



ECOSMO E2E v2.0: Generic modules of higher-trophic-level fish and macrobenthos functional groups compatible for two-way coupling to lower-trophic-level model hosts through FABM coupler

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Abstract. The ECOSMO E2E v2.0 model includes functional-group-type fish and macrobenthos modules that can be two-way coupled to N(nutrient) P(phytoplankton) Z(zooplankton) D(detritus) type lower-trophic level (LTL) models. The model has been reprogrammed from the previous version, ECOSMO E2E v1.0, into independent fish and macrobenthos modules. This new version utilises the conceptual advantage of the Framework for Aquatic Biogeochemical Models (FABM), which provides an interface for coupling ecosystem models of diverse types. The coupling is exemplified by employing three different LTL models widely used in Copernicus Marine Services applications (ECOSMO, ERSEM, and ERGOM). The flexible design of the ECOSMO E2E v2.0 allows it to be coupled to LTL models and applied to regions beyond the example given in this paper. We present a proof of concept showing the two-way coupling of the E2E v2.0 with these LTL models, implemented in the central North Sea. We use a 1D water column model based on the General Ocean Turbulence Model for simulating the physics. The control simulation includes one macrobenthos functional group and two fish functional groups: a predominantly planktivorous group and a predominantly benthopiscivorous group. The modelled annual cycle of fish production is consistent with the patterns observed in fish biomass estimates from the International Bottom Trawl Survey in the North Sea. We present a model intercomparison of simulations from coupling the E2E model with different LTL models to explore the ecosystem dynamics of the central North Sea. We assess the effects of two-way coupling between lower and higher trophic levels on plankton dynamics, nutrient cycling, and fish production. Two-way coupling induces stronger and more realistic top-down control on zooplankton and phytoplankton than simplified LTL closures, modifying both biomass and seasonal patterns. Macrobenthos enhance detritus remineralisation, leading to elevated bottom-layer nutrient concentrations. Fish production strongly depends on macrobenthos, and the impacts on LTL fields vary between models according to trophic structure. We show that differences in prey composition among different models further drive non-additive ecosystem responses that shape fish and macrobenthos production.



1 Introduction

Marine ecosystem models are typically designed to represent lower trophic level (LTL) ecosystem components and therefore include primary production, nutrient cycles, and carbon uptake. These processes are often addressed within a Eulerian modelling framework, as phytoplankton and zooplankton can be treated as passive tracers to a first approximation (Blackford et al., 2004; Daewel and Schrum, 2013; Maar et al., 2011; Schrum et al., 2006). However, in this approach, the Higher Trophic Levels (HTL) such as fish are only considered as closure terms, often by assuming an additional zooplankton mortality term. Thus, the HTL component, an important part of the marine food web, is missing in such models. The important HTL components of the marine food web include pelagic and demersal fishes and macrobenthos. The macrobenthos group represents the benthic fauna that inhabit the seafloor, including suspension or filter feeders and deposit feeders. Small pelagic fish are predominantly planktivorous and occupy the pelagic region of the ocean, while demersal fish prey on pelagic fish or benthos. A simple yet effective way of modelling this HTL ecosystem is to approximate them as functional groups, and separate them by functional traits, similar to functional groups for phytoplankton and zooplankton in an NPZD (Nutrient Phytoplankton Zooplankton Detritus) approach. This was demonstrated by Daewel et al. (2019) using an end-to-end model (ECOSMO E2E v1.0) for the marine ecosystems of the North Sea and the Baltic Sea. Other examples of functional-group-type HTL models are van Denderen et al. (2021), Blanchard et al. (2009) and Cheung et al. (2018). Other mechanistic approaches for modelling HTL include species-specific implementations using either a Lagrangian (Shin and Cury, 2001; Travers et al., 2009) or Eulerian schemes (Senina et al., 2020; Dragon et al., 2018).

An HTL model can be forced (forcing refers to the provision of fields of LTL variables that drive the model) using outputs from physical-biogeochemical models (e.g., temperature, current velocities, plankton biomass) or observational datasets that provide boundary conditions for the simulated higher trophic level. In a one-way coupling approach, variables such as phytoplankton or zooplankton biomass derived from the LTL model are typically used as external forcing to drive the HTL model. The second approach involves two-way coupling, which enables a full exchange of fluxes between the LTL and HTL components and ensures mass conservation. This substantially improves the realism of ecosystem dynamics and is more suitable for studying long-term and regional-scale processes (Dupont et al., 2023). In HTL modelling, an important consideration is how energy flows through trophic levels through bottom-up and top-down processes (Cury et al., 2003). Bottom-up control refers to situations where HTL dynamics are driven by the availability of lower trophic level prey and by biogeochemical processes. In contrast, top-down control occurs when HTL predators influence the abundance and distribution of organisms at lower trophic levels, thereby affecting overall ecosystem structure. In one-way coupling, changes in prey availability can still propagate upward to influence predators in the HTL model through bottom-up controls. However, the top-down feedback from predators to prey and to ecosystem processes represented in the LTL model is not resolved (Travers et al., 2009; Fulton, 2010). Two-way coupling incorporates the top-down and bottom-up feedback necessary for reproducing realistic ecosystem behaviour and is particularly important in systems with strong predator-prey interactions (Brown et al., 2004), as demonstrated in the end-to-end modelling framework of Daewel et al. (2019). Another example of a two-way coupled modelling approach is demonstrated in Powley et al. (2026).



55 Stand-alone HTL models are typically applied in a one-way coupled configurations (Shin and Cury, 2001). In some cases, two-way coupling is implemented, where plankton biomass from the LTL model serves as prey for fish, and fish-induced predation mortality feeds back to the plankton fields, maintaining dynamic and mass-consistent interactions between the trophic levels (Travers et al., 2007). A key limitation of existing end-to-end HTL models is their limited flexibility for two-way coupling with independent LTL models. This highlights the need for stand-alone HTL models that can be fully coupled in a two-way
60 manner with existing LTL systems. Here, we present independent generic modules of macrobenthos and fish functional groups developed from the ECOSMO E2E v1.0 by Daewel et al. (2019). The independent modules presented in this paper are named ECOSMO E2E v2.0 (hereafter referred to as E2E). E2E also ensures benthic-pelagic linkage to capture ecosystem feedback and exchange flux between benthic and pelagic fields. The run-time integration of the modules to hydrodynamic and LTL models is achieved via the Framework for Aquatic Biogeochemical Models (FABM; Bruggeman and Bolding (2014)).

65 The main objective of this paper is to describe the important aspects of the E2E modules. Further, the manuscript presents a case study demonstrating the portability of the modules with three LTL models that are widely used in Copernicus Marine Services applications (ECOSMO, ERSEM and ERGOM). The modelled ecosystem dynamics and intercomparison of the simulations are investigated using a water column model that requires minimal resources for computation. This simplification has come at the expense of the exclusion of physical processes such as horizontal advection and horizontal migration of fish.
70 We consider these to be reasonable approximations for a central North Sea location away from the coastal boundaries.

The paper is organised as follows. A description of the E2E model is given in Section 2. Section 3 presents a case study for the central North Sea, and briefly describes the 1D water-column hydrodynamic model and the three LTL model hosts used. The simulated ecosystem dynamics of the central North Sea, and an intercomparison of the model simulations are presented in Section 3. In this section, we also compare the effects of two-way coupling, macrobenthos' role in nutrient cycling, and their
75 influence on fish production across the three model couplings. Section 4 discusses the advantages and limitations of the HTL modules, along with recommendations for coupling E2E with other LTL models. Section 5 concludes the paper.

2 E2E

2.1 Model equations

The E2E model explicitly simulates carbon biomass for both fish and macrobenthos. Equations involved in the formulation of the E2E, briefly described here for the completeness of this paper, are based on Daewel et al. (2019).
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In the configuration used here, macrobenthos is modelled as a single functional group, only represented at the bottom water-column boundary in E2E and is not influenced by advection. The macrobenthos group feeds on phytoplankton (flagellates and diatoms), zooplankton (micro- and mesozooplankton), detritus and dissolved organic matter, and sedimentary particulate organic matter available at the bottom. For the macrobenthos functional group in E2E, consumption of each prey group is calculated using a Michaelis-Menten (Michaelis and Menten, 1913; Monod, 1942) functional response, with the grazing parameters and feeding preferences specified in the model parameterisation. The overall macrobenthos consumption is then calculated as the sum of the consumption of the different prey groups X (zooplankton and phytoplankton groups, detritus, dissolved organic
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matter and organic sediment). The grazing rate (G_{MB}) of macrobenthos on a prey X is then formulated accordingly as a function of the prey group's biomass concentration (C_X):

$$90 \quad G_{MB}(C_X) = \sigma_{(MB,X)} \frac{a_{(MB,X)} C_X}{r_{MB} + F_{MB}} \quad (1)$$

Here, F_{MB} , the total available food is given by,

$$F_{MB} = \sum_{x=1}^n a_{(MB,X)} C_X \quad (2)$$

$\sigma_{(MB,X)}$ is the grazing rate for macrobenthos on the prey X , $a_{(MB,X)}$ is the feeding preference of macrobenthos for the prey X , r_{MB} is the half-saturation coefficient and n is the number of prey groups available for macrobenthos. The total consumption

95 rate of macrobenthos is then estimated as the sum of the consumption rates of all prey items and is given by,

$$R_{MB(cons)} = C_{MB} \left(\sum_{x=1}^n G_{MB}(C_X) \right) \quad (3)$$

The macrobenthos production rate is a product of assimilation efficiency (γ_{MB}) and the total consumption ($R_{MB(cons)}$). The losses due to natural mortality ($m_{MB}C_{MB}$) and excretion ($\epsilon_{MB}C_{MB}$) are linearly dependent on C_{MB} .

$$\epsilon_{MB} = \mu_{MB} e^{\left(\frac{\theta_{MB}}{k} \times \frac{T-T_0}{T \times T_0} \right)} \quad (4)$$

100 Here, T is the temperature in K , T_0 is the reference temperature (273.15 K), k is the Boltzmann factor, μ_{MB} is the macrobenthos excretion rate and θ_{MB} is the temperature control excretion parameter. The loss term for macrobenthos due to fish predation is defined in the fish module. Similarly, the macrobenthos module imposes a predation loss of $C_{MB}G_{MB}(C_X)$ on prey X . The conservation equation for macrobenthos is then given by,

$$\frac{dC_{MB}}{dt} = \gamma_{MB}C_{MB} \left(\sum_{x=1}^n G_{MB}(C_X) \right) - m_{MB}C_{MB} - \epsilon_{MB}C_{MB} - \text{predation loss}|_{z=\text{bottom}} \quad (5)$$

105 The E2E fish module consists of one functional group of fish. The main principle governing the modelling of the fish functional group is that the group can utilise all resources in the water column. Its production depends on the vertically integrated prey and in each time step the fish biomass is redistributed based on the vertical distribution of the prey biomass. The horizontal migration of fish is not considered in this configuration as only a 1D water column is simulated. The grazing rate (G_{Fi}) of fish on a prey X is modelled similar to the macrobenthos group:

$$110 \quad G_{Fi}(P_X) = \sigma_{(Fi,X)} \frac{a_{(Fi,X)} P_X}{r_{Fi} + F_{Fi}} \quad (6)$$

