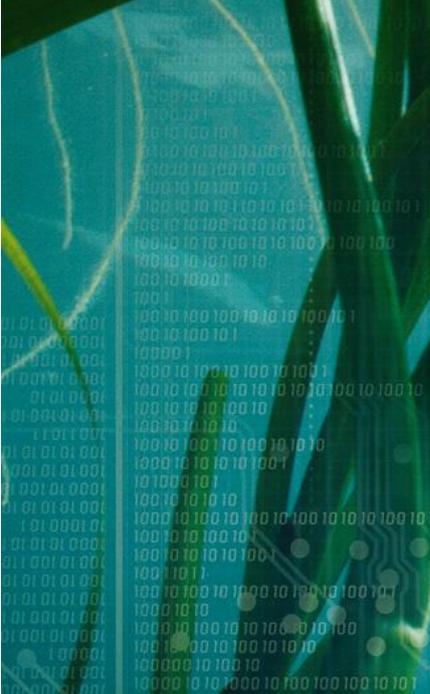


Development of Mechanistic Models

Short Technical Description of the Biogeochemical Models Applied for the Mechanistic Model Development



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Prepared for Danish EPA (Miljøstyrelsen, Fyn)
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*Eelgrass in Kertinge Nor
Photo: Peter Bondo Christensen*

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1 Summary

As part of the preparation towards the Danish River Basin Management Plans 2021-2027 the Danish Environmental Protection Agency (EPA) has initiated a number of mechanistic model developments with the aim of increasing the spatial coverage of models, improving the calibration/validation and hence the confidence of the Maximum Allowable nutrient Inputs (MAIs).

The mechanistic model complex development includes two regional models, three local-domain models and six estuary specific models.

- Two regional models are being developed: The North Sea model and the model covering the inner Danish waters (IDF). Regional models cover specific Danish water bodies and regional waters, such as the North Sea and a small part of the North Atlantic and the Baltic Sea, which is covered by the IDW-model (Inner Danish Waters). These models provide model results for specific water bodies but, equally important, provide boundaries to local-domain models and estuary specific models.
- Local-domain models: These models are developed to allow for resolving most small and medium-sized water bodies in the north-western Belt Sea, the south-western Belt Sea and the water bodies in and around Smålandsfarvandet.
- Specific estuary models: Six specific estuary (fjord) models are developed to allow for detailed modelling of the particular estuary.

Each of the different models consists of three specific modules: i) a hydrodynamic module (HD) computing water levels, current (speed and direction), salinity and water temperature, ii) a transport model (or advection/dispersion module - AD) computing the transport and dispersion of a specific biogeochemical component and iii) a biogeochemical module (or aquatic ecosystem models – AEM) computing changes in concentrations of a specific biogeochemical component due to fx primary production of grazing by zooplankton.

The model setup and calibration/validation of the physical models (HD and AD) are reported in a series of model specific technical notes. The specific model setup and calibration/validation of the biogeochemical models will be reported in a series of model specific technical notes (in progress), whereas the present technical note describes the overall functionality of the biogeochemical model (AEM) applied for the project.

The biogeochemical models developed and applied as part of the present project include the main components and processes that determine the state of the water quality and responding ecosystem changes (e.g. changes in eelgrass biomass) based on external factors like meteorology and nutrient supply. The models describe the turnover of organic matter and nutrients in the pelagic phase (water column) and benthic phase (at the seabed or sediments). The pelagic phase includes fx phytoplankton as well as inorganic and organic nutrients. The benthic part of the models includes fx sediment pools of nutrients and estimates the exchange of nutrients between the sediment and the water phase. The benthic part also describes biomass and growth of benthic vegetation (macroalgae, eelgrass and microbenthic algae at the sediment surface).

A mass balance module keeps track of the size, transport and exchange of the pools of organic matter and nutrients in the pelagic phase, in the sediment and in the benthic plants. Hence, the models are always mass-conserving.

In total, the biogeochemical model contains more than 50 primary state variables, whereof approximately half of these are associated with the benthic compartment, while the other half describes the pelagic system. Whereas the state variables describing the benthic system are

fixed to the seabed/sediment surface, the pelagic state variables are subject to dilution and transport (advection and dispersion) due to water movements.

