An approach for coupling higher and lower levels in marine ecosystem models and its application to the North Sea

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Abstract

End to end modelling is an attractive and rapidly developing approach to solve developing strategies in marine systems science and management. However problems remain in the area of data matching and sub-model compatibility. A mechanism and novel interfacing system (Couplerlib) is presented whereby a physical/biogeochemical model (GOTM-ERSEM) that predicts dynamics of the lower trophic level (LTL) organisms in marine ecosystems is coupled to a dynamic ecosystem model (Ecosim) that predicts food-web interactions among higher trophic level (HTL) organisms. Coupling is achieved by means of a bespoke interface which handles the system incompatibilities between the models and a more generic Couplerlib library which uses metadata descriptions in extensible mark-up language (XML) to marshal data between groups, paying attention to functional group mappings and compatibility of units between models. In addition, within Couplerlib, models can be coupled across networks by means of socket mechanisms.

As a demonstration of this approach, a food web model (Ecopath with Ecosim, EwE) and a physical/biogeochemical model (GOTM-ERSEM) representing the North Sea ecosystem were joined with Couplerlib. The output from GOTM-ERSEM varies between years dependent on oceanographic and meteorological conditions. Although inter-annual variability was clearly present, there was always the tendency for an annual cycle consisting of a peak of diatoms in spring, followed by (less nutritious) flagellates and dinoflagellates through the summer resulting in an early summer peak in the mesozooplankton biomass. Pelagic productivity, predicted by the LTL model, was highly seasonal with little winter food for the higher trophic levels. The Ecosim model was originally based on the assumption of constant annual inputs and, consequently, when coupled, pelagic species suffered population loss over the winter months. By contrast, benthic populations were more stable (although the benthic linkage modelled was purely at the detritus level). The coupled model was used to examine long term effects of environmental change, and showed the system to be nutrient limited, rela-
tively unaffected by forecast climate change, especially in the benthos. The stability of an Ecosim formulation for large higher tropic level food webs is discussed and it is concluded that this kind of coupled model formulation is better for examining the effects of long term environmental change than short term perturbations.

1 Introduction

End to end modelling is becoming a hot topic in marine systems primarily because of the need, implied by regulatory frameworks such as the Marine Strategy Framework Directive (MSFD) (http://ec.europa.eu/environment/marine/index_en.htm) for management of the marine systems to take into account distal effects of any deliberate or accidental anthropogenic changes to parts of the marine ecosystem. To this effect a paper describing a strategy of End to End modelling (Rose et al., 2010) has become a highly cited paper in the journal (Kenneth A. Rose, personal communication, 2013). However, the problem which remains is that the models that are used in an end to end modelling system are themselves complicated with many parameters. Joining such models end to end has been described as “Putting lipstick on a pig” (Rose, 2012), and an appeal is sometimes made to start with simpler models (Fulton et al., 2003).

Given the choice between constructing end to end model systems do novo and joining existing models together “Frankenstein Style” the former has a number of obvious advantages. The multiple models can benefit from a unified design process, can use a consistent co-ordinate system and model entity representation and can benefit from unified data input, output, visualisation, control and validation. Most importantly, the models can be aligned in terms of whether they are strategic models for exploring general principles, or tactical models designed to explore specific aspects of the system with a high degree of detail and domain specific knowledge (Levins, 1966). Joining models with widely differing focus will typically result in a combined model with only broad results for a narrow domain, and yet will still require a large amount of data to calibrate it. On the other hand, we are often forced to work with combining existing
models because of the existence of code, with updates and a user community and are constrained by the investment of time in the lengthy processes of calibrating and validating these models. We must, therefore take sociological aspects of the modelling process into account when producing end to end models.

In many cases the objective of the end to end modelling approach includes a high degree of prediction for example work packages 3 and 4 of the EU Framework programme 7 project Meece (www.meece.eu). However although it is possible to model phytoplankton blooms and short term fish stocks management fairly reliably there are a number of less tractable problems, including estimating the recruitment of young fish to the adult stock. It is a difficult function to quantify in models because it is dependent not only on the size of the parent stock, but also on interactions of the lower trophic level components of marine ecosystems, notably zooplankton, that are poorly understood and which are highly dependent on physical driving factors such as temperature, irradiation and wind (Cushing, 1996). Zooplankton modelling has always been the weakest link in the end to end chain and how such processes govern fish recruitment and population variability is still poorly understood (Minto et al., 2008).

Process-oriented coupled physical-biogeochemical models such as GOTM-ERSEM (Burchard et al., 1999, 2006; Baretta et al., 1997; Vichi et al., 2003) and POLCOMS-ERSEM (Lewis and Allen, 2009; Blackford et al., 2004) that predict changes in primary production and zooplankton abundance as outcomes of hydrodynamic and biogeochemical processes, are similarly not without limitation, an important one being their inability to capture top-down trophic impacts from higher grazers such as fish, which are not explicitly included.

Although lower trophic level components can quite easily be represented (albeit simply) in multi-species fisheries models such as Ecopath with Ecosim (EwE) (Christensen et al., 2005), representation of how environmental drivers influence the dynamics of higher trophic species is more challenging. In EwE, this is usually achieved using simple production and consumption forcing patterns, which gloss over biogeochemical processes, such as how the dynamics of the different nutrient components determine the
limitations of phytoplankton growth. With the knowledge that environmental changes can have drastic impacts on lower trophic level components such as phytoplankton (Richardson and Schoeman, 2004) and that fishing has strong impacts on the abundance and structure of fish stocks (e.g. Lotze et al., 2006), investigating how ecosystems respond to combined pressures necessitates that processes at lower and higher levels are linked. This is the basis of the present trend towards end-to-end modelling, whereby the connection of physics to fish and fisheries is made (Travers et al., 2007; Libralato and Solidoro, 2009; Rose et al., 2010). The end-to-end modelling of Kearney (2012) impressively links the NEMURO lower trophic level model with a 23 component EwE model, achieves ecosystem stability, intra and interannual variation in biomass of higher and lower trophic level species, though it does not encapsulate all the processes that lead to variation in fish populations, especially recruitment variation.

Whilst the realisation of effective end to end modelling systems for prediction will depend on the development of precise sub-models for some of these critical components, their development will also depend upon consistent systems for model integration and data exchange. Coupled LTL-HTL model systems should allow for iterative exchange of data among models, thus capturing important feedback processes within an ecosystem. Thus they should enable us to investigate ecological issues, such as how changes in phytoplankton abundance in shelf seas might be attributed simultaneously to abiotic drivers, such as nutrient inputs and changes to summer stratification or a reduction of predation on zooplankton by fish. Such complex interactions can only be understood through an end-to-end approach that combines physics, lower trophic levels and higher trophic levels.

