



Modelling the Food, Energy and Nature Transition in the North Sea

Toolbox design by WMR, NIOZ and Deltares

Author(s): Tobias van Kooten¹, Anouk Blauw², Johan van der Molen³, Tineke Troost², Silke van Daalen¹, Anieke van Leeuwen³, Karen van de Wolfshaar¹, Luca van Duren² & Lauriane Vilmin²

¹Wageningen Marine Research

²Deltares

³NIOZ Royal Netherlands Institute for Sea Research

Wageningen University &

Research report: C071/24

Modelling the Food, Energy and Nature Transition in the North Sea

Toolbox design by WMR, NIOZ and Deltares

Auteur(s): Tobias van Kooten¹, Anouk Blauw², Johan van der Molen³, Tineke Troost², Silke van Daalen¹, Anieke van Leeuwen³, Karen van de Wolfshaar¹, Luca van Duren² & Lauriane Vilmin²

¹Wageningen Marine Research

²Deltares

³NIOZ Royal Netherlands Institute for Sea Research

Wageningen Marine Research
IJmuiden, november 2024

Wageningen Marine Research report C071/24

Tobias van Kooten, Anouk Blauw, Johan van der Molen, Tineke Troost, Silke van Daalen, Anieke van Leeuwen, Karen van de Wolfshaar, Luca van Duren & Lauriane Vilmin, 2024. Modelling the Food, Energy and Nature Transition in the North Sea; Toolbox design by WMR, NIOZ and Deltares. Wageningen Marine Research report number C071/24. 41 pages.

Keywords: Ecosystem models, model trains, MONS.

Client Rijkswaterstaat Water Verkeer en Leefomgeving
 Attn.: Dr. T. Schellekens
 Griffioenlaan 2
 3526 LA Utrecht

This report can be downloaded for free from <https://doi.org/10.18174/679267>
Wageningen Marine Research provides no printed copies of reports

Wageningen Marine Research is ISO 9001:2015 certified.

© Wageningen Marine Research

Wageningen Marine Research, an institute within the legal entity Stichting Wageningen Research (a foundation under Dutch private law) represented by Drs.ir. M.T. van Manen, Director Operations

KvK nr. 09098104,
WMR BTW nr. NL 8113.83.696.B16.
Code BIC/SWIFT address: RABONL2U
IBAN code: NL 73 RABO 0373599285

Wageningen Marine Research accepts no liability for consequential damage, nor for damage resulting from applications of the results of work or other data obtained from Wageningen Marine Research. Client indemnifies Wageningen Marine Research from claims of third parties in connection with this application. All rights reserved. No part of this publication may be reproduced and / or published, photocopied or used in any other way without the written permission of the publisher or author.

A_4_3_2 V34 (2024)

Contents

1	Background	4
2	Research questions and approach	5
	2.1 Modelling toolbox approach	5
	2.2 Interaction and advice	6
3	Modelling toolbox	7
	3.1 Proposed model studies	7
	3.2 Initial model studies	8
	3.2.1 Ecosystem effects of lower trophic aquaculture	8
	3.2.2 Integral effects of climate change	9
	3.2.3 The food web consequences of large-scale hard substrate addition	10
	3.2.4 Fish life cycle connectivity through the larval stage	11
	3.2.5 Changes in bottom fishing and its ecosystem effects as a result of area closures (MPA and OWF)	13
	3.2.6 Integral effects of offshore wind development on seabirds and marine mammals	14
	3.3 Stakeholder feedback on initial studies	15
	3.4 Overview of models and couplings	16
	3.4.1 Models	16
	3.4.2 Physical models	16
	3.4.3 Biogeochemical models	17
	3.4.4 Higher trophic ecosystem and/or community models	19
	3.4.5 Single-species higher trophic level models	20
	3.4.6 Particle tracking models with behaviour	21
	3.4.7 Agent based simulation models	22
	3.4.8 Habitat suitability models	23
	3.4.9 Model coupling	26
4	Work plan	28
	4.1 Approach	28
	4.2 Priority actions	29
	4.2.1 Ecosystem effects of lower trophic aquaculture	29
	4.2.2 Integral effects of climate change	29
	4.2.3 The food web consequences of large-scale hard substrate addition	30
	4.2.4 Fish life cycle connectivity through the larval stage	31
	4.2.5 Changes in bottom fishing and its ecosystem effects as a result of area closures (MPA and OWF)	32
	4.2.6 Integral effects of offshore wind development on seabirds and marine mammals	33
	4.2.7 Development of generic toolbox	34
5	Interaction and advice	35
6	Quality Assurance	36
	References	37
	Justification	40

1 Background

The basis of the North Sea Agreement (NSA) is formed by three transitions which are envisioned on the Dutch North Sea in the coming decade:

- **Nature transition:** The NSA observes that the North Sea is a degraded ecosystem and there is a trend towards further degradation. This transition aims to return the ecosystem to a healthy state and keep it there.
- **Food transition:** The NSA states that a transition is required to a fishery and mariculture with clear long-term economic perspective, and in balance with the new situation on the North Sea (as resulting from these three transitions and other changes, such as climate change).
- **Energy transition:** The North Sea will be instrumental in delivering energy as an alternative to fossil fuels. This means that substantial space will be used for offshore wind farms and associated infrastructure (cables, substations, et cetera). The implementation of the Dutch ambition for OWFs must be balanced against competing spatial claims of other activities and functions at sea.

The NSA states that the key to successful implementation of these three transitions lies in understanding and focusing on the connections between them. This is not only required to minimize conflicts among sectors, activities, users and values, but is expected to also yield opportunities for novel combinations of functions and uses. With these expectations, the NSA observes that current knowledge of the North Sea ecosystem is insufficient to navigate a path through the three transitions. The MONS program was created to enhance understanding of the North Sea ecosystem and its response to human activities, and deliver the tools needed for good science-based policy advice to implement the three NSA transitions. This research plan focuses specifically on the development of model tools. An important requirement of these model tools is that they, collectively, can be used to study trade-offs between transitions. This means that models can be used to study, for example, the effects of various OWF scenarios on nature and the fishery. Or the effect of large-scale seaweed farming on ecosystem health. The ability to study these trade-offs is crucial to make well-informed management decisions based on the best available knowledge.

2 Research questions and approach

This project consists of two components. The first focuses on developing a collective, coherent, and consistent modelling toolbox to strengthen the knowledge base of the North Sea ecosystem, to better understand the effects of anthropogenic disturbances and to support the implementation of the food- nature- and energy-transitions as described in the North Sea agreement.

The second component consists of a proposal for how to use the developing modelling toolbox to provide advice on both the prioritization and implementation of other research projects within MONS and Wozep, as well as on how to periodically re-align the priorities within the modelling toolbox development with those of the relevant stakeholders (MONS and Wozep organization and the participants in the North Sea Agreement).

2.1 Modelling toolbox approach

The central research priority for this work is to develop a coherent and consistent toolbox of models, which can be collectively used (in various combinations) to study and give advice on the implementation of the three NSA transitions in the coming years. Because it is impossible to foresee all future policy needs, the consortium has defined a number of model studies for which there is consensus about their relevance. We then worked out the combinations of models required to tackle these. Throughout this report, we refer to these connected sets of models as 'model trains'. This has led to a list of models, many of which already exist, while others do not. Most of the existing models will require some degree of adaptation in order to function as part of the defined model trains. Some of the models which do not yet exist are planned to be developed as part of other MONS and/or Wozep projects. Others will have to be developed within the follow-up of this research plan.

The approach taken to design a modelling toolbox can be summarized in six steps, outlined below. Each includes a reference to the chapter or paragraph in this document where it is further developed:

1. Choose a limited number of model studies which address important challenges central to MONS and Wozep (Paragraph 3.1).
2. Get feedback from stakeholders within the North Sea Agreement, MONS and Wozep, and use this feedback to refine the results of item 1 (Paragraph 3.3).
3. Further develop these model studies, describing their relevance within MONS and Wozep and in relation to the transitions described in the North Sea Agreement (trade-offs between transitions, Paragraph 3.2).
4. Describe a model toolbox for each of these model studies, composed of one or more model trains (Paragraph 3.2), the components they contain and the required connections between them (Paragraph 3.4).
5. Combine the toolboxes from 4. to obtain a list of all required tools and couplings for the entire set of model studies (Paragraph 3.4).
6. Write research plans to develop selected tools and connections for each of the required components (Chapter 4), taking into account:
 - a. Other work ongoing and/or planned in MONS and Wozep
 - b. Upcoming projects and opportunities for related work, national as well as international (Horizon Europe, Nationale Wetenschapsagenda, etc.)

Carrying out these research plans will result in a set of models which can be connected together into a number of model trains, required for the example studies. Combining these with other ongoing work, and the required components which that will deliver, leads to a set of components and actions which are necessary to complete these model trains. However, our ambition is to set them up in a generic and flexible way which will also allow for other model train configurations, thus facilitating other model studies in the future. Hence, despite starting with specific model studies, the end product is aimed at a generic model toolbox.

An important aspect of complex (combinations of) models is uncertainty. A model is in essence a formal, mathematical description of how we assume (a part of) the ecosystem works. The degree of certainty about the underlying assumptions is an important consideration of the interpretation of model results. In this project, such model uncertainty pertaining to uncertainty about the mechanistic basis of ecosystem processes will be explored by implementing alternative assumptions and testing their effects when possible. Sometimes this will be explicit, when we test various different formulations, in other cases it will be conducted in the form of ensemble modelling, where we compare the output of several existing model confronted with identical input and scenarios.

Another source of uncertainty is parameter uncertainty. For mechanistic models we often assume fixed values for parameter values (such as reproduction, food intake, mortality, etc.). In reality, these values are often uncertain or variable in space and time. The effect of parameter uncertainty will be tested by either implementing stochastic versions of models (as for example in the KEC model train for seabirds), or by explicitly studying the sensitivity of model outcomes to changes in parameter values (sensitivity analysis).

2.2 Interaction and advice

The second part of this project consists of a proposal to:

1. Provide advice on the implementation and prioritization of other MONS and Wozep research and data collection projects. Many of those projects will either make use of or contribute to the model toolbox.
2. Regularly update the priorities within this project, together with the relevant stakeholders (MONS and Wozep organization and the participants in the North Sea Agreement). This way we make sure that the modelling toolbox remains relevant to the most important societal questions, even if these shift over the course of the project.

This is developed further in Chapter 5.

3 Modelling toolbox

3.1 Proposed model studies

In this chapter the model studies that were defined to act as relevant and 'no regret' example studies are listed and described in more detail. These studies are the result of group discussions inspired by the three transitions. They should be seen as highly relevant and representative studies which are considered inevitable in supporting the implementation of one or more of these transitions. Together, they cover a large range of topics and questions, guaranteeing a wide applicability of the resulting toolbox.

The defined studies are:

- Q1. Ecosystem effects of lower trophic aquaculture
- Q2. Integral effects of climate change
- Q3. The food web consequences of large-scale hard substrate addition
- Q4. Fish life cycle connectivity through the larval stage
- Q5. Changes in bottom fishing and its ecosystem effects as a result of area closures (MPA and OWF)

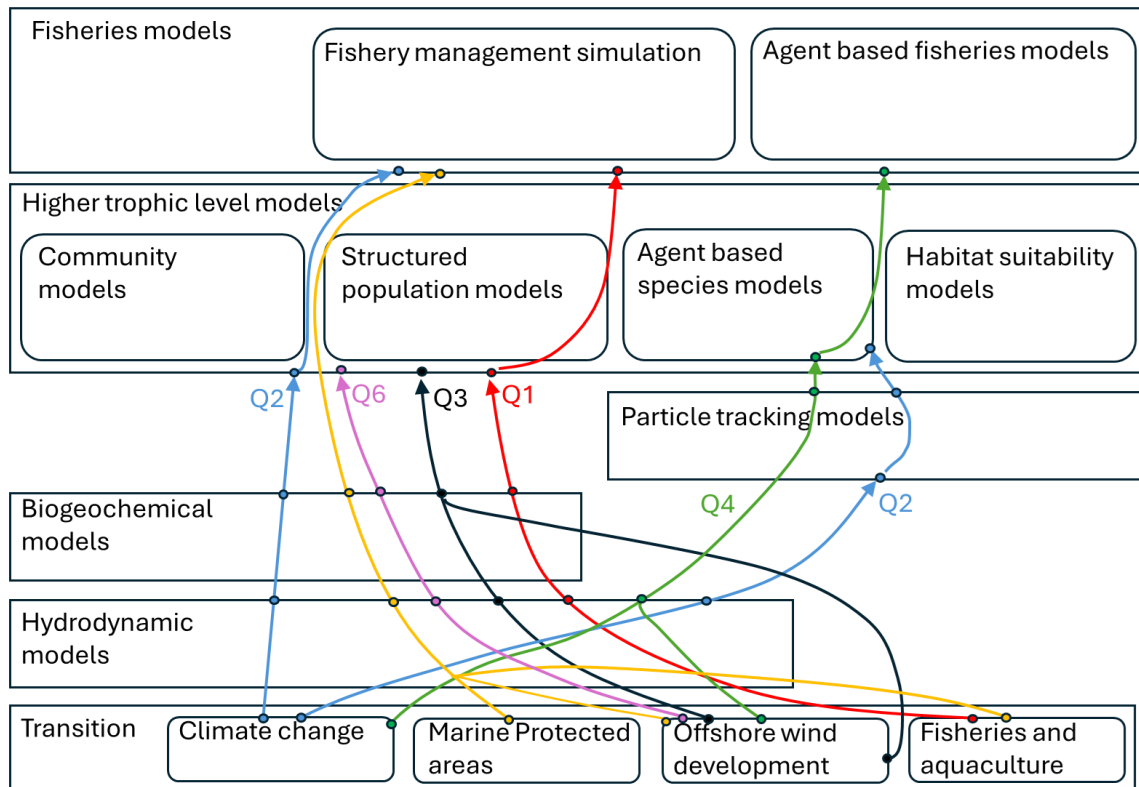


Figure 1. Schematic representation of model framework and how the model trains for the six proposed example model studies make use of the framework. Each model study is identified by Q and the number of the model study in the listing above. The arrows connect the different model components required to answer the question of the model study, indicated by a small circle where the arrow crosses the model component. The arrows start from the transition of which the impact is studied, but the output of each study will have consequences for each of the transitions and how they are dealt with. For some studies it is not yet clear which type of model in the group of higher trophic models will be used, so the circle is on the edge of the box for the group of models.

- Q6. Integral effects of offshore wind energy development on seabirds and marine mammals

The model toolbox which we aim to develop accommodates all these studies, but each study requires the use of a different subset of models (Figure 1). The underlying framework will be generic and suitable for many other relevant studies. Furthermore, while each of the proposed studies is inspired by a single transition, they are suitable to study trade-offs between the NSA transitions, as each is related to more than one transition (Figure 2). Most studies also incorporate elements of climate warming. Below we further describe each of these example studies and outline the required modelling toolbox.

	Transition			
Study	Nature	Energy	Climate	Food
Q1				
Q2				
Q3				
Q4				
Q5				
Q6				

Figure 2. overview of which transitions are addressed by the six research lines: green: nature transition, blue: energy transition, red: climate change, yellow: food transition.