Here, F_{Fi} , the total available food, is given by,

$$F_{Fi} = \sum_{x=1}^n a_{(Fi,X)} P_X \quad (7)$$



$\sigma_{(F_i,X)}$ is the grazing rate for the prey X, $a_{(F_i,X)}$ is the feeding preference of fish for the prey X and r_{F_i} is the half-saturation coefficient. Here, P_X and P_{F_i} are the vertically integrated prey and fish biomasses, respectively.

$$115 \quad P_X = \int_{z=\text{surface}}^{z=\text{bottom}} C_X dz \quad (8)$$

$$P_{F_i} = \int_{z=\text{surface}}^{z=\text{bottom}} C_{F_i} dz \quad (9)$$

The total fish consumption is first calculated from the vertically integrated prey biomass (P_X) and then distributed vertically based on the actual prey distribution (C_X) in each grid cell.

$$120 \quad R_{F_i(\text{cons})} = P_{F_i} \left(\sum_{x=1}^n G_{F_i}(P_X) \times \frac{C_X}{P_X} + G_{F_i} C_{MB}|_{z=\text{bottom}} \right) \quad (10)$$

The fish production rate is a product of the assimilation efficiency (γ_{F_i}) and the total consumption ($R_{F_i(\text{cons})}$). The fish group mortality rate ($m_{F_i} C_{F_i}$) is defined as linear. Biomass loss due to excretion ($\epsilon_{F_i} C_{F_i}$) is parameterised as a function of temperature (Gillooly et al., 2001; Clarke and Johnston, 1999).

$$\epsilon_{F_i} = \mu_{F_i} e^{\left(\frac{\theta_{F_i}}{k} \times \frac{T - T_0}{T \times T_0} \right)} \quad (11)$$

125 Here μ_{F_i} is the fish excretion rate and θ_{F_i} is the temperature control excretion parameter. Finally, the conservation equation for fish biomass is as follows,

$$\frac{dC_{F_i}}{dt} = \gamma_{F_i} R_{F_i(\text{cons})} - m_{F_i} C_{F_i} - \epsilon_{F_i} C_{F_i} - \text{predation loss} \quad (12)$$

The coupling of the E2E modules to the LTL model introduces additional sources and sinks in the governing equations of the LTL state variables. These modifications account for grazing by macrobenthos and fish and the associated changes in organic matter and nutrients resulting from HTL processes. The biomass loss due to predation by macrobenthos on the state variable C_X is given by

$$\frac{dC_X}{dt} \Big|_{z=\text{bottom}} = -C_{MB} G_{MB}(C_X) \Big|_{z=\text{bottom}} \quad (13)$$

Similarly, the biomass loss due to grazing by fish on the state variable C_X is given by

$$\frac{dC_X}{dt} = -P_{F_i} G_{F_i}(P_X) \frac{C_X}{P_X} \quad (14)$$

135 The detritus sources and sinks governed by losses due to fish and macrobenthos grazing and gains from the fraction of unassimilated fish consumption and mortality.

$$\frac{dC_{det}}{dt} = -P_{F_i} G_{F_i}(P_{det}) \frac{C_{det}}{P_{det}} - [C_{MB} G_{MB}(C_{det})]_{z=\text{bottom}} + (1 - \alpha_{DOM}) [(1 - \gamma_{F_i}) R_{F_i(\text{Cons})} + m_{F_i} C_{F_i}] \quad (15)$$



α_{DOM} is the fraction of unassimilated fish consumption and mortality that is allocated to dissolved organic matter, with the remaining fraction $1 - \alpha_{DOM}$ contributing to detritus. Dissolved organic matter terms complements detritus, receiving a fraction α_{DOM} of unassimilated fish losses and macrobenthos, while being grazed by macrobenthos.

$$\frac{dC_{DOM}}{dt} = -[C_{MB} G_{MB}(C_{DOM})]_{z=bottom} + \alpha_{DOM} [(1 - \gamma_{Fi})R_{FiCons} + m_{Fi}C_{Fi}] + ((1 - \gamma_{MB})R_{MBCons} + m_{MB}C_{MB}) \quad (16)$$

Sediment sources and sinks are also similar to detritus, with macrobenthos grazing acting as a sink, while the remaining fraction $1 - \alpha_{DOM}$ of macrobenthos losses contributes to the sediment pool.

$$\frac{dC_{sed}}{dt} = -C_{MB} G_{MB}(C_{sed}) + (1 - \alpha_{DOM}) [(1 - \gamma_{MB})R_{MB(Cons)} + m_{MB}C_{MB}] \quad (17)$$

The nutrient pool (PO_4 , NH_4) in the LTL model is enhanced by excretion from fish throughout the water column and from macrobenthos at the bottom boundary.

$$\frac{dPO_4/NH_4}{dt} = \epsilon_{Fi}C_{Fi} + \epsilon_{MB}C_{MB}|_{z=bottom} \quad (18)$$

Respiration is also parameterised based on excretion, scaled by a conversion factor, as follows.

$$\frac{dO_2}{dt} = -c_{C:O_2} [\epsilon_{Fi}C_{Fi} + [\epsilon_{MB}C_{MB}/\Delta z]_{z=bottom}] \quad (19)$$

2.2 Model coupling and configuration

The E2E modules are written in object-oriented Fortran 90. Their coupling, both with each other and with LTL or hydrodynamic models, is handled via FABM (Bruggeman and Bolding, 2014). FABM is a widely adopted flexible coupling interface that facilitates communication and data exchange between independent modules using a set of application programming interfaces. Modularity is a key strength of FABM, and this makes it possible to build complex biogeochemical food-web models by interconnecting self-contained modules. Each module operates without explicit spatial or temporal loops, and they rely on macros that allow seamless integration with high-performance computing frameworks. Spatially explicit variable arrays are managed by the host hydrodynamic model, allowing for efficient simulations across large grids. FABM is a core component of operational forecasting for the north-west European Shelf Seas and the Arctic Ocean under the CMEMS. More information and documentation, including a list of FABM-compatible models, can be found at <http://fabm.net/wiki>. Details on implementation and test cases for ECOSMO, ERSEM, ERGOM and other biogeochemical models implemented in FABM can be found at <https://github.com/fabm-model/fabm>.

In a coupled setup based on FABM, each module (e.g., fish, macrobenthos, plankton) can read from and write to shared state variables. Each module registers its required inputs (dependencies) and outputs (state or diagnostic variables) within FABM. This setup ensures dynamic feedback: changes in prey availability affect predator consumption and growth, while predator actions (e.g., grazing or excretion) feed back into nutrient and detritus pools. For instance, when the prey consumption by fish is estimated, it reduces the prey concentration in the LTL model by applying a negative flux to the corresponding prey



state variable (Equations 13–14). At the same time, the fish module can increase nutrient concentrations (e.g., NH_4 , PO_4) or detritus through excretion or mortality (Equations 15–19). Mass is conserved because all fluxes are handled within shared data structures. These features ensure consistency across all modules and allow for meaningful feedback loops. For example, the fish module's grazing reduces plankton biomass, which in turn can affect the fish growth rate. Similarly, macrobenthos feed on benthic detritus and, in turn be preyed upon by fish.

The model setup is handled through a human-readable configuration file in YAML format (<https://yaml.org/>). YAML files allow users to define prey for fish and macrobenthos as dynamically-sized arrays, specify multiple prey functional groups, each with distinct elemental compositions (C , N , P , Si), set rates for grazing, mortality, excretion, and half-saturation constants, identify target pools for excretion (e.g., NH_4 , PO_4), which are scaled to match the unit system of the host LTL model. Because these definitions are handled externally in the YAML file, users can modify or calibrate the model without recompiling the source code.

The E2E fish and macrobenthos modules are designed generically, making them adaptable to a wide range of LTL models. Rather than being hardcoded (or statically assigned) to specific plankton groups or unit conventions, these modules operate using generic variables such as prey, detritus, and dissolved organic matter. At runtime, these references are linked to the appropriate variables from the LTL model defined in the YAML file. Modules also use string-based checks to determine whether to track additional elemental stoichiometric composition (e.g., nitrogen, phosphorus, silica) for the prey items. For example, if the composition string includes 'n', then nitrogen compensation will be fed back to the LTL model. To ensure compatibility between models that use different unit systems, multipliers can be defined in the YAML file. For instance, if the LTL model outputs detritus in mol C kg^{-1} but the E2E module requires mg C m^{-3} , an internal multiplier handles the conversion. This modular and flexible approach ensures smooth integration, whether the host LTL model is a basic NPZD-type model or a more complex ecosystem representation. This flexibility allows users to minimise the need for heavy customisation when the LTL model evolves in the future. Further, the modules can be called multiple times in the YAML file to generate more than one functional group of fish or macrobenthos. A schematic diagram of the E2E modules illustrating the predation, mortality and excretion targets is given in Figure 1.

In this paper, we used two simplified fish functional-groups: a predominantly planktivorous group and a predominantly benthic-piscivorous group. Although this is a generalisation, this distinction has proven ecologically significant in several regions, such as the northern Atlantic (Thompson et al., 2025) and the northern Indian Ocean (Shankar et al., 2019; Vijith et al., 2023).

3 The North Sea case study

We used three LTL models in this study: ECOSMO, ERSEM and ERGOM. These three models have different strengths and weaknesses and their applications vary based on the specific regional ecosystems and issues they are designed to address. Important differences in the nutrient cycles, and pelagic and benthic biomasses in each model and the technical details of



the coupling are noted in this section. Table 1–3 list the important model parameters used while coupling E2E with the three models.

3.1 The physical model (GOTM)

The physical model is a 1D water-column model, GOTM (Burchard et al., 1999), set up for a central North Sea location (56°N, 3°E). The water column is 73 m deep and has 83 sigma coordinate levels. The model is integrated for 20 years with repeated annual forcing, and the final-year simulation is presented in the paper. The integration time step is 1800 s. The ECMWF ERA5 dataset (0.25° and hourly resolution) (Hersbach et al., 2020) is used for meteorological forcing. Nutrients (nitrate, phosphate, silicate, and oxygen) are initialised with climatological profiles obtained from WOA 2018 (Garcia et al., 2019). In addition, nutrients are relaxed to climatological profiles on a relaxation time scale of one year. Temperature and salinity are relaxed to the WOA 2018 climatological profiles every month. These relaxations are expected to compensate for the unaccounted processes (such as horizontal advection) in the 1D model. A $k-\epsilon$ turbulence model with a second-order closure is used with the minimum turbulent kinetic energy set to $10^{-6} \text{ m}^2 \text{ s}^{-2}$. The physical bottom roughness was set to 0.005 m. A horizontal gradient in surface elevation is prescribed at the sea surface to mimic tidal effects.