The principal challenges of coupling LTL models with HTL models include reconciling differences in how the models handle and represent important processes at different time and spatial scales (Rose et al., 2010). Whilst it is vitally important to test and understand how model behaviour is influenced by choices in the level of detail (one or many groups), the groups that are represented (size, age, bulk biomass) and the choice of time and spatial scales of processes (e.g. capturing seasonality), there is
also a need to be pragmatic. This means making choices that enable the models to be coupled and tested, either through comparison with empirical data or by their ability to generate plausible, testable hypothesis that are consistent with understanding.

The paper describes a methodology for coupling LTL and HTL models. The “Couplerlib” approach is generic, allowing for exchange of information between separate LTL and HTL models. In effect Couplerlib is a glue layer between different models, consisting of a library of routines for checking data consistency between models, carrying out data conversions and providing network protocols. It is not a universal coupler, which would be very difficult to achieve given the potentially enormous range of languages and calling conventions that models may use. Instead, the user is required to provide a compatible interface for use with Couplerlib; this being the “front end” used to input required information to setup and perform a model run.

In the specific example presented here, Couplerlib connects two models representing the dynamics of the North Sea ecosystem; GOTM-ERSEM (Burchard et al., 2006), a physical-biogeochemical model of the LTLs, and the food-web EwE model (Mackinson and Daskalov, 2007) of the HTLs. The two models are downloadable at www.gotm.net and www.ecopath.org respectively. In this case the EwE front end serves as the primary interface for Couplerlib, through which a graphical front-end for GOTM-ERSEM is called for specification of the LTL model run parameters.

To facilitate a clear understanding and promote further development of the methodological approaches, we describe the technical process of linking EwE to GOTM-ERSEM. Specific problems and solutions to overcoming them are discussed.

2 Methodology

2.1 Principles of model coupling

We can define a series of degrees of integration between models that require different coupling mechanisms:
a. Direct Coupling: coupled models share a memory space and are able to read and write directly into it. This requires the models to have the same way of storing basic data information for integer and floating point variables, which can present a number of problems. C/C++ and FORTRAN, for example have different array storage (row major and column major) which may require a glue layer to convert data order. Coupling between data that is stored alternately between models will require some form of indirection (i.e. pointers or arrays indexed via an index variable). Direct coupling will not allow any form of data conversion such as between units, grid resolutions or where functional groups are merged between models. Despite these limitations it is an attractive form of coupling because of its speed and simplicity, for example there is direct linking between the GOTM and ERSEM models in this example.

b. Managed Coupling. Managed Coupling uses a management layer between two models which is capable of data conversion, data validation, reorganisation, splitting and merging of data. It is possible to couple models with very different internal representations by incorporating the necessary glue layers within the management layer. Typically as well and data being transferred between models via the management layer, there is some form of control data which can specify how the data exchange is controlled. The Couplerlib system presented here is such a management layer, which stores control information via a system of XML files (Fig. 1).

c. Networked Coupling. This is an extension of managed coupling which can operate between processes and across the web. In order to achieve this, there need to be two copies of couplerlib with communication processes between each. Typically one of the processes is the master with capabilities for operator interaction and the rest are slaves operating under a system of messages between them. The Atlantis system (atlantis.cmar.csiro.au, Fulton, 2010) also implements a networked
coupling system between network components but is both data and control central, whereas Couplerlib is control central and data distributed.

d. Offline Coupling uses some form of file to store data so that multiple models can run, store data and allow a second model to process this model independently. Because of the slow nature of file reading Couplerlib implements offline coupling using netCDF files as a one-way only coupling.

2.2 Couplerlib design and specifications

A critical feature of Couplerlib is its ability to specify multiple models and interfaces between them and perform validation on these interfaces, only validated interfaces may link and exchange data. The principle behind this is that multiple coupling mechanisms may be provided, only some of which may be allowed in each situation. An example would be the provision of data in multiple types of grid and non-grid spatial format, which might require a conversion layer between the models, by specifying multiple models we can allow code for multiple conversion libraries to be incorporated within a model.

Existing approaches that have linked lower and higher trophic levels using single species and individual based approaches (for example Rose et al., 2007; Travers et al., 2009), define the linkages before the simulation is run. However, in connecting ERSEM to Ecosim we are confronted by the problem that the constituent components of Ecosim models are explicitly specified at runtime and ERSEM output is specified by means of a user invoked compiler. In this case it is necessary to develop a coupling mechanism where metadata information that is generated at runtime can still be cross-matched and validated.

For linking to EwE, which is Windows only, managed linking is only possible within a windows environment. The data store in Couplerlib is global and persistent, and is referenced by an enumeration (i.e. a list of items which is converted to a numeric sequence) of model and interface. In principle a single Couplerlib can be used to link
multiple models with multiple connections for different types of data between them. However, care must be taken to ensure that a frame of data (data for single model and interface combination) is only read after it is completely written; otherwise the data may be corrupted. Because programming libraries for multithreaded systems have various ways to signal events and suspend program execution on a thread, these mechanisms need to be provided by the interface to Couplerlib.

When Couplerlib operates in networked mode, each process or machine is required to have its own Couplerlib. The networked Couplerlibs are initially synchronised by reading metadata descriptions of all the models being linked from files that will be available on all machines as a Uniform Resource Identifier (Berners-Lee et al., 2005). At run time the networked Couplerlibs are synchronised on a need-to-know, object request basis (the receiving Couplerlib specifies what data the transmitting Couplerlib needs to send) even though validation has been carried out during the initial model loading phase. Data from a model is written to the local copy of Couplerlib and the remote copy synchronises its own copy when an instruction is received to fetch data. In addition to transferring data, the networked Couplerlib exchanges diagnostics and model output to be displayed remotely and controls the synchronisation of data (Fig. 2).

To ensure that coupled models are synchronised, Couplerlib uses the Berkeley Sockets Mechanism, specifically blocking sockets. By assigning each a station number, multiple models can connect using networked Couplerlibs.

2.3 Metadata information exchange and specification

Both EwE and GOTM-ERSEM are reconfigurable modelling frameworks which can emit metadata to describe their composition. In the case of GOTM-ERSEM the output data to be emitted is partly specified by a user specified list of variables which are then mapped into the main data array (known internally as the CC array) at source level, with parameter values being loaded from a FORTRAN namelist. The physics/LTL model GOTM has an optional front end GUI interface containing a parameter editor and the model specification can be adjusted during the data editing phase before the
core GOTM program starts up. GOTM-ERSEM has an internal array of metadata which
describes the model’s internal arrays in terms of full name, abbreviated name and unit
dimensions, which is created for each instantiation of the source code at the same
time as the CC array and describes internal as well as output variables. The Ecopath,
Ecosim and Ecospace programs also have a main data array where metadata is stored,
although dimensional information is specified for all data items together. This data array
can be changed at runtime by means of the editor built into EwE v6, if organisms are
added or deleted, for example.

