SEVENTH FRAMEWORK PROGRAMME THEME 7 Environment

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Project title: European Basin-scale Analysis, Synthesis and Integration

Deliverable 8.4 Report on final tuned food web & key species analyses for each region

Contributors: Mike Heath, Douglas Speirs,
Angus Cameron and David Morris, University of Strathclyde

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Theme 6 Environment

Dissemination Level		
PU	Public	X
PP	Restricted to other programme participants (including the Commission)	
RE	Restricted to a group specified by the consortium (including the Commission)	
CO	Confidential, only for members of the consortium (including the Commission)	

Deliverable 8.4 Report on final tuned food web & key species analyses for each region, is a contribution to

Task 8.2: Comparative analysis of North Atlantic marine food web structure and function. This Task will focus first, on performing comparative food web analyses, based on the principles of Ecopath, for a set of North Atlantic regions. Then, the Task will conduct scenario analyses of the effects of changing fishing and environmental conditions in each region.

The aim of the food web analyses will be to distil out of historic data via retrospective analyses , metrics to describe food web structure and function such as are required for the EU-MSFD indicators of good ecological status. The approach will be to harvest the new information on diet and abundance coming from the other WP's in EURO-BASIN, and merge this with existing data sets. These data will form the basis for applying the linear Ecopath equations to estimate the steady state annual flux of biomass in feeding networks representative of each of the study regions. The analysis will allow assessment of the role of key species in each region, ratios of production by integrated functional groups, and a variety of network metrics. For example, ratios of benthic/pelagic production and benthic invertebrate/demersal fish production which have been found to be diagnostic of ecosystem status in a variety of regions.

Analyses based on the linear Ecopath equations provide steady state estimates of biomass fluxes. However they do not allow scenario testing to determine, for example, the ecosystem consequences of changes in fishing patterns or environmental conditions. For this, a dynamic simulation system is required. Ecosim – the dynamic version of Ecopath – is one of a number of options for dynamic simulation and forward projection. However, Ecosim does not represent environmental effects on primary production or nutrient recycling, so is of limited use for investigating bottom-up effects on the food web. For EURO-BASIN, we will develop an alternative simulation system incorporating more explicit representation of low-trophic level and nutrient processes drawing on output from models developed in WP5 and WP6. Finally, scenario analyses with Ecosim will be used to investigate interacting effects of climate change and fishing on food web structure and functioning, including the examination of indicators representing good ecological status within the MSFD.

Responsible: USTRATH; Participants: ALL
Start month 1, end month 48

Executive Summary:
The deliverable takes to the form of three manuscripts. The first was published in Progress in Oceanography (2012; Ecosystem limits to food web fluxes and fisheries yields in the North Sea simulated with an end-to-end food web model). The second has been reviewed by Ecological Modelling and being revised according to referee comments (Identifying key parameters affecting North Sea fisheries: Global sensitivity analysis of a marine end-to-end ecosystem model). The third is in the late stages of preparation for submission, and was delivered as an oral presentation at the MASTS (Marine Science and Technology Scotland) Annual Science Conference, Edinburgh, in August 2013 (Dynamic food webs in a changing world: A trait-based modeling approach for describing shifting species composition within functional groups in response to changing temperatures.

As discussed in connection with earlier deliverables under Task 8.2, we did not pursue the use of Ecopath for the project, but rather developed a new food web model (StrathE2E; manuscript 1; Heath 2012), which incorporates a representation of biogeochemistry into a model of the marine food web extending from phytoplankton to birds and mammals. In this way the feedbacks of nutrient through the food web could be properly represented. The investigations of StrathE2E provided in this deliverable refer to the North Sea implementation of the model.

The manuscript for Ecological Modelling describes a global sensitivity analysis of the StrathE2E North Sea food web model, with respect the fisheries components. The majority of formal sensitivity analyses of ecosystem models to date have be of the ‘one-at-a-time’ type, where individual parameters are varied independently and the effect on output variables is assessed. However, these analyses an miss effects arising from non-linear interactions between parameters. The alternative ‘global analysis’ in which all parameters are varied simultaneously is massively computationally intensive requiring tens of thousands of model iterations.for modest parameter sets. StrathE2E is computationaly fast (~5 seconds for 100 year run on a desktop comuter), so a global analysis was feasible.

