SEVENTH FRAMEWORK PROGRAMME THEME 7 Environment

Collaborative project (Large-scale Integrating Project)

Project no: 246 933

Project Acronym: EURO-BASIN

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

Deliverable 8.5 Report on the pressures and processes causing structural ecosystem changes and key species dynamics

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Due date of deliverable: Oct 2013
Actual submission date: Oct 2013
Organisation name of the lead contractor of this deliverable: UN. STRATHCLYDE

Start date of project: 31.12.2010   Duration: 48 months
Project Coordinator: Michael St John, DTU Aqua

Project co-funded by the European Commission within the Seventh Framework Programme,
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 8.5 Report on the pressures and processes causing structural ecosystem changes and key species dynamics, 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 an in press manuscript to be published in *Ecology Letters* (**Understanding patterns and processes in models of trophic cascades**). The manuscript contains is a mathematical analysis of the factors which dictate trophic cascades in simple food web models, and a demonstration of top-down and bottom-up cascade effects in the StrathE2E North Sea food web model developed in BASIN Task 8.2. Simulating trophic cascades is a key goal of marine ecosystem modelling, and this paper identifies how components of such models affect the holistic cascade properties of the system as a whole.

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; Heath 2012; Deliverable 8.4), 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.

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

Summary of Ecology Letters manuscript

Understanding patterns and processes in models of trophic cascades.

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Accepted: Ecology Letters 2013

Abstract. Climate fluctuations and human exploitation are causing global changes in nutrient enrichment of terrestrial and aquatic ecosystems and declining abundances of apex predators. The resulting trophic cascades have had profound effects on food webs, leading to significant economic and societal consequences. However, the strength of cascades – that is the extent to which a disturbance is diminished as it propagates through a food web - varies widely between ecosystems, and there is no formal theory as to why this should be so. Some food chain models reproduce cascade effects seen in nature, but to what extent is this dependent on their formulation? We show that inclusion of processes represented mathematically as density-dependent regulation of either consumer uptake or mortality rates is necessary for the generation of realistic "top-down" cascades in simple food chain models. Realistically modelled "bottom-up" cascades, caused by changing nutrient input, are also dependent on the inclusion of density-dependence, but especially on mortality regulation as a caricature of e.g. disease and parasite dynamics or intra-guild predation. We show that our conclusions, based on simple food chains, transfer to a more complex marine food web model in which cascades are induced by varying river nutrient inputs or fish harvesting rates.

Key sections from the manuscript

We examined top-down and bottom-up cascade effects in the StrathE2E model (BASIN Task 8.2; Deliverable 8.4), which represents the fluxes of nutrient (nitrogen) through the North Sea ecosystem from dissolved inorganic to birds and mammals, and regeneration through excretion and mineralization of detritus (Heath 2012; see Appendix). The model incorporates Type-II functional relationships between each predator-prey couplet in the food web, chemostat-like regulation at the lowest trophic level and density-dependent (quadratic) mortality regulation of the upper trophic levels (top-levels plus most interior levels). External forcing factors include sea surface irradiance, temperature, hydrodynamic fluxes, freshwater input, river and atmospheric nitrate and ammonia inputs, ocean boundary nitrate, ammonia and suspended particulate concentrations, and density-independent fishery harvesting rates of shellfish, pelagic and demersal fish. Using simulated annealing to explore the parameter space, the stationary state of the model has been fitted to a suite of observed data from the North Sea collected between 1970 and 1999, whilst being forced by 1970-1999 average monthly external forcing data (Heath 2012). To expose cascading patterns, we compared the stationary annual mean abundances of model components in the fitted 1970-1999 simulation (hereafter referred to as the default run), with the equivalent values from scenario runs in which one of the external forcing factors (demersal fish harvesting rate, or river nutrient concentrations) was either doubled or halved.

Default model run

Model parameters were optimized by simulated annealing to identify the set providing the best fit of the stationary state model to a suite of observations on biomasses and fluxes in North Sea averaged over the period 1970-1999, whilst being driven by a repeating annual cycle of 1970-1999 monthly averaged driving variables. We refer to this as the 'default model run', and averaged the state variable abundances over a stationary annual cycle.

Scenario model runs

We defined 4 scenario runs of the model based on halving or doubling of various external driving time series: a) halving or doubling of the default nitrate and ammonia concentrations in inflowing river waters; b). halving or doubling of the default harvesting rate applied to demersal fish. For each model state variable X (averaged over a stationary annual cycle), the difference between default and scenario states was expressed as $\Delta X = \log_2(X_{scenario}/X_{default})$. Hence $\Delta X = 0$ corresponds to no difference between scenario and default, $\Delta X = 1$ to a doubling of abundance in the scenario run, and $\Delta X = -1$ to a halving.