Consequently the location in terms of numerical indexation within the data arrays of
the two models is not fixed at runtime. Indeed there is no guarantee that the necessary
data for a linked model run will even be available once the simulation starts, since the
user may remove a needed component from their model instance. The first stage of
model coupling is for each model to provide a specification of the data available for
linking, which it provides between model loading/editing and the start of the run. Each
model provides this information in XML format. The data is supplied in a hierarchical
manner, suitable for reading with the Document Object Model library (Le Hégaret et al.,
2009) with the following hierarchy:

```xml
<Model>
  <Description> Author, System, Languages
  <Interface>
    <Time Information> Periodicity, Start and Stop Times
    <Grid Information> Dimensions, Start and end, Resolution
  <DataItems> of type Phytoplankton, Zooplankton, Consumers, Resources
  <Name>
  <Symbol>
  <Chemical Consituent> Carbon, Nitrogen, Silicate, Phosphorous
  <Flux Direction> Concentration, Intake, Offtake,
```
Information on the dimensions of values is included in the metadata specification. If the dimension of a coupled variable differs between coupled models, such as density of a nutrient per unit volume, vs. density per unit area, Couplerlib checks in its conversion dictionary to find an appropriate dimensional converter and then applies the relevant conversion ratio to all values transferred between the models (in this case multiplying or dividing by water column depth).

The model specification is produced by combining a template file, which is an XML file describing the basics of each model (such as language and system), with variable-specific metadata provided dynamically by the model after loading/editing. The specifications for the coupled models are combined by use of a coupler specification which is also an XML file; this specifies the models to be linked as a number of interfaces. The coupler crosschecks for each interface in turn to see whether the connection is permissible. Permissible interfaces occur when the model and system information are permissible, the spatial and temporal dimensions are in range for the data, and there is a registered correspondence between all functional groups specified in the interface. So for each organism in the interface there must be a way of obtaining all nutrient concentrations and the time and area of the data must be consistent. The functional groups that are checked are only those which are specified as actually needing to be linked in the interface specification.

Alongside the XML files used for specifying the rules of the interface, schema (XSD) files can be used to validate the vocabulary and patterns of any human written XML file. For example the XML file will specify the axes used in the grid, whilst an XSD file will specify that a three dimensional grid will require three axis dimensions each of which will need a start co-ordinate, a length and a resolution. The XSD file is loaded into
a XML editor such as EditiX (www.editix.com) prior to creating or loading an XML file. It can also be located online via a URL so may reside in a cross-institutional repository. Its use is optional but will reduce run time errors in Couplerlib.

Couplerlib can be extended to the case where the functional group values are structured in some way (e.g. age or size). Additional metadata will define the number and specification of age/size classes. However, further conversion code would need to be supplied when one model outputs as size or age structured and only a single biomass values is needed.

However, it will often be the case that there is a disparity between the metadata produced by the two models to be coupled. The simplest is the use of different names by the two models, other situations arise where there is an inexact match of the functional group definitions between the two models: for example, the version of ERSEM used here has 5 different phytoplankton groups whereas the EwE North sea model has a single phytoplankton class. It is acceptable, within EwE to model the relative offtake of all the phytoplankton groups as a single value if the predation pressure on bulk phytoplankton in EwE can be assumed to apply equally to all phytoplankton groups, but the production and consumption of phytoplankton within GOTM –ERSEM vary between phytoplankton groups. We consider this to be a reasonable approximate because the ingestion of phytoplankton by zooplankton, modelled in ERSEM is much larger than that by higher trophic level species, modelled in EwE. The final case of disparity is where units of measurement vary between models, which occurs in this case as ERSEM expresses plankton concentrations in molar concentration units of C, N, P and Si and the EwE North Sea model in terms of tonnes per square kilometre of total biomass. These different conflicts are dealt with by a final XML file called the dictionary file. This specifies mappings between groups and units, unit conversions and synonyms. Furthermore items in the dictionary can be specified in terms of their context (models, interface and organism name). This is useful for exceptions to normal rules, such as greater wet-mass to dry mass ratios for jellyfish compared to most
organisms. The dictionary is searched when an exception is found between organism names, or unit names, during the coupling process.

2.4 Use of Graphical User Interfaces (GUIs) – model front ends

Both the EwE models and GOTM (and hence GOTM-ERSEM) have GUIs. In the case of EwE the interface is written in the .net programming environment for windows, and whilst programmed in Visual Basic, it uses an object structure which is fully accessible using Visual C++ and C#. The EwE system is runtime extendable using plugins which use the .net interface system to extend the object model of the underlying EwE system. Plugins are dynamically loaded as DLLs (executable code program extensions, which must be called from another executable). This plug-in architecture is used to couple EwE, via Couplerlib, to the GOTM-ERSEM front end. The GOTM interface, however, is written in Python, which is an interpreted language: the interface consists of a set of scripts and modules that require a Python interpreter to run. Accordingly an interpreter is embedded within the EwE plugin, together with python.net (Pythonnet.sourceforge.net): a. net compatible API that provides access to the Python interpreter.

The coupler plugin has a visual interface to select the directory where the coupler description XML files described previously are contained. This launches the Python interpreter to run the scripts which collectively make up the GOTM-ERSEM front end. These scripts enable the GOTM and ERSEM configuration files to be manipulated at run time and also for output data to be visualised. In turn, the Python-based front end communicates with the FORTRAN core of GOTM and ERSEM via a C wrapper layer – F2Py (Peterson, 2007). To enable coupling with external models, this layer has been expanded with interfaces for read-write access to relevant FORTRAN data objects, in particular the arrays that describe the values of biogeochemical state variables. Couplerlib is available to parse metadata and carry out the kind of managed data conversion described in the previous section. The net result of these various conversion and API layers is that meaningful data objects in GOTM-ERSEM are available from within EwE and vice versa.
2.5 The LTL and HTL models

The 1-D GOTM-ERSEM (Burchard et al., 2006) lower trophic level model was set up to represent a site in the Oyster Grounds (a muddy sand site immediately south of the Dogger Bank at 54°24′ N, 4°3′ E) with appropriate water depth (40 m), tidal velocities (M2 amplitudes of 30 cm s−1) and meteorological forcing. This parameterisation simulates the annual dynamics of a summer stratified site that is broadly representative of average behaviour over a large area of the central North Sea. Preliminary validation of this model is reported in Van Der Molen et al. (2012, 2015).