We analysed the sensitivities of fish and shellfish state variables in the model to key model drivers (hydrodynamics, boundary nutrients, temperature, fishing, light environment), and the biological parameters. The analysis revealed effects that were clearly a direct impact of external drivers, and those which were inditect effects due to cascade propagation through the food web. The analysis points to important sensitivities in the North Sea, but is also a hint as to the key drivers and parameters for implementing the model in other regions.

The manuscript on “trait-based modeling approach for describing shifting species composition” is groundwork for implementing the StrathE2E model in a time-series simulation mode to investigate the effects of trends in temperature, rather than running to an equilibrium state. The issue tackled is that a functional group in a model with given temperature response parameters will respond to a trend in temperature as if its implicit species composition remains constant. In reality, the species composition will adapt, so that the group becomes increasingly composed of warm-adapted species n response to a warming trend. As far as the model is concerned this implies a shift in temperature response parameters. But how can we implement this in the model?

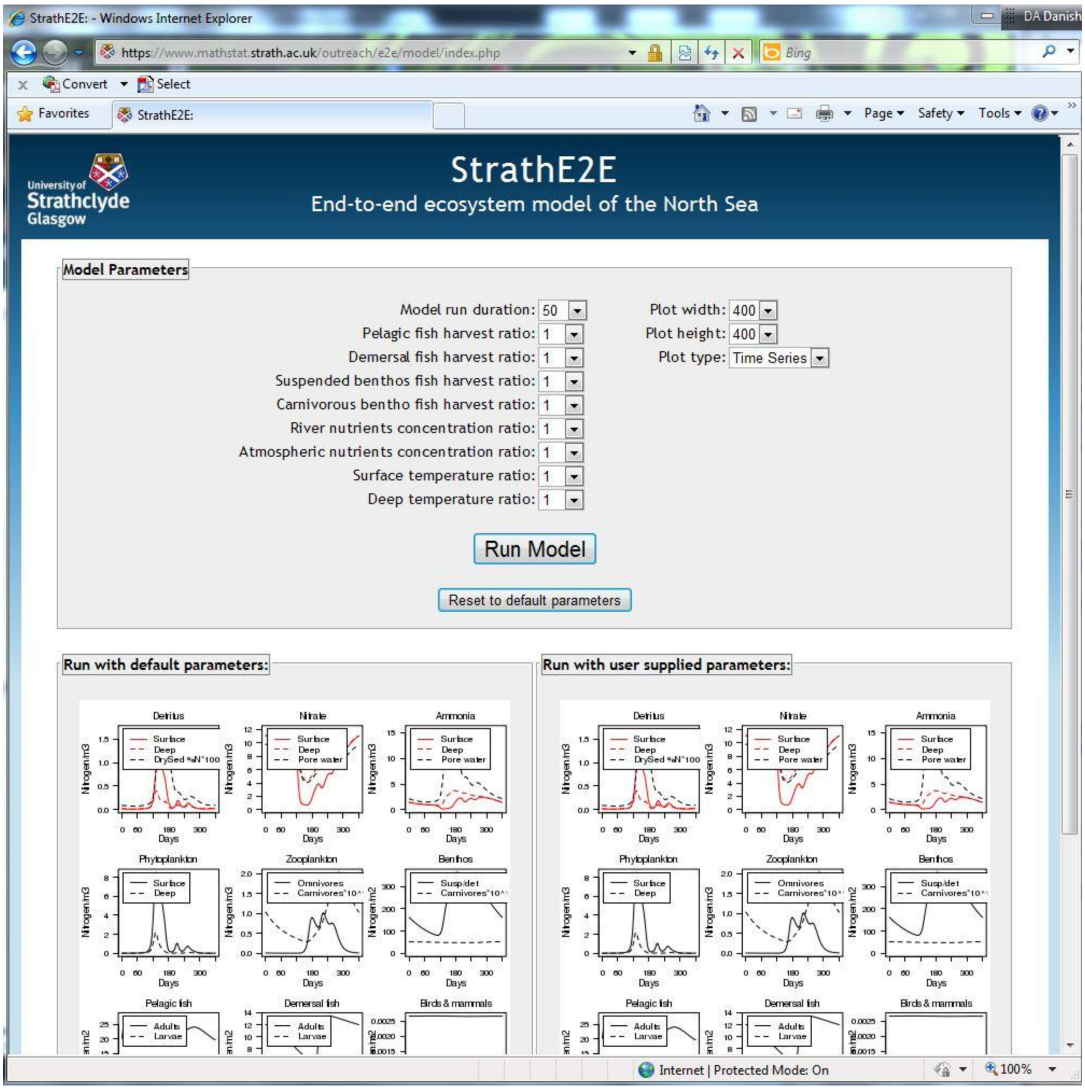
Relevance to the project & potential policy impact:

The objective in task 8.2 is to implement the end-to-end ecosystem model in a variety of regions of the northeast Atlantic, and test the hypothesis that, at the given level of species aggregation into functional groups, the system dynamics can be explained in terms of external physical, chemical and fisheries forcing, with a common parameter set despite differences in the species composition of the functional groups in each region. If this proves to be the case, then the model represents a powerful tool for assessing the high level management strategies required to achieve different societal goals for the ecosystem in a range of regional settings.

