European Commission

Marine Biodiversity Modelling Study

Independent Expert Report

Research and Innovation

Marine Biodiversity Modelling Study

European Commission
Directorate-General for Research and Innovation
Directorate B — Healthy Planet
Unit B.4 — Healthy Oceans & Seas
Contact Nicolas Segebarth
Email RTD-B4-ASSIST@ec.europa.eu
nicolas.segebarth@ec.europa.eu
RTD-PUBLICATIONS@ec.europa.eu
European Commission
B-1049 Brussels

Manuscript completed in November 2022
First edition

The information and views set out in this study are those of the authors and do not necessarily reflect the official opinion of the Commission. The Commission does not guarantee the accuracy of the data included in this study. Neither the Commission nor any person acting on the Commission's behalf may be held responsible for the use which may be made of the information contained therein.

PDF	ISBN 978-92-76-58698-2	doi:10.2777/213731	KI-03-22-114-EN-N

Luxembourg: Publications Office of the European Union, 2022

© European Union, 2022

Reuse is authorised provided the source is acknowledged and the original meaning or message of the document is not distorted. The European Commission shall not be liable for any consequence stemming from the reuse. The reuse policy of European Commission documents is implemented by Commission Decision 2011/833/EU of 12 December 2011 on the reuse of Commission documents (OJ L 330, 14.12.2011, p. 39).

For any use or reproduction of elements that are not owned by the European Union, permission may need to be sought directly from the respective rightholders.

Marine Biodiversity Modelling Study

Edited by

Fundación AZTI – AZTI Fundazioa

Guillem Chust (gchust@azti.es) – Project responsible
Xavier Corrales
Fernando González
Ernesto Villarino
Marina Chifflet
José A. Fernandes
Leire Ibaibarriaga
Ángel Borja
Martin Aranda
Eider Andonegui
Meritxel González
Xabier Irigoien
Dorleta García

MEMBER OF
BASQUE RESEARCH
& TECHNOLOGY ALLIANCE

2022 Directorate-General for Research and Innovation
Food, Bioeconomy, Natural Resources, Agriculture and Environment EN

Table of contents

EXECUTIVE SUMMARY

The European Commission tendered the study “Marine Biodiversity Modelling” [RTD/2021/MV/10] to pursue the identification and characterization of a subset of candidate biodiversity models that could contribute to the implementation of the European Digital Twin of the Ocean (EU DTO). The EU DTO will be an operational infrastructure for digital ocean services that aims to support decision-making capabilities by authorities to implement EU policies like the Marine Strategy Framework Directive (MSFD) but also by citizens and businesses operating at sea. Specific objectives of the project were:

1) Conduct a horizon scan to identify and map available modelling approaches used to hindcast, nowcast

2) Develop a comprehensive catalogue to classify available modelling approaches according to their characteristics

3) Propose a subset of the most meaningful models among major model typologies.

4) Assess whether these models can be used in the implementation of the Digital Twin Ocean and can improve the decision-making capacity under the MFSD.

Within this project, marine biodiversity/ecosystem models were defined as any modelling approach targeting marine biodiversity and/or ecosystem components (e.g., species abundance/occurrence or traits, functional groups and habitats) and considering (1) their interactions with multiple species and/or groups of species and/or trophic levels, (2) their associations with environmental variables (e.g., temperature, salinity, light availability, oxygen levels, and water movement), and (3) the impacts from human activities (e.g., fishing, aquaculture, alien invasive species, pollution, habitat modification, anthropogenic climate change).

The project (from January to October 2022) was structured in four phases.

The first phase of the project involved a horizon scanning that combined expert assessment and an extensive literature review. The literature review was performed using the Web of Science database. With a selection of relevant keywords related to four groups of information (modelling, environmental conditions, human activities and pressures, and marine ecosystems), 5212 articles and technical reports were identified. The horizon scan resulted in a total of 62 biodiversity/ecosystem models belonging to different model categories. These 62 biodiversity/ecosystem models were categorized as single species models (5), biogeochemical and lower trophic level models (7), species distribution models (6), community qualitative models (1), minimum realistic models (15), multispecies size-based models (11), multispecies individual-based models (4), mass based – food web models (3), and whole system or end-to-end models (10). Although most of the models were directly identified through literature screening, the initial list was carefully revised and extended. About one third of the models (18 models out of 62) were included based on suggestions from the project team and the Scientific Committee since they deemed important by the scientific community and had a potential use for the DTO. In addition, some of the model categories were pooled together by grouping similar models or to retain just a few important representatives. Species distribution models and biogeochemical and lower trophic level models were the most frequently used modelling approaches. The project team conducted a detailed review to record the main characteristics of each model and to assess their realized and potential ability to support the implementation of DTO and EU environmental policies. To assess these modelling approaches, the project team, together with the Scientific Committee, developed a scoring process. The scoring was organized in six major categories focusing on: (1) the ability of candidate models to produce outputs at different spatiotemporal scales; (2) the overall aim of each model, assessed in the context of the trade-off between generality, realism and precision proposed by Levins (1966); (3) the difficulty to setup and develop an operational version of the model; (4) the development practices followed by model development teams and their compromise with reproducible and open research; (5) the scope of the products derived from each model to support decision-making under MSFD; and (6) the potential and realized capability to couple each model to another existing models focusing either in purely physical or biogeochemical aspects of marine ecosystems, other trophic levels, or the impact of socioeconomic actors. The scoring process, together with expert judgement, led to the selection of the top ten candidate models.