3.2 LTL models and its coupling to E2E modules

3.2.1 ECOSMO (ECOSystem MOdel)

The ECOSMO LTL model used in this paper is based on Daewel and Schrum (2013). The evolution of the ECOSMO modelling framework can be found in Schrum et al. (2006) and Daewel and Schrum (2013). The ECOSMO II model includes three primary nutrient cycles: nitrogen, phosphorus, and silicon, crucial for understanding nutrient dynamics within the marine ecosystem. The model includes three functional groups of primary producers: diatoms, flagellates and cyanobacteria. The model resolves two zooplankton groups: herbivorous microzooplankton and omnivorous mesozooplankton. An integrated bottom sediment layer (sedimentary particulate organic carbon) is implemented to simulate fluxes between the water column and the sediment. The model validations presented by Daewel and Schrum (2013) and Daewel and Schrum (2017) show that ECOSMO can reasonably simulate ecosystem dynamics in the North Sea and Baltic Sea. The model has also been shown to simulate the general biogeochemistry of the Nordic and Arctic seas by comparing against in situ, satellite, and climatological data (Yumruktepe et al., 2022). The ECOSMO model is currently used as the marine biogeochemical model for operational forecasts of the Arctic Ocean (Copernicus Marine Service, 2024a) under the umbrella of CMEMS at the Arctic Marine Forecasting Centre.

The coupling of the E2E modules with ECOSMO is straightforward and follows a similar approach to that described in Daewel et al. (2019). The MB group feeds on flagellates, diatoms, microzooplankton, and mesozooplankton, as well as detritus, dissolved organic matter, and sedimentary organic matter. The first group of fish is predominantly planktivorous and feeds on meso- and microzooplankton. In addition, it can feed on macrobenthos and detritus. The second group of fish is pisci-benthivorous, and it preys mostly on the planktivorous fish group and macrobenthos. In addition, it can feed on mesozoo-



plankton and detritus. For each of the fish groups, the excretion and mortality fluxes target NH_4 , PO_4 , detritus and dissolved organic matter. The mortality rates of zooplankton groups are reduced to 80% of the rate used in ECOSMO II to account for the addition of the HTL groups.

3.2.2 ERSEM (European Regional Seas Ecosystem Model)

235 ERSEM is the most complex among the three considered LTL models. The ERSEM model used here is based on Butenschön et al. (2016). The model was originally developed to simulate the seasonal cycle of biogeochemistry and the pelagic and benthic food web of the North Sea (Baretta et al., 1995; Baretta-Bekker et al., 1997). A detailed description of the model, the history of its development and a list of various applications are available in Butenschön et al. (2016). ERSEM simulates the nutrient cycles of nitrogen, phosphorous, silicon, and iron in the marine environment. In the pelagic system, ERSEM includes
240 four types of phytoplankton (diatoms, picophytoplankton, nanophytoplankton, and microphytoplankton) and three types of zooplankton (nanoflagellates, microzooplankton, and mesozooplankton). ERSEM includes three detritus groups (R4, R6, and R8), but the current E2E coupling framework allows only one detrital target for the HTL components. Therefore, only the medium-sized detritus pool (R6) is used by the fish and macrobenthos modules, while the other detritus groups remain in the ERSEM model but are not accessed by the HTL modules. In the benthic system, ERSEM includes two types of bacteria
245 (aerobic and anaerobic). The interactions between these functional types are represented by fluxes of nutrients, carbon, and other chemical components. These fluxes are calculated based on the physiological processes of each functional type, such as uptake, respiration, excretion, and predation. The model also includes fluxes between the pelagic and benthic systems, such as sedimentation and resuspension. The benthic macrofauna (suspension feeders and deposit feeders) and meiofauna available in ERSEM are not used in this paper. ERSEM is used by the UK Met Office as the biogeochemical component in their operational
250 forecasting systems for the north-western European shelf seas within CMEMS (Copernicus Marine Service, 2024b).

The labels for variables given in this paragraph are as used in ERSEM. The choices of feeding and excretion targets were adopted to maintain consistency with the ECOSMO-E2E and ERGOM-E2E coupling configurations. In coupling with ERSEM, the macrobenthos group feeds on microphytoplankton (P4), diatoms (P1), mesozooplankton (Z4) and microzooplankton (Z5), as well as detritus (R6), labile dissolved organic matter (R1) and sedimentary organic matter (Q6). The mortality targets are
255 Q6 and R1, and excretion produces ammonium (N_4) and phosphate (N_1). Fish 1 predominantly feeds on Z4 and Z5 and is planktivorous. It also has a smaller grazing preference for R6 and macrobenthos. Fish 2 predominantly feeds on fish 1 and MB. In addition, it has a smaller grazing preference for Z4, R6 and macrobenthos. The mortality targets are Q6 and R1, and excretion produces ammonium (N_4) and phosphate (N_1). In ERSEM, units for nutrient concentrations of N_4 and N_1 are in mmol m^{-3} . Whereas in E2E, these concentrations are expressed in equivalent carbon units (mg m^{-3}). A suitable conversion is
260 performed in the E2E code to address this difference, as noted in the earlier section. Because ERSEM has a more detailed LTL structure, several alternative combinations of predation, mortality, and excretion pathways could be implemented. Therefore, the targets described above are used to ensure consistency and allow direct comparison with the ECOSMO-E2E and ERGOM-E2E simulations.



3.2.3 ERGOM (Ecological Regional Ocean Model)

265 ERGOM was originally developed to simulate Baltic Sea ecosystem dynamics and thus specifically address anoxia and hypoxia (Neumann, 2000; Neumann et al., 2002). ERGOM incorporates the nitrogen and phosphorus cycles. The pelagic ecosystem in ERGOM is represented by three functional groups of phytoplankton: large-cell, small-cell, and diazotrophic cyanobacteria. In ERGOM, the phytoplankton groups differ not only in growth rate but also in nutrient requirements. The model also includes a single group of zooplankton, which interact with the phytoplankton through grazing. The most recent versions of the model
270 are reported in Neumann et al. (2015, 2017). ERGOM was applied to the North Sea by Maar et al. (2011). ERGOM is used in operational forecasting systems for biogeochemistry of the Baltic Sea (Copernicus Marine Service, 2026).

The coupling of the ERGOM model to the E2E modules is as follows. The predation targets for the macrobenthos group are set to large-cell and small-cell phytoplankton, and zooplankton. The macrobenthos also feeds on detritus, dissolved organic carbon and sedimentary organic carbon. Fish 1 (planktivorous fish group) predominantly feeds on the only zooplankton
275 functional group available in ERGOM, and marginally on detritus and macrobenthos. Fish 2 feeds predominantly on fish 1 and macrobenthos. Fish 2 also feeds on detritus and zooplankton. The mortality and excretion targets are NH_4 , PO_4 , detritus and dissolved organic carbon. Nitrogen is the major currency in ERGOM and, therefore, scaling is used to convert the state variables to carbon units. These scaling multipliers are defined in the YAML file.

3.3 Model simulations

280 We have performed five primary experiment sets, each repeated for the three LTL models (ECOSMO, ERSEM, ERGOM).

1. LTL-only run: The model is configured without fish and macrobenthos, and the setup consists only of the NPZD variables of the chosen LTL model. This simulation serves as the baseline for understanding how the LTL model behaves in isolation, without top-down control from higher trophic levels.
2. Macrobenthos-only run: Only the macrobenthos group is coupled to the LTL model (without any fish). The purpose of
285 this simulation is to identify the role of benthic–pelagic coupling, focusing on how benthic detritus consumption and nutrient regeneration affect pelagic plankton productivity.
3. Control Run: The control simulation includes two fish functional groups and a macrobenthos group coupled to the LTL model. This model configuration represents the most complex ecosystem configuration.
4. LTL with 20% increased zooplankton mortality: This is equivalent to the LTL-only simulation, but with zooplankton
290 mortality rates increased by 20% compared to the LTL-only run. The increased zooplankton mortality is expected to mimic the effect of top-down control (predation) on zooplankton. This simulation allows comparison with runs that explicitly include HTL, assessing how well the mortality tuning replicates, or differs, from the inclusion of explicit HTL predation scenarios.



5. Fish-only run (without macrobenthos): This configuration involves two fish groups coupled to the LTL model without
the macrobenthos group. The purpose is to isolate the top-down effect of fish predation alone on zooplankton and to see
how it changes the LTL dynamics, without any benthic–pelagic coupling mediated by macrobenthos.

3.4 International Bottom Trawl Survey data

Daewel et al. (2019) used data on fish distribution in the North Sea collected by the North Sea International Bottom Trawl
Survey (IBTS), which is archived at the International Council for the Exploration of the Sea (ICES, 2012)([http://www.ices.
dk/Pages/default.aspx](http://www.ices.dk/Pages/default.aspx)). Daewel et al. (2019) sorted the fish data into pelagic and demersal groups and converted the data into
biomass using species-specific allometric relationships. The IBTS survey is carried out every year in the first quarter, and
for some years it is also sampled in the other quarters. For comparison with the biomass of the fish simulated in the model,
we construct the annual cycle using harmonic analysis (Risien and Chelton, 2008; Abhishek et al., 2023). Harmonic analysis
converts a time-series signal into a set of cosine waves that, when combined, recreate the original pattern. The first four
harmonics of the annual period (365.00, 182.50, 121.67, and 91.25 days) are used to build the annual cycle of the spatially-
averaged fish biomass data.

3.5 Control Run

This section presents the control simulations conducted using the E2E coupling with ECOSMO, ERSEM, and ERGOM. Each
simulation was run under identical physical forcing conditions to allow for a consistent comparison across model systems.

3.5.1 Modelled physical setting of the North Sea

In the central North Sea, temperature and salinity exhibit marked seasonal variations (Figure 2). During the winter months,
from December to February, the water column is well-mixed, with temperatures between 6 and 10°C and salinity levels around
34.9. As winter transitions to spring, the water column begins to stratify gradually. By summer, a strong thermocline develops
and the mixed layer becomes shallow (~20 m). The surface waters warm to approximately 18°C and salinity increases slightly
to about 35.0. In autumn, increased rainfall and river discharge contribute to fresher surface water, reducing salinity to around
34.7 while at the same time increased storm activity mixes the surface layer, deepens the mixed layer depth, and weakens the
thermocline. Cooling on the sea surface during winter leads to deep water convection and mixing of the water column. During
an annual cycle, temperatures range from 6°C to 18°C, while sea surface salinity varies between 34.7 and 35.0. The region
exhibits a pronounced annual cycle in penetrative shortwave radiation (Figure 2), with minimal light penetration in winter and
significantly stronger penetration during summer. In summary, the central North Sea experiences a clear annual cycle with
strong stratification during summer, while in winter, the water column is well-mixed. The seasonal stratification of the central
North Sea is discussed in Pohlmann (1996); van Leeuwen et al. (2015).



3.5.2 Modelled annual cycle of lower trophic level variables

The variability of nutrients in the central North Sea is affected by seasonal hydrodynamics (Figure 3). In winter, nutrients
325 are well-mixed and concentrations are relatively high throughout the water column. In summer, nutrients are depleted near
the surface within the mixed layer, while concentrations remain abundant below it. This annual cycle in nutrient distribution
is similar in all three simulations. However, the ERGOM model simulates slightly high nutrient concentrations, although
their seasonal patterns align closely with those simulated in the ERSEM and ECOSMO models. The ERGOM configuration
used here lacks a silicate component. The summertime depletion of near-surface nutrients in the central North Sea has been
330 previously noted by Daewel and Schrum (2013).