The North Sea EwE ecosystem model (Makinson and Daskalov, 2007) is a spatially averaged representation of the biomass of food-web components over the whole North Sea (ICES div IVa–c). It consists of 68 functional groups, which are both pelagic and benthic. However, in order to be consistent with ERSEM, this was extended by two new detritus groups (separating particulate organic matter (POM) into pelagic and benthic components and adding a new faecal POM group). The Lower trophic level groups used by both EwE and GOTM-ERSEM for pelagic and benthic components are listed in Table 1.

2.6 The biology of the coupling

The GOTM-ERSEM representation of the physics and primary production and the EwE representation of the higher trophic levels are coupled via biomass of pelagic plankton groups and nutrients returned to the water column via detritus (Table 1). Omnivorous zooplankton (Z4 in ERSEM), microzooplankton, bacteria and phytoplankton (Z5, Z6, B and P1–P5 in ERSEM) are chosen as the coupling groups. The most significant of these links is with omnivorous zooplankton, because in shelf seas it forms the principal pathway that connects the energy from the lower trophic food web with the higher trophic level consumers. The link between omnivorous and carnivorous mesozooplankton is handled in Ecosim rather than ERSEM (with predation by carnivorous Zooplankton turned off in ERSEM) to provide a better description of the closure of the
mortality of mesozooplankton (P. Rudaij, personal communication, 2010) Nutrients are returned to ERSEM from Ecosim within the particulate, dissolved and faecal detritus components, which required adding the faecal component in Ecosim. The 1-D version of GOTM-ERSEM captures the biogeochemical processes occurring in the water column, describing the plankton ecosystem from incoming solar radiation, via phytoplankton to zooplankton. The EwE model assumes that the biomass of all functional groups is distributed evenly throughout the model domain.

The coupling is by two unidirectional Couplerlib interfaces. ERSEM passes to EwE the biomass of the pelagic functional groups, while the amount of oftake by predators as a proportion of biomass is returned to ERSEM, as are the detritus fluxes which are added to the ERSEM detritus pools. The version of EwE used has been specially been adapted to run at a timestep of a single day, rather than a month. This is to prevent the accumulation of consumption over time long time steps leading to apparent overgrazing of omnivorous zooplankton. Internally GOTM and ERSEM run the North Sea model at a timestep of 10 min. Dynamics of the benthic components run separately in each model and thus shadow each other. The EwE component is affected by the temporal variability of the detritus, but not by the immediate variation of benthic conditions input experienced by the ERSEM model. Consequently the variability of the species which consume benthic components within EwE is less than those that feed heavily via the pelagic route.

ERSEM explicitly describes the concentrations of individual chemical elements (carbon, nitrogen, phosphorous and, for some functional groups, silicon). However EwE is a biomass only model (the ratios of carbon, nitrogen and phosphorous do not vary significantly between higher trophic level species). Consequently Couplerlib must estimate the stoichometric ratios of EwE model groups, such as detritus, when transferring biomass based values from EwE models back to GOTM-ERSEM. This can be done by using predefined ratios or by assuming the composition of incoming EwE variables matches the current elemental ratios of the target variables in ERSEM, as was done here. Also, care must be taken to ensure dimensional correctness; for example when
EwE models are expressed in terms of wet biomass, whereas in ERSEM they are expressed as g C m$^{-2}$. When the dimensions of values are included in the metadata specification, Couplerlib will check in its conversion dictionary to find an appropriate dimensional converter and then apply the relevant conversion ratio to all values transferred between the models.

2.7 EwE model re-parameterisation

The very first attempt to link the two models was not successful. Pelagic groups that feed off mesozooplankton in EwE overexploited the mesozooplankton during the winter period causing the death of the zooplankton populations and a consequent reduction in pelagic productivity. This was a result of the Ecosim model having being calibrated primarily on summer plankton levels to set the consumption to biomass level, albeit annualised i.e. the seasonality in plankton food production was not captured in EwE. In practice consumption is very much lower in winter months when the plankton population is lower but also the metabolic rate of the predatory fish is very much reduced. In addition to the reduced metabolism which follows an exponential temperature to metabolism law, there may be behavioural changes that reduce prey consumption still further. For example sandeels, which were observed to be one of the major predators of mesozooplankton, switch to being benthic between November and April (Engelhard et al., 2008) and so have zero consumption of plankton in winter months. To account for these phenomena, it was necessary to add a function to reduce predation of pelagic sources in winter months. Two forcing functions were used – one a purely metabolic model using a $Q_{10} = 2.0$ rule of temperature, with maximum temperature having a multiplier based on the original EwE model of 1., the other fitted the observations on sandeel populations of Englehard et al. (2008). In addition metabolic costs were reduced to 0.3 for adults and 0.0 for juveniles (this latter figure reflects the seasonal production of juveniles starting in the spring, and their migration from spawning grounds, so there will not be juveniles in the area modelled but the population still needs to be modelled and EwE allows only a fixed value for metabolic costs). The background mortality of the
zooplankton in ERSEM was reduced to a nominal value to take account of the fact that most mortality would be due to predation which is accounted for in the EwE model. Interestingly, the level of zooplankton predicted by the ERSEM model peaked at around the value used to calibrate EwE.

2.8 The coupling process in action

The main sequence of inter-model calls and data communication is illustrated in Fig. 3. It can be seen that there are six model components. At the ends of the stack of components are the EwE and GOTM models themselves (ERSEM is implemented as a library extension to GOTM but is interfaced through GOTM). Furthermore there is a front end interface to GOTM, which is written in Python and uses the Qt graphical interface components (Bruggeman and Bolding, 2007). Although the use of this component is optional, it provides useful on line data editing, file management and visualisation facilities, so the decision was made to couple the models via the front end to keep the existing functionality.

The six most important points of interface between the core and the GOTMlink plugin are indicated in Fig. 3, but there are additional points for documentation, identification and visual interaction with the plugin. Control passes from the EwE core to the plugin at those specific points where additional functionality can be provided by the GOTMlink interface. When the two models are coupled in the same process running on the same machine the two sides of the model (EwE plus its plugin and GOTM plus its GUI and Interface) operate on separate threads; that is to say, there are separate sequences of operations for the EwE and GOTM models. The EwE and GOTM interfaces signal directly when a step in one model is complete and the second model should take over, with execution of the first model suspended in a wait state. Using separate threads is essential where the component models are themselves multithreaded and may need to keep other threads such as the Graphical User Interface or network code running – EwE is like this, GOTM is not, but can be embedded within a multithreaded server, such as a network daemon. Data transfer is carried out by means of Couplerlib, which
provides marshalling of the data using external metadata specifications. However the two interfaces can exchange basic information about model status, time to run for, and the like through shared memory.