In addition to the primary state variables, there are a large number of important variables derived from the primary state variables. An example of a derived variable is the light intensity in the different layers (depths) of the water column. This is dynamically calculated based on the solar radiation at the water surface and the light attenuation down through the water column. The light attenuation is determined from the following state variables: chlorophyll, particulate organic matter (detritus), dissolved organic matter (CDOM), and inorganic (fine) sediment, as well as a constant expressing the water's own light absorption. In the models, the influence of waves and currents on the buildup of sediment and thus the light attenuation is coupled to the eelgrass biomass, so that increasing eelgrass biomass reduces the resulting light attenuation, by decreasing resuspension of sediment. Thus, there is a feedback mechanism in the models that describes the eelgrass's influence on lighting conditions.

In the following, the overall model principles are described shortly. More detailed description and specific model equations can be found in DHI (2019c).

2 Introduction

As part of the preparation towards the Danish River Basin Management Plans 2021-2027 the Danish Environmental Protection Agency (EPA) has initiated a number of mechanistic model developments with the aim of increasing the spatial coverage of models, improving the calibration/validation and hence the confidence of the Maximum Allowable nutrient Inputs (MAIs).

For each model, the development consists of a 3D hydrodynamic model describing the physical system; water levels, current, salinity and water temperatures and the development of the biogeochemical (ecosystem) model describing the governing biogeochemical pelagic and benthic parameters and processes like nutrient and carbon dynamics, phytoplankton, dissolved oxygen, primary production, etc. The model structure is modular, meaning that a hydrodynamic model is developed independently of the biogeochemical model.

The mechanistic model complex developed as part of the present project includes two regional models, three local-domain models and six estuary specific models.

- Regional models: Two regional model are being developed: The North Sea model and the model covering the inner Danish waters (IDF). Regional models cover specific Danish water bodies and regional waters, such as the North Sea and a small part of the North Atlantic and the Baltic Sea, which is covered by the IDW-model (Inner Danish Waters). These models provide model results for specific water bodies but, equally important, provide boundaries to local-domain models and estuary specific models.
- Local-domain models: These models are developed to allow for resolving small and medium-sized water bodies in the north-western Belt Sea, the south-western Belt Sea and the water bodies in and around Smaalandsfarvandet.
- Specific estuary models: Six specific estuary (fjord) models are developed to allow for detailed modelling of particularly estuaries.

Each of the different models consists of three specific modules: i) a hydrodynamic module (HD) computing water levels, current (speed and direction), salinity and water temperature, ii) a transport model (or advection/dispersion module - AD) computing the transport and dispersion of a specific biogeochemical component and iii) a biogeochemical module (or aquatic ecosystem models – AEM) computing changes in concentrations of a specific biogeochemical component due to fx primary production of grazing by zooplankton.

The model setup and calibration/validation of the physical models (HD and AD) are reported in a series of model specific technical notes (DHI 2019d – DHI 2019n). The specific model setup and calibration/validation of the biogeochemical models will be reported in a series of model specific technical notes (in progress), whereas the present technical note describes the overall functionality of the biogeochemical model (AEM) applied for the project.

The present model description is an update of the report by Erichsen & Timmermann (2017) with the aim to describe RBMP 2021-2027 biogeochemical models.