As a consequence of the distribution of water-column nutrients and the penetration of light, the evolution of plankton vari-
ables in the central North Sea is also strongly seasonal, with peak productivity during the spring and summer (Figure 4). Key
patterns in plankton variability reveal a late spring bloom of phytoplankton, including both flagellates and diatoms. This spring
bloom is evident in all three models. During the summer months, from July to September, flagellates and diatoms exhibit a
335 subsurface biomass maximum. An additional near-surface bloom of flagellates occurs from September to November within the
mixed layer in the ERGOM model simulation. Microzooplankton and mesozooplankton occur in the summer and extend their
presence until early autumn in all three simulations. Maxima of zooplankton biomass occur at the base of the mixed layer in the
subsurface during late summer. The zooplankton distribution simulated by ERGOM is coherent with the modelled flagellate
distribution.

340 According to Greenstreet et al. (1997), zooplankton biomass in the North Sea follows a pronounced seasonal cycle, with total
zooplankton biomass increasing from 10.31 gWW m^{-2} (wet weight in gram per square metre) in winter (quarter 1) to a peak
of 21.59 gWW m^{-2} during spring–early summer (quarter 2), before declining to 16.59 gWW m^{-2} in late summer–autumn
(quarter 3) and 12.68 gWW m^{-2} in autumn–winter (quarter 4). Fransz et al. (1984) further showed that copepods exhibited
a distinct subsurface biomass maximum associated with the chlorophyll maximum, indicating that the vertical distribution of
345 zooplankton closely followed that of their phytoplankton prey. These characteristics are consistent with the model simulations.

Overall, a sequential bloom pattern is observed in the central North Sea, beginning with diatoms, followed by flagellates,
then microzooplankton, and finally mesozooplankton. This sequential pattern is consistent with continuous plankton recorder-
based studies (Reid et al., 2003), sample data analysis (Rodríguez et al., 2000), and modelling studies (Daewel and Schrum,
2013).

350 The detritus, occurring below the mixed layer and extending to the seafloor, and benthic sedimentary organic carbon peak
during the summer (Figure 5). A uniform sinking velocity of 5 m day^{-1} is prescribed for detritus in all three model configura-
tions. Here, ERSEM shows concentrations much lower compared to ERGOM and ECOSMO. ERSEM includes three detritus
size classes: small, medium, and large particulate organic matter. Although small-sized detritus also shows considerable con-
centrations in the simulation, only medium-sized detritus is used in the coupling. Therefore, the total detrital pool accessible
355 to the E2E model is lower.



3.5.3 Modelled annual cycle of fish and macrobenthos

Figure 6 shows the simulated distributions of fish 1 and fish 2 groups among the three model configurations. Among the models, ERGOM simulated the lowest fish biomass, while ERSEM simulated the highest. Across models, fish 2 biomass is lower than fish 1 biomass. In the ECOSMO and ERGOM models, both fish 1 and fish 2 show high biomass during late summer through autumn, predominantly concentrated below the mixed layer. In the ERSEM and ECOSMO simulations, fish 1 displays a subsurface biomass peak in summer and remains high throughout the water column from late summer to the end of autumn.

The macrobenthos biomass cycle peaks in summer in ECOSMO and ERSEM, and in winter in ERGOM, reaching a minimum in spring (Figure 7c–e). Notably, fish 1 shows distinct seasonal variability, while fish 2 does not exhibit a clear seasonal pattern in integrated biomass. In all three models, biomass of fish 1 begins to increase in early summer. These aspects (the seasonality of fish 1 and its higher biomass compared to fish 2) are also evident in the estimated climatology of the catch per unit effort from the IBT survey (Figure 7b). ERSEM simulates the highest fish 1 production, ECOSMO shows intermediate values, and ERGOM produces the lowest fish production overall, with fish 2 remaining very low compared to fish 1 in all three simulations. Fish 1 in ERGOM does not exhibit seasonal variability due to the extended temporal availability of prey. Also, it is important to note that the model-simulated fish biomass shown in this figure cannot be quantitatively compared with the IBT survey climatology, as the model outputs are expressed in terms of fish production potential (biomass in grams per unit volume), while the IBT survey data are reported as catch per unit effort (Hoyle et al., 2024).

The three model simulations generally exhibit similarities and the models provide a complementary view of the seasonal ecosystem of the central North Sea, despite the differences noted above. All three models show consistent patterns for plankton, fish, and macrobenthos, although with varying magnitudes, and capture the essential aspects of the seasonal dynamics in the central North Sea. Although differences in fish biomass could be reduced by tuning feeding preferences or grazing rates, we kept these rates within a consistent range to ensure comparable settings across models. Adjusting these rates considerably would undermine the goal of an intercomparison.

3.5.4 Grazing rates of fishes and macrobenthos

Figure 8 shows the grazing rates (Eqs. 1 and 6) of fish 1, fish 2, and macrobenthos on their respective prey, helping to explain the seasonal differences in HTL production. In ECOSMO and ERSEM, the grazing rate of fish 1 on microzooplankton is highest in early summer, while the grazing rate on mesozooplankton increases later in summer. Outside this period, the grazing rate of fish 1 shifts predominantly towards macrobenthos, reflecting the reduced availability of zooplankton after summer. In ERGOM, where only one zooplankton group is represented, fish 1 grazing is dominated by zooplankton during spring and early summer, while grazing on macrobenthos becomes relatively more important during winter. Grazing on macrobenthos occurs throughout the year, although at lower rates during periods of high zooplankton availability.

Fish 2 shows a stronger dependence on benthic prey. In ECOSMO, the grazing rate of fish 2 on fish 1 is highest in spring, after which the grazing rate on macrobenthos becomes dominant for the rest of the year. In ERSEM, the grazing rate of fish 2



on fish 1 is higher during spring, autumn, and winter, whereas the grazing rate on macrobenthos is relatively higher in summer. In ERGOM, the grazing rate of fish 2 indicates that macrobenthos is the primary prey throughout the year.

390 A seasonal shift in macrobenthos grazing is evident (Figure 8), but with differing patterns across models: in ECOSMO, macrobenthos grazing shifts from a mixed diet of sediment and detritus towards predominantly detritus in late summer and autumn; in ERSEM, grazing remains largely sediment-dominated; whereas in ERGOM, it is dominated by detritus during summer and autumn, with sediment being relatively more important outside this period. Macrobenthos also grazes to some extent on diatoms in both ECOSMO and ERGOM, but not in ERSEM. In contrast, moderate grazing on flagellates occurs in ERSEM and
395 ERGOM, but not in ECOSMO. Macrobenthos can only consume diatoms or flagellates when these phytoplankton groups reach the bottom layer, so differences in the way the models simulate their vertical distribution (Figure 4) could lead to contrasting feeding patterns. Overall, this indicates that even with an identical macrobenthos model, differences in pelagic fields across LTL models lead to markedly different macrobenthos grazing patterns, highlighting the strong influence of pelagic–benthic coupling on model outcomes.

400 Several patterns observed in fish production can be better understood through the grazing rates given in Figure 8. In the ERSEM model, the subsurface peak in fish 1 biomass during the summer (Figure 6) coincides with increased feeding on both mesozooplankton and microzooplankton, highlighting the importance of zooplankton availability in supporting pelagic fish growth. In the ERGOM model, elevated concentrations of detritus promote the growth of macrobenthos, which ultimately serves as a key food source for both fish groups. Variations in prey composition and availability across models directly in-
405 fluence the spatial and temporal patterns of fish and macrobenthos production. Fish are known to exhibit an opportunistic feeding behaviour, adjusting their diet based on the availability of different prey groups (Travers-Trolet et al., 2025). Due to these compensatory feeding mechanisms, similar fish biomass patterns can emerge across different model simulations, despite differences in LTL dynamics, as shown in this paper.

3.6 Impact of coupling the HTL modules

410 We have carried out five sets of simulations, as listed in Section 3.3, which differ only in selected biological components. Here, we use our results to present a testable hypothesis on how the addition or removal of an HTL functional group might impact the ecosystem of the central North Sea.

3.6.1 Role of macrobenthos

The impact on the distribution of detrital and benthic sediments owing to the macrobenthos group is assessed using the difference between the macrobenthos-only and LTL-only runs, and the difference between the control and fish-only (without
415 macrobenthos) runs. Figure 5 shows that, in the control run, both detrital and bottom sedimentary carbon peak during summer (May–July) in all three simulations. Consequently, the macrobenthos biomass begins to increase in July, reaches a maximum in August or September, and then declines (Figure 7). Assessment of the actual grazing rates indicates that macrobenthos primarily feed on detritus and sediment (Figure 8). The impact of macrobenthos on carbon dynamics is evident in Figure 9,
420 where simulations including macrobenthos show lower detritus concentrations, particularly in ECOSMO and ERGOM during



summer to autumn, whereas in ERSEM the detritus response is weaker. In the case of the ERSEM simulation, the detrital concentrations are relatively low, and hence the grazing of macrobenthos is mostly restricted to sedimentary carbon. The effect on the bottom sediment is more pronounced and persistent than on detritus, with strong reductions during summer and autumn when macrobenthos biomass is high (Figure 9). A comparison of the concentrations of nutrients in the bottom layer revealed
425 that the presence of macrobenthos generally leads to higher near-bottom nutrient concentrations in ECOSMO, ERSEM, and ERGOM, although the magnitude differs between models and between nitrate and phosphate (Figure 10). In the ERGOM-E2E coupling, the response is dominated by macrobenthos-mediated remineralisation, which enhances nutrient recycling and results in elevated nutrient concentrations in the presence of macrobenthos.

The analysis shows that macrobenthos significantly influence the redistribution and remineralisation of detritus and benthic
430 sediment, thus affecting nutrient concentrations in the bottom layer of the water column consistently across all three models. Previous observational studies (Braeckman et al., 2014) and modelling studies (Zhang et al., 2019, 2021) have also shown that macrobenthos play a key role in benthic-pelagic coupling in the North Sea by modulating biogeochemical cycling.

3.6.2 Top-down control by HTL groups

Here, we compare the control run with the LTL-only and mortality-tuning (+20% zooplankton mortality) runs. An increased
435 zooplankton mortality represents a simplified top-down control, usually adopted to close the LTL simulations (Daewel et al., 2014). Figure 11 shows that incorporating HTL modules reduced the concentrations of micro- and mesozooplankton in ECOSMO and ERSEM. Additionally, it altered the seasonality of zooplankton, which in turn affected phytoplankton distribution (Figure 11). In contrast, the changes driven by the increased zooplankton mortality in the LTL-only simulation reduced zooplankton concentrations without affecting its seasonal pattern. Furthermore, the phytoplankton groups responded to changes
440 in zooplankton groups following the inclusion of HTL modules, indicating a top-down control. Specifically, flagellate and diatom concentrations increased. Additionally, the timing and magnitude of phytoplankton biomass change differed between the simulation with explicit HTL modules and the setup that simulated the food-web closure by enhancing zooplankton mortality (Figure 11). In the ERGOM model, which includes only a single zooplankton group, the feedback patterns resulting from the addition of HTL modules and from increased zooplankton mortality are not similar (Figure 11).

445 In summary, we show that including the HTL groups (as in the control run) leads to a stronger top-down control on the zooplankton compared to a fixed +20% zooplankton mortality. The results indicate that even simplified zooplankton representations can transmit top-down effects to phytoplankton groups when coupled to HTL modules. Nevertheless, the distribution of these feedbacks depend on the structure of the lower-trophic-level food web, highlighting the importance of food-web complexity in shaping ecosystem responses.