Comparison of scenario and default model results

The results showed several key features:

1) Halving and doubling of demersal harvesting rates led to inverse responses throughout the water column food web (Fig.1). However, this was not universally the case in the recycling food web, with water column ammonia, corpses, and carnivorous/scavenging benthos all showing a positive response to both halving and doubling of demersal harvesting rate. This occurred because corpses, which constituted a significant portion of the diet of carnivorous/scavenging benthos, were produced by a combination of fishery discards, and quadratic density dependent mortality terms applied to upper trophic components of the food web. Corpse production showed a U-shaped response to demersal harvesting rates (Heath 2012). Carnivorous/scavenging benthos abundance was close to a local minimum with respect to fish harvesting rates in the default model run.

2) The conceptual top-down alternating responses were evident along some trophic pathways, e.g. demersal fish, pelagic fish, omnivorous zooplankton, phytoplankton,

nitrate. However, carnivorous zooplankton were anomalous in this respect, always responding in the same direction as their main prey (omnivorous zooplankton). In the model, carnivorous zooplankton were both predators on fish larvae (pelagic and demersal), and prey of adult fish. Hence the connectivity of carnivorous zooplankton in the food web was complex.

3) Changes in demersal fish landings responded negatively to both a doubling and halving of the harvesting rate. This was because landing under the default harvesting rate were close to the maximum sustainable yield, so any change in harvesting rate was guaranteed to produce a decrease in landings. Conversely, pelagic landings responded positively and negatively to a doubling and halving of demersal harvesting rate respectively due to connectivity between demersal and pelagic fish in the food web.

4) In marked contrast to the patterns above, doubling of river nutrient concentrations produced an increase in stationary annual average abundances throughout the entire web (Fig. 2). Conversely, halving river nutrients produced a decrease throughout the web.

In summary, doubling or halving of river nutrient concentration had a similar relative effect on all the functional groups in the food web, corresponding approximately to the archetypal bottom-up cascade (Fig. 3). Top-down forcing by doubling or halving demersal fish harvesting rate, produced alternating positive and negative responses between lower functional groups but, due to compartmentalisation of the benthic and pelagic sub-systems, this depended on how the groups were formed. Carnivorous zooplankton, that feed on omnivorous zooplankton (but also on fish larvae), changed together, as did carnivorous and sedimentary feeding benthos. However the dominant feature of the top-down forced profiles, was a strong attenuation of the response with decreasing trophic levels (Fig 1, 2 and 3).

We identify a need to distinguish between different types of regulatory processes in the formulation of ecosystem models.

Our results showed that different forms of density-dependence generate very different cascade dynamics in food chain models. From a modelling perspective, this indicates a need to see the various mathematical forms of density-dependence not simply as devices to confer stability in population dynamics models, but as formal representations of particular biological processes. So, there is not necessarily one form which fits all situations, and different forms are not necessarily mutually exclusive. The issue is not the general primacy of consumptive vs non-consumptive (density vs trait-mediated) effects in nature or in models (Schmitz *et al.* 2004). Rather, it is the combination of such regulatory processes at different points in the system that permit model food webs to respond in different ways to both top-down and bottom-up forcing factors.

Three types of regulatory factors stand-out as requiring consideration in models. The first is cannibalism which clearly constitutes a density-dependent mortality in the context of individual species. However, the equivalent regulatory process in a model which only resolves guilds or functional groups implicitly includes predation between species. It is tacitly assumed that this can also be represented as a density-dependent mortality. The second is trait mediated effects or predator avoidance behaviours induced by the fear of being eaten (Brown & Kotler 2004, Hammerschlag, & Trussell 2011). These take a wide range of species-specific forms, the effects of which can be represented by consumer density-dependent regulation of species uptake rates. However, it is very unclear that equivalent processes act at the scale of species guilds. The third is largely unobserved agents such as disease organisms or parasites (Lafferty *et al.* 2008) which may also lead to density-dependent regulation of their hosts (Tompkins & Begon 1999). Explicit representation in food chain models will rarely be possible and then only in a species-specific context. However, density-dependent mortality may be a simple way to implicitly account for these missing regulatory effects.

References

Brown, J.S. & Kotler, B.P. (2004). Hazardous duty pay and the foraging cost of predation. *Ecol. Lett.*, 7, 999-1014.

Hammerschlag, N. & Trussell, G.C. (2011). Beyond the body count: Fear of predators can affect ecosystem function (Reply to Estes *et al.,* 2011. *Science*, 333, 301-306). *Science*, published online 11 November 2011, http://www.sciencemag.org/content/333/6040/301/reply#sci_el_15579

Heath, M.R. (2012). 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, 42-66.