3 Application of mechanistic models in environmental studies

Dynamic mechanistic models focusing on water quality have for more than four decades provided important support for the management of lakes, estuaries and coastal waters (Fath et al. 2011; Janssen et al. 2015). Since the early start in the 1970s, the models have evolved continuously, and with the steadily increasing CPU capacity, spatial resolution, spatial coverage and/or biogeochemical details have been expanded. The earliest mechanistic models focused on plankton growth, the associated nutrient dynamics and dissolved oxygen (e.g. Di Toro et al. 1971; Thomann et al. 1974; Nyholm 1977; 1978). Later, driven by the ambitions to mimic “real nature”, water quality models gradually turned into aquatic ecosystem models (AEMs) by introducing several phytoplankton groups, zooplankton, biotic benthic state variables such as filter feeders and deposit feeders, and carbon and nutrient pools as well as dynamics in the sediment, etc. (e.g. Baretta et al. 1995; Butenschön et al. 2016). While the pitfalls posed by overly complex models (i.e. overfitting resulting in reduced reliability) is recognised by some modellers, for instance Friedrichs et al. (2007), quantitative evaluation of the appropriate model complexity is rare. As a rule of thumb, models should only be as complex as needed to address specific questions. Furthermore, inclusion of new state variables without firm knowledge of their role in the ecosystem and associated processes and rates should be avoided. Therefore, excess CPU capacity may be better used on increasing the spatial resolution and the coverage as well as temporal resolution than on enhancing the complexity of the ecosystem description. Higher temporal resolution is, for example, more beneficial when transport time scale dominates over the scale of the biogeochemical processes, implying that advection plays an important role in distributing soluble and planktonic state variables (Frayse et al. 2013).

Today, AEMs are applied as management tools to evaluate the efficiency of eutrophication mitigation strategies (Thieu et al. 2010) and other actions related to, for instance, climate change (Neumann 2010; Meier et al. 2011a). In a recent survey, about 80% of the respondents (environmental managers and decision-makers) representing 25 states across the USA replied that they used models (statistical and/or mechanistic) or model results in their management of aquatic ecosystems (Fitzpatrick et al. 2016).

Results from detailed science-based mechanistic models can be difficult to incorporate in a management framework and such issues might be the reason for reluctance of managers in several EU countries to adopt mechanistic modelling as a general tool. A way forward was demonstrated by Nobre et al. (2005) who combined mechanistic modelling to estimate current and pristine status of chemical and biological components not quantified and fed the model output - and monitoring data - into a screening tool (Assets) to grade eutrophication status into five classes: High, Good, Moderate, Poor and Bad.

Collective modelling efforts, especially by the Baltic NEST Institute (BNI) and HELCOM, have previously paved the way for the Baltic Sea Action Plan in which MAIs are set for the regional water bodies of the Baltic Sea. In addition, numerous model studies have been carried out to clarify the impacts of nutrient loads on the environmental status of different water bodies in Europe (Neumann & Schernewski 2005; Carstensen et al. 2011; Lenhart et al. 2010; Thieu et al. 2010; Meier et al. 2011b). Thorough studies have also been made of individual Danish estuaries (Kuusemäe et al. 2016).

The application of mechanistic models in a relatively large part of the Danish WFD water bodies was first attempted as part of the development of the Danish RBMP 2015-2021. This work is reported in Erichsen & Timmermann (2017).

In the development of mechanistic models as part of the Danish RBMP 2021-2027, the key question is how to calculate the maximum allowable input (MAI) of nutrients supporting maintenance/achievement of good ecological status (GES) of the coastal water bodies governed by the WFD. Furthermore, the models should also be applicable for assessment of climatic

changes, assessment of reference chlorophyll-a values and potential assessment of seasonal response to nutrient loadings.

In the following sections, the models developed are described in more detail.

3.1 Nutrient loads and circulations

In the preparation of RBMP 2015-2021 two indicators were in use: Summer chlorophyll-a and summer- K_d . The chlorophyll-a is intercalibrated and was – and still is – an indicator of phytoplankton biomass whereas K_d was used as a proxy for the potential depth limit of eelgrass. At present, the indicators to be used as part of RBMP 2021-2027 are still under evaluation. Summer-chlorophyll-a will be included, and the inclusion of light, as a proxy for eelgrass depth limit, is still to be finally defined, why the model should be capable of describing those parameters.