3.6.3 Non-additive effect of HTL groups

Here, we examine whether the simultaneous presence of fish and macrobenthos produces a response in plankton dynamics that cannot be explained as the simple sum of their individual effects. Using the LTL run as the baseline, we compare the anomalies in the macrobenthos-only, fish-only, and control runs relative to this baseline. Figure 12 shows that the control response is not



uniformly reproduced by either the macrobenthos-only or fish-only runs, indicating non-additive ecosystem responses. This is expected, as fish and macrobenthos interact not only through separate grazing pathways, but also through predation and competition.

The magnitude and sign of the anomalies vary across functional groups and among models. In both ECOSMO and ERSEM, mesozooplankton is reduced in control and macrobenthos-only configurations relative to the LTL baseline, but the strength of the reduction differs depending on whether only one HTL component or both are present. In ERSEM, the strongest response occurs in flagellates, which increase markedly in all three configurations, while diatoms and zooplankton generally decrease. In ECOSMO, the responses are more mixed: flagellates increase in the control run, mesozooplankton decreases, and diatoms respond most strongly in the fish-only configuration. These patterns show that the combined HTL effect is not a simple linear combination of the separate fish and macrobenthos effects. The absence of the Fish–LTL bar for ERGOM in Figure 12 reflects the very weak fish-only effect in this model, with the overall HTL response being dominated by the macrobenthos contribution.

Overall, the figure demonstrates that differences in prey composition and trophic interactions can generate non-linear, model-dependent responses in plankton, so that adding fish and macrobenthos together does not simply reproduce the sum of their isolated effects. These results underline that two-way coupling of fish and macrobenthos can produce non-additive behaviours in plankton communities, reinforcing the need for two-way coupling in ecosystem models. Such interactions could not be reproduced if the HTL models are run with LTL forcing, such as in a one-way coupling. Previously, several studies (Shin et al., 2010; Travers et al., 2009; Cury et al., 2008) have also proposed that two-way coupling between the HTL and plankton models leads to emergent ecosystem behaviours that cannot be replicated by forcing the HTL model with LTL variables.

3.6.4 Role of MB in fish dynamics

Here, we test the hypothesis that the presence of macrobenthos is essential to model fish production in the central North Sea by comparing the control run with the fish-only simulation, in which macrobenthos are excluded (Figure 13). The model responses differ markedly among the three LTL configurations, indicating that the role of macrobenthos strongly depends on the underlying trophic structure.

In ECOSMO, removal of macrobenthos causes an almost complete collapse of fish 2 biomass, whereas fish 1 biomass increases strongly. The grazing diagnostics suggest that, in the absence of macrobenthos, fish 1 can maintain high production by feeding on zooplankton and detritus, while fish 2 loses an important prey source and is no longer sustained. In ECOSMO, fish 1 remains comparatively resilient, with an increase relative to the control run, because it continues to exploit zooplankton effectively in the absence of macrobenthos. In ERSEM, the exclusion of macrobenthos also reduces fish 2 biomass, but the decline is less severe than in ECOSMO. The grazing rates indicate that fish 2 in ERSEM relies mainly on fish 1 when macrobenthos are absent, which helps sustain some production even without benthic prey. Fish 1, in ERSEM, remains comparatively resilient, with only a moderate reduction relative to the control run, because it grazes on zooplankton effectively. The strongest dependence on macrobenthos is seen in ERGOM. In this model, both fish 1 and fish 2 collapse almost completely when macrobenthos are removed. This reflects the limited planktonic prey field available in ERGOM to sustain fish production. Thus, macrobenthos acts as a critical trophic link in this configuration.



Overall, Figure 13 shows that macrobenthos is particularly important for sustaining fish 2 across all three models, while its importance for fish 1 is model dependent. In ECOSMO, the absence of macrobenthos indirectly favours fish 1 through the absence of competition, whereas in ERSEM fish 1 remains supported by pelagic prey, and in ERGOM both fish groups depend strongly on macrobenthos. These results are consistent with the idea that benthic prey form an important component of fish production in the central North Sea. They also highlight that the sensitivity of higher trophic levels to macrobenthos depends on how prey diversity and trophic pathways are represented in the host LTL model. Previous studies have similarly emphasised the role of the benthic system, particularly macrobenthos, as an important food source for fish in the North Sea. Daewel et al. (2019) showed in a three-dimensional ECOSMO-E2E simulation that macrobenthos is vital for maintaining the seasonal dynamics of fish production in the North Sea, while in the Baltic Sea fish depend more strongly on zooplankton than on macrobenthos. The paper by Greenstreet et al. (1997) highlights the essential role of the benthic, particularly macrobenthic, system as a major food source for benthic fish in the North Sea. The contrasting responses across ECOSMO, ERSEM, and ERGOM in Figure 13 underline the importance of representing trophic structure realistically in coupled lower- and higher-trophic-level models.

4 Discussion

The compatibility of the generic E2E modules with multiple LTL models offers a clear advantage for model intercomparison. Another key advantage of the newly developed E2E modules is their flexibility to simulate complex interactions without the need to recompile the model code. This is made possible by defining new fish or macrobenthos groups directly in the YAML configuration file. Further, users can define different feeding preferences and rates based on their research decisions, rather than being based solely on the choices given here. Such flexibility is particularly valuable for realistic ecosystem applications where detailed trophic interactions are necessary (Shin et al., 2010; Cury et al., 2003). The modular E2E framework offers a powerful platform for addressing ecosystem dynamics beyond the North Sea and Baltic Sea by adjusting feeding preferences and parameters. The two other biogeochemical models used by CMEMS for operational forecasting are BFM (Álvarez et al., 2023) and PISCES (Aumont et al., 2015). The E2E fish and macrobenthos modules are, in principle, transferable and can be coupled to these models, provided that they are compatible with FABM and share a trophic structure similar to that of ECOSMO, ERSEM, or ERGOM.

Most parameters in the model coupling were kept identical across the three models to ensure consistency in the comparison. This allows differences in model outcomes to be primarily attributed to differences in pelagic ecosystem structure rather than parameter choices. A more systematic and objective parameter optimisation approach would further strengthen such comparisons. In future work, parameterisation frameworks such as the toolbox developed by Nguyen et al. (2025) could be applied to ensure consistent and data-constrained tuning across models.

As discussed by Daewel et al. (2014, 2019), the E2E modelling demonstrated in this paper by implementing two-way coupling with the generic modules enables a more dynamic representation of zooplankton mortality. This approach shifts the traditional closure problem in NPZD models from zooplankton mortality to fish mortality. Nevertheless, this approach also



520 has challenges, such as the simplification of fish as functional groups and the representation of their horizontal migration (in a three-dimensional implementation), which are discussed in detail in Daewel et al. (2019).

5 Conclusions

The ECOSMO E2E model includes HTL modules for fish and macrobenthos functional groups. These modules are easily portable and can be coupled with LTL models like ECOSMO, ERSEM, and ERGOM, which are widely used in CMEMS applications. In general, the E2E modules can also be linked with other LTL models, that are capable of simulating various phytoplankton, zooplankton, detritus, dissolved organic matter, and sediment functional groups. The plug-and-play capability of these E2E modules was tested using a case study designed for the central North Sea. This case study also compared coupled model simulations from different LTL model hosts. We conducted five different simulations for each LTL-E2E model combination, taking advantage of the plug-and-play functionality. The following hypotheses were tested:

- 530 1. The macrobenthos plays a significant role in redistributing and remineralising detritus and benthic sediment, which affects nutrient concentrations in the bottom water layer.
2. The two-way coupling of HTL groups to the LTL model exerts a stronger top-down control on zooplankton populations than a closure of LTL model with a fixed increase in zooplankton mortality. The two-way coupling can lead to emergent behaviours in plankton communities, showing that the combined effects of macrobenthos and fish are not simply additive.
- 535 3. The presence of a macrobenthos functional group is crucial for simulating fish production in the central North Sea.
4. Variations in prey composition and availability across LTL models influence the spatial and temporal patterns of fish and macrobenthos production. Fish can adjust their diet opportunistically, leading to similar simulations across coupled models, even with dissimilar prey fields.

The 1D analysis presented in this study demonstrates that structural differences in model design can significantly influence HTL variables, such as fish biomass, and alter feedback within the food web. Extending this framework to a more complex 3D coupled modelling study would therefore be a valuable next step. Such an approach could also provide the basis for a multimodel ensemble.

Code and data availability. The E2E model source code and test cases, including forcing, initial, and output files, are available at <https://doi.org/10.5281/zenodo.20413770> (Vijayakumaran, 2026). E2E is also available from <https://codebase.helmholtz.cloud/GCOAST/ecosmoe2e>, accessible to users with login credentials. A user manual providing the information required to obtain, compile, configure, and run the E2E models described in this manuscript using the archived one-dimensional GOTM–FABM–E2E test cases with different lower-trophic-level host models (ECOSMO, ERSEM, and ERGOM) is available as a supplement. Documentation for GOTM, FABM, and the lower-trophic-level host models can be found in the references cited in this paper.



550 *Author contributions.* Conceptualization: VV, UD. Methodology: VV, UD, RM, HP, JB, JH, AL, GL, CS. Formal analysis: VV. Writing – original draft: VV. Writing – review & editing: RM, JB, JH, HP, GL, AL, CS, UD.

Competing interests. The contact author has declared that none of the authors has any competing interests.

Acknowledgements. VV acknowledges the valuable discussions during the NECCTON annual meetings held in Liège (March 2024) and Trieste (March 2025). Model computations were performed on DKRZ Levante HPC system. The colour palettes used in this paper are based on the Scientific Colour Maps developed by Crameri (2018). ChatGPT was used to assist with language editing.

555 *Financial support.* This research has been supported by the European Union's Horizon Europe Research and Innovation Action (Grant Number 101081273)



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Table 1. E2E model parameters used for macrobenthos in the ECOSMO, ERSEM, and ERGOM couplings. ERGOM values are shown in parentheses and ERSEM values in square brackets, but only where they differ. A dash in parentheses indicates that the parameter is not used in ERGOM.

Parameter	Description	Value
m_{MB}	Mortality rate (day^{-1})	0.001
ϵ_{MB}	Excretion rate (day^{-1})	0.025
r_{MB}	Grazing half-saturation (mmol C m^{-3})	0.1 (0.2)
$\sigma_{MB,Det}$	Grazing rate on detritus (day^{-1})	0.1
$\sigma_{MB,Sed}$	Grazing rate on sediment (day^{-1})	0.1
$\sigma_{MB,DOM}$	Grazing rate on DOM (day^{-1})	0.1
$\sigma_{MB,Ps}$	Grazing rate on flagellates (day^{-1})	0.1
$\sigma_{MB,Pd}$	Grazing rate on diatoms (day^{-1})	0.1
$\sigma_{MB,Zs}$	Grazing rate on microzooplankton (day^{-1})	0.1 (-)
$\sigma_{MB,Zl}$	Grazing rate on mesozooplankton (day^{-1})	0.1
$a_{MB,Det}$	Feeding preference for detritus	0.1
$a_{MB,Sed}$	Feeding preference for sediment	0.1
$a_{MB,Dom}$	Feeding preference for DOM	0.1
$a_{MB,Pf}$	Feeding preference for flagellates	0.15
$a_{MB,Pd}$	Feeding preference for diatoms	0.2
$a_{MB,Zs}$	Feeding preference for microzooplankton	0.15 (-)
$a_{MB,Zl}$	Feeding preference for mesozooplankton	0.2

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Table 2. Same as Table 1, but for fish 1.