The second phase of the project involved a detailed characterization of selected candidate models through careful review of each model and interviews with model development teams. Biogeochemical models which were relevant have been suppressed to the list since most models identified are already mature and made operational within CMEMS ocean forecasting centres. The following table lists the ten selected models:

Abbreviation	Model Name	Model type	Website
APECOSM	Apex Predators ECOSystem Model	Multispecies size-based models	https://apecosm.org/
Atlantis	Atlantis Ecosystem model	Whole system or end-to-end models	http://atlantis.cmar.csiro.au
EwE	Ecopath with Ecosim	Multispecies size-based models	https://ecopath.org
ECOSMO-E2E	ECOSystem MOdel-End to End	Whole system or end-to-end models	https://hereon.de/institutes/coastal_systems_analysis_modeling/matter_transport_ecosystem_dynamics/models/
ECOTRAN e2e	Top-down linear solution to bottom-up, end-to-end model	Whole system or end-to-end models	
Macroecological	Macroecological model	Multispecies size-based	
NORWECOM.E2E	Norwegian Sea Ecosystem End-to-End Model	Whole system or end-to-end models	https://bio.uib.no/te/research/norwecom.php
OSMOSE	Object-oriented Simulator of Marine ecOSystem Exploitation	Multispecies individual-based models	https://www.osmose-model.org
SEAPODYM	Spatial Ecosystem And POpulation DYnamics Model	Multispecies individual-based	http://www.seapodym.eu/
StrathE2E	StrathE2E2: End-to-End Marine Food Web Model	Whole system or end-to-end models	https://outreach.mathstat.strath.ac.uk/apps/StrathE2EApp/

The third phase involved the assessment and validation of interim results by biodiversity modelers to document the capability of each proposed model to contribute to DTO implementation and to support MSFD policy. In this analysis, we prepared and sent a questionnaire to each model development teams to gather further details on the main characteristics and capabilities of each model. From the information provided by model experts, we synthetized the main strengths and weaknesses of each modelling approach and identified potential synergies arising from the combined use of alternative biodiversity/ecosystem models.

The fourth phase was devoted to the synthesis of results, their validation, and public dissemination of all information gathered during the project through an online workshop with model users, model experts and stakeholders. In this workshop, the potential contributions of biodiversity models to the DTO were discussed.

The main outputs of the project included documenting and reporting of all the results of the project and the development and curation of three databases detailing: the output of the literature review; the characterization of 62 relevant modelling approaches identified in the initial assessment; and the in-depth analysis of the ten selected models. Selected models simultaneously embrace the complexity of marine food webs intertwined with multiple interacting environmental stressors, and account for the impact of human activities on the marine environment. Development teams align with open and reproducible research practices promoted by the European Commission. These models can also be integrated into coupled workflows interacting both with physical and socioeconomic models, with the potential to contribute to the development of the DTO and boost the implementation of EU environmental policies.

The databases produced by this study and referred to in this report are available for download on Zenodo: https://doi.org/10.2777/213731

RÉSUMÉ

La Commission Européenne a commandé l'étude "Modélisation de la biodiversité marine" [RTD/2021/MV/10] afin d'obtenir l'identification et la caractérisation d'un ensemble de modèles de biodiversité qui pourraient contribuer à la mise en œuvre du « European Digital Twin of the Ocean » (EU DTO, Jumeau Numérique Européen de l'Océan). Le EU DTO sera une infrastructure opérationnelle de services océaniques numériques, visant à accompagner et aider les prises de décision des autorités pour mettre en œuvre les politiques de l'UE telles que la Directive-cade de Stratégie pour le Milieu marin (Marine Strategy Framework Directive, MSFD), mais aussi des citoyens et des entreprises opérant en mer. Les objectifs spécifiques du projet étaient :

1) Mener une analyse prospective pour identifier et cartographier les approches de modélisation disponibles utilisées pour effectuer des simulations rétrospectives, actuelles et prévisionnelles de la biodiversité et des écosystèmes marins.

