) 2960–2971, <http://dx.doi.org/10.1016/j.ecolmodel.2009.08.017>.
- [23] M. Hartvig, K.H. Andersen, J.E. Beyer, Food web framework for size-structured populations, *J. Theor. Biol.* 272 (2011) 113–122, <http://dx.doi.org/10.1016/j.jtbi.2010.12.006>.
- [24] A.G. Rossberg, J.E. Houle, K. Hyder, Stock-recruitment relations controlled by feeding interactions alone, *Can. J. Fish. Aquat. Sci.* 70 (2014) 1447–1455, <http://dx.doi.org/10.1139/cjfas-2012-0531>.
- [25] A.G. Rossberg, R.I. Shii, T.A. Memiya, K. Itoh, The top-down mechanism for body-mass-abundance scaling, *Ecology* 89 (2008) 567–580, <http://dx.doi.org/10.1890/07-0124.1>.
- [26] A.G. Rossberg, *Food webs and biodiversity: foundations, models, data*, Wiley, 2013.
- [27] S. Mackinson, Combined analyses reveal environmentally driven changes in the North Sea ecosystem and raise questions regarding what makes an ecosystem model’s performance credible? *Can. J. Fish. Aquat. Sci.* 46 (2014) 31–46, <http://dx.doi.org/10.1139/cjfas-2013-0173>.
- [28] D. Pauly, Anecdotes and the shifting baseline syndrome of fisheries, *Trends Ecol. Evol.* 10 (1995) 430, [http://dx.doi.org/10.1016/S0169-5347\(00\)89171-5](http://dx.doi.org/10.1016/S0169-5347(00)89171-5).
- [29] D. Pauly, J. Alder, E. Bennett, V. Christensen, P. Tyedmers, R. Watson, The future for fisheries, *Science* 302 (2003) 1359–1361, <http://dx.doi.org/10.1126/science.1088667>.
- [30] D. Pauly, V. Christensen, Primary production required to sustain global fisheries, *Nature* 374 (1995) 255–257, <http://dx.doi.org/10.1038/374255a0>.
- [31] M. Coll, E. Akoglu, F. Arreguin-Sánchez, E.A. Fulton, D. Gasuel, J.J. Heymans, et al., Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach, *Rev. Fish. Biol. Fish.* 25 (2015) 413–424, <http://dx.doi.org/10.1007/s11160-015-9386-x>.
- [32] S. Fletcher, Converting science to policy through stakeholder involvement: An analysis of the European Marine Strategy Directive, *Mar. Pollut. Bull.* 54 (2007) 1881–1886, <http://dx.doi.org/10.1016/j.marpolbul.2007.08.004>.
- [33] R. Barciela, R. Mahdon, P. Miller, R. Orrell, J. Shutler, AlgaRisk[®] 08: A pre-operational tool for identifying and predicting the movement of nuisance algal blooms, *Environment Agency Science Report: SC070082/S*, Bristol, UK, 2008.
- [34] J.D. Shutler, M.A. Warren, P.I. Miller, R. Barciela, R. Mahdon, P.E. Land, et al., Operational monitoring and forecasting of bathing water quality through exploiting satellite Earth observation and models: the AlgaRisk demonstration service, *Comput. Geosci.* 77 (2015) 87–96, <http://dx.doi.org/10.1016/j.cageo.2015.01.010>.
- [35] OSPAR, Convention for the Protection of the Marine Environment of the North-East Atlantic, 2007.
- [36] OSPAR, OSPAR Workshop Report on Eutrophication Modelling, (<http://www.cefas.defra.gov.uk/media/351984/workshop-Report-Eutro-Modelling.pdf>) 2007.
- [37] H.-J. Lenhart, D.K. Mills, H. Baretta-Bekker, S.M. van Leeuwen, J. van der Molen, J.W. Baretta, et al., Predicting the consequences of nutrient reduction on the eutrophication status of the North Sea, *J. Mar. Syst.* 81 (2010) 148–170, <http://dx.doi.org/10.1016/j.jmarsys.2009.12.014>.
- [38] HM Government, *Marine Strategy Part One: UK initial assessment and Good*

- Environmental Status. Crown Copyright, Defra, London, UK, 2012.
- [39] J.J. Heymans, U.R. Sumaila, V. Christensen, Policy options for the northern Benguela ecosystem using a multispecies, multifleet ecosystem model, *Prog. Oceanogr.* 83 (2009) 417–425, <http://dx.doi.org/10.1016/j.pocean.2009.07.013>.
- [40] ICES, Interim Report of the Working Group on Multispecies Assessment Methods (WGSAM), Stockholm Sweden, 2013.
- [41] É.E. Plagányi, D.S. Butterworth, A critical look at the potential of Ecosim to assist in practical fisheries management, *Afr. J. Mar. Sci.* (2004) 261–287.