Parameter	Description	Value
m_{F1}	Mortality rate (day^{-1})	0.001 (0.00113)
ϵ_{F1}	Excretion rate (day^{-1})	0.001 (0.00113)
r_{F1}	Grazing half-saturation (mmol C m^{-3})	0.7
$r_{F1,MB}$	Grazing on MB half-saturation (mmol C m^{-3})	0.9
γ_{F1}	Assimilation efficiency	0.7
$\sigma_{F1,Det}$	Grazing rate on detritus (day^{-1})	0.0001
$\sigma_{F1,MB}$	Grazing rate on macrobenthos (day^{-1})	0.005
$\sigma_{F1,Zs}$	Grazing rate on microzooplankton (day^{-1})	0.033 (-)
$\sigma_{F1,Zl}$	Grazing rate on mesozooplankton (day^{-1})	0.033
$a_{F1,Det}$	Preference for detritus	0.1
$a_{F1,MB}$	Preference for macrobenthos	0.1
$a_{F1,Zs}$	Preference for microzooplankton	0.4 (-)
$a_{F1,Zl}$	Preference for mesozooplankton	0.4

Table 3. Same as Table 1, but for fish 2.

Parameter	Description	Value
m_{F2}	Mortality rate (day^{-1})	0.0005 (0.00055)
ϵ_{F2}	Excretion rate (day^{-1})	0.001 (0.00105)
r_{F2}	Grazing half-saturation (mmol C m^{-3})	0.7
$r_{F2,MB}$	Grazing on MB half-saturation (mmol C m^{-3})	0.9
γ_{F2}	Assimilation efficiency	0.65
$\sigma_{F2,Det}$	Grazing rate on detritus (day^{-1})	0.0001
$\sigma_{F2,MB}$	Grazing rate on macrobenthos (day^{-1})	0.0045 [0.004]
$\sigma_{F2,Zl}$	Grazing rate on mesozooplankton (day^{-1})	0.001
$\sigma_{F2,F1}$	Grazing rate on fish 1 (day^{-1})	0.0045 [0.004]
$a_{F2,Det}$	Preference for detritus	0.1
$a_{F2,MB}$	Preference for macrobenthos	0.4
$a_{F2,Zl}$	Preference for mesozooplankton	0.1
$a_{F2,F1}$	Preference for fish 1	0.4

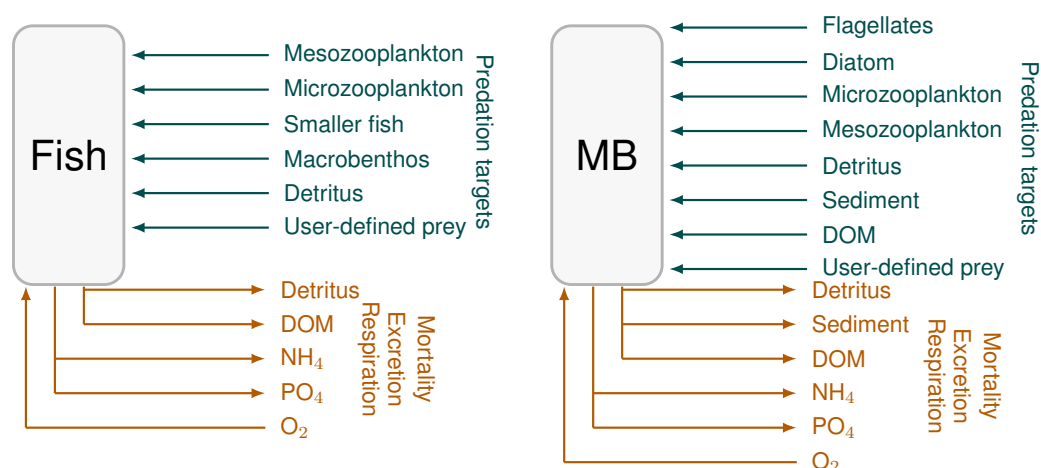


Figure 1. Schematic diagram of the E2E model showing the predation, mortality, and excretion targets required for coupling to the host LTL model.

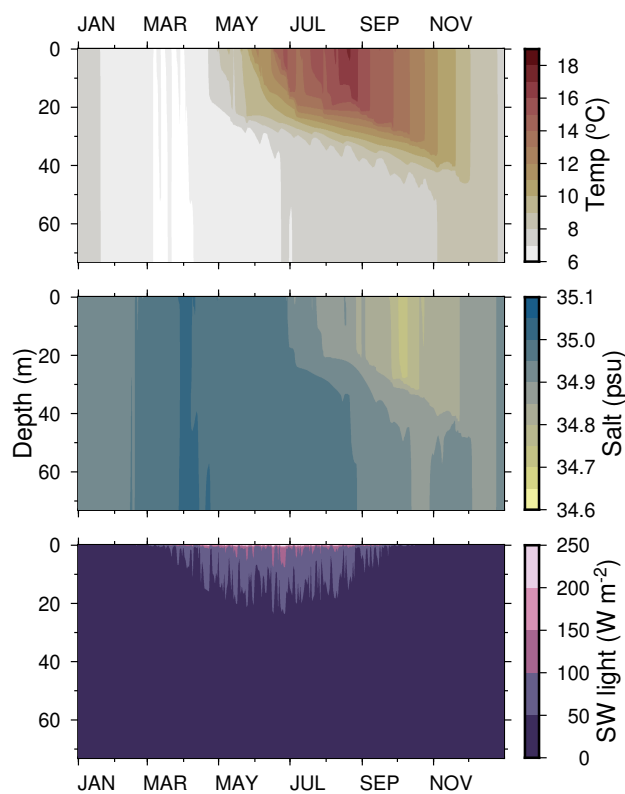


Figure 2. Control run simulation of the annual cycle of temperature, salinity and penetrating shortwave light in the central North Sea.

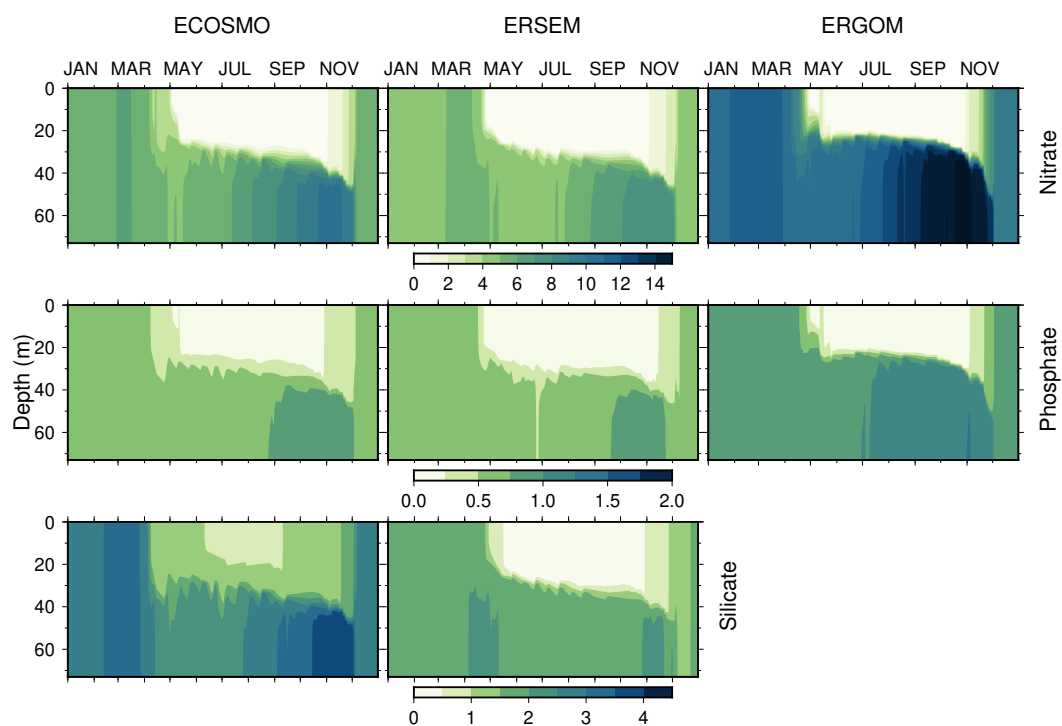


Figure 3. Nutrient variables in the control-run simulations across the three models: ECOSMO (first column), ERSEM (second column), and ERGOM (third column). All the variables are reported in mmol m^{-3} .

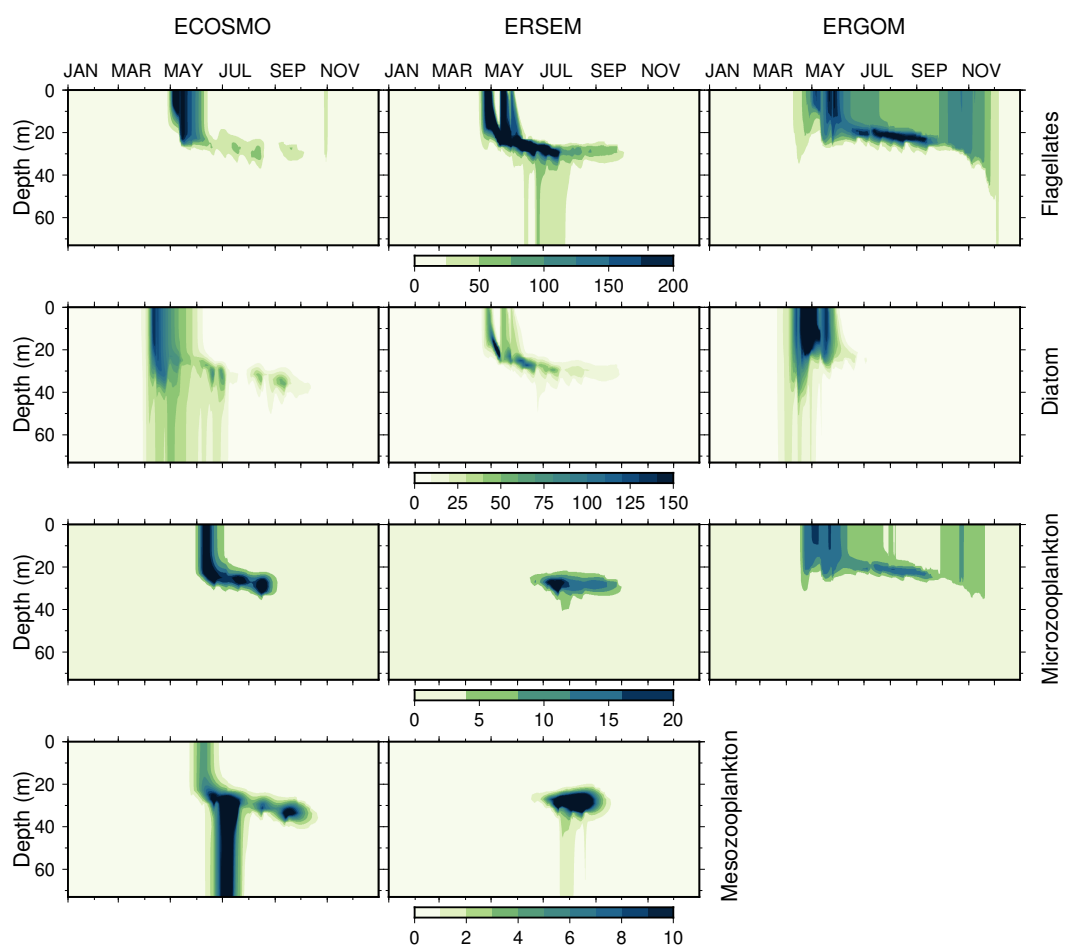


Figure 4. Pelagic state variables (flagellates, diatoms, micro and mesozooplankton) in the control-run simulations across the three models: ECOSMO (first column), ERSEM (second column), and ERGOM (third column). Note that only one zooplankton class is available in ERGOM. All the variables are reported in mg C m^{-3} .