In networked mode the GOTM and EwE sides cannot communicate directly since they do not share common memory. Instead everything goes via Couplerlib. The EwE and GOTM sides have their own copies of Couplerlib. The two Couplerlibs will exchange information using TCP/IP sockets so that the receiving end of a data transfer makes a copy from information requested from the sender Couplerlib. Information used to synchronise the models and give information on model state such as waiting, finished and error conditions for various operation is sent via a separate pair of sockets and diagnostic information is sent to the Couplerlib which is attached to the graphical console (the EwE GOTMlink plugin in this case).

The GOTMlink plugin includes an interface to the model coupling facilities. There are four user initiated operations: GOTM model load, Edit, Run and Visualize. Only the run call operates beyond the GOTM GUI into GOTM itself. Instantiation of the EwE model is controlled through the EwE GUI. When the EwE and GOTM models are loaded they export their specifications to separate XML files. These are made available, together with the user provided interface specification and dictionary to Couplerlib. Data, such as the timestep, and the start and stop times are transferred from GOTM to EwE sides (so they can be available before EwE produces its XML metadata). The bulk of the data is transferred via Couplerlib. The critical call to Couplerlib is the CheckIF call, which loads all the metadata specifying the interface, and cross checks this against the specifications of the component models. Providing this is consistent, the GOTM and EwE threads are synchronised to ensure that the Ecosim module has been started, resulting in the EcoSimRunInitialized call being sent from the EwE core to the plugin. Both component models can then use GetIFAddress to locate the position of the data that will be transferred in the Couplerlib data store.

The main loop consists of repeated calls to the GOTM library, requesting simulation for a particular length of time, equal to the EwE time step. After every call the GOTM ar-
ray holding the values of biogeochemical state variables is accessed and its values are stored in Couplerlib. The EwE part of the model will wait for these data to be written, and then fetch the values it requires, using Couplerlib to carry out any conversion between units or between functional groups. After updating the values of coupled variables in EwE in this fashion computation continues with the EwE calculations for a single time step. When complete, updated EwE data are written to a different frame of the Couplerlib repository and GOTM must synchronise and then read the data. The changes in biogeochemical state variables during the EwE time step are output to Couplerlib as (dimensionless) relative changes, which can be applied directly across all vertical layers of the GOTM-ERSEM water column without violating mass conservation. Finally if EwE has finished (the Simulation Ending Interface call is made) GOTM can be made to terminate early and cleanup called to ensure data are written to output files.

3 Results

3.1 One dimensional two way coupling between LTL and HTL

Here the results from the application of Couplerlib to coupling the LTL and HTL models of the North Sea are described. Results are produced separately but concurrently by the EwE and GOTM-ERSEM parts of the model.

Within ERSEM, the dynamics of Zooplankton are constrained by the dynamics of 5 phytoplankton groups, the most important of which are, diatoms flagellates and dinoflagellates (Fig. 4a–c). Two years of the 40 year run are examined in detail: 1970 and 1971. There is an annual dynamic, with silicon dependent diatoms peaking in March–April and then being limited by silicon availability. The dynamics into the summer are then determined by the growth first of flagellates and dinoflagellates that lead to the gradual reduction in the zooplankton peak. The transition between a phytoplankton community dominated by diatoms and one dominated by dinoflagellates was observed in the North Sea EwE model calibration exercise (Mackinson and Daskalov, 2007).
However there is also considerable annual variation and seasonal variation in diatom and dinoflagellate numbers during the summer period.

In Fig. 4d the omnivorous zooplankton dynamics are indicated. Between 1970 and 1971 there is a considerable difference in the timing of the peak as a result of differences in the diatom bloom. These differences are likely to have profound, though not completely understood effects on recruitment on pelagic fish in the following year.

An examination of the effect on a number of functional groups is shown in Fig. 5. Each graph shows the changes in fish population numbers away from the calibrated levels at the start of the simulation (based on the 1990 calibration data). A significant rebalancing between functional groups occurs as a result of the introduction of the seasonal lower trophic levels. That the coupled model should give different answers is not surprising, given that (i) there is a switch from a non seasonal model to a seasonally driven one (ii) the ERSEM model is calibrated for a single point, the EwE model is for the whole North Sea (iii) It has been shown that for large models small changes in the growth of a single population can have drastic consequences for the population of the North Sea (Rossberg, 2013). (iv) Communities are subject to periodic shifts in species within a guild e.g. Sardine and Anchovy cycles (Chavez et al., 2003). Given these differences between the models we cannot expect a congruency between coupled and uncoupled models, nor can we predict the likely population of a single species based on meteorological data alone, because it is hard to estimate recruitment in a mixed species environment. Nevertheless a stable long-term equilibrium may be found, as the trophic network with Ecosim readjusts. There is a considerable rebalancing between pelagic groups, for example Herring numbers decline (probably a result of the difficulties of modelling this migratory fish in a static model with no space, no larval dynamics and limited seasonality). With extensive recalibration we can produce a useful operating model to examine how changes in the physical and lower trophic level environment may further affect the ecosystem balance between multiple species.
3.2 Long term effects of changes in the physical environment on fish biomass

The coupled model was run using synthesised weather data based on the IPCC climate change scenarios A1B (which is a rapid global industrial growth scenario with a mixture of fossil and non-fossil fuels resulting in around 3.2° of warming) and B1 (with limited industrial growth and an emphasis on CO$_2$ reduction resulting in 2.4° of warming) (Nakicenovic et al., 2000). The nutrient scenario was either high (representing the level of nutrients found in the eutrophic Southern North Sea) or low (with half the levels of N, and P) (Table 2).