Access to Data and/or model code (where relevant):

The StrathE2E model is now available as a C-object for running in the R Statistical Environment, and is developed as a web application www.mathstat.strath.ac.uk/outreach/e2e/

For the model code, contact Michael Heath m.heath@strath.ac.uk



Report:

The following report is based on two manuscripts and one conference proceedings:

Heath, Michael (2012). Ecosystem limits to food web fluxes and fisheries yields in the North Sea simulated with an end-to-end food web model. Progress In Oceanography: 102 (2012) pp. 42-66. 10.1016/j.pocean.2012.03.004
Open Access version http://www.zenodo.org/record/884?ln=en#.UlPrSxBKszR

Morris et al (submitted). Identifying key parameters affecting North Sea fisheries: Global sensitivity analysis of a marine end-to-end ecosystem model, Ecological Modelling

Cameron et al 2013. Dynamic food webs in a changing world: A trait-based modeling approach for describing shifting species composition within functional groups in response to changing temperatures, Abstract of oral presentation at the MASTS Annual Science Conference

Summary of Manuscript 1

Ecosystem limits to food web fluxes and fisheries yields in the North Sea simulated with an end-to-end food web model.

Michael R. Heath

University of Strathclyde, Department of Mathematics and Statistics, Livingstone Tower, Glasgow, G1 1XP, UK. E-mail: m.heath@strath.ac.uk

Progress in Oceanography, 102, 42-66 (2012)

Model summary description:

The model simulated fluxes of a single nutrient element (nitrogen), between bulk mass state variables representing classes of detritus, dissolved nutrient, phytoplankton, benthos, zooplankton, fish, and top-predators. The state variables were further resolved to represent two depth layers in the water column, and a seabed sediment layer (Fig. 1). Rates of exchange between the mass compartments were described by a set of ordinary differential equations. Key features of the model were:

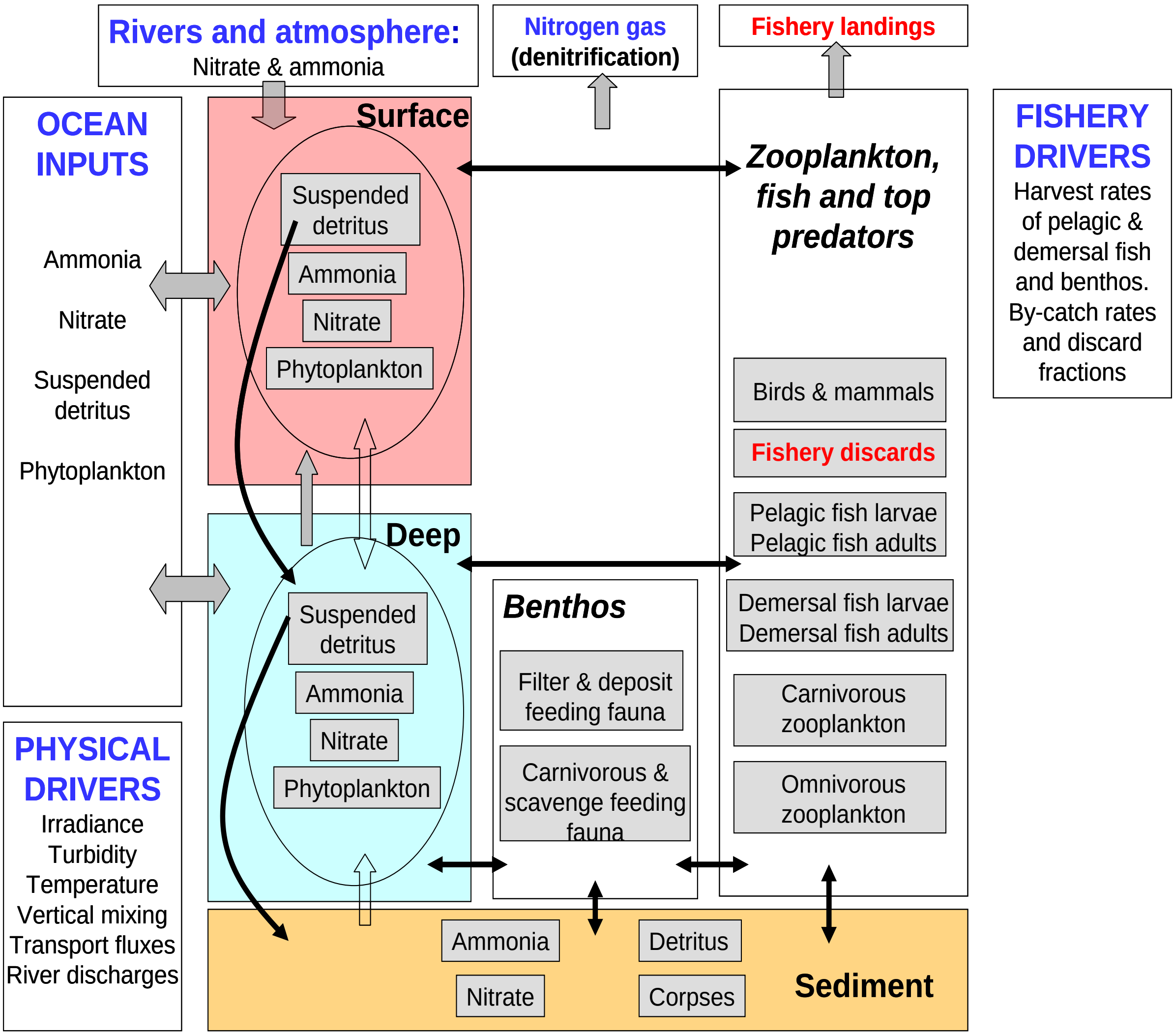
- External sources of nitrogen were from phytoplankton, detritus, nitrate and ammonia advected into the model domain by ocean currents, atmospheric deposition and river inputs of nitrate and ammonia.
- Exports of nitrogen from the model (sinks) were phytoplankton, detritus, nitrate and ammonia advected out of the model domain, nitrogen gas produced by denitrification, and fishery landings.
- Phytoplankton, detritus, nitrate and ammonia in the water column were subject to vertical exchange between depth layers (by sinking of particulate material and mixing). Detritus,

ammonia and nitrate were subject to vertical exchange between the water column and sediment.
- Uptake of dissolved ammonia and nitrate by phytoplankton was confined to the surface layer and modeled according to a Type–II function scaled by the depth averaged daily irradiance. Maximum uptake rate was temperature dependent according to a Q_{10} function, but the half-saturation coefficient was temperature independent.
- A constant proportion of phytoplankton per day was converted to detritus.
- Uptake of prey by all classes of predators was described by Type-II functions with prey and temperature-dependent maximum uptake rates. The half-saturation coefficient was independent of both temperature and prey.
- Fixed proportions of food ingested by predators were assimilated, excreted to ammonia, and defaecated to detritus.
- Predators excreted a temperature-dependent proportion of their body mass per day to ammonia, according to a Q_{10} function.
- Predators were subjected to a density-dependent mortality rate, which created a flux to corpses.
- A proportion of corpse mass was converted to detritus per day, and similarly detritus to ammonia, ammonia to nitrate, and nitrate to nitrogen gas (denitrification). The proportions were temperature dependent according to a Q_{10} function.
- Fish were resolved into two demographic stages – larvae (including eggs), and adults. Adults shed a fixed proportion of their mass per day to larvae during prescribed time intervals each year. A fixed proportion of larvae were promoted to adults per day during a different prescribed interval.
- Adult fish and benthos categories were subject to harvesting which removed a proportion of their mass per day as catch. A fraction of the catch was returned to the food web as fishery discards, the remainder was regarded as landings which were a sink.
- Benthos categories additionally suffered a by-catch mortality which was a fixed fraction of the demersal fish harvesting rate. This by-catch was passed directly to fishery discards.
- The proportion of catch discarded was constant for pelagic fish and benthos, but scaled with adult abundance for demersal fish, to caricature the shift in fish size distribution towards smaller individuals with declining abundance in demersal fish communities.