2) Développer un catalogue complet pour classer les approches de modélisation disponibles selon leurs caractéristiques.

3) Proposer un ensemble des modèles les plus significatifs parmi les principales typologies de modèles.

4) Évaluer si ces modèles peuvent être utilisés dans la mise en œuvre de l'EU DTO et peuvent améliorer la capacité de prise de décision dans le cadre de la MFSD.

Dans le cadre de ce projet, les modèles de biodiversité/écosystème marin ont été définis comme toute approche de modélisation ciblant la biodiversité marine et/ou les composantes de l'écosystème (par exemple, l'abondance/l'occurrence ou les caractéristiques des espèces, les groupes fonctionnels et les habitats) et prenant en compte (1) leurs interactions avec plusieurs espèces et/ou ou groupes d'espèces et/ou niveaux trophiques, (2) leurs associations avec des variables environnementales (par exemple, la température, la salinité, la disponibilité de la lumière, les niveaux d'oxygène et le mouvement de l'eau), et (3) les impacts des activités humaines (par exemple, la pêche, aquaculture, espèces exotiques envahissantes, pollution, modification de l'habitat, changement climatique anthropique).

Le projet (de janvier à octobre 2022) était structuré en quatre phases.

La première phase du projet impliquait une analyse prospective combinant une évaluation par des experts et une analyse documentaire approfondie. La revue de la littérature a été réalisée à l'aide de la base de données Web of Science. Avec une sélection de mots-clés pertinents liés à quatre groupes d'informations (modélisation, conditions environnementales, activités et pressions humaines et écosystèmes marins), 5212 articles et rapports techniques ont été identifiés. L'analyse prospective a abouti à un total de 62 modèles de biodiversité/écosystème appartenant à différentes catégories de modèles. Ces 62 modèles de biodiversité/écosystème ont été classés en modèles d'espèce unique (5), modèles biogéochimiques et de niveau trophique inférieur (7), modèles de distribution d'espèces (6), modèles qualitatifs de communauté (1), modèles réalistes minimaux (15), des modèles multi-espèces basés sur la taille (11), des modèles multi-espèces basés sur les individus (4), des modèles de réseau trophique basés sur la masse (3) et des modèles du système entier dit « de bout en bout » (10). Bien que la plupart des modèles aient été directement identifiés grâce à la recherche documentaire, la liste initiale a été soigneusement révisée et étendue. Environ un tiers des modèles (18 modèles sur 62) ont été inclus après suggestion de l'équipe du projet et du comité scientifique car ils étaient jugés importants par la communauté scientifique et avaient une utilisation potentielle pour le DTO. De plus, certaines catégories de modèles ont été regroupées car similaires ou pour ne retenir que quelques représentants importants. Les modèles de répartition des espèces et les modèles biogéochimiques et de niveau trophique inférieur ont été les modèles les plus fréquemment utilisés. L'équipe du projet a mené un examen détaillé pour enregistrer les principales caractéristiques de chaque modèle et évaluer leur capacité réelle et potentielle à aider à la mise en œuvre des politiques environnementales du DTO et de l'UE.

Pour évaluer ces approches de modélisation, l'équipe du projet, en collaboration avec le comité scientifique, a développé un processus de notation. La notation a été organisée en six grandes catégories axées sur: (1) la capacité des modèles à produire des résultats à différentes échelles spatio-temporelles; (2) l'objectif global de chaque modèle, évalué dans le cadre du compromis entre généralité, réalisme et précision proposé par Levins (1966); (3) la difficulté de mettre en place et de développer une version opérationnelle du modèle; (4) les pratiques de développement par les équipes et leur compromis pour une recherche reproductible et ouverte; (5) la portée des produits dérivés de chaque modèle pour aider à la prise de décision dans le cadre de la MFSD; et (6) la capacité potentielle et effective de coupler chaque modèle à un autre modèle existant se concentrant soit sur les aspects purement physiques ou biogéochimiques des écosystèmes marins, soit sur d'autres niveaux trophiques, soit sur l'impact des acteurs socio-économiques. Le processus de notation, associé au jugement d'experts, a conduit à la sélection des dix meilleurs modèles.