3.2 Initial model studies

In the six initial studies we describe below, we develop a series of modelling frameworks and connections between them, to address critical knowledge gaps regarding effects of the North Sea nature, energy and food transitions. The different frameworks represent state-of-the art approaches to deal with questions that range from baseline hydrodynamics resolved in vertical columns of seawater, to the behaviour of fishers in a spatial grid. The different frameworks therefore also deal with input in their own ways. We incorporate, for example, models that are fully data-driven system accounts including short-term temporal resolution. At higher trophic levels, we incorporate dynamic models for fish populations that are based on first principles and which only rely on data to ensure correct species-specific physiology. In parallel to this, we use statistical habitat suitability models which predict the spatial distribution of fish based on quarterly survey data.

In addition to the modelling frameworks for the model studies, another crucial component is the connections between these. The connections are parts that still mostly need to be developed within the project, because these are not straightforward and often non-existent. For example, to address questions about higher trophic levels we need productivity of food sources as input. Food sources may be animal species at a lower trophic level or based on primary production. For boundary conditions, we may then aim to couple this high trophic level model by its food productivity, to a spatially highly resolved hydrodynamics model. However, if we look at a higher-trophic level model without explicit spatial structure, we need to translate the spatial signal from the hydrodynamics model to a food productivity level or range that contains space implicitly or not at all. For several of the six initial model studies, the element of connecting the individual models of the model train is the biggest challenge.

3.2.1 Ecosystem effects of lower trophic aquaculture

As part of the food transition, the Dutch government aims to facilitate low trophic aquaculture (LTA) within the perimeter of wind farms. Earlier studies for e.g. PROSEAWEED and FutureMARES have indicated that LTA is likely to affect the environmental conditions inside and outside the wind farm areas. These effects occur in conjunction with the effects of wind turbines and climate change on the environment, ranging from physical processes (stratification and mixing) to impacts on the marine food web. Offshore wind farms impact horizontal transport and vertical mixing of nutrients and hence influence primary production. Seaweed aquaculture takes up nutrients from the surrounding water and hence yields will be directly influenced by the presence of wind farms. In the current models the impact of aquaculture cultivation structures on hydrodynamics (slowing down of currents inside a farm and increased transport laterally) are not taken into account. Particularly in periods with large biomasses of seaweed or shellfish on the lines, this effect is likely considerable and can lead to depletion of nutrients or phytoplankton inside the farm, influencing both yields and the overall effect of a farm on local ecosystem dynamics.

Based on previous work (projects PROSEAWEED and FutureMARES), large-scale seaweed cultivation can remove significant amounts of nutrients from the system, reducing phytoplankton primary production over large areas and potentially negatively impacting the carrying capacity for other ecosystem components. Shellfish aquaculture will take up phytoplankton and organic matter from the water, which is likely to reduce the food availability to zooplankton and higher trophic levels feeding on zooplankton, such as some fish species. At the same time, the high local grazing rates of shellfish will have an impact on nutrient regeneration, which will feed back on primary production. This study will be geared towards unravelling the intricate links between climate, wind farms, and LTA farms at different spatial and temporal scales.

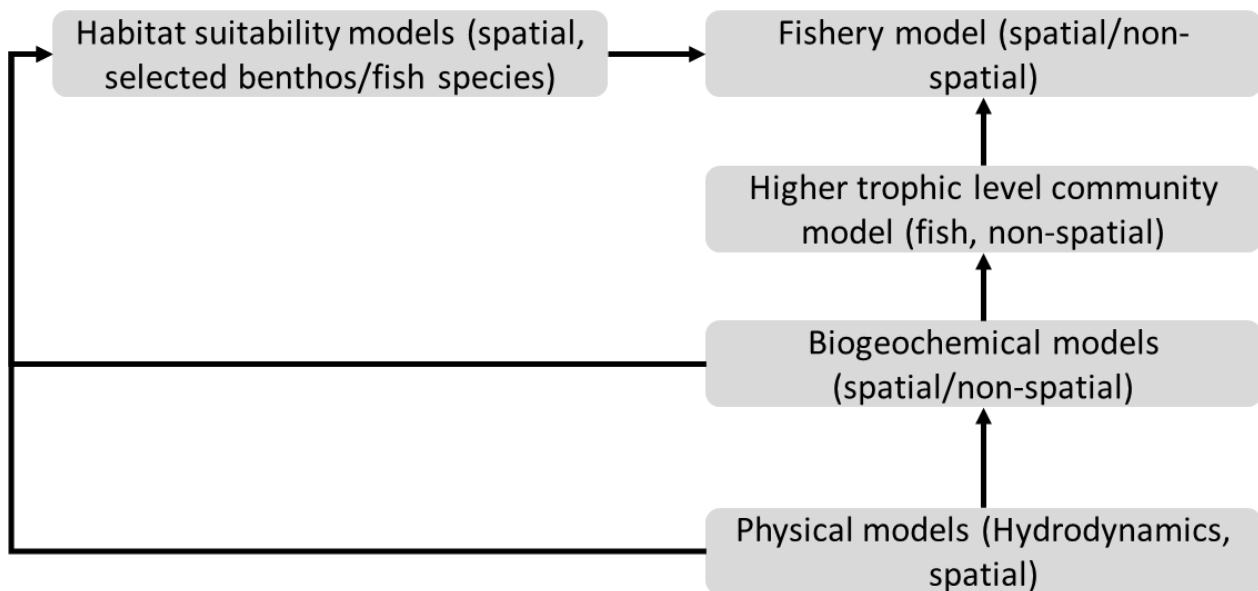


Figure 3. Schematic view of the model train for the study of lower trophic aquaculture (3.2.1; pressure: A shift of local phytoplankton primary productivity towards seaweed production), as well as for the integral effects of climate change (3.2.2; pressure: changing temperature and hydrodynamics).

3.2.1.1 Models

To simulate the processes related to lower trophic aquaculture described above, we connect various model components and create links for these connections (Figure 3). The impact of the aquaculture infrastructure on the currents, in combination with climate change impacts, will be simulated using a hydrodynamic model. Uptake of nutrients, phytoplankton dynamics, and impact of organic matter on primary production and zooplankton dynamics will be simulated using a 3D biogeochemical model that incorporates zooplankton as variable. If zooplankton is not included in a specific biogeochemical model an alternative approach could be to approximate the impact on zooplankton dynamics with an empirical model approach, such as a statistical model, using output from biogeochemical models. We also aim to combine hydrodynamic and biogeochemical models hosted by Deltares and NIOZ respectively. An alternative approach to simulation of seaweed and shellfish growth and food uptake in a biogeochemical model could be to use the DEB-based model developed by WMR, with input from a biogeochemical model. In the Deltares biogeochemical models, the DEB model parameters from WMR are fully integrated. For the simulation of impacts on higher trophic levels, mechanistic fish community models as well as habitat suitability or statistical models will be used.

3.2.2 Integral effects of climate change

Evidence of climate change effects on the North Sea ecosystem has already been observed - for example, migration of species northwards due to increases in water temperature. However, climate change not only affects temperature-related habitat suitability, it also has more complex bottom-up effects on ecosystems. In response to climate change, future river loads (water and nutrients) to the coasts will change, affecting nutrient gradients off the coasts and subsequent primary production. It is expected that river discharges will increase in winter and decrease in summer. The increase in atmospheric CO₂ also leads to ocean acidification that can be detrimental, especially for shell-forming species. Furthermore, apart from increasing water

temperatures, heating of the system may also affect physical processes such as stratification. Stratification can affect SPM dynamics, nutrient availability near the water surface and re-oxygenation in deeper waters. It is one of the main factors influencing the level of primary production and timing of the spring blooms, which forms the base of the marine food web. This, in turn, can affect the intensity and timing of zooplankton growth, which many fish species time their migration and spawning patterns on. The models at the base of the model train can also simulate secondary effects of climate change such as changes in storm frequency and intensity, so that these can be included as well. Because they are connected to changes in river runoff (through precipitation), we can also include changes in nutrient loading on the system.

We will analyse how future climate change scenarios for meteorology (temperature, wind, radiation, precipitation), atmospheric CO₂ and freshwater inputs will affect abiotic conditions and biogeochemistry in the North Sea including acidification. We will investigate how this affects the distribution of commercial fish species and the habitat suitability for a selection of sensitive and priority species (with an initial focus on fish and benthos species). We aim at investigating these effects both in terms of mid/long-term trends/average effects (up to 2050-2100) and for extreme events (e.g. marine heat waves).

3.2.2.1 Models

In this theme, we investigate bottom-up effects of climate change on the food transition (commercial fish species) and the nature transition (habitat suitability for priority species). The proposed model train (*Figure 3*) starts from the basis of 3D process-based modelling for abiotic conditions (hydrodynamics, salinity and temperature). These abiotics are coupled to process-based biogeochemical models which simulate bottom-up biological productivity of algae and grazers (benthos and zooplankton).

We will use several different process-based models to simulate the abiotic and biogeochemical environment, which will be used to force models for fish community dynamics, accounting for spatially explicit distribution, as well as non-spatial fish population and community models.

Alternatively, we will use the outputs for abiotic and biogeochemical conditions as input for habitat suitability models, based on knowledge rules or empirical relationships for selected priority and sensitive species (e.g. sand eels, reef building species, arctic quahog).

This theme will need extensive data for the forcings of 3D models in the context of future climate scenarios. These include hydrodynamic and biogeochemical boundary conditions for our 3D models, meteorology and river inputs (discharge, temperature and nutrient concentrations). Depending on the species we want to investigate in terms of habitat suitability, data to define knowledge rules that are not yet included in our models will be needed. For a number of benthic invertebrates and fish species this data can be obtained from existing ICES and WMTL surveys. For other species (pelagic fish and zooplankton), the MONS-funded zooplankton and pelagic fish survey results can be used (MONS ID 14-16 and 23), as well as data sets from NWA projects, such as the recently funded No-Regrets.

3.2.3 The food web consequences of large-scale hard substrate addition

With the expansion of OWF in the North Sea substantial areas of hard substrate are added to the ecosystem, which may present opportunities and challenges for organisms, for example the growth of filter feeders or the loss of sandy seafloor, but it is unclear whether such effects would be mostly positive or negative. While other developments, such as floating solar energy generation, could introduce even more hard substrates in the future, we focus here on OWF as it is the most concrete and pressing source. Introduced hard substrates may attract fish species by providing food or shelter (e.g. gadoids), but productivity of the benthic (invertebrate) community may be affected through introduction of hard substrates which could deter (flatfish) species that forage on sandy bottoms. These unknowns are addressed in this study in which we aim to elucidate the immediate and long-term impact of introduced hard substrate on the demersal food web structure and dynamics.

The possible effects of addition of hard substrate in sandy bottom areas can be viewed in light of the nature transition but also in light of the food transition, especially concerning the impacts for demersal fisheries. Fishing is not allowed in offshore wind farms, due to safety issues, making the area around the turbines a refuge for fish. We will analyse how the (aggregative) behaviour of demersal fish species and changing spatial distributions in response to the creation of hard substrate impacts demersal fisheries. When introduced hard substrate creates large refuges for fish, as actual shelter and as no-take zone, the spatial

distributions of fish that fisheries rely on may be skewed towards these closed areas, impacting potential yields in areas that remain open to fisheries.

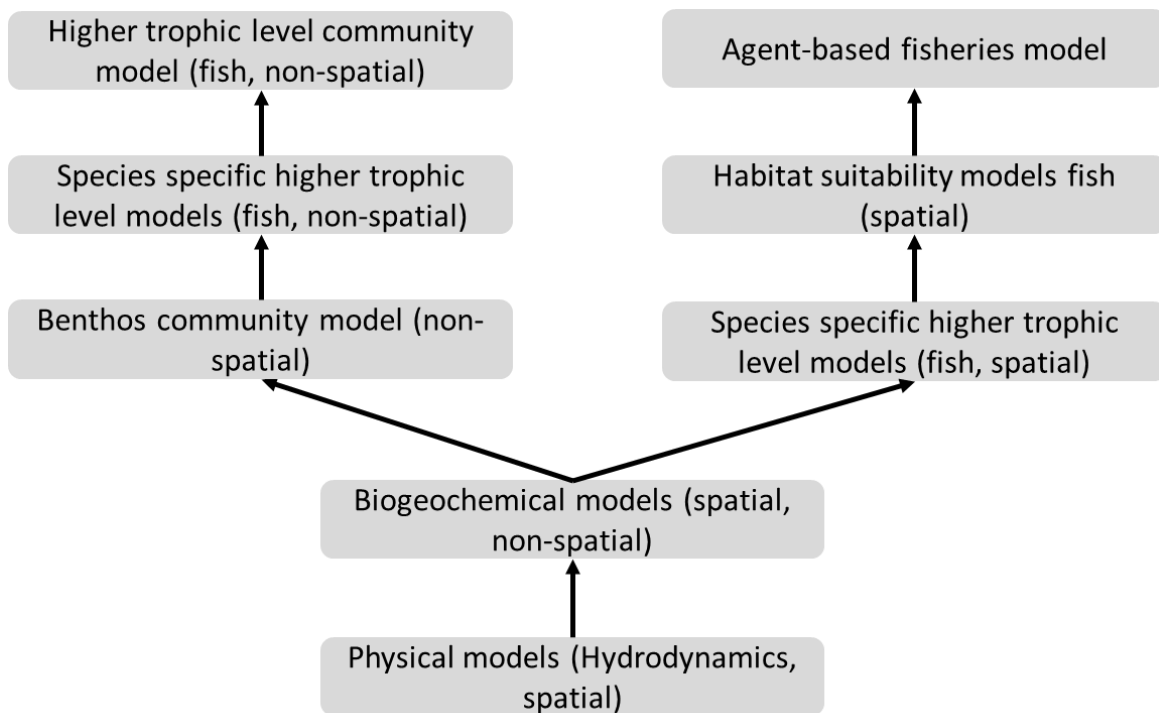


Figure 4. Schematic view of the model train for the food web effects of large-scale hard substrate addition, where the pressure on the ecosystem is the presence of hard substrate introduction from offshore wind turbines.

3.2.3.1 Models

In this theme we aim to connect food web functioning with fisheries outcomes. This model train allows us to address questions concerning the food transition (by studying effects of hard substrate on demersal fisheries) and to address questions concerning the nature transition (by analysing effects of hard substrate addition for food web dynamics and structure). We envision two similar model trains (*Figure 4*), which differ in the spatial resolution at the higher trophic levels. Both start from a spatial hydrodynamic model, coupled to various biogeochemical models, varying in spatial complexity. In one model train, the biogeochemistry layer sets the primary resource productivity for a non-spatial benthos community model which accounts for species' size-structure and dynamic interactions. The demersal fish population model that we couple to the benthos community model, accounts for food- and temperature dependent physiological processes, yielding population abundances and size-structure as outcomes. This model train ends with a demersal fish community model including dynamic predator-prey interactions between demersal fish populations and the benthic community.

The other model train builds on the same biogeochemistry baseline as described above but couples this to a different model for demersal fish population dynamics, here accounting for behavioural dynamics and a spatially explicit distribution. This spatial component is crucial to elucidate the distribution of targeted fish stocks in a statistical (data-driven) model. The fish stock distribution model informs an agent-based model for fishers at the top level of this model train. In this level the focus is on the impact of introduced substrates (in large spatial areas) on the spatial distribution of fishing activity.