The populations of marine species affected by changes in the environment are grouped in seven blocks: Microbes (plankton and bacteria), higher level invertebrates (shrimps, crabs, bivalves etc.), small and medium pelagic fish (herring, mackerel, sand eels etc.), Demersal fish (cod, haddock etc. but not flatfish), Flatfish (sole, plaice etc. excluding skates and rays), sharks (including skate and rays) and a block containing marine mammals and birds. The populations of those species relative to the current temperature and nutrient scenario (baseline) in the four scenarios for temperature and nutrients are shown in Fig. 6. It may be seen that the system is very much nutrient limited, especially in pelagic species (where there is a proportional relationship between nutrients and biomass). In large benthic species and mammals the relationship is less than linear (i.e a 30% reduction in biomass for a 50% reduction in nutrients). The effect of warming is relatively small and greatest for pelagic species and higher trophic level predators such as sharks, and negligible for the microbes. Two explanations for this higher trophic level effect are that nutrients limit the microbial populations whilst increased temperature increases rates of turnover of microbes and hence nutrients, and that there is strong negative feedback on predated populations which are predated at a higher rate when predator populations increase.
4 Discussion and conclusions

Demand for scientific advice on the ecosystem approach to resource management will require predictive tools capable of exploring the impacts of environmentally driven influences and management actions on the sustainability of resources and dependent industry. It requires models linking physical and biogeochemical processes with food-web and fisheries dynamics. However such a link may serve to expose the weak links in the end to end chain of model relationships. Critical limitations of some of the underlying models include: weak understanding of factors determining recruitment in commercial fish populations (Minto et al., 2008), seasonal dynamics of lower and mid trophic level components and prediction of zooplankton components.

The technical innovation of the coupling processes and the solutions to the ecological problems that emerged has exposed both technical and ecological issues of reconciling the two models, the key points of which are discussed below.

In principle Couplerlib is designed to handle coupling of any groups among models, but in this example only the plankton groups are coupled. The reason for this lies in the effort/benefit ratio, the argument being that plankton groups form the main energy conduits through which environmental changes get translated in to changes in secondary productivity, and poor correspondence between the benthic components of the two North Sea models means a lot of effort would be spent for little marginal gain. Having the dynamics of the benthic components in each model run separately is taken as providing a useful point of comparison.

The example coupling, links a 1-D LTL model calibrated using parameters from the North Sea “Oyster Grounds” with the HTL food web model whose parameters are spatially averaged over the whole North Sea. While the parameters used to represent each model differ to in their degree of spatial specificity, we do not see this giving rise to conceptual or technical issues that cannot be reconciled. First, the Oyster Grounds is a site close to the tidal mixing front that divides summer stratified with the mixed region to the south. Although it simply cannot capture fully the diversity between a mixed
site in the southern North Sea and a deep strongly stratified location in the northern North Sea, it is nevertheless representative of the dynamics of a large area of the central North Sea. Second, both models utilise many rate and state parameters from a much a wider area of the North Sea or are indeed specified even more generally. The internal consistency of each of the separate models might thus imply that each could be considered as rather general representations of the North Sea ecosystem. From a technical point of view, the practical arguments for coupling these non-spatially resolved models are compelling; the coupling allowing proof of concept on the technical methods and early identification of key ecological issues before extending to spatially resolved models. We believe that the main issues have been resolved and plans are in place to tackle coupling spatially resolved models, knowing full well the new issues will emerge, such as capturing the dynamics of annual migrations for some species.

Plankton growth in ERSEM is regulated by four elements: carbon (C), whose production depends on light and temperature, nitrogen (N), phosphorous (P) and silicon (Si). With the particular parameterisation chosen for the Oyster ground model, it has been seen that N is not generally limiting and that light, as expected, is only limiting during the winter months, and that Si and P are more limiting in spring. However, since we have fixed the total amount of these elements and the model is closed, these results are a consequence of our particular choice of initial conditions rather than being a true model “prediction”. The dynamics of silicon dynamics is more interesting. In particular diatoms, which are more “digestible” by mesozooplankton, bloom in early spring and then are replaced by the flagellates and dinoflagellates as the Si concentration drops, a result consistent with Broekhuizen et al. (1995). The possible biological consequences of this are discussed by Officer and Ryther (1980). One consequence of the Si dependency is that Si is only gradually accumulated as a result of inflow from rivers and thus does not change much from one year to the next, so that the total diatom production level is constant from one year to the next although timing of spring bloom will vary from year to year in relation to temperature and light. There is apparent inter-annual variation between the timings of the growth of the different phy-
toplankton peaks, the importance of which will depend on the ability of zooplankton to incorporate biomass form the different phytoplankton groups. This single point or average model cannot represent the inter-annual variation in phytoplankton bloom location resulting from inter-annual variation in weather combined with ocean currents. For example where plankton bloom location varies in space from year to year the effect on the higher trophic level species will depend on the ability of that species to move with the plankton bloom location.

Another issue is that of spatial pattern of biomass production across the whole of the North Sea, which can vary considerably across time. For example, data used in a meta-analysis by Broekhuizen et al. (1995) showed considerable variation in summer peak omnivorous zooplankton numbers with populations off the Norway coast (Box 3 in their paper) having a peak between days 100 and 180, whilst populations off Denmark (Box 10) were low until after day 150 and stayed high between day 180 to 270 a late summer bloom. Overall the original ERSEM parameterisation placed too much emphasis on the spring diatom bloom as a source of production and so gave a pattern of productivity which did not lead to a stable ecosystem. The current parameterisation which peaks around day 180 gives a better estimate of mean mesozooplankton biomass, even though the nutrient model which gives rise to it requires some refinement to fit to observed levels.

There are a number of known divergences from observations for the ERSEM model: for carnivorous zooplankton there is under prediction in winter and too great a rise in spring (avoided by moving this group to EwE); and for microzooplankton there is an over estimate of densities (although this may be as a result of errors in the observations) (Broekhuizen et al., 1995). Modified EwE parameterisations have been made to correct for these: for example setting consumption for herring to be very low in winter and adjusting the maintenance cost of herring downwards, in order to prevent this underestimation leading to broader erroneous trophic effects, as a result of erroneous herring deaths. In the long term improvements to the zooplankton component of ERSEM may remove the need for some of these corrections. In the short term these results
raise a number of issues about the dynamics of planktonivorous species such as herring. Given the paucity of zooplankton during the winter months, how do they manage to survive over winter? The answers seem to be multifaceted; herring switch prey over the winter months (Blaxter and Hunter, 1982), herring are migratory and may move to extend the season of availability of food (Corten, 2000) and herring do seem to exist in a negative energy balance over winter leading to loss of condition. All these aspects are of potentially great interest for researchers and should be incorporated into future versions of the underlying models.

The timeframe of the constituent models is critical to their interoperability. This has often been characterized in terms of timestep, but reality is much more complex than that. GOTM is a model that makes use of very high resolution temporal data, to represent the effects of short term weather conditions and tides, at a temporal resolution that is sub-hourly. The biological component of ERSEM can respond to these changes in a matter of days because some of the functional groups, e.g. bacteria and diatoms can respond over this timeframe. In the same way the Ecosim model has these components with P/B ratios of 30 year$^{-1}$ or more suggesting that the daily timeframe is more appropriate for simulation than the default monthly timeframe. However Ecosim is a model that relies on empirical calibration which is usually annual, although some attempts have been made to make seasonal Ecosim models with quarterly recalibration (Althauser, 2003). In the current context it would seem that there is a need for seasonal adjustment of parameter values (especially of P/B ratios, basal metabolic rate and starvation mortality). Data for this calibration are not generally available at high frequency, however.