La deuxième phase du projet impliquait une caractérisation détaillée des modèles sélectionnés grâce à un examen approfondi de chaque modèle et aux échanges avec les équipes de développement de modèles. NB : les modèles biogéochimiques qui étaient pertinents ont été supprimés de la liste car la plupart des modèles identifiés sont déjà matures et rendus opérationnels au sein des centres de prévision océanique CMEMS. Le tableau suivant liste les dix modèles sélectionnés :

Abréviation	Nom du modèle	Type de modèle	Site web
APECOSM	Apex Predators ECOSystem Model	Modèles multi-espèces basés sur la taille	https://apecosm.org/
Atlantis	Atlantis Ecosystem model	Modèles du système entier ou « end to end »	http://atlantis.cmar.csiro.au
EwE	Ecopath with Ecosim	Modèles multi-espèces basés sur la taille	https://ecopath.org
ECOSMO-E2E	ECOSystem MOdel-End to End	Modèles du système entier ou « end to end »	https://hereon.de/institutes/coastal_systems_analysis_modeling/matter_transport_ecosystem_dynamics/models/
ECOTRAN e2e	Top-down linear solution to bottom-up, end-to-end model	Modèles du système entier ou « end to end »	
Macroecological	Macroecological model	Modèles multi-espèces basés sur la taille	
NORWECOM.E2E	Norwegian Sea Ecosystem End-to-End Model	Modèles du système entier ou « end to end »	https://bio.uib.no/te/research/norwecom.php
OSMOSE	Object-oriented Simulator of Marine ecOSystem Exploitation	Modèles multi-espèces basés sur les individus	https://www.osmose-model.org
SEAPODYM	Spatial Ecosystem And POpulation DYnamics Model	Modèles multi-espèces basés sur les individus	http://www.seapodym.eu/
StrathE2E	StrathE2E2: End-to-End Marine Food Web Model	Modèles du système entier ou « end to end »	https://outreach.mathstat.strath.ac.uk/apps/StrathE2EApp/

La troisième phase impliquait l'évaluation et la validation des résultats intermédiaires par les modélisateurs de biodiversité afin de documenter la capacité de chaque modèle proposé à contribuer à la mise en œuvre du DTO et à appuyer la politique MSFD. Dans cette analyse, nous avons préparé et envoyé un questionnaire à chaque équipe de développement des modèles pour recueillir plus de détails sur les principales caractéristiques et capacités de chaque modèle. À partir des informations fournies par les experts en modélisation, nous avons synthétisé les principales forces et faiblesses de chaque approche de modélisation et identifié les synergies potentielles découlant de l'utilisation combinée de modèles de biodiversité/écosystème.

La quatrième phase a été consacrée à la synthèse des résultats, à leur validation et à la diffusion publique de toutes les informations recueillies au cours du projet par le biais d'un atelier en ligne avec les utilisateurs de modèles, les développeurs des modèles et les parties prenantes. Dans cet atelier, les contributions potentielles des modèles de biodiversité au DTO ont été discutées.

Les principaux résultats du projet comprenaient la documentation et la communication de tous les résultats du projet ainsi que le développement et la conservation de trois bases de données (DB) détaillant : les résultats de l'analyse documentaire ; la caractérisation de 62 approches de modélisation pertinentes identifiées lors de l'évaluation initiale ; et l'analyse approfondie des dix modèles sélectionnés. Les modèles sélectionnés englobent simultanément la complexité des réseaux trophiques marins et de leurs relations avec les multiples facteurs de stress environnementaux, et tiennent compte de l'impact des activités humaines sur l'environnement marin. Les équipes de développement s'alignent sur les pratiques de recherche ouvertes et reproductibles promues par la Commission Européenne. Ces modèles peuvent également être intégrés dans des travaux interagissant à la fois avec des modèles physiques et des modèles socio-économiques, avec le potentiel de contribuer au développement du DTO et de stimuler la mise en œuvre des politiques environnementales de l'UE.

Les bases de données développées au cours de cette étude sont disponibles pour téléchargement en accès libre sur Zenodo : https://doi.org/10.2777/213731

MARINE BIODIVERSITY MODELLING STUDY

1. Background and objectives

1.1. Background

Oceans play a key role for human well-being as they provide valuable and vital ecosystem services such as food provision, climate regulation, carbon sequestration, oxygen production, energy, mineral and genetic resources, and cultural and recreational services (Barbier et al. 2011, Stocker 2015). Particularly, coastal areas provide advantages for human settlement because marine environment sustains diverse activities including fishing, industry, trade and tourism (Barragán and de Andrés 2015). Nearly 40% of the world's population lives within 100 km of the coast and this percentage is increasing (Agardy et al. 2005).