3.2.4 Fish life cycle connectivity through the larval stage

In this theme we will address the question: What is the sensitivity of survival, condition, and connectivity of the larval stages of selected fish species to climate change and offshore wind farms, and how does this affect fish populations?

Offshore wind farms are expected to change currents and stratification, and to provide hard substrates for filter feeding organisms. Climate change is also expected to change water temperatures and stratification.

These factors influence fish larvae as they affect spawning in space and time, food availability and development rates, and transport between spawning grounds and nursery areas. They also affect mortality rates through additional predation and temperature-related effects. The combination of these changes is likely to modify the connectivity landscape between spawning and nursery grounds, and hence affect year class strengths of among others commercial fish species and subsequently influence fish populations and the fishing industry. In this theme we will further develop and apply particle tracking approaches to disentangle and assess these effects on larval connectivity and extend this to fish populations. We will focus on species that are expected to be sensitive to these changes (such as flatfish), or for which effects have already been observed (e.g. sole and plaice).

3.2.4.1 Models

The sequence of models will be built based on existing particle tracking suites for Delft3D and GETM. These existing methods consist of a hydrodynamics model coupled offline with a particle tracking model that includes vertical migration behaviour, and temperature-dependent growth and mortality.

We will first apply these existing particle tracking models of Deltares and/or NIOZ to a series of model scenarios with and without wind farms, with and without climate change, and with combinations of the two for, e.g., contrasting years. Subsequently, we will add a Dynamic Energy Budget (DEB) approach for development of individual particles in one of or both these models. This will enable the models to account for effects of spatial and temporal variations in temperature and in food fields on the condition and survival of larvae, as well as changes in those food fields induced by climate change and offshore wind farms. Parallel to this development, we will develop a coupling to a fish population model that accounts for spatial interactions between juvenile populations in nearshore nursery areas and adult populations offshore and life cycle closure. This coupling should work for both the classical and DEB-based particle tracking model versions. To study potential effects on fishing yield, a fishery management model will be coupled to the fish model.

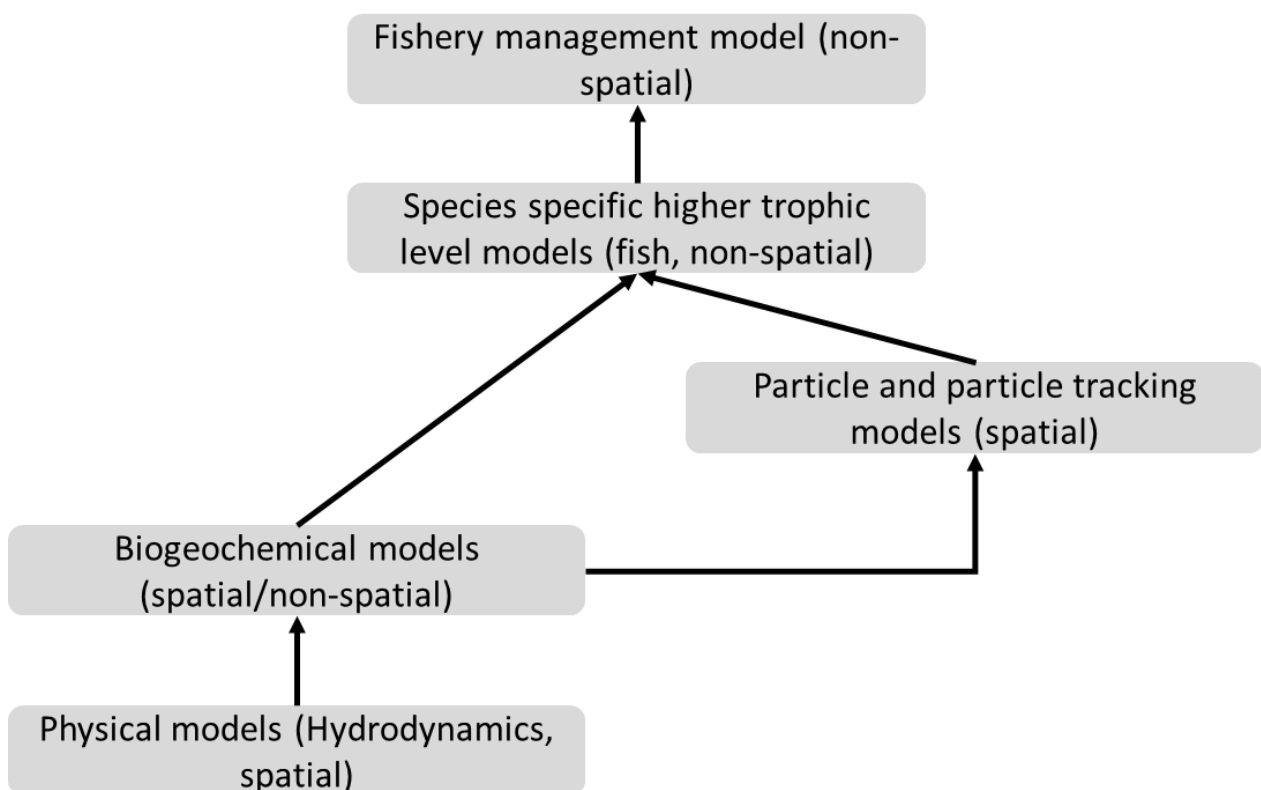


Figure 5. Schematic view of the model train for fish life cycle connectivity through the larval stage, where the main pressure studied will be the changes in temperature and associated hydrodynamical changes, as well as changes in the timing of essential phenomena such as peaks in food abundance.

3.2.5 Changes in bottom fishing and its ecosystem effects as a result of area closures (MPA and OWF)

An important measure to conserve nature in Dutch waters is the implementation of Marine Protected Areas (MPAs), where no fishing is allowed. Aside from these areas specifically designated for marine conservation, fishing activities are also banned from Offshore Wind Farms (OWF). Fishing quota are not adjusted to account for the lost fishing area, and fishers will most likely fish elsewhere to compensate for lost catch opportunities. This means that the implementation of both the nature and energy transitions will lead to large-scale relocation of fishing effort in the North Sea. This study aims to understand what this means for the North Sea marine ecosystem and how the effects can be managed, taking into account the effect of such management on the fishery.

We will set up a sequence of models to study the trade-offs between the nature, energy and food transitions, through the displacement of fishing effort from closed areas to areas which remain open. We will consider ecological feedbacks in the food web (such as indirect effects through competition and predation), spatial effects (such as spillover from closed areas), and fisher behaviour (such as displacement to new fishing grounds or switching to new fishing gears).

Using our combined models, we will be able to study how different degrees and locations of closed areas and associated management actions (such as effort and gear restrictions) affect marine nature and fishery. For such scenarios, we will potentially be able to study the net effects on benthic ecosystem quality, abundance, productivity and size distribution of commercial and non-commercial fish species and economic indicators of the fishery.

3.2.5.1 Models

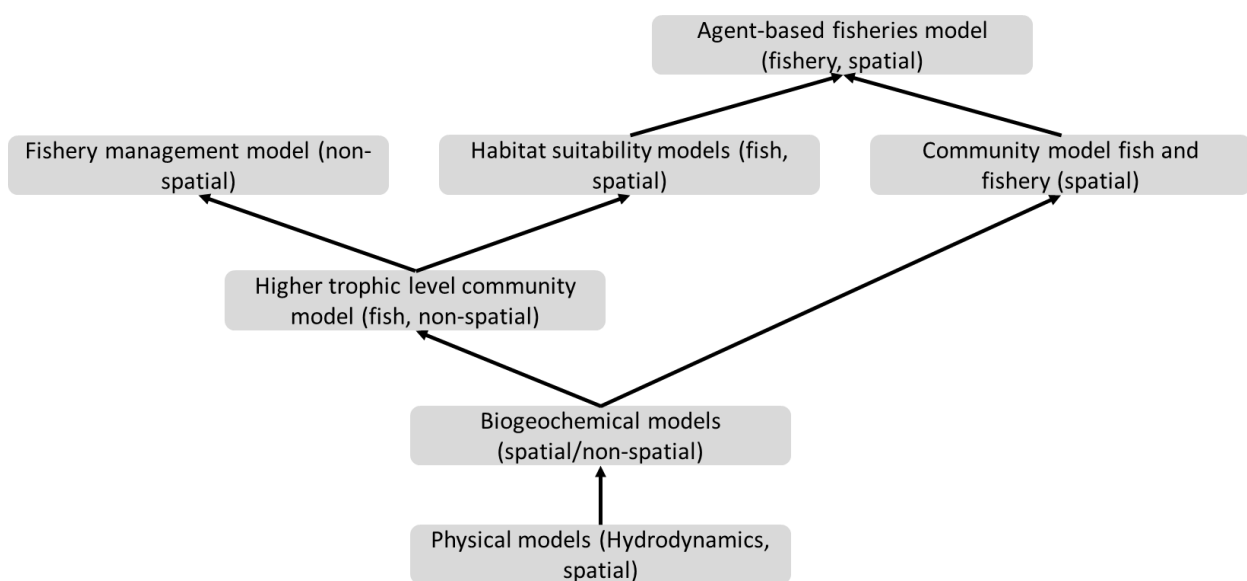


Figure 6. Schematic view of the model train to study the ecosystem effects of bottom fishing closures from OWF and MPAs. The pressure studied here is the redistribution of bottom fishing effort, from closed areas to those remaining open.

The model train required to study the effect of spatial fishing redistribution on the benthos, fish and fishery (Figure 6) consists of several parallel tracks which take different approaches. A model is required which can provide the productivity which fuels the benthic invertebrate food web. There are several options, of varying complexity. Ersem includes a benthic invertebrate food web, and can hence directly provide 'fish food productivity' without the need for a separate benthic invertebrate community model. There are also two models of varying complexity (DEMONS, relatively simple, and D-Water Quality, more complex) which can be coupled to the WMR benthos community model, or can provide estimates of benthic invertebrate abundances directly. A non-spatial fish community model (distinguishing between open and closed areas) will be developed by WMR in a separate project, which will be connected to the benthos community model and

various fishing models (with or without a habitat suitability model for spatial distribution). Both an agent-based fleet dynamic model as well as a simpler fishing effort and intensity model will be available to model the fishery behaviour and catches. Habitat suitability models, which describe the relative abundance of species or functional groups in space, dependent on biotic and abiotic factors (depth, temperature, food availability, etc.) will be used to connect the non-spatial models to spatially explicit models.

3.2.6 Integral effects of offshore wind development on seabirds and marine mammals

Offshore wind farms affect seabirds and marine mammals in various ways. Direct effects result from increased presence of man-made structures (turbines, maintenance and construction vessels), which can cause seabird displacement and habitat loss. Underwater noise affects marine mammal behaviour and there are suggestions that this is also the case for certain seabird species. Finally, seabird mortality increases when individuals are struck by turbine blades. The strength and importance of each of these effects varies between species. There are also indirect effects through the potential effect of OWFs on the food landscape for seabirds and marine mammals. There are indications that wind turbines locally attract fish, which could in turn make them attractive for seabirds and marine mammals looking for prey. Offshore wind turbines also potentially decrease the amount of stratification and wave action over larger areas. Such effects could cause changes in the productivity and/or distribution of small planktivorous fish, which are the main food source for many seabirds as well as marine mammals. It can be expected that direct and indirect effects interact in unexpected ways: if local prey increases attract seabirds to turbines, where they suffer higher mortality, the net effect of turbines on the seabird population is highly complex. In this study, we aim to understand the relative importance of these various effects and their interactions on the distribution and abundance of (selected) species of seabirds and marine mammals.

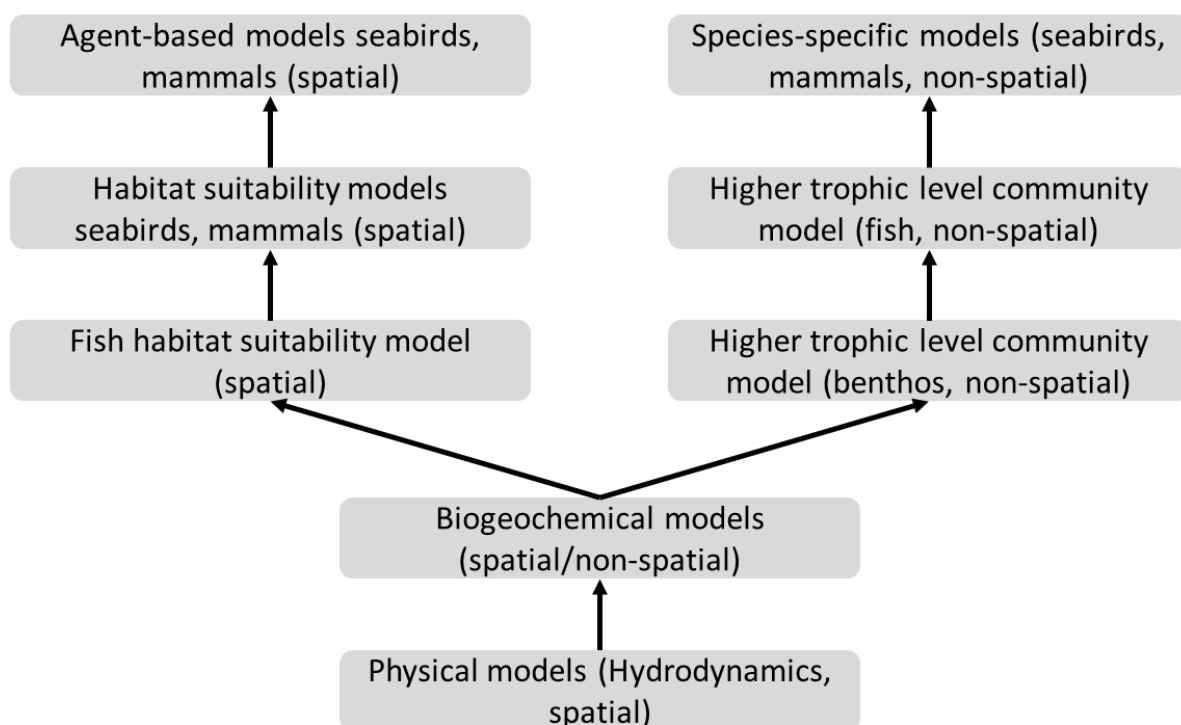


Figure 7. Schematic view of the model train to study the integral effects of OWF development on seabirds and marine mammals. The pressure here is the presence of Offshore wind turbines, with effects both above and below water.

Offshore wind development forms the core of the energy transition as described in the NSA, and seabirds and marine mammals are of prime conservation interest as part of European legislation. As such, they are crucial in the nature transition in the NSA. This research hence directly addresses the trade-off between those two transitions. For certain seabirds, bycatch from fishing vessels has become an important food source, so trade-offs with the food transition can also be explored at a later stage.