The major factors governing the development of phytoplankton in offshore Danish waters are nutrient loadings and hydrography, both of which are tightly coupled with meteorology. In inlets and shallow estuaries, the biomass of benthic filter feeders filtering the bottom water also has a decisive influence on phytoplankton concentrations (Møhlenberg 1995). Total nutrient loads from Danish land to Danish marine waters averaged 62.0 kton N and 2.3 kton P in 2016 (Jensen et al. 2018). Loads to in the inner Danish waters (Kattegat south of the Skagen-Gothenburg cross-section, the Belt Sea and the Western Baltic Sea) account for approximately 70% of the N-load and 80% of the P-load, and the remaining loads were discharged to the North Sea/Skagerrak area. Other important external nutrient sources for the inner Danish waters are atmospheric deposition, nutrients in inflowing water from the Skagerrak and Baltic Sea and direct runoff from Sweden and Germany to the area. Along with the land-based loads and exchanges with adjacent seas, nutrients are continuously recycled in the water column and sediments by heterotrophic activity (bacteria, zooplankton and higher trophic levels).

Two field studies carried out in the Bay of Aarhus (1990-1991) and in the south-eastern Kattegat (1988) estimated that the yearly nitrogen remineralisation rates (primarily in the form of $\text{NH}_3\text{-N}$) ranged from 40 to 50 g N m^{-2} (Kaas et al. 1990; Jørgensen et al. 1996), suggesting that the recycling of nitrogen was at least a magnitude higher than the present-day land-based Danish nitrogen load. Both runoff and mineralisation show pronounced seasonal variation, but with a mirroring pattern; runoff peaks during wet winter months when the soil is saturated with water and crop growth is light limited, while the remineralisation in the water column and the sediment grossly follows temperature and peaks during late summer and autumn. Therefore, land-based runoff is important during early spring as it fuels the algae spring bloom, while demineralised nutrients are the main driver of summer and autumn production. However, winter run-off also constitutes a proportion of the mineralisation of nutrients later in the season, relative to total nutrient inputs and the standing stock of bioavailable nutrients in the system.

3.2 Model description

All dynamic mechanistic models are set up using DHI's model software; for hydrodynamic modelling MIKE 3 HD Flexible Mesh (FM) (DHI 2019a) was applied and for biogeochemical modelling the numerical MIKE solver ECO Lab model was employed (DHI 2019b).

Altogether eleven different models are developed (see Figure 3-1): A regional model covering the North Sea, a regional model covering the waters from Skagen-Gothenburg to the Bothnian Bay (the entire Baltic Sea), a local model covering the water bodies in the Northern Belt Sea, a local model covering the water bodies in the Southern Belt Sea, a local model covering the water bodies in and around the Smaalandsfarvand, and six estuary specific models: Ringkøbing Fjord, Nissum Fjord, Limfjord, Mariager Fjord, Odense Fjord and Roskilde Fjord. The specific features of the HD model setup and input data for the different models are described in

individual documents for each model (DHI 2019d – DHI 2019n), and similar documents describing the biogeochemical models (in progress). In the present technical note, we describe the mechanisms behind the biogeochemical models used for the different estuaries, and thus, this document forms a background documents in progress.



Figure 3-1 The eleven models developed covers the North Sea, the waters from Skagen-Gothenburg to the Bothnian Bay (the entire Baltic Sea), the Northern Belt Sea, the Southern Belt Sea, the Smålandsfarvand, Ringkøbing Fjord, Nissum Fjord, Limfjord, Mariager Fjord, Odense Fjord and Roskilde Fjord.

3.2.1 Biogeochemical model

The numerical MIKE solver ECO Lab comprises a set of standard models (templates) that is used as basis for describing the processes relevant for a particular biogeochemical model. In the RBMP model development process, two well-established templates are adapted into the biogeochemical models – one, which simulates the ecosystems covered by the model for the inner Danish waters and the North Sea model (regional models), and one, slightly different, which is implemented in the estuary specific models but also for the local models (having a focus on the local estuaries). The basic structure of the two models is identical. They both include interactions between the pelagic and the benthic compartments, and in the development towards RBMP 2021-2027, more details are being included in the regional models therefore the two models to a large extent describe the same features within the pelagic-benthic interactions.

As an example, the estuary models include a two-layer sediment model, and for the regional models this is also the case for the RBMP 2021-2027 (not included in the regional models used for the RBMP 2015.2021). However, due to resolution in especially shallow areas more focus is on e.g. benthic vegetation in the local models whereas the models applied in the regional models have more pelagic algae species included.