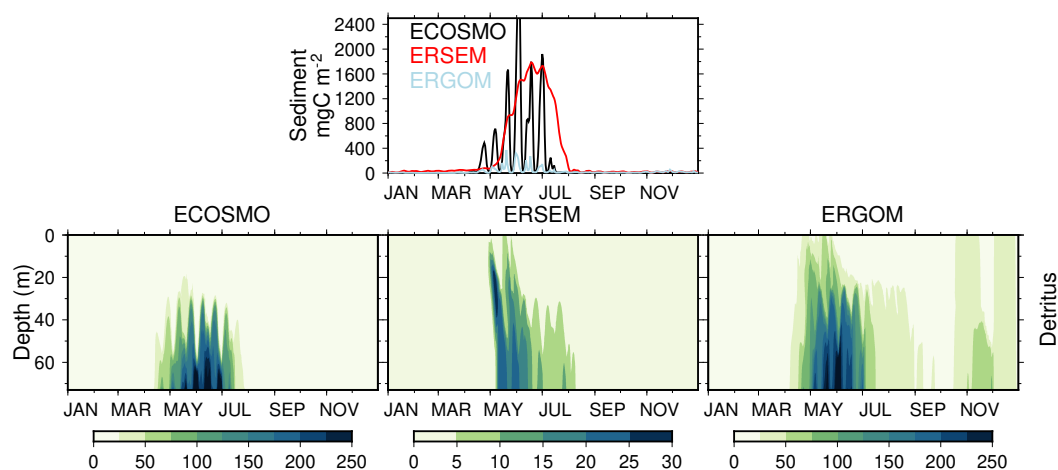


Figure 5. Benthic sedimentary carbon and detritus in the control-run simulations for each of the three models. Note that a different colour palette was applied to ERSEM because the simulated ranges differ substantially with other two models. Detrital concentrations are reported in mg C m^{-3} .

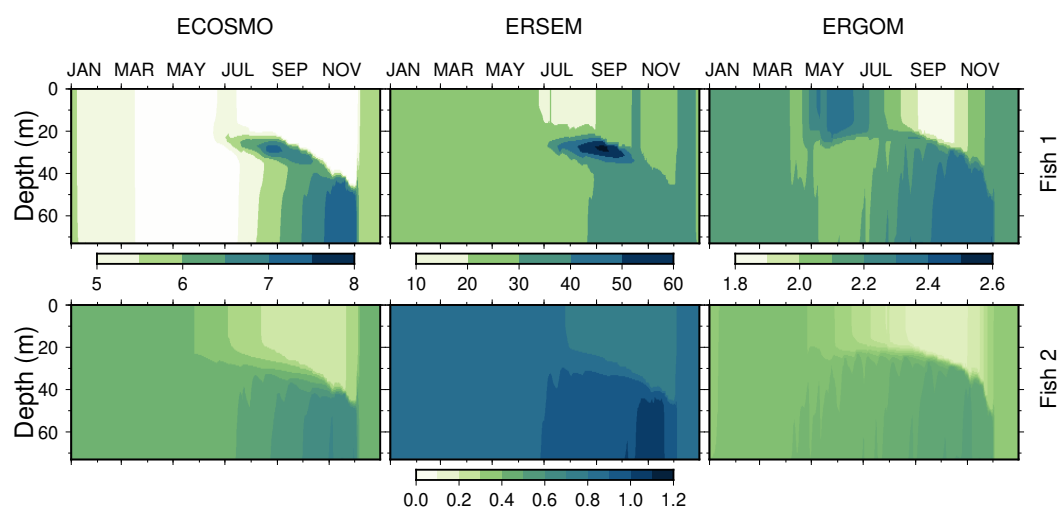


Figure 6. Fish 1 and fish 2 groups in the control-run simulations across the three models: ECOSMO (first column), ERSEM (second column), and ERGOM (third column). All water-column variables are reported as biomass in mg C m^{-3} . Different colour scales are used in each panel to emphasise temporal variability; comparisons should therefore be interpreted in terms of patterns.

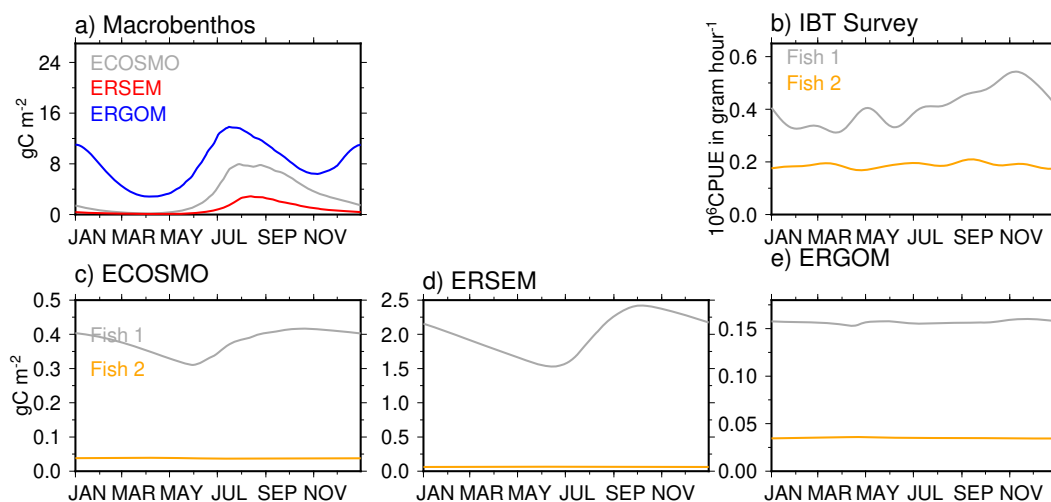


Figure 7. The simulated biomasses of (a) macrobenthos and water-column integral of fish 1 and fish 2 during an annual cycle (c–e). Pelagic and demersal fish biomass estimated from IBT survey is shown in (b).

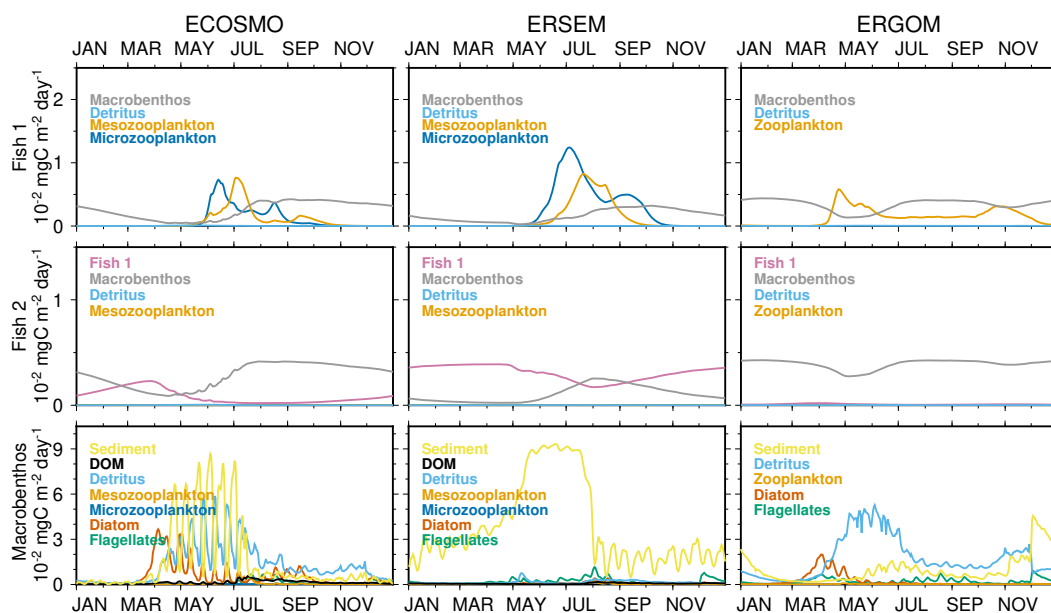


Figure 8. Grazing rates for fish 1 (first row), fish 2 (second row), and macrobenthos (third row) on prey items for each of the LTL models coupled to E2E.

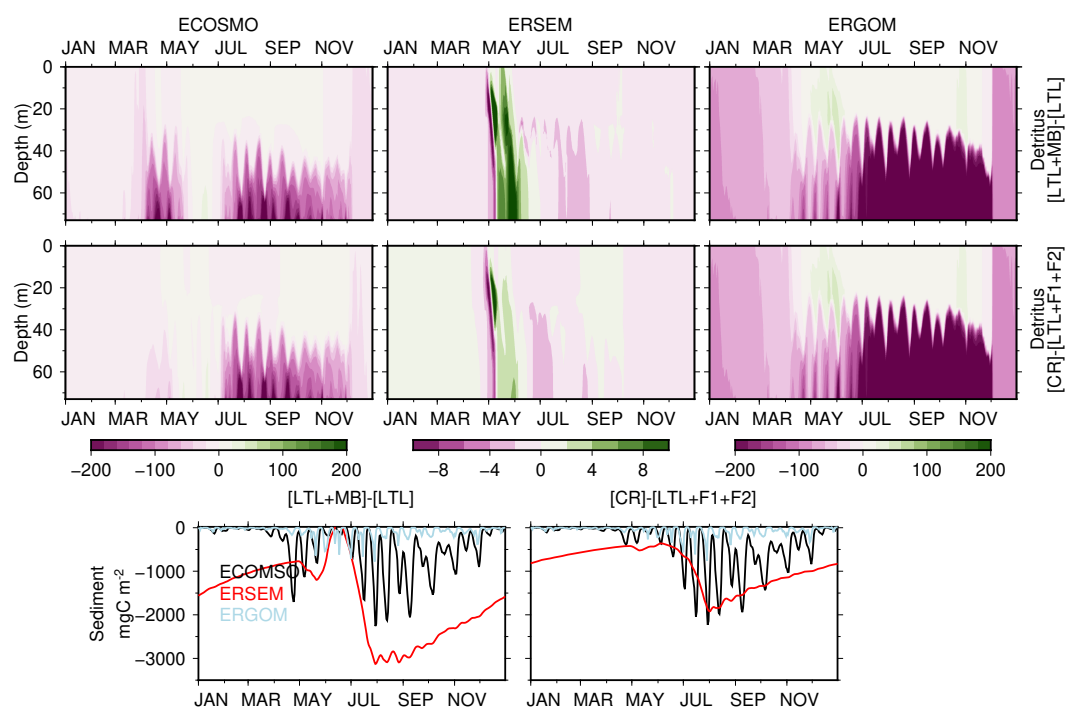


Figure 9. Differences in detritus and bottom sediment between the macrobenthos-only and LTL-only runs, and between the control run and the fish-only run (without macrobenthos), in each of the three LTL models. Detrital concentrations are reported in mg C m^{-3} .