3.2.6.1 Models

To model the effects of reduced stratification and wave action on the production and distribution of fish food, a coupled hydrodynamic and biogeochemical model is required which can relate the presence of OWF to the distribution, productivity and abundance of phyto- and zooplankton. These models can be connected to benthos- and fish community models, which need to have sufficient detail to model the productivity and abundance of the fish or benthos which is edible to seabirds and marine mammals (*Figure 7*). The food availability and dynamics can in turn be coupled to individual-based models (agent-based models as well as structured population models) of seabird and marine mammal populations. Fish and benthos models are generally not spatially explicit. In order to couple these models to spatially explicit individual-based simulation models, habitat suitability models can be used to create maps of the (relative) abundance of species or functional groups, based on local biotic and abiotic factors (such as temperature, distance to spawning grounds, depth, etc.). The same approach can be used for non-spatial seabird and marine mammal population models.

3.3 Stakeholder feedback on initial studies

The six initial model studies were presented at the stakeholder meeting and reflected upon, although not all model studies were discussed in equal detail during the meeting.

Different stakeholders each have their own perspective, leading to different questions and remarks. LVVN has a focus on the food transition (fisheries), Stichting De Noordzee focuses on the nature transition and the energy companies on the energy transition. We find it important to recognize each of these perspectives, and to make sure the scope of our modelling frameworks encompass their full breadth. We feel that this is matched in the proposed modelling studies, as each relates to more than one of the transitions.

Remarks and questions per topic are given below. The issues raised are listed here as is, but will be valuable guiding input for developing the annual research plans for the model framework in the coming years.

Ecosystem effects of lower trophic aquaculture

It is suggested (Jakob Asjes, RWS) that mariculture is currently not considered a viable business model, even though experiments with companies are being done. This suggests that questions on model study 1, dealing with the effects of lower trophic aquaculture may be less urgent to address. On the other hand, it might be worthwhile to address the boundaries of mariculture: if studies reveal which levels of mariculture yield severe effects on the ecosystem, then companies can assess if such effects are hampering economic development, before maricultural developments take place. Jaap van der Meer (WUR/WMR) is currently supervising a PhD student on this topic, concerning the effects of seaweed culture on nutrient dynamics and competition with other primary producers.

Changes in bottom fishing and its ecosystem effects as a result of area closures (MPA and OWF)

The model study 5, on the effects of area closure, was also discussed during the stakeholder meeting. Fisher representatives mention that sole, the most important demersal stock, is no longer found on the more traditional spawning grounds during the spawning season, and they suggest that that could be caused by human constructions such as wind parks and powerlines. Avoidance or attraction of OWF by fish will have consequences at stock level and at socio-economic level. Assumptions on fish avoidance of wind parks need to be complemented with scenarios where fish are attracted to OWF, such as plaice, crab and cod, which can be found in higher densities in OWF.

Changes in fisher behaviour in turn can affect fish stocks and the food web. Attention needs to be given to these aspects as well. Will the planned transition of the fishery industry also be considered in this context? Climate change also needs to be considered as driver of change in spatial occurrence of stocks. Some stakeholders advocate that in addition, one should look at the effects of closed areas on nature in a broad sense, beyond commercially exploited species and the effect of local closure at North Sea scale. Other stakeholders fear that such broadened approach will cause loss of focus on bottom trawling and dilute energy to come to useful answers and insights.

Additionally mentioned was the option to perform a study comparing the impact of one large versus multiple small, closed areas, with in total identical surface area, on the food web and North Sea fisheries.

Integral effects of offshore wind development on seabirds and marine mammals

According to LVVN this topic has high priority, and they mentioned it would be great if the proposed seal tagging experiments can be incorporated in this study. This topic relates strongly to Wozep.

Is food also part of the integral effects, given that fishers, birds and marine mammals share resources?

General remarks

As a more general remark on the proposed model studies attention is drawn to a more integral approach of all these topics. Can cumulative effects be addressed? Is there a way to compare effect sizes between these studies and can such an approach be used for trade-offs? It is seen as an important challenge to make clear how the trade-offs between the transitions depend on the way in which these transitions are implemented.

How do these themes relate to the nature transition? Is nature treated as a result or as a scenario?

Can we make use of and/or relate to KRM threshold values, with contribution from Stichting De Noordzee?

Can species-specific protection plans be used or addressed in the proposed model studies, for example in addition to area closure?

There is a general call to be very consistent and clear in terminology. For example, there can be no confusion about the definitions of terms like 'observation', 'assumption' or 'contribution'. Usages of broad terms such as 'habitat', 'carrying capacity' can cause misunderstanding because interpretation may differ between people.

How will uncertainty be dealt with? Each model has its own level of uncertainty and while each model is state-of-the-art, outcomes can be unsure and are not to be considered as absolute truth. It is important to acknowledge uncertainty and treat it as such. Methods such as sensitivity analysis exist to quantify uncertainty.

LVVN asks for incorporating sand extraction in the proposed model studies because this activity will increase and sole densities in sand pits may actually increase.

LVVN remarks that climate change may also mean a 5-degree lowering of temperature due to changes in current.

LVVN is interested in how the transitions relate to each other. It would be nice if relations can be considered in the models.

3.4 Overview of models and couplings

3.4.1 Models

Combining the models required for all proposed model trains reveals that there is a lot of overlap among them, meaning that many models are needed in two or more model trains (Table 1). The most generally required models are those for the lower trophic levels. There is also considerable variation in how specifically the various models are named. This often reflects differences in the state of development. For example, the indicated 'fish community model' is still to be chosen and/or developed and therefore a specific name is not given. This is different for, for example, the D-water quality model, which is an established and well-developed model for the North Sea water quality. Below we provide more detail on each model. For models already available, we discuss their state of development relative to the model studies proposed here, and their past applications.

3.4.2 Physical models

Physical ocean models calculate water levels, currents, temperature, salinity and in some cases transport. Implementations range from stationary state analytical models for a single location to 3D numerical

hydrodynamical models that simulate changes in physical variables in space and time. Increased levels of simplification reduce the applicability of these models to specific situations, so for realistic situations 3D numerical hydrodynamical models are usually used. There are quite a few of these models available in the engineering and scientific communities, which strongly overlap in their implemented processes and capabilities, but also have differences. We give more detail about the models used by Deltares and NIOZ below.

These hydrodynamics models can be fitted with particle tracking models that can trace the trajectories of water parcels or physical particles ranging from e.g. microplastics to shipping containers, or biological particles such as eggs or larvae from a source location to a destination. Some of these can also account for particle behaviour, such as floating or sinking, or vertical swimming. Particle tracking models are often used to investigate (changes in) connectivity between source and destination areas. Also, for particle tracking models we will give more detail about the ones used by Deltares and NIOZ below.

3.4.2.1 Delft 3D D-flow FM

D-Flow Flexible Mesh (D-Flow FM) is the hydrodynamic simulation module of the Delft3D FM Suite developed by Deltares. D-Flow FM implements a finite volume solver on a staggered unstructured grid. The higher-order advection treatment and near-momentum conservation make the solver very suitable for supercritical flows, bores and dam breaks. The handling of wetting-and-drying makes it suitable for flooding computations. The continuity equation is solved implicitly for all points in a single combined system. Optionally, non-linear iteration can be applied for very accurate flooding results. Furthermore, Coriolis forcing, horizontal eddy viscosity, tide generating forces and meteorological forcings were added, making the system suitable for tidal, estuarine or river computations. The D-Flow FM module of the Delft3D FM 2024.03 release fully supports hydrodynamic modelling for 2D horizontal applications and 3D applications for transport of salinity, temperature, and conservative tracers. In the D-Flow FM, Sigma-coordinates, Z-coordinates, and Z-Sigma-coordinates are possible in the vertical. Depending on the application, one of these co-ordinate systems can be chosen. For deep water applications (roughly deeper than one kilometre) Z-Sigma-coordinates are preferred. In this way, relatively thin Sigma-layers of a few meters near the surface can be combined with Z-layers of an increasing thickness in deeper parts. For 3D modelling, three turbulence models are available: algebraic, k-epsilon and k-tau. Vertical transport can be solved both explicitly and implicitly. Temperature modelling is supported either using the composite heat flux model or the excess heat flux model, which can both be driven by space-and-time varying meteorological datasets. Time integration is done explicitly for part of the advection term, and the resulting dynamic time-step limitation is automatically set based on the Courant criterium. The possible performance penalty can often be remedied by refining and coarsening the computational grid at the right locations. D-Flow FM models can be run as parallel computations on distributed-memory high-performance computing clusters. The Deltares water quality model (D-Water Quality) can be coupled to Delft3D and D-Flow-FM.

3.4.2.2 GETM

The General Estuarine Transport Model (GETM) is an open-source community hydrodynamics model (Burchard & Bolding, 2002, www.getm.eu). It solves the hydrostatic shallow-water hydrodynamics equations in 3D, and includes water temperature and salinity. It also includes turbulence calculations through the 1D General Ocean Turbulence Model (GOTM) model (Burchard et al., 1999, gotm.net). GETM supports cartesian, spherical and curvilinear horizontal Arakawa-C grids, and a range of vertical grid types (Z, sigma, general) that can be fixed or adapt dynamically. Coupling pathways run via GOTM, facilitating a seamless 1D-3D testing environment. NIOZ maintains North-west European Shelf, North Sea, Wadden Sea, and Eastern and Western Scheldt model setups for GETM. GETM has a generic facility to include friction by structures in the water column, that relies on user-supplied subroutines for specific types of structures. GETM and GOTM use the generic FABM coupler, and NIOZ has a native coupler to ERSEM-BFM.

3.4.3 Biogeochemical models

Biogeochemical models simulate the dynamics of nutrients and groups of species that typically are weak swimmers so they stay in one place or move with the currents. These models are typically based on conservation laws for nutrients. The simplest type of these models are NPZD (Nitrogen, Phytoplankton, Zooplankton, Detritus) models which simulate one nutrient, one phytoplankton group, one zooplankton group and one type of detritus. More complex models have larger numbers of these components. These

primarily pelagic models can be equipped with a benthic model which improves the representation of nutrient recycling. Also, these benthic models range from simple (benthic return models) to complex. The latter can include multiple vertical layers, multiple types of bacteria and macrofauna.

Biogeochemical models are typically coupled with a hydrodynamics model that supplies it with physical environmental conditions and facilitates spatial transport of the ecosystem components. We give more detail about the models used by Deltares and NIOZ below.

3.4.3.1 D-water quality

The D-Water Quality module simulates the far- and mid-field water and sediment quality due to a variety of transport and water quality processes. To accommodate these, it includes several advection diffusion solvers and an extensive library of standardized process formulations with the user-selected substances. The process formulations are organized in a modular way, so that models with different levels of complexity can be created in a flexible way. However, for the North Sea applications of D-water quality always a similar set of processes and process parameter values is used: GEM (Blauw et al., 2009). This includes 4 nutrient variables: nitrate (including nitrite), ammonium, ortho-phosphate and silicate. It includes 4 phytoplankton groups: diatoms, flagellates, *Phaeocystis* and dinoflagellates. The properties of these phytoplankton groups (such as growth rate and chlorophyll to carbon ratio) are adapted to the specific local environmental conditions, using the BLOOM modelling approach. Additionally, one particulate organic matter fraction for each nutrient (N, P, Si) is included, both in the water column and in the sediment. Oxygen concentrations and benthic filter feeders are included in the North Sea model applications as well. For the modelling of benthic filter feeders the DEB-model, developed by WMR, is integrated in D-Water quality (D-WAQ). In DEB-models (Dynamic Energy Budget) the growth and metabolic processes per individual depend on the size of the individual, following the DEB theory developed by Kooijman (2010). Some special versions of the model also include carbonate variables (TIC and alkalinity), seaweed or zooplankton. Also, the modelling of zooplankton uses the DEB-model approach, integrated in D-WAQ. D-water quality can be run in an online coupling with D-FLOW-FM or stand-alone, with hydrodynamic input from Delft3D or other hydrodynamic models. In case Delft3D is used as hydrodynamic basis the spatial grid can be aggregated to reduce the simulation time. This option is not available yet for D-FLOW FM.

3.4.3.2 ERSEM

There are currently three distinct biogeochemical models that were derived from the common ancestor ERSEM (European Regional Seas Ecosystem Model, coded in Fortran-77) that was developed in the late 1980's (Baretta et al., 1995). The original ERSEM contained four nutrients, five phytoplankton groups, bacteria and two relatively basic benthic modules. The three modern versions are: BFM (Biogeochemical Flux Model, maintained by INGV, Italy), ERSEM-BFM (maintained by NIOZ), and FABM-ERSEM (maintained by PML, UK). Each has a different history, and partly different capabilities. BFM is a completely re-coded version (Fortran-95) of the original ERSEM model created in the early 2000's by NIOZ and INGV, with an optimised architecture (Vichi et al., 2007). BFM is mainly intended for deep, clear-water ocean and Mediterranean simulations, and contains a simple benthic return model. Recently, BFM was modified to work with the FABM coupler. ERSEM-BFM is based on the BFM code and was developed by NIOZ and Cefas since the mid-2000's, but is optimised for shallow turbid-water applications such as the North Sea (e.g., Van Leeuwen et al., 2013). It contains North-Sea specific phytoplankton parameterisations including *Phaeocystis* colonies, a sediment resuspension and turbidity module (van der Molen et al., 2017), a macroalgae farming module (van der Molen et al., 2018), and a benthic module. The benthic module has recently been extended such that the benthic biogeochemistry is strongly influenced by the activity of burrowing fauna. This version is currently being implemented in 3D following testing in 1D. FABM-ERSEM is a version that was re-coded by PML with contributions by Cefas to use the FABM coupler in the early 2010's (Butenschon et al., 2016), and was based on a partly modernised version of the original ERSEM code. It contains one of the original benthic modules, cocolithophores, and iron cycling. It is used for both open ocean and shelf sea applications. ERSEM-BFM is in the last stages of a major upgrade, and the coupling to a modern version of 3D GETM is in progress. An important development within this project will be to test FABM-ERSEM with GETM and/or couple it to Delft 3D D-flow FM.

3.4.3.3 DEMONS

Demons is a DEB based ecosystem model of the North Sea (van der Meer et al. 2022) using nitrogen, carbon and phosphate as base nutrients. Current model components are primary producers, consumers, decomposers, described as V1 morphs with structure and reserves (Kooijman 2010). Synthesizing units were developed for use of stoichiometry and to maintain mass balance (van der Meer et al. 2022). Detritus is described by its origin of the components. It is a closed system, that has been applied to 0-D and 1-D, but will be extended to 2-D based on North Sea compartments. While the 3-D counterparts rely on fine detail in time and space they are heavy on complexity and computational time, Demons is more simple and therefore quick. It can be used to explore how various ecosystem processes, such as the mode of trophodynamic control or the processes that limit phytoplankton and zooplankton growth, depend on various model parameters and assumptions. Current developments include improvement of how phosphate is implemented, the development of a 3D version and the possible consequences of nutrient competition between phytoplankton and seaweed. In addition, the effects of pelagic vs benthic grazing will be studied.

3.4.4 Higher trophic ecosystem and/or community models

These models describe the interactions among species (benthos and higher trophic levels) or functional groups (for example filter feeding bivalves or schooling small pelagic fish). They are often phrased as systems of ordinary differential equations, with a variable for each species or functional group. These are generally derivatives of the classical Lotka-Volterra predator prey model from the 1920's, which can readily be expanded for more species or functional groups. Ecopath with Ecosim is the most well-known of these. They have also been expanded to include stage structure (de Roos et al 2008, Petrik et al 2019). In recent years, community models which define species as a distribution over a continuous size spectrum have also become available (Andersen et al 2016). Here, the species or functional group concept is fully replaced by a size-based specification of the ecological role of individuals, but hybrid formulations which retain some degree of species- or functional group-level variation are also available (Hartvig et al 2011).