- [42] B.S. McIntosh, J.C. Ascough, M. Twery, J. Chew, A. Elmahdi, D. Haase, et al., Environmental decision support systems (EDSS) development – challenges and best practices, *Environ. Model. Softw.* 26 (2011) 1389–1402, <http://dx.doi.org/10.1016/j.envsoft.2011.09.009>.
- [43] M. Nilsson, A. Jordan, J. Turnpenny, J. Hertin, B. Nykvist, D. Russel, The use and non-use of policy appraisal tools in public policy making: an analysis of three European countries and the European Union, *Policy Sci.* 41 (2008) 335–355, <http://dx.doi.org/10.1007/s11077-008-9071-1>.
- [44] A. Wesselink, A.J. Challinor, J. Watson, K. Beven, I. Allen, H. Hanlon, et al., Equipped to deal with uncertainty in climate and impacts predictions: lessons from internal peer review, *Clim. Change* (2014), <http://dx.doi.org/10.1007/s10584-014-1213-1>.
- [45] D. Ludwig, M. Mangel, B. Haddad, Ecology, conservation, and public policy, *Annu. Rev. Ecol. Syst.* 32 (2001) 481–517, <http://dx.doi.org/10.1146/annurev.ecolsys.32.081501.114116>.
- [46] J. Harwood, K. Stokes, Coping with uncertainty in ecological advice: lessons from fisheries, *Trends Ecol. Evol.* 18 (2003) 617–622, <http://dx.doi.org/10.1016/j.tree.2003.08.001>.
- [47] A. Petersen, *Simulating Nature: A Philosophical Study of Computer-model Uncertainties and Their Role in Climate Science and Policy Advice*, Second ed., CRC Press, Abingdon, UK, 2012.
- [48] P.H.M. Janssen, A.C. Petersen, J.P. van der Sluijs, J.S. Risbey, J.R. Ravetz, A guidance for assessing and communicating uncertainties, *Water Sci. Technol.* 52 (2005) 125–131.
- [49] Defra, *Biodiversity and Ecosystems Evidence Plan*, Department for Environment, Food & Rural Affairs, 2013.
- [50] Defra, *Climate change evidence plan*, Department for Environment, Food & Rural Affairs, 2013.
- [51] R.E. Chandler, Exploiting strength, discounting weakness: combining information from multiple climate simulators, *Philos. Trans. A Math. Phys. Eng. Sci.* 371 (2013) 20120388, <http://dx.doi.org/10.1098/rsta.2012.0388>.
- [52] TEEB, *The Economics of Ecosystems and Biodiversity: Ecological and Economic Foundations*, Earthscan, London and Washington, 2010.
- [53] C. Hattam, J.P. Atkins, N. Beaumont, T. Börger, A. Böhnke-Henrichs, D. Burdon, et al., Marine ecosystem services: linking indicators to their classification, *Ecol. Indic.* 49 (2015) 61–75, <http://dx.doi.org/10.1016/j.ecolind.2014.09.026>.
- [54] *UK National Ecosystem Assessment*, UK National Ecosystem Assessment Synthesis of the Key Findings, UNEP-WCMC, Cambridge, UK, 2014.
- [55] S.R. Gari, A. Newton, J.D. Icelly, A review of the application and evolution of the DPSIR framework with an emphasis on coastal social-ecological systems, *Ocean Coast. Manag.* 103 (2015) 63–77, <http://dx.doi.org/10.1016/j.ocecoaman.2014.11.013>.
- [56] B. Fisher, R.K. Turner, P. Morling, Defining and classifying ecosystem services for decision making, *Ecol. Econ.* 68 (2009) 643–653, <http://dx.doi.org/10.1016/j.ecolecon.2008.09.014>.
- [57] R.B. Thorpe, W.J.F. Le Quesne, F. Luxford, J.S. Collie, S. Jennings, Evaluation and management implications of uncertainty in multispecies size-structured model of population and community responses to fishing, *Methods Ecol. Evol.* 6 (2015) 49–58, <http://dx.doi.org/10.1111/2041-210X.12292>.
- [58] M.A. Spence, P.G. Blackwell, J.L. Blanchard, Parameter uncertainty of a dynamic multi-species size spectrum model, *Can. J. Fish. Aquat. Sci.*, in preparation.
- [59] A. Gelman, J. Carlin, H. Stern, D. Dunson, *Bayesian data analysis*, Third ed., Taylor & Francis Group, Boca Raton, Florida, USA, 2013.
- [60] I. Vernon, M. Goldstein, R.G. Bower, Galaxy formation: a Bayesian uncertainty analysis, *Bayesian Anal.* 5 (2010) 619–670, <http://dx.doi.org/10.1214/10-BA524>.