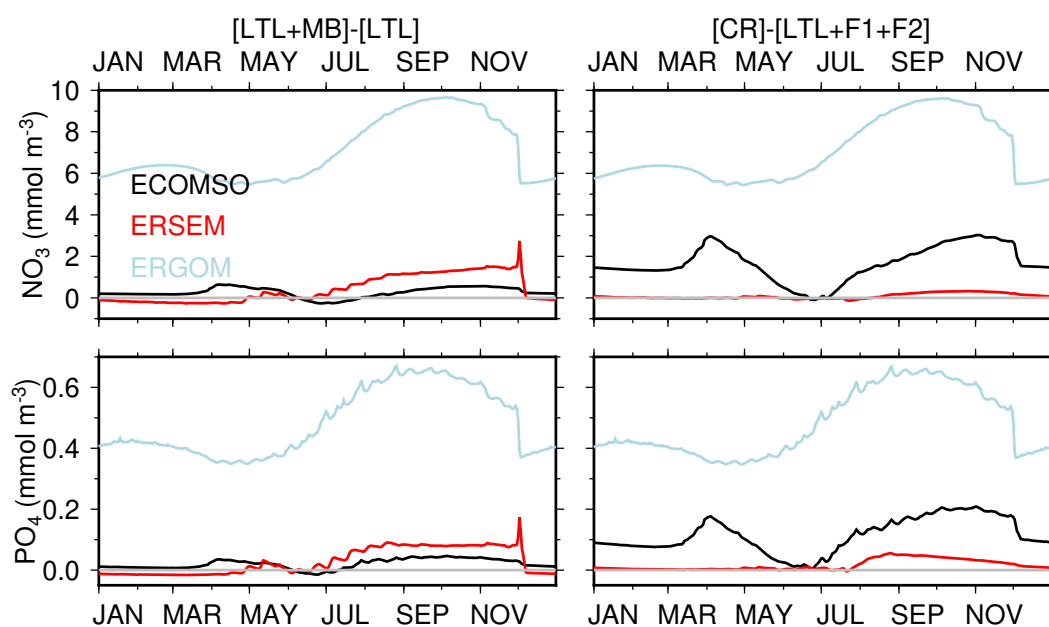


Figure 10. Differences in near-bottom nitrate and phosphate concentrations between the macrobenthos-only and LTL-only runs, and between the control run and the fish-only run (without macrobenthos), in each of the three LTL models coupled to E2E.

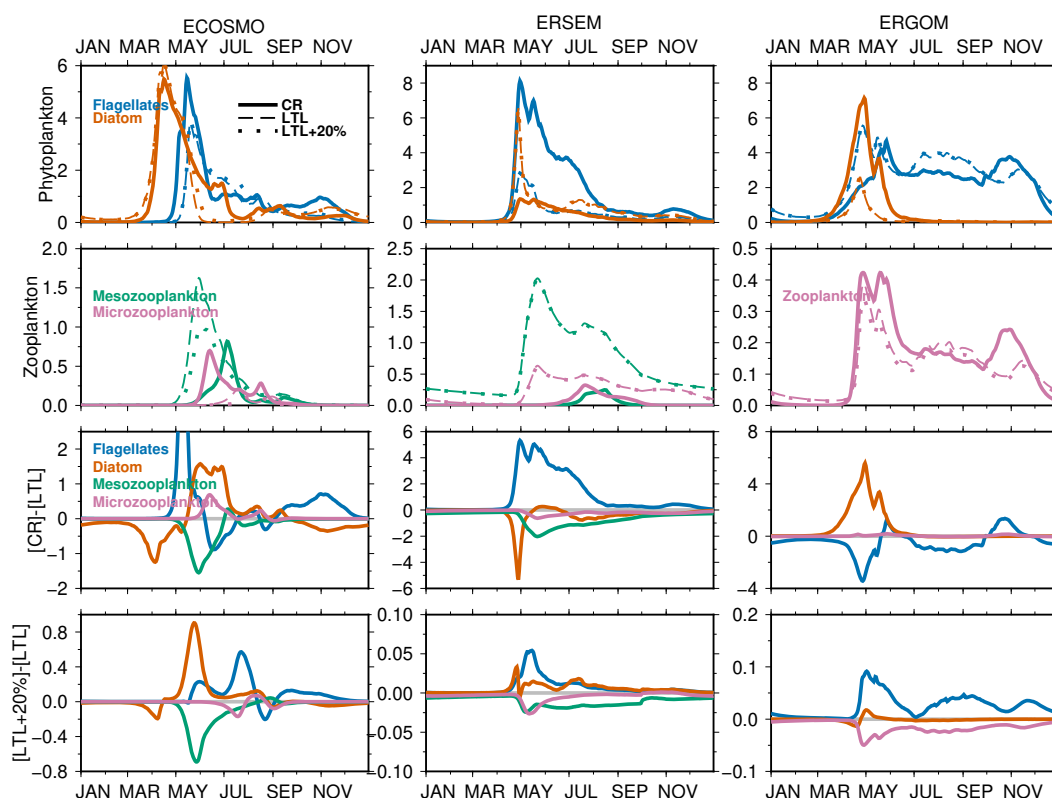


Figure 11. First and second rows show, respectively, the distributions of phytoplankton and zooplankton from the three models in the control run (solid lines), the LTL-only run (dashed lines), and the LTL run with increased zooplankton mortality (dotted lines). The third and fourth rows show the differences in the water-column-integrated concentrations of flagellates, diatoms, mesozooplankton, and microzooplankton between the control and LTL-only runs, and between the LTL-only run and the LTL run with increased zooplankton mortality. Each column represents one LTL model. All variables are integrated over the water column (g C m^{-2}).

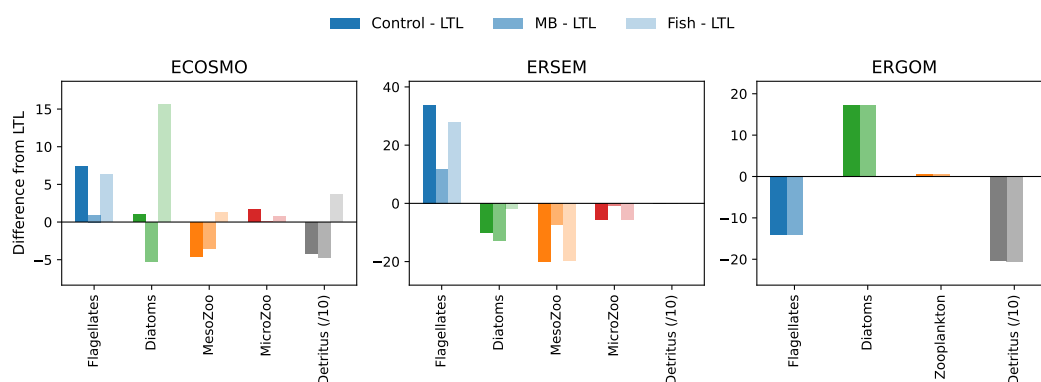


Figure 12. Comparison of the differences in plankton groups relative to the baseline LTL run in the three models. Each panel shows bars for Control - LTL, MB - LTL, and Fish - LTL simulations. The x-axis shows the functional groups (flagellates, diatoms, mesozooplankton, microzooplankton, and detritus) in vertical text. All variables, integrated over the water column and the annual cycle, are given in 10^9 mgC m^{-2} , except for detritus, which is given in $10^{10} \text{ mgC m}^{-2}$.

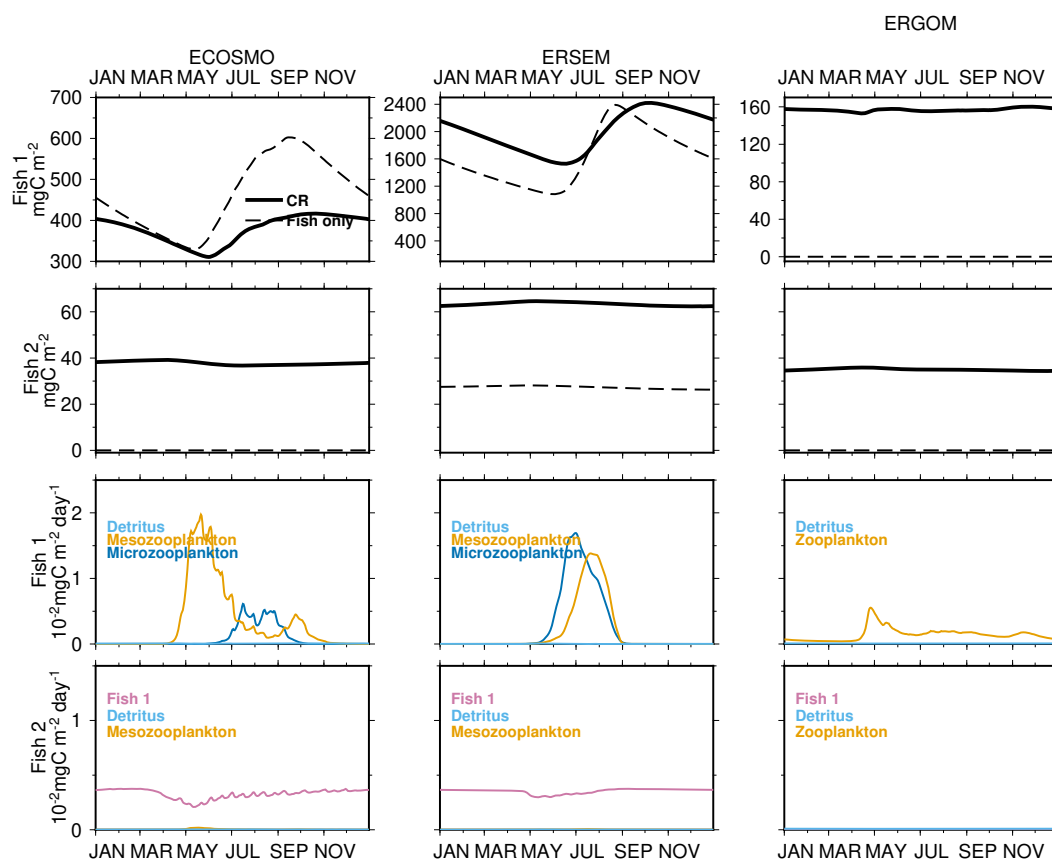


Figure 13. The first and second rows show the fish 1 and fish 2 simulated in the fish only (without macrobenthos) simulation, with all water column integrated variables shown in mgC m^{-2} . The third and fourth rows show the grazing rates for fish 1 (third row), fish 2 (fourth row). Each curve represents the rate of grazing of fish functional groups on its prey items.