3.4.4.1 Benthos community model

This model was developed to study the effects of bottom trawling on the benthic food web. It includes both the direct mechanical effect of trawling on benthos, as well as the indirect effects through the manipulation of fish abundance (van de Wolfshaar et al, 2020). It describes the benthic invertebrate community as biomass distributed over functional groups (predators, filter feeders and detritivores) rather than species. Each of these groups is split into biomass of adults and juveniles, because they engage in different ecological interactions.

The model takes as input the food abundance for filter feeders and detritivores, and its output is biomass available as food for fish and some seabirds (such as common scoters, *Melanitta nigra*). Fish abundance and trawling intensity could also be forcing variables from an external source (another model). The model in its current form does not include a distinction between areas open and closed to fishing, but this can readily be implemented and would be a requirement for its application in most of the planned model studies.

3.4.4.2 Fish community model

Fish form the connection between the lower trophic levels (benthos and zooplankton) and top predators (seabirds, marine mammals, sharks). They are also the target of fisheries and can be predators themselves. Because fisheries management is species-oriented, the models available for fish are often single-species models. This also means our knowledge of fish life history and dynamics in the North Sea is strongly skewed towards commercially fished species. The model studies proposed here require a broader tool which includes most, if not all fish biomass. For the planned work, we will require a functional group level model of the fish community in the North Sea.

3.4.4.3 OSMOSE

OSMOSE is a size-based, object-oriented, spatially explicit model, or individual based model, that describes the fate of fish based on feeding, growth, reproduction and mortality, using a super-individual approach. This implies that each 'school' consists of identical fish of the same species, with the same size, age and location. Each school feeds, moves, may get eaten or suffers from fishing mortality (van de Wolfshaar et al. 2021). Fish may consume other fish but also external resources provided by lower trophic level models; such as

zooplankton and different types of macro-invertebrates. This creates a dynamic food web, in which non-linear interactions play a role on the outcome of scenarios relative to a baseline scenario. The model has been used to study the sensitivity of higher trophic levels to different lower trophic level input (van de Wolfshaar et al. 2021) and different levels of fishing effort for bottom trawling and both bottom trawling and pelagic fishing (Lynam et al. 2023). Together with Hereon (Hamburg, Germany) a study is being done to study food web effects of wind parks serving as MPA (Benkort et al. in prep). Recent developments in the H2020-SEAwise project have resulted in an updated version with the addition of two fish species (now 14) and 14 metiers instead of 4 fleets, representing the bulk of fish biomass and metiers in the North Sea (Binch et al. In prep). Fishing mortality is now a function of fish size, gear, catchability for a certain species-metier combination and an effort distribution in space and time. With this model version the effects of MPA's based on the 30% area closure for bottom trawling by 2030 have been studied (Binch et al. in prep). At this moment, scenarios are done to assess combined effects of MPA's and climate change, where climate change is accounted for by using predicted habitat use for the species involved and external resources based on ERSEM climate runs that include macro-invertebrates (Binch et al. work in progress). In the H2020-SEAwise project also ecological and fisheries indicators were developed and applied to both OSMOSE versions (Lynam et al. 2023, Binch et al. in prep). The next aim for SEAwise is to develop an agent-based fishery module which allows for a dynamic representation of the fleet with simple behaviour rules based on state-of-the-art socioeconomics (collaboration with Wageningen Economic Research and other SEAwise partners). Both OSMOSE versions in their current form do not include temperature dependent physiological rates, nor do they include physiological and environmental drivers of movement.

3.4.4.4 Fishery management simulation

Fishing mortality in ecological models is often implemented as a constant mortality rate. However, fishing mortality is a complex outcome of fisher behaviour and management regulations. While it is possible to construct a complex agent-based model of individual fishers, this is not always the best approach (for reasons of computational limitations and generality). Therefore, we will also implement a more abstracted model of dynamic fishing mortality, including the practice of annual quota dependent on recent estimates of stock abundance and distribution, as well as catch-dependent fishing intensity (i.e. fishers 'giving up' when their revenue falls below a threshold). Such abstractions can readily be coupled to the fish community models and can be used to compare various fisher behaviour and fishery management scenarios and their outcome under various transitions and climate change scenarios.

3.4.5 Single-species higher trophic level models

Higher trophic level (HTL) models simulate the dynamics of the populations of one or more selected species that can move around relatively independently from the currents. Because this movement is usually poorly understood, it cannot be simulated based on first principles. Hence, these models are usually formulated to provide information about population dynamics and species interactions at the spatial scale of the basin of interest. These models can include distinct life stages of the species they simulate. Recent developments include adding spatial components to these models, these then tend to include prescribed horizontal movement. Below, we provide more detail about HTL models used at WMR and NIOZ.

3.4.5.1 Fish species specific population model

For a number of relevant species, detailed individual-level descriptions of growth, energetics, feeding and reproduction are available (e.g. Cod, plaice, sole, herring, brown shrimp). Such models can be used to study the effects of disturbances on the population growth rate and other relevant indicators (Soudijn et al 2020). They can also be implemented into the framework of physiologically structured population models (De Roos & Persson, 2013) to study population and community responses to changes in environmental factors (van Leeuwen et al 2013). Such models are particularly suited to study non-lethal effects of anthropogenic disturbance on population and community dynamics, and many of such effects play a role in the trade-off between the transitions (for example: underwater noise effects on feeding opportunities, changes in visibility affect foraging efficiency, concentration of prey around wind turbines affects feeding opportunities and competition, etc). Most existing models do not include temperature-dependence, but methods to add this are available (van de Wolfshaar et al 2008, Ohlberger 2011, Dye et al. in prep).

3.4.5.2 Structured population models seabirds

Structured population models describe a population as a frequency or number distribution over states. Most often these states are individual age and/or reproductive activity. This is for example the case for the matrix population models for seabirds used for the KEC (Kader Ecologie en Cumulatie; Soudijn et al 2022), where a distinction between juvenile, breeding and non-breeding adults is used. Other models use a more elaborate physiological state, such as individual body size and energy reserves. Such models are relatively rare for seabirds, perhaps because they are often parameterized based on experimental determination of parameter values, which are not available for seabirds. However, they have been used successfully, in particular to study the non-lethal effects of human disturbance in other taxa (e.g. Cod; Soudijn et al 2020, cetaceans; Hin et al 2019). There are statistical methods available to estimate parameters based on individual-level dynamics (weight, caloric intake) and the potential of these methods can be explored. The advantage of these models is that they can translate non-lethal energetic costs for individuals to population-level vital rates on the basis of physiological mechanisms. Such non-lethal effects occur frequently as a result of anthropogenic disturbances. An example is the increased energetic cost of flying further to find food when an OWF is built near a breeding colony.

3.4.5.3 Structured population models marine mammals

Structured population models (as described above for seabirds) have been successfully used to understand the effects of sonar use on marine mammals (Hin et al 2023). For a number cetacean species relevant to the North Sea, parameterized individual-level energy budget models are available, which can be used in population models. For both North Sea-relevant seal species, models are not available, but individual-level parameters can likely be collated from literature.

3.4.6 Particle tracking models with behaviour

In particle tracking models, the transport of particles can be simulated at a resolution that is higher than the grid of the underlying hydrodynamic model. This approach is called a Lagrangian approach, in contrast to the Eulerian approach where all concentrations are averaged per grid cell. ERSEM and D-WAQ are examples of Eulerian models. The transport of the particles in Lagrangian models is based on the currents in the underlying hydrodynamic model. Additionally, the position of the particles is affected by random dispersion. In some applications the position of particles is also affected by behaviour: such as swimming for fish larvae and jellyfish. Also, concentrations of particles can be affected by processes, such as decay or evaporation of oil slicks. Models of individual behaviour (IBMs) simulate (part of) the life history of an individual or a group of identical individuals as it responds to (changes in) its immediate environment. Such responses can be flying, swimming or feeding behaviour, growth, reproduction, mortality, or a combination of those. Growth, reproduction and/or mortality can be represented by empirical relationships with environmental variables such as temperature. IBMs can be run stand-alone, or associated with a particle of a particle tracking model that moves around in the environmental space of a hydrodynamics model or a coupled hydrodynamics-lower trophic level ecosystem model. Here, we provide more detailed information about the larval behaviour models used by Deltares and NIOZ.

3.4.6.1 D-part

D-part is the particle tracking software developed by Deltares. It can be coupled to Delft3D or D-FLOW-FM. In both cases, apart from the physical transport also additional processes can be simulated such as swimming, vertical migration and evaporation. It has been applied to simulate the behaviour of fish larvae, jellyfish and oil slicks. There are 2 versions of particle tracking available at Deltares: one that is coupled to Delft3D and one that is based on D-FLOW-FM. The former uses curvilinear grids and the latter uses flexible mesh sizes to enable the use of fine mesh sizes in nearshore coastal waters and more coarse mesh sizes in offshore waters. The D-part version coupled to D-FLOW-FM is relatively new and some functionalities, such as swimming behaviour by fish larvae, are only available yet in D-Part coupled to Delft3D. Vertical migration of particles is included in both versions.

3.4.6.2 GITM

The General Individuals Transport Model (GITM) is a Lagrangian particle tracking model that was developed to run offline using NetCDF files with stored hydrodynamics from GETM (van der Molen et al., 2015). It assumes that the hydrodynamics data are on an Arakawa-C grid (cartesian or spherical, curvilinear is not (yet) available), and sigma or general vertical coordinates (Z not available), and uses that grid for the particle tracking calculations. It uses a semi-analytical approach to obtain accurate predictions of particle advection, and includes a random walk method for particle diffusion that uses time-varying diffusion based on turbulence calculated by the hydrodynamics model. GITM includes a flexible propagule development and behaviour module, that uses a super-individual approach. This approach assumes that each particle represents a number of identical individuals, that can develop, die, have vertical migration behaviour, and be transported. Propagule development is included through several temperature-dependent egg and larvae development equations. Mortality is also implemented through several temperature-dependent equations. It is easy to add alternative development equations. Vertical migration behaviours include fixed depth, constant vertical velocity, density-dependent vertical velocity, motion towards given depths, and diurnal and tidally cued vertical migration behaviour. These behaviours can be combined. Particle settlement can be delayed until a combination of certain environmental conditions is met. Species-specific behaviours can be implemented by specifying a user-defined number of subsequent egg and larval development stages through a simple text file. Each stage can have its own growth, mortality and vertical migration definitions. NIOZ has species-specific development and behaviour settings for a range of species in the North Sea (e.g., Van der Molen et al., 2018).

3.4.7 Agent based simulation models

Agent based simulation models explicitly simulate a (large) number of individuals which interact with their environment and each other. The advantage of such models is that they can deal with variation among individuals in a very natural way, because each individual is modelled explicitly. For this same reason, such models are often computationally intensive and this often limits the number of individuals that can be simulated. These models are usually applied to organisms or people exhibiting more complex behaviours, often in a spatially explicit setting. They have for example been used to study the behaviour of shrimp fishers choosing where and when to fish under various management scenarios (Beier et al 2023) and to estimate the impact of OWF-related habitat loss on seabird mortality (Van Kooten et al 2019).

3.4.7.1 Agent based models seabirds

A number of agent based models for relevant seabird species have been developed at WMR over the last years (van Kooten et al, 2019; Soudijn et al 2022). These have generally been used to estimate the impact of habitat loss from OWF on seabird mortality. These models will be developed further by WMR in the coming years, in related projects. Those models will become an integral part of the toolbox developed here, and are expected to be used to assess how behaviour mediates the response of seabirds to changes in the environment, such as the availability of nesting sites, food from fishery discards, emergence of OWFs and climate warming effects on the seabird food landscape.

3.4.7.2 Agent based models marine mammals

These models will have the same function in the modelling toolbox as the agent based models of seabirds described above. They combine assumptions and knowledge about individual behaviour of animals with environmental changes, and can be used to generate predictions and hypotheses about the net effect of

these. WMR has agent-based models of seal and porpoise populations available (Chudzinska et al 2021, Chudzinska et al 2024).

3.4.7.3 Agent based model fishers

Two complimentary approaches are in development. Agent based models for fishers are currently in development at Wageningen Economic Research. These models are strongly based on empirical relationships, consider a large number of factors and as a result will be highly complex. They are developed using the DISPLACE framework (see displace-project.org). A simpler (but also agent-based) approach is in development at WMR (the Artemis framework, van Kooten et al. in prep). The Displace models will be suited to make predictions based on many simultaneous projected environmental changes. The Artemis approach is more suited to study how general mechanisms (such as environmental uncertainty, strength of competition) influence the outcome of fishing and management strategies. This makes both frameworks valid tools to study trade-offs between the transitions, but at different levels of detail.

3.4.8 Habitat suitability models

Habitat suitability models relate environmental conditions (both biotic and abiotic) to the suitability for a particular species or group of species. Often, these models are statistical models (GLMs, GAMs, etc) which relate observations of biota to the local environment in which the observation was made (for example, depth, seafloor substrate, temperature, etc.). While suitability conditions are often derived directly from data, an alternative is that the rules governing habitat suitability are derived from the literature based on published information about suitable conditions for particular species. An example of this latter approach is D-eco impact which Deltares has developed for a number of species, in particular filter feeding benthic invertebrates. The planned models for fish, seabirds, marine mammals and fishers are examples of statistical habitat suitability models driven by empirical observations.

Both model types can be used to create habitat suitability maps when they are used to calculate local habitat suitability across a map, based on the relevant prevailing local conditions. This can also be conducted along scenario studies, for example for climate change or area closure to fishery. This allows us to study how particular scenarios affect habitat suitability for species or species groups across space and time.

A limitation of habitat suitability maps is that they are built on information of species presence or abundance, with the assumption that this is entirely driven by habitat quality. There could be many constraints that limit the validity of this assumption, such as migration barriers (good locations cannot easily be reached), conditions that were different in the past (individuals have not yet 'grown into' the newly suitable area), or an area of very good conditions outside the study area (conditions in the study area are fine, but they are even better elsewhere). These limitations do not invalidate the use of habitat suitability models entirely, but they do require care in how they are used and how their results are interpreted. Here, we see them as tools to generate an estimate of the potential spatial distribution of non-spatial model output.

3.4.8.1 D-eco impact

At Deltares the D Eco Impact software is designed for habitat suitability analyses. It has native couplings to D Flow-FM and D Water quality, but can also read input data on environmental variables from generic formats, such as NetCDF files. This approach calculates a habitat suitability index between 0 and 1 to indicate to what extent environmental conditions in a certain place and time are suitable for the occurrence of a certain species or species group. The habitat suitability is typically calculated through a combination (multiplication or minimum rule) of suitability indices (between 0 and 1) for a range of relevant environmental variables. Most often these are static maps based on model results, bathymetry maps or satellite data. The indices can be calculated with different types of functions, such as block functions (crisp thresholds), linear optimum functions or more complex relations between an environmental variable and species abundance.