- [61] M. Strong, J.E. Oakley, J. Chilcott, Managing structural uncertainty in health economic decision models: a discrepancy approach, *J. R. Stat. Soc. Ser. C* 61 (2012) 25–45, <http://dx.doi.org/10.1111/j.1467-9876.2011.01014.x>.
- [62] J. Rougier, D.M.H. Sexton, Inference in ensemble experiments, *Philos. Trans. A Math. Phys. Eng. Sci.* 365 (2007) 2133–2143, <http://dx.doi.org/10.1098/rsta.2007.2071>.
- [63] A. Patt, S. Dessai, Communicating uncertainty: lessons learned and suggestions for climate change assessment, *Comptes Rendus – Geosci.* 337 (2005) 425–441, <http://dx.doi.org/10.1016/j.crte.2004.10.004>.
- [64] A.G. Patt, D.P. Schrag, Using specific language to describe risk, *Clim. Change* 61 (2003) 17–30, <http://dx.doi.org/10.1023/A:1026314523443>.
- [65] M.D. Mastrandrea, K.J. Mach, G.K. Plattner, O. Edenhofer, T.F. Stocker, C.B. Field, et al., The IPCC AR5 guidance note on consistent treatment of uncertainties: a common approach across the working groups, *Clim. Change* 108 (2011) 675–691, <http://dx.doi.org/10.1007/s10584-011-0178-6>.
- [66] D. Spiegelhalter, M. Pearson, I. Short, Visualizing uncertainty about the future, *Science* 333 (2011) 1393–1400, <http://dx.doi.org/10.1126/science.1191181>.
- [67] A.M. MacEachren, A. Robinson, S. Hopper, S. Gardner, R. Murray, M. Gahegan, et al., Visualizing geospatial information uncertainty: what we know and what we need to know, *Cartogr. Geogr. Inf. Sci.* 32 (2005) 139–160, <http://dx.doi.org/10.1559/1523040054738936>.
- [68] K. Brodlić, R. Allendes Osorio, A. Lopes, A review of uncertainty in data visualization, in: J. Dill, E. Rae, D. Kasik, J. Vince, P. Chung Wong (Eds.), *Expanding the Frontiers Visual Analytics and Visualization*, Springer-Verlag, London, UK, 2012, pp. 81–109, http://dx.doi.org/10.1007/978-1-4471-2804-5_6.
- [69] D. Paterson, E. Defew, J. Jabour, Ecosystem function and co-evolution of terminology in marine science and management, in: M. Solan, R. Aspden, D. Paterson (Eds.), *Marine Biodiversity and Ecosystem Functioning: Frameworks, Methodologies, and Integration*, Oxford University Press, Oxford, 2012, pp. 24–33.
- [70] R. Naidoo, A. Balmford, R. Costanza, B. Fisher, R.E. Green, B. Lehner, et al., Global mapping of ecosystem services and conservation priorities, *Proc. Natl. Acad. Sci. U.S.A.* 105 (2008) 9495–9500, <http://dx.doi.org/10.1073/pnas.0707823105>.
- [71] N. Jobstvogt, N. Hanley, S. Hynes, J. Kenter, U. Witte, Twenty thousand sterling under the sea: estimating the value of protecting deep-sea biodiversity, *Ecol. Econ.* 97 (2014) 10–19, <http://dx.doi.org/10.1016/j.ecolecon.2013.10.019>.
- [72] A. McQuatters-Gollop, D.E. Raitos, M. Edwards, Y. Pradhan, L.D. Mee, S. J. Lavender, et al., A long-term chlorophyll dataset reveals regime shift in North Sea phytoplankton biomass unconnected to nutrient levels, *Limnol. Oceanogr.* 52 (2007) 635–648, <http://dx.doi.org/10.4319/lo.2007.52.2.0635>.
- [73] T.P. Hughes, D.R. Bellwood, C. Folke, R.S. Steneck, J. Wilson, New paradigms for supporting the resilience of marine ecosystems, *Trends Ecol. Evol.* 20 (2005) 380–386, <http://dx.doi.org/10.1016/j.tree.2005.03.022>.
- [74] M.T. Tomczak, J.J. Heymans, J. Yletyinen, S. Niiranen, S.A. Otto, T. Blenckner, Ecological network indicators of ecosystem state and change in the Baltic Sea, *PLoS One* 8 (2013) 1–11, <http://dx.doi.org/10.1371/journal.pone.0075439>.
- [75] A.J. Kenny, H.R. Skjoldal, G.H. Engelhard, P.J. Kershaw, J.B. Reid, An integrated approach for assessing the relative significance of human pressures and environmental forcing on the status of large marine ecosystems, *Prog. Oceanogr.* 81 (2009) 132–148, <http://dx.doi.org/10.1016/j.pocean.2009.04.007>.