The equilibrium property of Ecosim has been much discussed (e.g. Plaganyi and Butterworth, 2004) as have the implications of the foraging arena concept (limits on access of prey to predators) that result in creating a model with stable representation of assemblages of many species (Ahrens et al., 2011). Another property of the foraging arena concept is the stabilising effect of additional weak interactions (Pinnegar et al., 2004) similar to the weak link regulatory system outline by McCann et al. (1998)
and in contrast to the finding of the relative instability of more complex model food webs as outlined by Pimm (1991). The consequences of the high connectivity of the North Sea EwE model and existence of weak linkages are that small oscillations arising from the short term dynamics in ERSEM are damped in the higher trophic levels. This is particularly the case for functional groups whose P/B is low because the inter-seasonal effects are, in effect, spread over many years. Moreover, trophic interactions among benthic and pelagic components serve to stabilise dynamics in the higher trophic levels because some consumers are able to select prey from either domain.

On the other hand an age or size structured model where an organism undergoes competition or predation restricted by size would be less connected, since only part of the relevant populations would be competing, might have less damping and may have tightly coupled oscillations or instability. Models which use Lotka–Volterra type competition and predation models also tend to be less stable because both predator and prey density oscillations fully affect predation amounts (Goh, 1977). The Ecosim – ERSEM coupling may be a good representation of dynamics resulting from large scale shifts in input, and less good for examining intra-year differences, i.e. good at examining shifts due to climate change less good at effects of weather, because, unforced, Ecosim solves for an equilibrium (in effect a fixed point attractor, resulting from the equilibrium between predation and the vulnerability factor), rather than simulating short term dynamics of predator-prey interactions which may be affected by growth rate fluctuations which are influenced by weather.

Differences in biomass and productivity between, often quite closely related species vary considerably between the original North Sea Ecosim model and the coupled model. However both of these results are an encapsulation of a complex spatiotemporal dynamic because there are seasonal fluctuations in the abundance of many of these species. To make a detailed predictive coupled model would require calibration in time and space, to ascertain, for example, the changes in diet composition which occur in time and space. When seasonal variation in productivity is included (e.g. by coupling models or adding in seasonal forcing), temporal calibration in Ecopath with
Ecosim requires consideration of seasonal effects on long-term equilibrium, and given that Ecosim may have multiple equilibria, coupling may cause instability in equilibria in some circumstances.

Does the short term behaviour matter when considering long-term environmental change? In terms of the pelagic system the answer would seem very much to be yes. Over-winter survival of everything from small pelagic fish to seabirds seems to depend upon reserves built up in the previous season, and variation in survival and recruitment is generally considered to be influenced by bottom-up constraints on feeding. In the modelling exercise reported here it was found that overwinter survival often depended on sufficiently rapid growth of plankton populations in spring when a fish’s metabolism was increasing. It was necessary to ensure that the forcing functions used to limit winter feeding were matched the timing of the spring bloom. Further software development could enable this matching to be automatic. This development could be used to model situations, such as the case of Moroccan sardine populations, where timing between zooplankton peaks and conditions favourable for spawning influences recruitment (Machuo et al., 2009). We can use experimental plankton studies to make a sensitive calibration of planktonic response to short term meteorological variation, but our ability to explore the effect of climate change on the whole ecosystem, particularly its higher trophic level components, and to predict typical weather in future years is very limited.

The addition of a process oriented model such as GOTM-ERSEM to EwE may allow us to express the relationships between the drivers of change and the consequences. However, the relative insensitivity of EwE to short term perturbations begs a number of questions as to its suitability in studies on the likely consequences of climate perturbations to the ecosystem. Firstly the fixed seasonality of Ecosim may not adequately represent the results of shifts in the timing of variable onset events such as plankton blooms, but could be incorporated by adding a run time updated forcing function to the feeding via a plugin within Ecosim. Secondly Ecosim is limited in its ability to represent the effect of environmental variation on transient stages of the life cycle of marine or-
ganism such as the pelagic larvae of fish and benthic invertebrates. This is because of the lack of a model of short term drivers, and components for body condition, and the calibration of the multi-stanza model based on a Von Bertalanfy growth curve which is based on the growth curve of sharks and does not represent larval stages well (Urban, 2002). The North Sea model calibration, consequently, pays little attention to these stages. Recognising such limitations, we are however faced with a practical dilemma; the need for data and modelling tools that help address the pressing research question about how ecosystem respond to change limits the usefulness of the model as a tool for management. The pragmatic route must be to use the modelling capability we have and use it to help learn how to do better in the future.

Alongside the issue of time is that of space. For some parameter values there were times of the year when either prey or predators became severely depleted because of availability of prey, but in reality the patchiness of and interconnectedness of areas with different prey levels would lead to rapid recolonisation of the area by new predators and prey. An example of spatiotemporal local severe depletion was that of the Bay of Biscay anchovy in 2005 (Borja et al., 2008). To address this, an Ecospace model (the spatial equivalent of Ecosim) can be linked to the ERSEM model within GETM, the spatialized version of GOTM; this will allow us to model the temporal shift of marine organisms in response to the spatiotemporal dynamics of both marine plankton and fishing pressure. However, spatial biogeochemical models require considerable computational resources to run in most practical situations (typically of the order of a week or more time on a cluster for a 100 year run). The single column GOTM-ERSEM model requires about 90 s year$^{-1}$ to run on an Intel i5 processor, and combined with the integrated front end, makes it much more suitable for exploratory parameterisation, teaching and prototyping than the larger models.

In the realm of biogeochemical modelling there are a number of different models (e.g. Nemo-PISCES, Aumont et al., 2003; Madec et al., 1991; ECOSMO, Schrum et al., 2006; Ecoham, Pätsch and Kühn, 2008) which model the dynamics of plankton in response to changes in the geochemical model. The differences between the
model stem from the number of plankton groups and the treatment of the benthos. However the treatment of the environment as a three dimensional grid lends itself to a common interface with Ecosim and Ecospace (its 2 dimensional equivalent) though a specification of Couplerlib with 2 dimensional data elements and appropriate metadata specification. Ultimately, however the choice of modelling system will depend on the kind of data available and the parameters collected, because model parameterisation is a time consuming and costly part of any modelling process. The choice of ERSEM for both 1 dimensional and 3 dimensional modelling is as a result of the use of this model for the North Sea area being examined.