In the following, the basic characteristics of the biogeochemical models is briefly described, and in Table 3-1 the similarities and differences between the models are highlighted.

The general biogeochemical model adapted for the RBMP-model development describes the relationships and interactions between nutrients and primary producers. The biogeochemical model consists of two major sub-modules: the pelagic system and the benthic system. A schematic representation of the pelagic cycling of carbon (C), nitrogen (N) and phosphorous (P) is given in Figure 3-2.

Biogeochemical model – pelagic compartment

Most biogeochemical AEMs include two to three (or more) phytoplankton functional groups in order to simulate the seasonal variations in phytoplankton biomass and composition (see Box 3.1). Three typical variables included are i) a diatom state variable to represent a non-motile, silicate-dependent trait having low light requirements and relying on turbulence to prevent sedimentation; ii) a flagellate variable to allow for neutrally buoyant cells; iii) a colony-forming cyanobacteria variable to represent N_2 fixing species inhabiting brackish waters (< 10-12 psu) that have an ability to aggregate in surface waters during calm periods and exhibit a steep growth response with increasing temperature.

Phytoplankton growth is the result of primary production minus losses. Where production mainly is controlled by nutrient and light availability as well as temperature, losses comprising respiration, grazing and sedimentation. In the models used for the RBMP the nutrient dependency of phytoplankton is described by a two-step process. Firstly, the inorganic nutrients are taken up into an internal pool of the algal cells, following the Michaelis-Menten kinetics for nutrient uptake as a function of the ambient nutrient concentration. Following the uptake, algal growth is described according to the Droop quota model (Droop 1968) for growth as a function of the intracellular nutrient concentration (Morel 1987; Haney & Jackson 1996; Erichsen & Rasch 2001). Details on how these processes are solved mathematically are available in Lessin & Raudsepp (2006), DHI (2019b) and DHI (2019c).

The nutrients in the pelagic compartment originate from external sources (river and direct discharges, atmospheric deposition, etc.), pelagic recycling, as described in the beginning of this section (section 3), and “internal loading” from the sediments driven by mineralisation of organic matter produced in the water column (or by benthic plants harvesting inorganic nutrients from the water column).

In the IDW model (including the Baltic Sea), nitrogen is also made available through nitrogen fixation (N_2) by cyanobacteria. N_2 fixation is an important source of N to the Baltic Sea, and some estimates suggest that N_2 fixation is comparable to the total land-based N load to the

Baltic Sea (Neumann & Schernewski 2008). Since significant occurrences of cyanobacteria are rare in the local model areas¹ and in the model specific estuaries, this process is not included in the models applied for those areas. Hence, based on experience from numerous model implementations, DHI decided to use three functional groups to represent the phytoplankton dynamics of open waters and one phytoplankton state variable for eutrophic estuaries.

Box 3.1: Inclusion of phytoplankton diversity in AEM models

Generally, the phytoplankton community in the sea consists of numerous species exhibiting differences in morphology, size and density, affinity to nutrient uptake, capability to store nutrients, N₂ fixation, light requirement, buoyancy regulation, maximum growth rate, mixotrophy and susceptibility to grazing loss (Litchman & Klausmeier 2008; Klais et al. 2017). Such plankton diversity cannot be represented in mechanistic models, which may question the results if nutrient (or hydrographic, light) conditions are imposed that lay outside the range used for model calibration. Generally, small-sized individuals and taxa are most competitive at low nutrient concentrations (say at historic “reference conditions”), while larger individuals and taxa (e.g. diatoms, dinoflagellates, chlorophytes) benefit from higher and pulsed nutrient inputs to surface waters (Edwards et al. 2012; Litchman et al. 2015). In the Baltic Sea, seasonal variation in phytoplankton traits roughly reflects the variation in meteorology and hydrography, Kattegat being an exception as diatoms dominate here through all seasons (Klais et al. 2017). Recent model exercises predict lower phytoplankton concentrations and reduced cell size in a future warmer ocean characterised by more oligotrophic surface waters (Morán et al. 2010; Acevedo-Trejos et al. 2014), reflecting the allometric scaling of nutrient uptake efficiency that is part of such models (Ward et al. 2013). As an alternative or a supplement to a trait-based approach with several phytoplankton state variables, implementing plasticity in phytoplankton processes, for example temporally varying nutrient loads and light affinity for growth, may allow tracking of seasonal variation in phytoplankton biomass using only one state variable (Lefevre et al. 2003).