The model was implemented as a C-object for the R statistical environment version 2.11.1 (R Development Core Team 2005), and output values of the state variables and fluxes at daily time intervals. The model is also being developed as a web application - see **www.mathstat.strath.ac.uk/outreach/e2e**

The run-speed of the model is an important feature (<5 seconds for 100 years simuation). This enables automatic parameter optimisation using simulated annealing to fit the model to a suite of observations, and global sensityinty analysis (see below), both of whish are computationally intensive tasks.

Figure 1 Schematic showing the North Sea food web model components and driving variables, in relation to physical structures (surface water layer, deep water layer, and sediments).



Summary of Manuscript 2

Identifying key parameters affecting North Sea fisheries: Global sensitivity analysis of a marine end-to-end ecosystem model.

David J. Morris, Douglas C. Speirs, Angus I. Cameron, Michael R. Heath

University of Strathclyde, Department of Mathematics and Statistics, Livingstone Tower, Glasgow, G1 1XP, UK. E-mail: m.heath@strath.ac.uk

Submitted: Ecological Modelling – currently being revised following referee comments

Abstract:

A variety of end-to-end ecosystem models, that include bottom-up and top-down pressures have been developed which can be used to explore the combined effects that fishing, environmental change and nutrient inputs will have on fisheries. Here we present the results of a two step global sensitivity analysis conducted on an end-to-end model (StrathE2E) parameterised for North Sea fisheries. The Morris elementary effects method (Morris, 1991) was used to screen the static and driving parameters of StrathE2E. This identified 34 parameters that ranked as influential on the model outputs. These were examined using Sobol sensitivity analysis (Sobol, 1990; Saltelli, 2002 as reviewed by Saltelli et al. 2008), to produce quantitative sensitivity indices for total and first order effects. The model outputs examined represented the biomasses of four fisheries guilds; suspension feeding benthos; carnivorous benthos; demersal fish and pelagic fish. The results indicated that these guilds are influenced by different parameter sets. Fishing rates were the most influential parameter affecting demersal and pelagic fish biomass. Suspension feeding benthos were most sensitive to changes in temperature while pelagic fish may also be affected by this parameter indirectly through trophic connections in the food web. Metabolic changes relating to biomass conversion was the most influential parameter affecting the carnivorous benthos guild. This parameter was also identified as influential for the other guild outputs and is of pertinence as it may be affected by a range of environmental drivers including pH. The non-linearities identified in model responses and interactions between the parameters highlight the appropriateness of using global rather than local methods for the sensitivity analysis of fishery models.

Key discussion points

The outputs of StrathE2E considered by the sensitivity analysis focused on fishery biomasses. The analysis produced similar results for the larval and adult stages of each of the fish guilds as could be expected. However, in terms of modelling the impact that environmental changes will have on marine species, it is notable that the different guilds in the StrathE2E model are sensitive to different parameters and drivers. This suggests that responses to these changes will differ between the guilds. StrathE2E does not model individual species, but by identifying which parameters are influential to the model in the steady state it is possible to identify which guilds are most likely to be affected by climate change either leading to changes in total biomass production or species composition.

For the suspension feeding benthos, deep temperature was the most influential driver. If StrathE2E is accepted as an accurate representation the food web of the North Sea, changes in deep temperature will have a direct impact on the resultant biomass of suspension feeding benthos. This driver is obviously of pertinence in the context of climate change, as increasesof 0.2 to 0.6°C per decade have been recorded in the seas around the UK and Ireland. The influence of this parameter also concurs with studies that show temperature as the major environmental factor affecting benthic filter feeders development, distribution and recruitment (reviewed by Byrne 2011). Deep nitrate and the thickness of the deep layer were also identified as influential drivers and parameters in StrathE2E, as were parameters associated with primary production. In the model, mechanisms for the transfer of nitrogen to the benthic filter feeding guild exist through the deep layer detritus, deep phytoplankton, and secondary producers. The parameters identified therefore reflect the importance of primary production over secondary production for the transfer of biomass to the filter feeding guild. The three parameters that have a dominant influence on the carnivorous/scavenging benthos guild are related to internal processes. This suggests members of this guild are relatively unaffected by the environmental drivers examined and external influences but are largely governed by their metabolism. This is in contrast to the suspension feeding benthos where only two of the internal processes (biomass conversion and excretion) were identified as having any significant influence. Therefore factors affecting metabolic parameters, may play an important role in determining the biomass of this guild.