Lafferty, K.D., Allesina, S., Arim, M., Briggs, C.J., De Leo, G., Dobson, A.P., Dunne, J.A., Johnson, P.T.J., Kuris, A.M., Marcogliese, D.L., Martinez, N.D., Memmott, J., Marquet, P.A., McLaughlin, J.P., Mordecai, E.A., Pascual, M., Poulin, R. & Thieltges, D.W. (2008). Parasites in food webs: the ultimate missing links. *Ecol. Lett*., 11, 533-546.

Tompkins, D.M. & Begon, M. (1999). Parasites can regulate wildlife populations. *Parasitol. Today*, 8, 311-313.

Schmitz, O.J., Krivan, V. & Ovadia1, O. (2004). Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecol. Lett*., 7, 153–163.

Figure 1 Changes in stationary annual average abundances of ecosystem components in the North Sea food web model parameterized against observations collected during 1970-1999 (Heath, 2012), as a result of doubling (left) and halving (right) the demersal (benthivorous and piscivorous) fish harvesting rate. Numerical values of the change are indicated by a $\log_2$ scale, so that +1 represents a doubling of abundance relative to the 1970-1999 model, and -1 indicates a halving of abundance. Boxes with dashed outlines represent fishery landings and hence export fluxes out of the system. Black arrows indicate uptake fluxes, green arrows indicate fishery harvests. Fluxes due to excretion and death are not shown for clarity.