¹ Cyano-bacteria might influence the model results in some water bodies in and around the Smaalandsfarvand. However, for most of the very local water bodies within that model domain, this is not the case.

State variables & processes

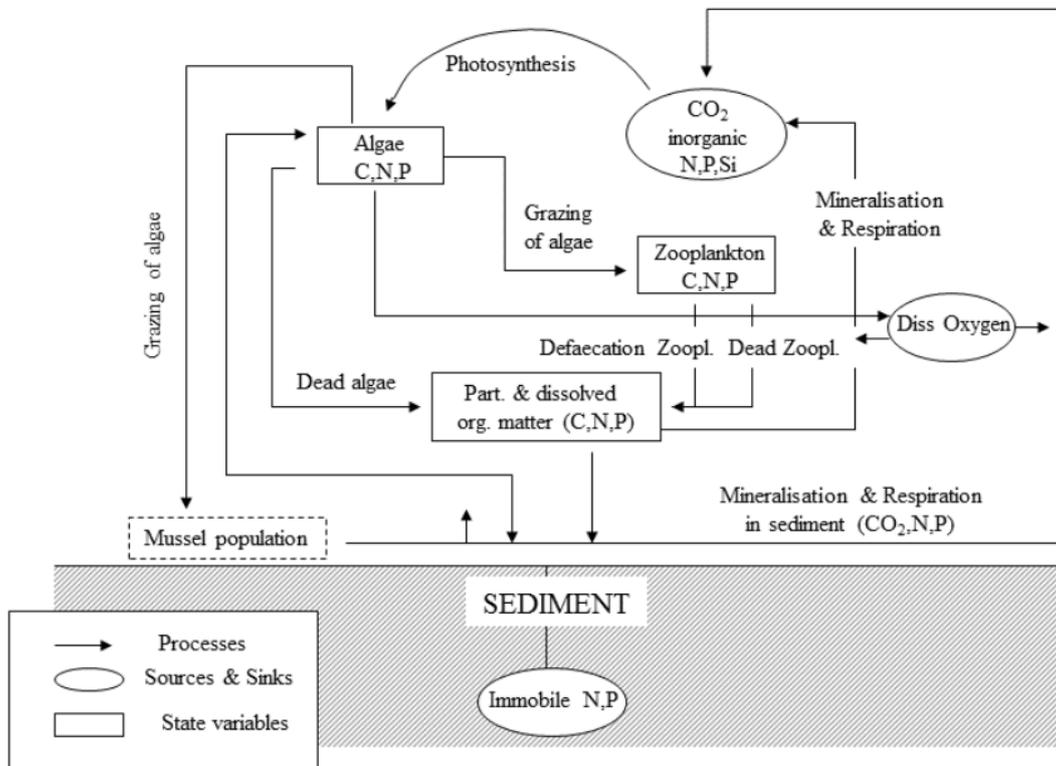


Figure 3-2 Simplified structure of the pelagic ecological module. For details on the sediment module, see Rasmussen et al. (2009).

Grazing and decomposition “transform” phytoplankton to zooplankton and detritus (particulate and dissolved organic matter, including C, N and P), respectively. The fate of detritus includes sedimentation and mineralisation in the “microbial loop”, which consists of mainly bacterially driven processes, leading to the remineralisation of dissolved and particulate organic matter that (re-)supply N and P to phytoplankton. Several AEMs explicitly represent members in the microbial loop (bacteria → heterotrophic flagellates → ciliates) and allow bacteria to compete with phytoplankton for nutrients (e.g. ERSEM; Vichi et al. 2007). Other AEMs take a simpler approach whereby a proportion of the detritus (at a temperature-dependent rate) is directly remineralised to inorganic nutrients (e.g. Yool et al. 2011). The two types of MIKE ECO Lab models adopted in this study use the latter approach; the mineralisation of organic matter by bacteria is parameterised (mainly based on temperature) without explicitly including the bacterial biomass as a state variable.