D-Eco Impact computes the spatial ecological impact assessment based on the relevant variables provided in a data cube and the ecological criteria (knowledge rules or functions) provided through the input file. Examples of variables that can be provided in the data cube are temperature, water depth, nutrient concentration, or sediment classes. This data can originate from expert knowledge, field measurements,

satellite imagery or model results. This data sources first need to be converted to a single data cube. In this data cube all variables are provided on the same spatial resolution, but the temporal resolution can vary in between variables.

D-Eco Impact:

- Operates on all relevant spatial or temporal resolutions scales (small scale, local, global, short term, long term).
- Allows for a flexible spatial schematization (point, polygon, grid mesh).
- Is expandable due to the code is written in Python and is provided open source.
- Ease of use by operating through and input file or as a python library.
- Can be connected to multiple modelling software output as long as this follows the international standard for the UGRID NetCDF format (e.g. Delft-FM 2D3D, Delft3D 4, wflow, iMOD).
- Adheres to the Interoperable and Reproduceable concepts of FAIR data processing, due to version numbering, the sharing of data through data cubes (UGRID NetCDF) and the input configuration (YAML).

D-Eco-impact models are already available for the following reef building species: flat oyster, northern horse mussel, Sabellaria and Lanice.

3.4.8.2 Statistical habitat suitability models

WMR has developed a number of statistical habitat models based on the annual surveys it conducts for fish species. There are also recent models available for selected seabirds, as well as for fishing activity. Habitat suitability models for marine mammals are also available, both in house (WMR) as well as through international collaborations. While there are basic versions of these models available, they are of varying quality and work will be needed to improve them in order to use them in the proposed model studies.

Statistical models are already available for the ocean quahog and sand eel.

In addition to the traditional statistical habitat suitability models, machine learning techniques, such as using "Random Forest" algorithms can be very powerful, provided that the underlying datasets are sufficiently large. The random forest algorithm splits the dataset in subsets. A random forest is an ensemble of decision trees that are combined to produce a single result. Decision trees are a category of algorithms that can be used for tasks such as regression and classification. These have been applied by Deltares for several habitat suitability studies, using spatially explicit data on presence / absence and maps of abiotic and biotic conditions.

Table 1. Model instruments emerging from model trains described for the proposed studies and the ecosystem components they relate to, sorted by model type. See main text for details.

Model type	Number	Model name	1. Lower trophic aquaculture	2. Integral climate change	3. fish, hard substrate, turbines	4. Larval fish and climate change	5. Changes in bottom fishing	6. OWF on seabirds and marine mammals	Hydrodynamics	Sediment	Light	Nutrients	Macrophytes	Phytoplankton	Zooplankton	Benthos	Demersal fish	Pelagic fish	Birds	Marine mammals	Fishers
Physical models	1.1	Delft 3D D-flow FM	x	x		x	x	x	x												
	1.2	GETM	x	x	x	x	x	x	x												
	1.3	Particle tracking module				x									x	x	x	x			
Biogeochemical models	2.1	D-water quality	x	x		x	x	x		x	x	x	x	x		x					
	2.2	ERSEM	x	x	x	x	x	x		x	x	x	x	x	x	x					
	2.3	DEMONS	x	x			x	x			x	x		x	x	x					
Higher trophic ecosystem and/or community models	3.1	benthos community model			x		x	x								x					
	3.2	Fish community model	x	x			x	x									x	x			
	3.3	OSMOSE					x										x	x			x
	3.4	Fishery management simulation					x														x
Single-species higher trophic level models	4.1	Fish species specific population models		x	x	x											x	x			
	4.2	population models seabirds		x				x											x		
	4.3	population models marine mammals		x				x												x	
Particle tracking models with behaviour	5.1	D-PART				x									x		x	x			
	5.2	GITM				x									x		x	x			
Agent based simulation models	6.1	Agent based models seabirds						x											x		
	6.2	Agent based models marine mammals						x												x	
	6.3	Agent based model fishers			x		x	x													x
Habitat suitability models	7.1	D-eco impact	x	x			x	x								x	x				
	7.2	statistical habitat suitability models		x	x		x	x									x	x	x	x	x

3.4.9 Model coupling

An individual model can never cover the entire marine ecosystem including human activities on all spatial, temporal, and process scales. Models such as the ATLANTIS model that do cover the entire marine ecosystem, including fishing and fishing-related socio-economics, (<https://research.csiro.au/atlantis/>) inevitably have to accept a coarser resolution in space, time, or process detail. Instead of trying to capture the whole ecosystem within one universal model, models focussing on different parts of the ecosystem can be made to work together. Their coupling facilitates information flow between the models. For instance, a lower trophic level model can simulate zooplankton concentrations, that could be used as a food source for a fish population model. Or a hydrodynamics model can provide flow fields to a particle tracking model. When building our model trains, we will inevitably have to couple models. This section gives an introduction to the potential types of coupling and some of the issues related to each.

3.4.9.1 Offline and online coupling

Broadly speaking, there are two main kinds of coupling: offline and online coupling. For offline coupling, models are run separately and in serial, and each model provides input to the next through information stored in one or more data files. With online coupling, models are typically run in parallel in lock-step, exchanging information at regular intervals directly through the computer memory.

Offline coupling is the simplest form of coupling, and hence the easiest to achieve. Each model in the sequence is run separately, with only minimal changes. The only requirement is that output from one model is in a form which can be used as input for the next model. This could be a manual process, or it can be automated (scripted). The biggest drawback of offline coupling is that feedback processes between models cannot be included directly. Indirect inclusion of feedback processes might be considered through iterative approaches. For instance, if a lower trophic level model is used to provide zooplankton as food for a fish model, the zooplankton mortality in the lower trophic model could be adapted depending on the amount consumed by fish in the higher trophic model, and both models could be run several times until the results converge. However, if the models are large and convergence is slow, this approach becomes impractical. Hence, offline coupling is most effective when feedback processes can be ignored.

With online coupling, feedback processes are automatically incorporated. To achieve this the models have to run on the same computing system, share some of the computer memory, and be subject to a joint time stepping procedure. Depending on the used protocol, the models even have to be written in the same programming language. This is obviously more complicated to achieve than offline coupling. Online coupling is easiest to achieve if the models share a common representation of space and time. These requirements mean that online coupling is not feasible for all potential combinations of models. Online coupling can be made somewhat easier by using generic couplers, such as FABM (Bruggeman & Bolding, 2014; <https://github.com/fabm-model/fabm>) or interfaces such as the 'Basic Model Interface' (<https://csdms.colorado.edu/wiki/BMI>) and OASIS (Craig et al., 2017; <https://oasis.cerfacs.fr/en/home/>). These use standard protocols for data sharing and time stepping. Using such generic couplers still requires modifications to the individual model codes that can be substantial, but for some models these have already been built in.

An alternative option which can be considered an indirect way to couple models is to use one model to derive parameterisations for use in another model. This is most similar to offline coupling, but instead of directly using output from one model as input in another, the output of one model is used to determine the shape of certain relationships (for instance dose-effect curves) which can be used in another model.

3.4.9.2 Match and mismatch

Coupling models is easiest if they match seamlessly (in spatial scale and domain, time step, units, etc). However, in reality, this is hardly ever the case as different models usually have different histories and purposes. Two models may both include some of the same processes, for instance a lower trophic level model and a higher trophic level model may both include zooplankton, but be implemented in different ways. Or two models may not share the same 'currency', for example if one is based on conservation of carbon and the other on conservation of nitrogen and phosphorus. In such cases additional effort and the application of assumptions is required to make models work together.

Models may also not share the same resolution in space and time. For instance, many biogeochemical models have high spatial resolution, while most fish stock assessment models work on a basin scale. Coupling these would require radical spatial averaging to transfer information from a biogeochemical model to a stock assessment model, or a very strong assumptions to feed information back as spatially resolved fields. Alternatively, one model may work with a time step of seconds, while the other calculates annual changes.

Such matches and mismatches affect the potential for coupling: for good matches, online coupling is possible, but as the level of matching decreases, offline coupling may turn out to be the only feasible option. For the construction of our model trains, a realistic assessment of the similarities among models and a vision on how to solve inevitable issues is essential. For new couplings, we will preferentially use generic methods, or design a common method if that does not exist (e.g. adopt a common intermediate file format for offline coupling with associated conversion scripts or re-designed I/O routines). Generic couplers will result in more possible model coupling functionality, but their use also requires much greater effort than a case-by-case solution. The decision what to use cannot be taken beforehand.

4 Work plan

4.1 Approach

This is a long research project, with many dependencies. A lot of the required work will only become clear once preceding steps are completed. In addition, we expect some of the work required for this project to emerge from other research, outside this project or even outside MONS or Wozep. This makes it very challenging to map out all the work required in this project beforehand. Therefore, we take a stepwise approach, where we define a longlist of actions required to obtain high-quality model instruments for the studies described in Chapter 3. From this longlist we then prioritize actions to tackle in the first year, based on the wish to develop first versions of working model trains by the end of year 1.

While we cannot guarantee that this goal (a working model train for each of the six defined studies by the end of year 1) can be achieved, setting it ensures that we focus on the most relevant obstacles. The risk of this approach is that we are too opportunistic, which could jeopardize the quality of the final model trains. To prevent this, we will also reserve time to discuss and plan more structural high-quality solutions, which can then be implemented later on in the project.

We foresee an annual process where the consortium, in collaboration with the client, determines the focus and actions for each coming year. The section below serves as a starting point for these discussions, but will need to be updated each year. It is hence meant as the starting point of an evolving document. Other important sources of input for these updates (and the annual selection of actions) are shifting priorities in policymaking, results from our work in this project, other MONS/Wozep research, as well as scientific developments elsewhere.

By taking this approach, we implement a cycle of continuous improvement, but also ensure that we have actual results early on in the project. In this way we balance the provision of timely and relevant results against scientific rigour and quality, and make sure that we can adapt to shifts in research and policy priorities during the project. Still, the overall model train framework as shown in Figure 1 is generic enough to be accommodate different types of model studies. So, it will likely be appropriate, even if the focus of policy priorities shift over time.

Despite the focus on the six example model studies, it is important to reiterate that these can also be subject to change. They are all marked as highly relevant currently, but their relevance is also subject to shifts in science and policy priorities. This could lead to revision or removal over time, or the addition of new studies of higher priority.

The model trains required for the six model studies show many overlaps. Therefore, we aim to develop generic technical solutions that meet the requirements posed by the six model studies. We will work in parallel on the six model studies and the development of a generic toolbox, to make sure that: 1) we check the suitability of the generic solutions for the six types of studies and 2) we have first prototypes for each type of research question already in the first year. These may first be based on existing model components and coupling methods that can be implemented most easily ('low hanging fruit'). In later years these can be generalized or developed further to enable flexible combinations of model components and cross validation of approaches. The cross validation of different combinations of model components is expected to deepen our understanding of the ecosystem and the added value of complex approaches over simplified approaches. It will also help to quantify uncertainties in model approaches. The process and actions to work towards more generically applicable tools is outlined below in paragraph 4.2.7.

4.2 Priority actions

4.2.1 Ecosystem effects of lower trophic aquaculture

Strategy:

At present there are a few small-scale trials with offshore aquaculture, but no significant commercial cultivation. Work in projects such as ProSeaweed have indicated that there are likely limits to upscaling LTA due to critical limits on ecological carrying capacity. This may or may not limit the business case for offshore aquaculture. Our aim in this project is to quantify the potential ecological impact and yield of different intensities of such aquaculture. This can support future permitting and business plans for aquaculture activities. This research question was not prioritised at the stakeholder workshop in July 2024, so we will spend limited effort on it, using currently available tools. Future work on this topic will strongly depend on the growing insights within MONS and other projects on the viability of the business case for offshore LTA.

First year actions:

- Update model simulations done by Deltares for EU-projects FutureMares and ULTFARMS and the ProSeaWeed project with the latest versions of D-FLOW-FM and D-WAQ.
- Collaborate with PhD project led by Jaap van der Meer on this subject, using the DEMONS model, towards a joint evaluation of feasibility and potential impacts of lower trophic aquaculture in offshore wind farms in the North Sea.
- Collaborate with Wozep-funded Ecosystem effects of offshore wind project and MONS ID 20 and 30 for fish models.

Later steps:

- Continue to collaborate with the PhD student of Jaap van der Meer towards a joint evaluation of feasibility and potential impacts of lower trophic aquaculture in offshore wind farms in the North Sea.
- Cross validation of Deltares seaweed module with the WMR model using a DEB approach to enhance understanding, for quality control and better understanding of uncertainties.
- Include Deltares seaweed module in standard release of D-WAQ after further testing, quality control and cross validation with DEMONS approach.

4.2.2 Integral effects of climate change

Strategy:

The impact of climate change on the ecosystem will be simulated by running climate change scenarios with hydrodynamic models and biogeochemical models. Model results from meteorological models (for example by KNMI and CMCC) will be used as input for the hydrodynamic and biogeochemical models. These include all meteorological forcing and atmospheric deposition and river discharges (based on changes in precipitation on land). The results of the hydrodynamic and biochemical models will be used as input for other model components, such as the particle tracking model, fish community models and habitat suitability models so assess potential impacts on higher trophic levels and commercial fish species. In the hydrodynamic and biogeochemical models the combined impacts of climate change and different scenarios of wind farm and MPA developments can be assessed. This work is connected with that under the NO-REGRETS proposal tasks 3.1 (Hydrodynamics and sediments) and tasks 7.2 (Climate Change), and will benefit greatly from funding of that proposal.

Current state: technical solutions for coupling the DFLOW-FM model with the climate models by CMCC are available. For the GETM model the scripts to convert the output from climate models to GETM input still need to be created.

First year actions:

- Run climate change scenarios with D-FLOW-FM and D-WAQ and create input files for model tools for higher trophic levels. This enables the first assessments of climate change impacts on some prioritised fish species which will give a first estimate of potential consequences for and seabird species and marine mammals which feed on them.

Later steps:

- develop coupling scripts for GETM with CMCC and run parallel climate change scenarios with GETM for cross validation with the D-FLOW-FM scenarios and for quantification of uncertainties.
- Simulate climate change impacts on some fish and seabird and marine mammal species with GETM input.
- Evaluate added value of linking to KNMI climate change model outputs, with more spatial resolution but smaller model domain.
- Extend climate change scenarios for more species and species groups of higher trophic levels.

4.2.3 The food web consequences of large-scale hard substrate addition

Strategy:

In this study we will couple dynamics at higher trophic levels in the food web as well as behavioural dynamics of fishers to the lower trophic levels. These couplings are the challenging component of this study, because we will need translations of model output variables in different units and dimensions. Output from lower trophic level models will be summarized (spatially and temporally) and initially provide ranges of bottom up resource productivity levels to inform the potential population growth of higher trophic levels (first model train). In the spatially explicit branch of the study (second model train), we will keep the spatial dimension and higher temporal resolution of the model output from lower trophic levels and connect this to the species-specific, spatially structured models for fish populations.

In the first year, the existing D-WAQ model will be expanded by including mussels on pillars (as part of existing other projects). The development of couplings between hydrodynamic and lower-trophic level models as targeted in the other initial studies links here directly (themes 1-6). We will first prioritize the non-dynamic coupling of the benthic community model output to the productivity of fish resources. The single-species population model for fish will be parameterized based on the choice for a focal species (however parameterization, including temperature and food-dependence for cod *Gadus morhua* exists). The first year will therefore focus on the range of input in the fish population model and the variation in possible population abundance and structure as output.