- [76] L. Wu, W. Cai, L. Zhang, H. Nakamura, A. Timmermann, T. Joyce, et al., Enhanced warming over the global subtropical western boundary currents, *Nat. Clim. Change* 2 (2012) 161–166, <http://dx.doi.org/10.1038/nclimate1353>.
- [77] A.N. Tidd, Y. Vermard, P. Marchal, J. Pinnegar, J.L. Blanchard, E.J. Milner-Gulland, Fishing for space: fine-scale multi-sector maritime activities influence fisher location choice, *PLoS One* 10 (2015) e0116335, <http://dx.doi.org/10.1371/journal.pone.0116335>.
- [78] J.C. Blackford, J.I. Allen, F.J. Gilbert, Ecosystem dynamics at six contrasting sites: a generic modelling study, *J. Mar. Syst.* 52 (2004) 191–215, <http://dx.doi.org/10.1016/j.jmarsys.2004.02.004>.
- [79] J.I. Allen, J.T. Holt, J. Blackford, R. Proctor, Error quantification of a high-resolution coupled hydrodynamic-ecosystem coastal-ocean model: Part 2. Chlorophyll-a, nutrients and SPM, *J. Mar. Syst.* 68 (2007) 381–404, <http://dx.doi.org/10.1016/j.jmarsys.2007.01.005>.
- [80] J. Van der Molen, J.N. Aldridge, C. Coughlan, E.R. Parker, D. Stephens, P. Ruardij, Modelling marine ecosystem response to climate change and trawling in the North Sea, *Biogeochemistry* 113 (2013) 213–236, <http://dx.doi.org/10.1007/s10533-012-9763-7>.
- [81] A. Yool, E.E. Popova, T.R. Anderson, Medusa-1.0: a new intermediate complexity plankton ecosystem model for the global domain, *Geosci. Model Dev.* 4 (2011) 381–417, <http://dx.doi.org/10.5194/gmd-4-381-2011>.
- [82] M.R. Heath, Ecosystem limits to food web fluxes and fisheries yields in the North Sea simulated with an end-to-end food web model, *Prog. Oceanogr.* 102 (2012) 42–66, <http://dx.doi.org/10.1016/j.pocean.2012.03.004>.
- [83] J.M. Andrews, W.S.C. Gurney, M.R. Heath, A. Gallego, C.M. O'Brien, C. Darby, et al., Modelling the spatial demography of Atlantic cod (*Gadus morhua*) on the European continental shelf, *Can. J. Fish. Aquat. Sci.* 63 (2006) 1027–1048, <http://dx.doi.org/10.1139/f06-006>.
- [84] D.C. Speirs, W.S.C. Gurney, S.J. Holmes, M.R. Heath, S.N. Wood, E.D. Clarke, et al., Understanding demography in an advective environment: modelling *Calanus finmarchicus* in the Norwegian Sea, *J. Anim. Ecol.* 73 (2004) 897–910, <http://dx.doi.org/10.1111/j.0021-8790.2004.00857.x>.
- [85] M.R. Heath, M.A. Culling, W.W. Crozier, C.J. Fox, W.S.C. Gurney, W.F. Hutchinson, et al., Combination of genetics and spatial modelling highlights the sensitivity of cod (*Gadus morhua*) population diversity in the North Sea to distributions of fishing, *ICES J. Mar. Sci.* 71 (2014) 794–807, <http://dx.doi.org/10.1093/icesjms/fst185>.
- [86] W.S.C. Gurney, K. Preedy, Fisheries Research Services Final Scientific Report: Spatially Explicit Model for Haddock Populations in Northern UK Waters. ROAME Report for Project MF0761, 2008.
- [87] C. Darby, T. Hutton, J. Andrews, W.S.C. Gurney, D. Beveridge, J. Hiddink, Investigations into closed area management of the North Sea cod, Department for Environment, Food & Rural Affairs Report SFCD15, 2006.
- [88] A.G. Rossberg, A complete analytic theory for structure and dynamics of populations and communities spanning wide ranges in body size, *Adv. Ecol. Res.* 46 (2012) 427–521, <http://dx.doi.org/10.1016/B978-0-12-396992-7.00008-3>.
- [89] D.C. Speirs, E.J. Guirey, W.S.C. Gurney, M.R. Heath, A length-structured partial ecosystem model for cod in the North Sea, *Fish. Res.* 106 (2010) 474–494, <http://dx.doi.org/10.1016/j.fishres.2010.09.023>.
- [90] M.-J. Rochet, J.S. Collie, S. Jennings, S.J. Hall, Does selective fishing conserve community biodiversity? Predictions from a length-based multispecies model, *Can. J. Fish. Aquat. Sci.* 68 (2011) 469–486, <http://dx.doi.org/10.1139/F10-159>.