Especially, in the Baltic Sea and the estuary systems, substantial amounts of dissolved organic matter (DOM) are discharged from the rivers and contribute to the turnover of organic matter and influence light conditions. Two fractions of dissolved organic matter are represented in the models: Labile dissolved organic matter (LDOM) and coloured dissolved organic matter (CDOM). Each of the three states of organic matter (detritus, LDOM and CDOM) is represented by three dynamic state variables (OC, ON and OP).

Grazing on phytoplankton by zooplankton (micro- and mesozooplankton) may have a regulating effect on the phytoplankton biomass, and the intensity of grazing can be a determinant reason for development of an algal bloom. Mesozooplankton, representing copepods, consists of a lumped biomass encompassing all 12 active grazing stages. Growth efficiencies and dependence on phytoplankton concentrations are based on the energy budget for *Acartia tonsa* (Kiørboe et al. 1985) and stage duration/growth rate dependence on temperature comes from Hirst & Shearer (1997). Regular zooplankton monitoring data on Danish waters after 1997 are

sparse and formal model calibration is thus not possible. However, our modelling results showing seasonal variation with a peak in microzooplankton about a month after the spring bloom and a peak in mesozooplankton in July (30-60 $\mu\text{g carbon L}^{-1}$) are consistent with earlier studies from Kattegat (Kjørboe & Nielsen 1994; Nielsen and Kjørboe 1994). The models do not include heterotrophs (predators) at higher trophic levels than zooplankton and loss by predation is integrated in the death rate of the zooplankton. Hence, predation on meso-zooplankton – whether by fish or jelly fish etc. – is handled by an unnaturally high zooplankton death rate, described by a quadratic function of zooplankton biomass.

In summary, the pelagic ecosystem model computes the concentration of phytoplankton (as carbon and chlorophyll-a), zooplankton, detritus and dissolved organic matter as well as the nutrient and dissolved oxygen content of the water phase. For more details, DHI (2019b) and DHI (2019c) may be consulted.

Biogeochemical model – sediment compartment

Benthic-pelagic coupling encompasses numerous processes (sedimentation, filtration, nutrient uptake in benthic plants, bioturbation, mineralisation, resuspension, predation) that drive the exchange of solutes, particles and organisms between the pelagic and benthic compartments (Griffiths et al. 2017). The nutrients in the pelagic compartment originate, among other sources, from “internal loading” from the sediments due to mineralisation of organic matter. The internal sediment loading varies according to the size of the biogeochemically available pools of C, N and P in the sediment together with bottom oxygen concentrations, water temperature and the bottom water exchange.

The applied MIKE ECO Lab model integrates the pelagic and benthic compartments. Both the regional models and the estuary models include two sediment layers. Sensus the Soetaert et al. (2000) definition, the models applied for the RBMP 2021-2027 are characterised as “level 4-3½”.

The degradation of the organic C, N and P pools of the sediment (utilising oxygen or nitrate as electron acceptors) releases N and P to the sediment pore water. The rate of degradation depends on the availability of oxygen (or NO_3) and the C:N ratio in the sediment. A minor fraction of the organic pool (C, N and P) is immobilised depending on the C:N ratio in the sediment (the fraction increases with increasing C:N ratio). Nitrate in the pore water can be denitrified to N_2 . Inorganic pore water P can bind to oxidised iron (Fe^{+++}) when the sediment is oxidised, and when the sediment is “reduced” (Fe^{++} being the dominant form) the inorganic P is released to the pore water again. The inorganic nutrients in the sediment exchange with nutrients in the water phase and, hence, the sediment may either act as a sink or a source of inorganic nutrients to the water above the sediment. For details of the sediment model, we refer to Rasmussen et al. (2009).