This setup will allow us to study how the (large-scale) addition of hard substrate affects the benthic community (its dynamics and structure). Moreover we will study the consequences of changes in the benthic community for the bigger food web. The research questions in this study are:

1. Does large-scale addition of hard substrate affect the benthic community productivity? And in which direction?
2. How do different benthic resource productivity levels result in different fish population abundance and type of regulation (bottlenecks)?
3. How does large-scale addition of hard substrate affect the regional distribution of fish species? (Spatial model train)
4. What are the effects of changes in regional fish species distributions on the behaviour of fishers?

Later steps:

In later years the coupling between higher trophic level models and the hydrodynamic and biogeochemical models will be extended to a larger fish species community and improved where necessary (congruently with theme 5). The outcomes in the first year will be leading for improvements and further analyses of the fish population and community models.

The model train addressing above research questions 3 and 4 relies on existing frameworks to model the spatial distribution of fish species. However, the agent-based model for fishers and how to couple this element are new and will be developed in concert with MONS ID 28 and 29.

Further challenges to be addressed post first year developments include improving benthic-pelagic coupling of nutrient and carbon flows in the D-WAQ approach. Currently only mussels on pillars are available, but the impact of benthic filter feeders is so far ignored. We continue to develop the fish species-specific and

community models to test the use of input variables from lower trophic levels and we aim for accounting for such input variables in the most dynamic way possible.

Parts of this study's goals overlap with other initial studies: Lower trophic level modelling is crucial to all studies and we will collaborate through this ecological level. Coupling lower-trophic level models to higher trophic levels will be implemented for plaice in the study on Fish life cycle connectivity. We will collaborate on the development of the coupling of this fish population model with the lower trophic level implementations. All of the higher trophic level models indicated for this study overlap with the models needed in study 5 Changes in bottom fishing due to area closures, therefore, we will collaborate on the development of the fish community model (early version).

4.2.4 Fish life cycle connectivity through the larval stage

Larval survival and settling is commonly understood to determine year-class strength for commercial fish species (e.g. Van der Veer et al, 2024) and hence is a driver for population dynamics and potential feedbacks on spawning. This likely also holds for other species. Larval survival and settling depends on connectivity between spawning and nursery grounds through ocean currents and larval behaviour, in combination with food availability, growth, and mortality through e.g. starvation, predation and disease. Larval connectivity is typically studied using Lagrangian particle tracking models (e.g. Van der Molen et al., 2018). Despite being adequate first indicators of connectivity, such models include only simple parameterisations for growth and mortality, and full life cycle feedbacks through adult population dynamics are not included. More realistic inclusion of growth using spatially and temporally varying food fields from biogeochemical models is possible, as was done in a study focussing specifically on the comb jellyfish *Mnemiopsis leidyi* (Van der Molen et al 2015). More generic approaches are possible by using Dynamic Energy Budget models (e.g. Flores-Valiente et al, 2023) to calculate the development of particles representing larvae. Using such combined models would improve our ability to simulate and understand the effects of larval-stage food availability on recruitment and year-class strength, and how this responds to climate change and introduction of offshore wind farms (in addition to potential changes in ocean currents).

Including adult population dynamics models will allow improved understanding of climate and OWF interactions with the full life cycle. There are currently no integrated initiatives to push these developments, and existing particle tracking models are typically used as-is (e.g., as planned in the OR ELSE project). Moreover, the particle tracking models used by NIOZ and Deltares each have specific capabilities and currently work only with their own hydrodynamical models preventing interoperability. A modest development effort is included in the recently awarded NO REGRETS project (Task 5.1) to include temperature-dependent growth formulations of the GITM model in D-PART. This theme aims to robustly address these gaps and gain improved knowledge and capability to simulate and understand effects on human-induced environmental changes on marine species life cycles. Where possible, we will use field observations and knowledge generated using new zooplankton imaging observations carried out in the MONS ID 14 en 15 and NO REGRETS projects. The results of changing recruitment dynamics and year class strength will also have ramifications for fishery. At the same time, fishery affects the abundance and size distribution of the fish stock. Once available (expected in 2026 and further), we will use models for fish and fishery developed in MONS IDs 20, 28, 29 and 30 to study this interaction.

Strategy:

The aim is to set up combinations of models that can address the spatial and temporal sensitivity of survival, condition, and connectivity between spawning and nursery areas of the larval stages of selected fish species to climate change and offshore wind farms, and how does this affect fish populations. Deltares and NIOZ have particle tracking models that include individual development and behaviour, but these can be improved substantially by adding a Dynamic Energy Budget (DEB) approach, with which WMR has experience. Also, these models can provide important connectivity and larval survival information that can be used in species-specific HTL models for fish to investigate effects on population dynamics. We will develop the required methods for NIOZ/WMR software, and then roll it out to Deltares software to facilitate joint testing and intercomparison. The development will be carried out using a step-wise approach, starting with constructing full life cycle model trains using existing components before implementing improvements and refinements.

We envisage that choices on how to proceed will be made depending on the results and insights obtained in previous steps. Implementation of model code changes will be carried out by the institutes maintaining the individual codes, while aiming for improved inter-operability and transparency.

First year actions:

We will start with setting up a test case for a species of choice (likely plaice, *Pleuronectes platessa* L.) with the existing particle tracking models, using existing data and comparing with earlier studies (e.g., Hufnagl et al., 2013) (**Month 1-6**). The larval development of plaice is well-known, and the larval connectivity is likely sensitive to climate change because plaice spawn at a specific water temperature, so global warming may result in earlier spawning or more northerly spawning, both of which may lead to different transport trajectories and food availability. Then we will design and implement an offline coupling to provide connectivity information to the species-specific HTL model for fish (**Month 5-7**), resulting in two model trains (one at NIOZ using GETM-GITM and one at Deltares using Delft3d-D-Part). With these, we will run a historic reference scenario and carry out an intercomparison of results of the two model trains, and address the research questions (see 3.2.4) for the first time (**Month 8-11**). The intercomparison between the results of the two model trains will provide a measure for uncertainty, as well as potential points for improvement. Finally, we will identify and formulate an online coupling method to couple the DEB model to both particle tracking models (**Month 11-12**). At the end of the first year we will make a plan for the next year (**Month 12**).

Later steps:

Subsequent steps include implementing the couplings to the DEB model in both particle tracking models (this may require translation of the DEB model into Fortran) (**Year 2**), testing using synthetic food fields and then including food fields from the biogeochemical LTL models (**Year 2-3**). The resulting model trains can then be used to analyse and identify potential bottlenecks in larval stage development and/or connectivity related to dynamic food availability, as well as effects on and feedbacks from the dynamics of the adult populations (**Year 3-4**). Finally, one or both of the model trains can be applied to climate change and wind farm scenario runs, and other species of interest (**Year 4-6**).

4.2.5 Changes in bottom fishing and its ecosystem effects as a result of area closures (MPA and OWF)

A crucial issue in this study is related to how the complex dynamic interaction between fish, benthic fish food and fisher behaviour will interact in response to area closures. The fisher behaviour is part of the MONS ID 28 and 29 projects, which are currently ongoing. We will wait for the first outcomes of those before implementing complex fisher models. The MONS ID 20 and 30 projects, which will start in early 2025, will develop fish community models and species-specific models which can be used to assess the behavioural response of fish. In the initial phase of this project, we will focus on adapting the existing WMR benthos functional model so that it can handle area closures, can be coupled to the fish community model, and can be forced using primary productivity timeseries which are output from biogeochemical models.

Strategy:

The aim is to set up a relatively coarse functional group based model of the fish community, which can be used to study meaningful questions, at a high level of abstraction, already in the first year (this work is part of MONS ID 20 and 30). The results of this work (and that in other developments within MONS) will then be used to guide future additions and refinement of the model suite. This includes connecting the fish community models to other food web component models.

First year actions:

In the first year, we will extend the existing WMR benthos functional community model to include areas that are open and closed to fishing. In the simultaneous MONS ID 20 and 30 projects, we will also formulate a first version of a functional fish community model, where fish feed on benthos, detritus, planktonic food and/or other fish. This first version will focus on the benthic soft-sediment fish community. We will then couple these two models dynamically, so that fish feeding is removed from the relevant benthic groups. To do this, we will assume the closed areas are highly fragmented, which means that fish can move between open and closed areas very quickly. This way, we do not (yet) need to distribute the fish over the open and

closed areas. Fishing will be included in the open areas. It will be implemented in a more dynamic way, with effort determined by a combination of quota and fish abundance. There will be no explicit spatial structure in these models, other than a distinction between open and closed areas for the benthos.

This setup will allow us to study how quota-based fishery works out when areas of the seabed are closed to fishing. The research questions in this study are:

1. How is seafloor recovery in closed areas related to seafloor effects of increased fishing effort in the areas which remain open?
2. What are the consequences of such closures for the efficiency of the fishery (as expressed in catch per unit effort), and how does efficiency trade off against seafloor recovery in closed areas?
3. How does the answer to 1. and 2. above depend on fishing quota?

We will also make first steps towards statistical habitat distribution maps for fish.

The work on the fish community model and the fishery management model, as well as the fish habitat distribution maps, are conducted within a separate project (MONS ID 20 and 30). The work on extending the benthos community model and the coupling to the fish model are budgeted within the current project.

Later steps:

In the following years, we will implement a distinction between open and closed areas in the fish community model. The fish community model may also be extended to include more functional groups and/or life history variation. We will also implement a way to take into account climate warming and differences between closed areas for nature conservation and closed areas for offshore wind farms. We will include offline coupling to models of phyto- and zooplankton so that scenarios of OWF effects on productivity can be assessed for their effects on the fish community and the fishery on it. The fish community model will also be coupled (on- or offline) to models of top predators (seabirds and marine mammals), which enables studies of indirect interactions between predators and fishery.

4.2.6 Integral effects of offshore wind development on seabirds and marine mammals

The most challenging aspect concerning the study of integral effects of offshore wind development on marine mammals and seabirds will be linking changes in fish distribution and productivity to seabird and marine mammal distribution, fitness and population abundance.

Within the MONS/ Wozep project Deltares has made model simulations to estimate the impact of turbulence induced by offshore wind farms on primary production and benthic filter feeders. Further developments are ongoing to also include the competition between zooplankton and benthic filter feeders in these model simulations. Model development for seal species by WMR is included in the MONS research plan for marine mammals (Siemensma and Asjes, 2023) as well. And a multi-annual MONS/Wozep project on modelling seabird populations is just starting up. For these taxa, we will first allow model development in those projects, and connect them into the model trains in later years. The initial focus here will be on harbour porpoises, which are by far the most abundant cetaceans in the North Sea (Hammond et al 2021). For this species, no comparable modeling projects are planned, but several important building blocks are already available. The approach we plan to develop for harbour porpoises can be used later to also connect seabirds and seals, and is hence of generic value to the model train project.

Strategy:

Ultimately, the aim is to develop an integrated suite of model tools to estimate the impact of offshore wind farm development on harbour porpoises and seabirds. In this integrated approach the direct impacts of wind farms on currents, mixing and primary and secondary production will be translated to impacts on higher trophic levels. The models for higher trophic levels will consist of statistical habitat suitability models which can be used to predict spatial distribution, an agent-based simulation model to translate environmental changes and anthropogenic disturbances to population-level parameters, and a physiologically structured population model to study the population impact of the (trade-offs between the) NSA transitions.

First year actions:

The focus in the first year will be to couple the existing model for harbour porpoise or a seabird to the hydrodynamic and biogeochemical models developed in MONS/Wozep, as a first demonstration of the integrated ecosystem approach. Currently, agent-based models exist for harbour porpoises that can be used to link prey intake to vital rates (probability of surviving and producing and weaning calves), and hence, population growth (Chuzindska et al. 2024). However, within these models, the relationship between prey abundance and prey feeding (i.e. the functional response) is highly simplified. Therefore, we will refine the relationship between harbour porpoises and their main prey species in the existing model. Multi-species functional response estimates for harbour porpoises in this area are already available (Ransijn et al. 2021) and these will serve as a starting point for including more realistic estimates of energy intake in the existing bioenergetic models. By combining prey availability and prey requirements from the energetics model this framework will then be used to derive a first estimate of the potential carrying capacity of the harbour porpoise population in the (Southern) North Sea.

Later steps:

In later years the coupling between higher trophic level models and the hydrodynamic and biogeochemical models will be extended to more species and improved where necessary. Based on the first year results the HTL models will also be refined in an iterative approach. A challenge towards including an explicit spatial component will be to include a realistic movement model for individual porpoises. This spatially-explicit version could then be used in combination with habitat suitability maps when these become available from other MONS projects (e.g. MONS research ID 159). Other opportunities for model improvement are incorporating temperature-dependence of metabolic processes (e.g. maintenance costs, thermoregulation) to be able to forecast effects of climate change and better represent seasonal patterns of energy expenditure.

4.2.7 Development of generic toolbox

Strategy:

At the start of the project some combinations of model components are already technically feasible where other combinations are not yet possible. We start building model trains for the six types of questions based on the combinations of model components that are already existing. These may not be sufficient to address all ecosystem interactions for all six questions. We will start developing technical solutions supporting these missing links, making sure that these technical solutions are as much as possible generic for different model components and not specific to individual combinations of model components.

First year actions:

Based on the initial model trains proposed for the six research questions we will identify commonalities in required technical solutions and start developing the highest priority links. The easiest way to couple model components is through an offline (one-way) coupling, in a common data format. So, this is expected as a first step. Next the information from model components with a high spatial resolution (hydrodynamic models and biogeochemical models) needs to be aggregated in space and time to enable the use of their model output as input for model components with lower spatial resolution (such as fish population or bird population models).

Later steps:

More complicated links between model components are links that are interactive, so where data flows are exchanged between model components in two directions. Also links between different types of hydrodynamic models and biogeochemical models require more complex technical solutions. An example of such a link is the combined use of D-FLOW-FM with ERSEM, or GETM with D-Waq.

5 Interaction and advice

Apart from model development, coupling and application, this project has an important advice and evaluation component, consisting of three main tasks:

- a. Advise on content and connections of other MONS and Wozep research projects which are related to the model toolbox, either because they receive input or because they deliver components (data, knowledge) to components of the model toolbox.
- b. The continuous critical evaluation of the model toolbox as it is being developed, in order to ensure its quality and applicability, and advise on adjustments where needed.
- c. Further development of scenarios which are relevant studies to apply the model toolbox. These will be centered around the trade-offs between the three NZA transitions, but their details will depend on shifting policy priorities as well as novel scientific insights as the project develops.

This advisory work is expected to last throughout the MONS program, up to and including 2030. The advisory work will be carried out in an iterative annual cycle. This will be the responsibility of an advisory board which will consist of representatives of each of the three institutes forming the consortium of this assignment.

The proposed cycle starts on the annual MONS/Wozep day, where the results of all projects are presented annually. These presentations will include those of the model development and application components of this project. After the annual presentation day, the advisory board will produce a brief document with

- reflections on the presented developments and results, with special emphasis on the uncertainties in the models and what those mean for the outcomes,
- potential consequences for the planned model toolbox development in the coming year, and
- recommendations for other related MONS/Wozep projects planned in the year ahead,
- summarize results and developments in other relevant (non-MONS/Wozep) projects that the main participant or other project team members are involved in and highlight potential opportunities for the MONS/Wozep model toolbox to benefit from those developments.
- Based on the above, a concise year plan will be formulated describing the goals and actions for the coming year within the scope of this project.