By far the most important parameter for both demersal and pelagic fish guilds was their respective fishing rates. This is unsurprising, as it is well documented that fishing can have a direct effect on fish numbers. Using StrathE2E, Heath (2012) reported that demersal fishing and pelagic fishing affected the resultant biomass of both the demersal and pelagic fish guilds, thus highlighting linkages between them. The sensitivity analysis concurs with this observation, but further indicated that demersal fishing is far more influential to pelagic fish biomass than pelagic fishing is to demersal fish biomass. Heath (2012) also examined the effect of fishing on the benthic productivity conducting a preliminary one-at-a-time analysis using StrathE2E. This suggested that demersal fishing rates affected the benthic food web. Although fishing rates do exert an influence on the benthic guilds, this is insignificant compared to the parameters already identified.

Previous examination of marine ecosystem models has indicated that while fishing is an important influence on fish biomass, it is not a deterministic response, as complex food web interactions between species, and trophic levels make species responses difficult to predict (Mackinson et al. 2009; Speirs et al. 2010). The differences observed between the total and first order sensitivity indices of the fishing parameters concurred with this, indicating that within the model, fishing was very influential but interactions with other parameters did occur to produce the resultant outputs.

A difference between the pelagic and demersal guilds was that significant interactions occurred between many of the parameters to influence the demersal guild biomass, while the pelagic guild was influenced by fewer parameters, with less interactions between them. This is likely to be a reflection of the extensive linkages of the demersal species to both the benthic, demersal and pelagic food webs, while the pelagic fish species were limited to the pelagic web (Heath 2012). Because of these linkages, to cause substantial changes in the output biomass of the demersal guild multiple parameters may need to be changed, in comparison to the pelagic guild output where alteration of single parameters could elicit a notable response. This suggests that the pelagic guild will respond differently, and be more susceptible to environmental changes compared to the demersal guild.

The combined effects of climate change and ocean acidification are likely to affect multiple parameters, including metabolic and environmental drivers simultaneously across guilds, affecting the food web structure of marine ecosystems. In the StrathE2E model, the benthic guilds displayed very different parameter sensitivities, with suspension feeding benthos being directly affected by multiple external and internal drivers, and carnivorous benthos by only a few internal drivers. For pelagic and demersal fish, the results of the StrathE2E sensitivity analysis, reiterates concerns that alterations in food web productivity due to ocean acidification and climate change will in turn affect fisheries productivity (Le Quesne and Pinnegar 2012). Parameter changes are likely to be more influential on larval fish stages than their adult counterparts and recent studies have indicated that it is these stages that will be affected most by ocean acidification (Baumann et al. 2012; Frommel et al. 2012). However, these changes will be relatively minor when compared to the effect that commercial fishing has on total demersal and pelagic fish biomasses.

In conclusion, a global sensitivity analysis was conducted on StrathE2E, an end to end marine ecosystem model. It identified that the fishery guilds of the model were influenced by different environmental drivers and parameters. Future studies using StrathE2E will need to determine what the impacts of changing these parameters are, particularly in the context of climate change, and try and determine the nature of the interactions observed.

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Summary of Manuscript 3

Dynamic food webs in a changing world: A trait-based modeling approach for describing shifting species composition within functional groups in response to changing temperatures.

Angus I. Cameron, David Morris, Douglas C. Speirs and Michael R. Heath

University of Strathclyde, Department of Mathematics and Statistics, Livingstone Tower, Glasgow, G1 1XP, UK. E-mail: m.heath@strath.ac.uk

Abstract of oral presentation at the MASTS Annual Science Conference

The stability and persistence of ecosystems worldwide currently face an unprecedented threat from global climate change. In ecosystems dominated by ectothermic organisms, such as in marine environments, the major threat is posed by temperature increases. Understanding the role of temperature in shaping natural communities is therefore fundamental to studying the impact of climate change on ecosystems and food-webs.

The effect of changing temperature on ectotherm communities has two components: the immediate effects on physiological traits of individuals (Dell et al., 2011) and long term effects on the distribution and abundance of species which can exist in a given geographic region (Diamond et al., 2012). Predicting the impact of the latter on communities will be extremely difficult and in the context of food web models, where the unit of interest is often a functional group rather than an individual species, it may be more useful to explore how temperature related traits in a community may change with increasing temperatures.

Here we present a dynamic trait-based model which encapsulates both short-term physiological effects and long-term species composition changes within functional groups. The model was explored analytically and found to closely match the output from models where a functional group was modelled as an explicit assemblage of individual species with distinct temperature-based traits.

The dynamics of species composition changes within a functional group are shown to be potentially important for persistence in the face of rising temperatures. By implementing the model within a food chain simulation scheme we show that faster response times are most

important for persistence at lower trophic levels.

References

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