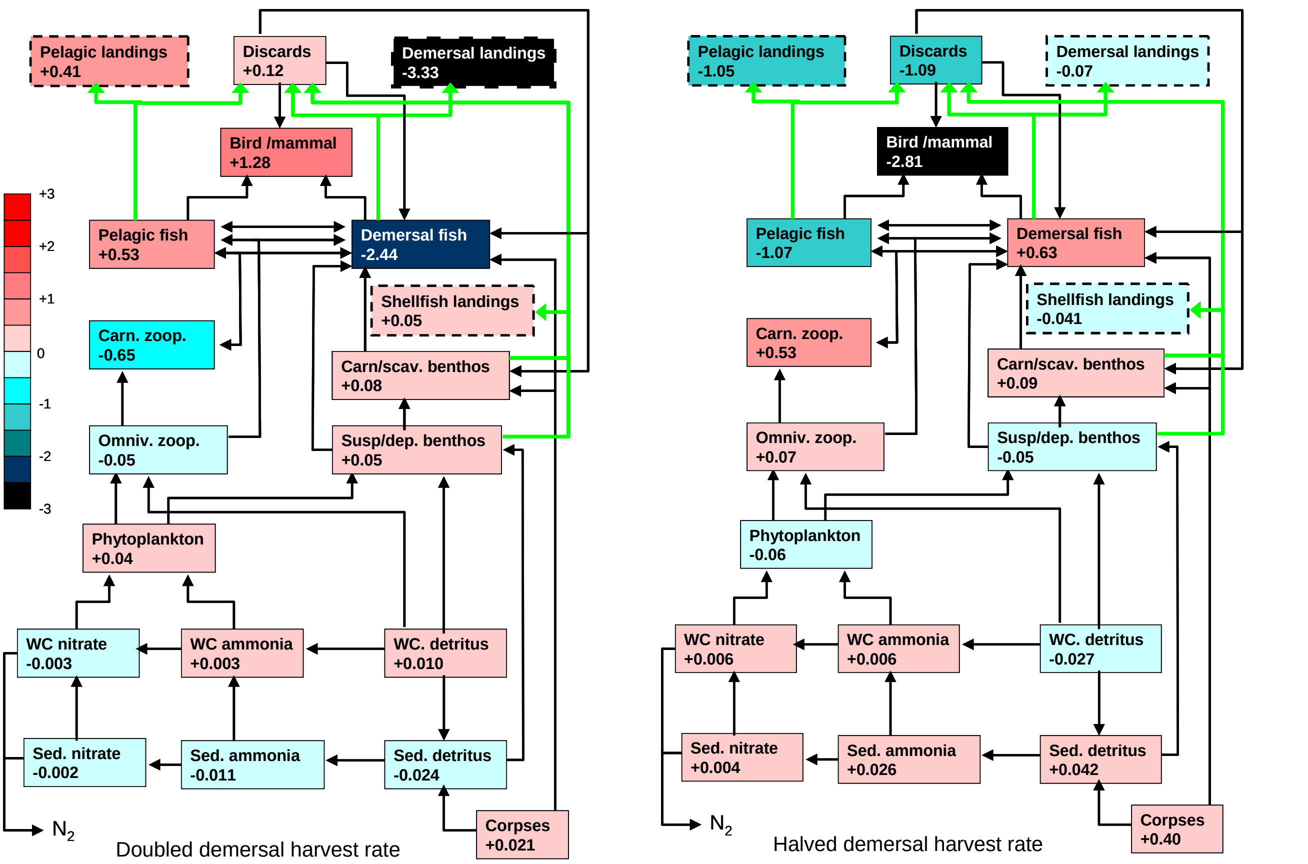

Figure 2 As Fig. 1 but showing the response to doubling and halving the concentrations of nitrate and ammonia in rivers flowing into the North Sea.

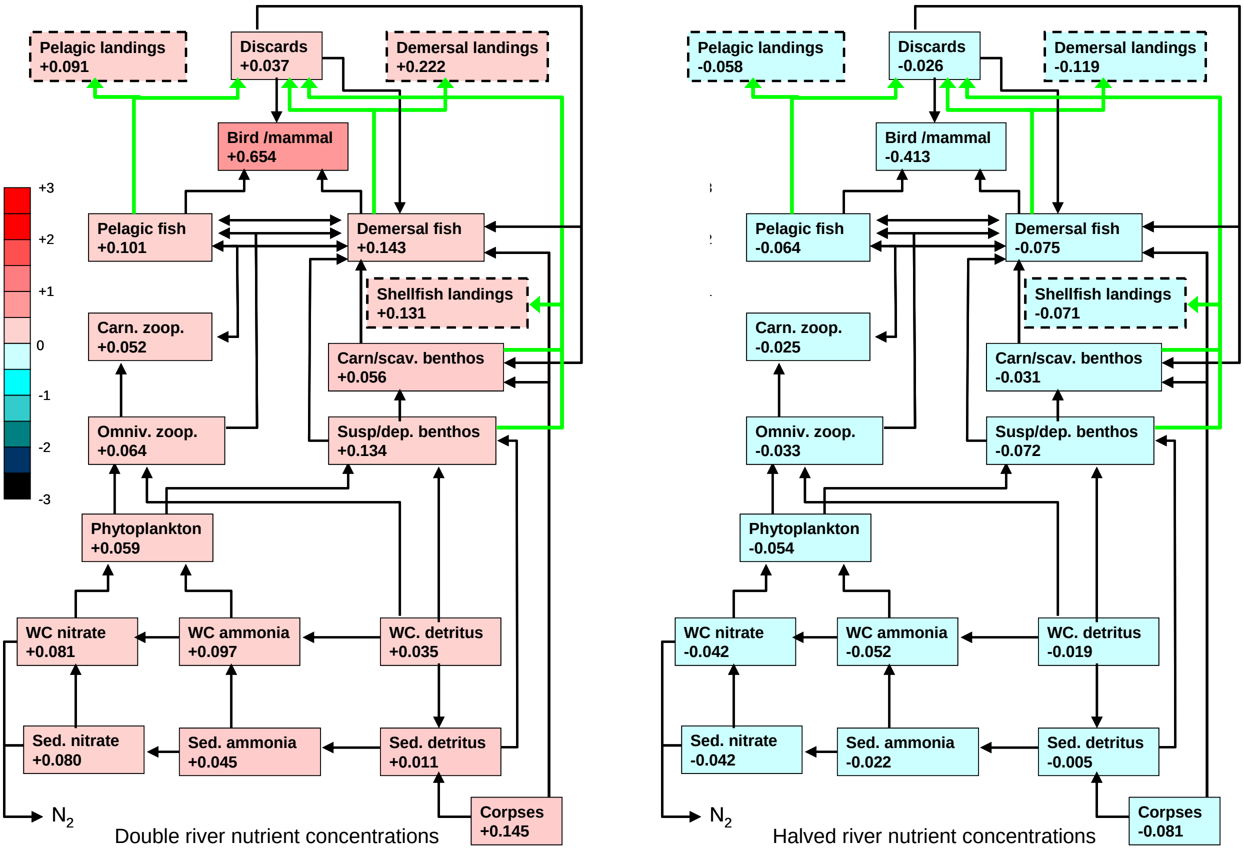

Figure 3. Proportional response in the stationary state annual average biomass of food web components in the North Sea food web model (Heath 2012), for (upper row) top-down forcing with 0.5x (left) and 2x (right) the default fishing pressure on demersal stocks, and (lower row) 0.5x and 2x river inputs of nitrate and ammonia. The proportional response is calculated as $\log_2$(abundance with altered forcing factor/abundance with default forcing factor).