These points will be presented to and discussed with representatives of MONS/Wozep at a separate (half- or full day) meeting after the MONS/Wozep day. This meeting can also include more in depth presentations of model results where necessary. After one round of comments a final year plan for the following 12 months for this project will be published. The approval of this year plan will be the basis for continuation of the project, except when other agreements are made for specific project components.

The year plan can also include suggestions for workshops and/or discussion meetings with (members of) the NSA stakeholder group.

To monitor the progress in the work plan and to be able to adapt to changes in the policy and/or research priorities as they occur, quarterly progress meetings between the advisory board and representatives of MONS/Wozep will be organized in the quarters where there is no year plan meeting. Informal discussions between these parties are expected to be initiated by either side whenever they are deemed relevant.

A prerequisite for the advisory board to carry out this assignment is that it is well-informed about the plans for research as part of the MONS and Wozep projects. The relevance of the advice would be strengthened if the board would receive information regarding planned new research projects before the annual MONS/Wozep day.

6 Quality Assurance

Wageningen Marine Research utilises an ISO 9001:2015 certified quality management system. The organisation has been certified since 27 February 2001. The certification was issued by DNV.

References

- Andersen, K.H., Jacobsen, N.S., Farnsworth, K.D. 2016. The theoretical foundations for size spectrum models of fish communities. *Canadian Journal of Fisheries and Aquatic Sciences*. 73(4): 575-588. <https://doi.org/10.1139/cjfas-2015-0230>
- Baretta, J.W., Ebenhöf, W., and Ruardij, P. 1995. The European Regional Seas Ecosystem Model, a complex marine ecosystem model, *J. Sea Res.*, 33, 233–246.
- Beier, U., van Oostenbrugge, H., Hin, V., van Kooten, T., Quirijns, F., Salz, P., van de Wolfshaar, K., Klok, A., Melis, E., Taal, K., Hamon, K., & van der Valk, O. 2023. Ecologische en sociaaleconomische effecten van alternatieve beheersscenario's voor de garnalenvisserij. *Wageningen Marine Research rapport; No. C053/23*. Wageningen Marine Research. <https://doi.org/10.18174/637047>
- Blauw, A. N., Los, H. F., Bokhorst, M., & Erftemeijer, P. L. (2009). GEM: a generic ecological model for estuaries and coastal waters. *Hydrobiologia*, 618, 175-198.
- Bruggeman, J., Bolding, K. 2014. A general framework for aquatic biogeochemical models. *Environmental Modelling & Software* 61, 249-265. <https://doi.org/10.1016/j.envsoft.2014.04.002>
- Burchard, H., Bolding, K. 2002. GETM – A General Estuarine Transport Model. Scientific Documentation, *Tech. Rep. EUR 20253 EN*, European Commission.
- Burchard, H., Bolding, K., Villareal, M.R. 1999. GOTM—a general ocean turbulence model. Theory, applications and test cases. *Tech. Rep. EUR 18745 EN*, European Commission.
- Butenschön, M., Clark, J., Aldridge, J.N., Allen, J.I., Artioli, Y., Blackford, J., Bruggeman, J., Cazenave, P., Ciavatta, S., Kay, S., Lessin, G., van Leeuwen, S., van der Molen, J., de Mora, L., Polimene, L., Sailley, S., Stephens, N., and Torres, R. 2016, ERSEM 15.06: a generic model for marine biogeochemistry and the ecosystem dynamics of the lower trophic levels. *Geoscientific Model Development* 9, 1293-1339, doi:10.5194/gmd-9-1293-2016.
- Chudzinska, M., Nabe-Nielsen, J., Smout, S., Aarts, G., Brasseur, S., Graham, I., Thompson, P., McConnell, B. 2021. AgentSeal: Agent-based model describing movement of marine central-place foragers. *Ecological Modelling*, 440, Article 109397. <https://doi.org/10.1016/j.ecolmodel.2020.109397>
- Chudzińska, M., Klementisová, K., Booth, C., Harwood, J. 2024. Combining Bioenergetics and Movement Models to Improve Understanding of the Population Consequences of Disturbance. *Oikos*, e10123. <https://doi.org/10.1111/oik.10123>.
- Craig A., Valcke S., Coquart L., 2017. Development and performance of a new version of the OASIS coupler, OASIS3-MCT_3.0, *Geoscientific Model Development*, 10, pp. 3297-3308, doi: <https://doi.org/10.5194/gmd-10-3297-2017>
- De Roos, A. M., Persson, L. 2013. Population and community ecology of ontogenetic development. Princeton University Press, Princeton, New Jersey, USA.
- De Roos, A. M., Schellekens, T., Van Kooten, T., Van De Wolfshaar, K., Claessen, D., Persson, L. (2008). Simplifying a physiologically structured population model to a stage-structured biomass model. *Theoretical Population Biology*, 73(1), 47-62. <https://doi.org/10.1016/j.tpb.2007.09.004>
- Flores-Valiente, J., Lett, C., Colas, F., Pecquerie, L., Aguirre-Velarde, A., et al. (2023) Influence of combined temperature and food availability on Peruvian anchovy (*Engraulis ringens*) early life stages in the northern Humboldt Current system: A modelling approach. *Progress in Oceanography* 215, pp.103034.
- Hammond, P. S., Lacey, C., Gilles, A., Viquerat, S., Börjesson, P., Herr, H., Macleod, K., Ridoux, V., Santos, M. B., Scheidat, M., Tellmann, J., Vingada, J., Olen, N. 2021. Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys. In Sea Mammal Research Unit, University of St Andrews, UK.
- Hartvig, M., Andersen, K.H., Beyer, J.E., 2011. Food web framework for size-structured populations. *Journal of Theoretical Biology* 272 (1), 113-122
- Hin, V., Harwood, J., de Roos, A. M. 2019. Bio-energetic modeling of medium-sized cetaceans shows high sensitivity to disturbance in seasons of low resource supply. *Ecological Applications*, 29(5), e01903. <https://doi.org/10.1002/eap.1903>
- Hin, V., De Roos, A. M., Benoit-Bird, K. J., Claridge, D. E., DiMarzio, N., Durban, J. W., Falcone, E. A., Jacobson, E. K., Jones-Todd, C. M., Pirotta, E., Schorr, G. S., Thomas, L., Watwood, S., Harwood, J.

2023. Using individual-based bioenergetic models to predict the aggregate effects of disturbance on populations: A case study with beaked whales and Navy sonar. *PLoS ONE*, 18(8), e0290819. Article e0290819. <https://doi.org/10.1371/journal.pone.0290819>
- Hufnagl, M., Peck, M.A., Nash, R.D.M., Pohlmann, T., Rijnsdorp, A.D. (2013). Changes in potential North Sea spawning grounds of plaice (*Pleuronectes platessa* L.) based on early life stage connectivity to nursery habitats. *J Sea Res* 84: 26– 39
- Kooijman, S.A.L.M. 2010. Dynamic energy budget theory for metabolic organisation. 3rd Edition, Cambridge University Press, Cambridge.
- Lynam, C., Thorpe, R., van de Wolfshaar, K. E., Puts, M., Corrales, X., Romagnoni, G., Tsagarakis, K., Potier, M., Papantoniou, G., Halouani, G., Heath, M., Kempf, A., Taylor, M. Jacobsen, N. S., 2023. SEAWise Report on the effects of fishing on food webs and community diversity aimed at populating the MSFD Descriptor 4 and based on food web and end-to-end modelling. Technical University of Denmark. Online resource. <https://doi.org/10.11583/DTU.25158746.v1>
- Petrik, C. M., Stock, C. A., Andersen, K. H., van Denderen, P. D., Watson, J. R. 2019. Bottom-up drivers of global patterns of demersal, forage, and pelagic fishes. *Progress in Oceanography*, **176**, 102124. <https://doi.org/10.1016/j.pocean.2019.102124>
- Ransijn, J.M., Hammond, P.S., Leopold, M.F., Sveegaard, S., Smout, S.C. 2021. Integrating Disparate Datasets to Model the Functional Response of a Marine Predator: A Case Study of Harbour Porpoises in the Southern North Sea. *Ecology and Evolution* 11, 23:17458-70. <https://doi.org/10.1002/ece3.8380>
- Siemensma, M. & Asjes, J., Visie MONS zeezoodieren 2023. Uitwerking onderzoeksplan. 2024.
- Soudijn, F. H., van Donk, S., Leopold, M. F., van der Wal, J. T., Hin, V. (2022). *Cumulative population-level effects of habitat loss on seabirds 'Kader Ecologie en Cumulatie 4.0'*. (Wageningen Marine Research report; No. C007/22). Wageningen Marine Research. <https://doi.org/10.18174/565601>
- Soudijn, F. H., van Kooten, T., Slabbekoorn, H., & de Roos, A. M. (2020). Population-level effects of acoustic disturbance in Atlantic cod: a size-structured analysis based on energy budgets. *Proceedings. Biological sciences*, 287(1929). <https://doi.org/10.1098/rspb.2020.0490>
- van de Wolfshaar, K.E., van Denderen, P.D., Schellekens, T., van Kooten, T.. 2020. Food web feedbacks drive the response of benthic macrofauna to bottom trawling. *Fish Fish.*, 21, pp. 962-972.
- van de Wolfshaar, K. E., de Roos, A. M., & Persson, L. (2008). Population feedback after successful invasion leads to ecological suicide in seasonal environments. *Ecology*, 89(1), 259–268. <https://doi.org/10.1890/06-2058.1>
- Van De Wolfshaar, K. E., Daewel, U., Hjøllø, S. S., Troost, T. A., Kreuz, M., Pätsch, J., Ji, R. & Maar, M. 2021. Sensitivity of the fish community to different prey fields and importance of spatial-seasonal patterns. *Marine Ecology Progress Series*.680, p. 79-95
- Van Der Meer, J., Hin, V., Van Oort, P., & Van De Wolfshaar, K. E. (2022). A simple DEB-based ecosystem model. *Conservation Physiology*, 10(1), Article coac057. <https://doi.org/10.1093/conphys/coac057>
- Van der Molen, J., van Beek, J., Augustine, S., Vandensteenbrugge, L., van Walraven, L., Langenberg, J., van der Veer, H.W., Hostens, K., Robbens, J., Pitois, S., (2015). Modelling survival and connectivity of *Mnemiopsis leidyi* in the southern North Sea and Scheldt estuaries. *Ocean Sci.* 11, 405-424, 2015. doi:10.5194/os-11-405-2015
- Van der Molen, J., Ruardij, P., and Greenwood, N. (2017). A 3D SPM model for biogeochemical modelling, with application to the northwest European continental shelf. *Journal of Sea Research* 127, 63-81.
- Van der Molen, J., Ruardij, J., Mooney, K., Kerrison, P., O'Connor, N.E., Gorman, E., Timmermans, K., Wright, S., Kelly, M., Hughes, A.D., Capuzzo, E., 2018. Modelling potential production of macroalgae farms in UK and Dutch coastal waters. *Biogeosciences* 15, 1123-1147, DOI <https://doi.org/10.5194/bg-15-1123-2018>.
- Van der Molen, J., van Beek, J., Augustine, S., Vandensteenbrugge, L., van Walraven, L., Langenberg, J., van der Veer, H.W., Hostens, K., Robbens, J., Pitois, S., 2015. Modelling survival and connectivity of *Mnemiopsis leidyi* in the southern North Sea and Scheldt estuaries. *Ocean Sci.* 11, 405-424, 2015. doi:10.5194/os-11-405-2015
- Van der Molen, J., Garcia, L., Whomersley, P., Callaway, A., Posen, P., Hyder, K. (2018) Modelling connectivity of larval stages of sedentary marine communities between offshore structures in the North Sea. *Scientific Reports*, 8:14772. DOI:10.1038/s41598-018-32912-2
- Van der Veer, H.W., Witte, J.IJ., Flege, P., van der Molen, J., Poesz, S.S.H. (2024). Spatial and temporal variability in larval connectivity of North Sea plaice *Pleuronectes platessa* between spawning grounds and coastal European nurseries. *Marine Ecology Progress Series* 733, 111-127. <https://doi.org/10.3354/meps14552>

- van Kooten, T., Soudijn, F., Tulp, I., Chen, C., Benden, D., & Leopold, M. (2019). *The consequences of seabird habitat loss from offshore wind turbines, version 2: Displacement and population level effects in 5 selected species*. (Wageningen Marine Research report; No. C063/19). Wageningen Marine Research. <https://doi.org/10.18174/496173>
- van Leeuwen, S.M., van der Molen, J., Ruardij, P., Fernand, L., Jickells, T., (2013). Modelling the contribution of deep chlorophyll maxima to annual primary production in the North Sea. *Biogeochemistry*, 113, Issue 1 (2013), Page 137-152. DOI 10.1007/s10533-012-9704-5.
- van Leeuwen, A., Huss, M., Gårdmark, A., Casini, M., Vitale, F., Hjelm, J., Persson, L., & de Roos, A. M. (2013). Predators with multiple ontogenetic niche shifts have limited potential for population growth and top-down control of their prey. *The American naturalist*, 182(1), 53–66. <https://doi.org/10.1086/670614>
- Vichi, M., Pinardi, N., and Masina, S.: A generalized model of pelagic biogeochemistry for the global ocean ecosystem, Part I: Theory, *J. Marine Syst.*, 64, 89–109, 2007.

Justification

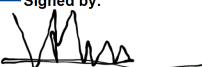
Report: C071/24

Project Number: 4316100367

The scientific quality of this report has been peer reviewed by a colleague scientist and a member of the Management Team of Wageningen Marine Research

Approved: Dr. V. Hin
Scientist

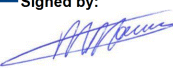
Signature:

Signed by:

79DC85A9E898445...

Date: 21 november 2024

Approved: Dr. A.M. Mouissie
Business Manager Projects

Signature:

Signed by:

291E7A4CA7DB419...

Date: 21 november 2024

Wageningen Marine Research
T +31 (0)317 48 70 00
E imares@wur.nl
www.wur.nl/marine-research

Visitors'address

- Ankerpark 27 1781 AG Den Helder
- Korringaweg 7, 4401 NT Yerseke
- Haringkade 1, 1976 CP IJmuiden



With knowledge, independent scientific research and advice, **Wageningen Marine Research** substantially contributes to more sustainable and more careful management, use and protection of natural riches in marine, coastal and freshwater areas.

The mission of Wageningen University & Research is "To explore the potential of nature to improve the quality of life". Under the banner Wageningen University & Research, Wageningen University and the specialised research institutes of the Wageningen Research Foundation have joined forces in contributing to finding solutions to important questions in the domain of healthy food and living environment. With its roughly 30 branches, 7,700 employees (7,000 fte), 2,500 PhD and EngD candidates, 13,100 students and over 150,000 participants to WUR's Life Long Learning, Wageningen University & Research is one of the leading organisations in its domain. The unique Wageningen approach lies in its integrated approach to issues and the collaboration between different disciplines.