There is considerable debate about whether the components of end to end models should be simple or complicated. Very often we are faced with models and sub models that are both over complicated, in the sense that they contain too many parameters and components (Fulton et al., 2003) and over simplistic in that they contain what can certainly be described as simplifying formulations and may even be seen as dysfunctional formulations (Anderson and Mitra, 2009). This sterility of this debate has been acknowledged in a number of forums (e.g. the WGIPEM ICES working group http://www.ices.dk/community/groups/Pages/WGIPEM.aspx) along with the general conclusion dating back to William of Occam that things should be as complicated as necessary but no more so. What are needed therefore, are not so much simple models as simple conclusions that are likely to be robust to uncertain small scale and detailed assumptions and limitations in model formulation. We are a long way off capturing all the physical, biological and human conditions that will enable us to predict the cod in the North Sea in 50 years time, but we at least are starting to have the tools that enable us to integrate important scientific findings within a whole ecosystem context.

In conclusion, linking two very different models has produced a system which is richly expressive of the kinds of interactions of the different functional groups that form pelagic ecosystems and the causes of dynamics, including temperature, nutrient ratios and biological components of the system. It is not at this stage very precise (Levins, 1966) because it models a spatial area as a single point in space and because of
a number of known limitations not just of the underlying ERSEM and EwE models, but also of spatiotemporal variability of marine data. Nevertheless the linked model represents a considerable advance on verbal arguments because it can demonstrate the likely relative magnitude of these effects in a wider context of nutrient dynamics and marine fisheries management.

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References


An approach for coupling higher and lower levels in marine ecosystem models

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### Table 1. ERSEM and EwE function groups mapped.

<table>
<thead>
<tr>
<th>EwE Group No</th>
<th>EwE group</th>
<th>ERSEM group</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>51</td>
<td>Carnivorous zooplankton</td>
<td>Carnivorous mesozooplankton (Z3) but moved to EwE</td>
<td>Copepods</td>
</tr>
<tr>
<td>52</td>
<td>Herbivorous and omnivorous zooplankton (copepods)</td>
<td>Omnivorous mesozooplankton (Z4)</td>
<td>Copepod nauplii, copepodites, microzooplankton</td>
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<tr>
<td>53</td>
<td>Gelatinous zooplankton</td>
<td></td>
<td></td>
</tr>
<tr>
<td>54</td>
<td>Large crabs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>55</td>
<td>Nephrops</td>
<td></td>
<td></td>
</tr>
<tr>
<td>56</td>
<td>Epifaunal macrobenthos (mobile grazers)</td>
<td>Epibenthic predators (Y1)</td>
<td>Cross reference Group</td>
</tr>
<tr>
<td>57</td>
<td>Infaunal macrobenthos</td>
<td>Filter feeders (epifauna/infauna) (Y3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Deposit feeders (infauna) (Y2)</td>
<td></td>
</tr>
<tr>
<td>58</td>
<td>Shrimp</td>
<td></td>
<td></td>
</tr>
<tr>
<td>59</td>
<td>Small mobile epifauna (swarming crustaceans)</td>
<td></td>
<td></td>
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<tr>
<td>60</td>
<td>Small infauna (polychaetes)</td>
<td>Deposit feeders (infauna) (Y2)</td>
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<td></td>
<td></td>
<td>Infaunal predators (Y5)</td>
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<td>Sessile epifauna</td>
<td>Filter feeders (epifauna/infauna) (Y3)</td>
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<td></td>
<td></td>
<td>(Y3)</td>
<td></td>
</tr>
<tr>
<td>62</td>
<td>Meiofauna</td>
<td>Meiofauna (Y4)</td>
<td></td>
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<td>63</td>
<td>Benthic microflora (incl. Bacteria, protozoa)</td>
<td>Aerobic benthic bacteria (H1)</td>
<td></td>
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<tr>
<td></td>
<td>Planktonic microflora (incl. Bacteria, protozoa)</td>
<td>Anaerobic benthic bacteria (H2)</td>
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<td>Microzooplankton (Z5)</td>
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<td></td>
<td>Heterotrophic flagellates (Z6)</td>
<td>up to 20 µm SED</td>
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<td>Phytoplankton (autotrophs)</td>
<td>Diatoms (P1) Flagellates (P2)</td>
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<td>Picophytoplankton (P3)</td>
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<td>Large phytoplankton (P4)</td>
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<td></td>
<td></td>
<td>Small diatoms (P5)</td>
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**Table 2.** Climate change scenarios used in the model predictions.

<table>
<thead>
<tr>
<th>Scenario</th>
<th>N Concentration</th>
<th>P Concentration</th>
<th>Warming</th>
</tr>
</thead>
<tbody>
<tr>
<td>A1B1 – High Nut.</td>
<td>10 mmol m(^{-3})</td>
<td>1.0 mmol m(^{-3})</td>
<td>+3.2°C</td>
</tr>
<tr>
<td>A1B1 – Low Nut.</td>
<td>5 mmol m(^{-3})</td>
<td>0.5 mmol m(^{-3})</td>
<td>+3.2°C</td>
</tr>
<tr>
<td>B1 – High Nut.</td>
<td>10 mmol m(^{-3})</td>
<td>1.0 mmol m(^{-3})</td>
<td>+2.4°C</td>
</tr>
<tr>
<td>B1 – Low Nut.</td>
<td>5 mmol m(^{-3})</td>
<td>0.5 mmol m(^{-3})</td>
<td>+2.4°C</td>
</tr>
</tbody>
</table>
Figure 1. Outline of the information sources in the form of XML files and model components between two models running in network mode with a twin copies of Couplerlib.
Figure 2. Data transfers between a network of four linked models running in network model, with transfers of control messages, data and diagnostic information, using a mixed point to point and central client model.
Figure 3. Sequence of operations when GOTM-ERSEM is linked with Ecopath with Ecosim (EwE) in managed model. Grey box is part of model that is run repeatedly on a daily timestep.
Figure 4. GOTM-ERSEM prediction for the dynamics of 4 Plankton types – (a) Diatoms, (b) Flagellates (c) Dinoflagellates and (d) Omnivorous mesozooplankton within a water column over a two year period using synthetic meteorological data 1970–1971.
Figure 5. Dynamics of size commercial fish species under the linked ERSEM – EwE model 1960–2000 simulation.
Figure 6. Changes in relative biomass of 7 classes of functional groups under differing conditions of warming and nutrient availability (see Table 2 for definitions).