3.2.1.1 Biogeochemical model – benthic production

All eleven AEMs include a description of the benthic primary producers. Four different benthic primary producers are included: perennial (“brown”) macroalgae typified by fucoid species, annual macroalgae (e.g. filamentous brown algae and *Ulva* sp.), benthic microalgae and the flowering plant eelgrass (*Zostera marina*).

As for the pelagic primary production, the benthic primary production depends on water temperature, nutrient availability and availability of photosynthetic active light, and the relations between the different factors and growth differ between groups. Besides growth regulation factors, perennial macroalgae need hard substrate to attach to, and eelgrass requires appropriate sediment (appropriate sediment is related to bulk density). An important distinctive characteristic is that macroalgae (annual and perennial) can only utilise inorganic nutrients from the water phase, whereas eelgrass can take up nutrients from the sediment pore water as well. Hence, eelgrass can grow in areas and seasons with low nutrient concentrations in the water if pore water nutrient concentrations are sufficiently high. Analogously, two nutrient sources are available to benthic microalgae growing on sediments, namely pore water nutrients in sediment

and nutrients in overlaying water. As for phytoplankton, the internal pools of N and P drive the growth of the different groups and the pools are described explicitly for eelgrass, benthic microalgae and macroalgae. Accumulation of internal nutrients (resulting in low C:N and C:P-ratios) during winter and spring allows continued growth when external nutrients become depleted in surface waters (Pedersen & Borum 1996).

Finally, the light dependency varies between the different benthic groups as do losses. Losses include respiration, decay, grazing and loss of parts of plants. Dead organic material is partly returned to the water phase and partly to the organic pools of the sediment. In this way, the benthic primary producers contribute to the organic and inorganic nutrient pools in the model. More details on the benthic primary production model can be found in Kuusemäe et al. (2016).

3.2.1.2 Distinctions between regional models and estuary models

An overview of the similarities and differences between the two types of models developed and applied, the regional models and the estuary models, is given in Table 3-1.

Table 3-1 Overall similarities and differences between the open water model and the estuary models.

	Model components	North Sea model and IDW model	Estuary models
Pelagic compartment model	Phytoplankton C, N and P	Three algae groups: diatoms, flagellates and cyanobacteria. Growth rates, light dependency, sedimentation/buoyancy etc. differ between groups. Cyanobacteria capable of N fixation.	One lumped phytoplankton group. Growth rates and light dependency change between spring and summer/autumn.
	Zooplankton, C	Two groups of zooplankton: micro- and mesozooplankton.	One lumped zooplankton group.
	Benthic filter feeders	Not modelled explicitly, but effects by filter feeders are included.	Not modelled explicitly, but effects by filter feeders are included.
	Inorganic nutrients, NH ₄ , NO _x , PO ₄ , Si	Si included.	Si not included.
	Organic matter, C, N, P and Si	Si included.	Si not included.
	Inorganic sediment	An empirical relation is implemented linking modelled shear stress (wave and current generated) at the seabed, 2D-maps of inorganic and organic sediment pools and concentrations of particulate matter in the water phase to light regime.	An empirical relation is implemented linking modelled shear stress (wave and current generated) at the seabed, 2D-maps of inorganic and organic sediment pools and concentrations of particulate matter in the water phase to light regime.
	Dissolved oxygen	No structural differences.	
	Hydrogen sulphide	No structural differences.	
Benthic compartment model	Primary producers C, N and P Macroalgae Microbenthic algae Eelgrass	Loss of ignition and seed-burrowing effects of the lug worm <i>Arenicola</i> not included.	Sediment bulk density is part of the possibilities for eelgrass to recolonise as well as part of a description of losses based on <i>Arenicola</i> burrowing activity.
	Organic matter	Si included.	Si not included.
	Inorganic nutrients	Si included.	Si not included.
	Inorganic sediment	An empirical relation is implemented linking modelled shear stress (wave and current generated) at the seabed, 2D-maps of inorganic and organic sediment pools and concentrations of particulate matter in the water phase to light regime.	An empirical relation is implemented linking modelled shear stress (wave and current generated) at the seabed, 2D-maps of inorganic and organic sediment pools and concentrations of particulate matter in the water phase to light regime.

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