As human population has grown, the use of marine resources and the impacts of anthropogenic activities on marine ecosystems have intensified, spread and diversified (Halpern et al. 2015, Halpern et al. 2019). Marine ecosystems have been altered at high rates in a global context over the last decades as a consequence of escalating pressure from the cumulative impact of global, regional and local stressors, including climate change, biological invasions and direct human pressures such as overexploitation of marine resources, pollution and habitat modification (Costello et al. 2010, Halpern et al. 2019). These anthropogenic impacts come from the activities of multiple sectors such as fisheries, aquaculture, oil and gas extraction, shipping, sea bed mining, marine renewable energy, desalination plants, tourism and urban and coastal development (Vierros et al. 2015). Given the range of human activities, stressors often co-occur in time and space, especially in coastal areas and, therefore, managing coastal and marine resources is becoming increasingly complex. As a result, most marine ecosystems are subjected to the impacts of multiple stressors (Halpern et al. 2015, Halpern et al. 2019) and the ability of the oceans to support human well-being is in a critical point (Worm et al. 2006, Duarte et al. 2020). Therefore, there is a need to restore and maintain marine ecosystems in healthy, productive, and resilient condition so they can provide the ecosystem services.

At the onset of UN Decade of Ocean Science for Sustainable Development, reconciling the sustained provision of ecosystem goods and services with the recovery and conservation of healthy marine ecosystems has emerged as a major challenge to ensure human well-being (Borja et al. 2020, Duarte et al. 2020, Pendleton et al. 2020). At European level, the Marine Strategy Framework Directive (MSFD; Directive 2008/56/EC), seeks the achievement of "clean, healthy and productive" oceans (i.e., good environmental status) and the sustainable use of ecosystem services, emphasizing the importance of healthy ecosystems as a prerequisite for ecosystem services to be provided. In addition, the European Commission launched the Mission "Restore our Ocean seas and waters by 2030". This Mission, part of Horizon Europe and in the context of the European Green Deal, aims in the next decade to restore the health of our oceans, seas and waters, in line with the UN Decade on ecosystem restoration (Waltham et al. 2020). Within this context, the Digital Twin of the Ocean (DTO) initiative will play an important role by integrating existing and new data sources and developing digital, high-resolution, multi-dimensional and near real-time representation of the global ocean. This initiative aims to provide better understanding of the ocean and to connect, engage and empower citizens, governments, and industries by providing them with the capacity to inform their decisions.

Quantifying past, current and future status of marine ecosystems under the MSFD is critical to inform decision making. Within this context, biodiversity/ecosystem models are powerful tools as they provide a framework for integrating available information about trophic interactions, interactions with environmental factors and human pressures such as fishing and climate change (Plagányi 2007, Heymans et al. 2018). They have been proven useful to provide understanding of the structure and functioning of marine ecosystems, estimate the impact of anthropogenic activities, assess the influence of environmental variability (including anthropogenic climate change), explore the effect of alternative policies and plausible changes in marine ecosystems conditions as a consequence of climate change such as temperature and primary production, and provide support to the decision-making process (Plagányi 2007, Acosta et al. 2016, Collie et al. 2016, Heymans et al. 2018).

Different reviews of existing modelling approaches have been undertaken within the European context to assess the ecosystem status in support of the MSDF and inform decision-making (Hyder et al. 2015, Piroddi et al. 2015, Lynam et al. 2016). However, as a result of an intense research, larger data availability, increasing understanding of marine ecosystems and their processes, and the development of computing technology, there has been an increase in the number and in the development of such modelling frameworks during the last years (Heymans et al. 2018, Tittensor et al. 2018). Therefore, within the context of the UN Decade of Ocean Science for Sustainable Development, the European Green Deal, the ongoing review of the MSFD, and the Digital Twin of the Ocean, there is a need to identify which of the existing models, to date, have the potential to directly support policies and management decisions with the aim to restore marine ecosystems and promote a sustainable use of marine resources.

1.2. Project objectives

The main objective of the project is to determine how marine biodiversity/ecosystem models currently either in use or under development can be used to implement the Digital Twin Ocean and improve, in particular but not only, the decision-making capacity under the MFSD (Fig.1). Specific objectives of the project are:

1) Conduct a horizon scan to identify and map available modelling approaches used to hindcast, nowcast and forecast marine biodiversity and ecosystems.

2) Develop a comprehensive catalogue to classify available modelling approaches according to their characteristics.

3) Propose a subset of the most meaningful models among major model typologies.

4) Assess whether these models can be used in the implementation of the Digital Twin Ocean and can improve the decision-making capacity under green deal policies such as the Maritime Spatial Planning Directive (MSPD) or the Marine Strategy Framework Directive (MFSD).

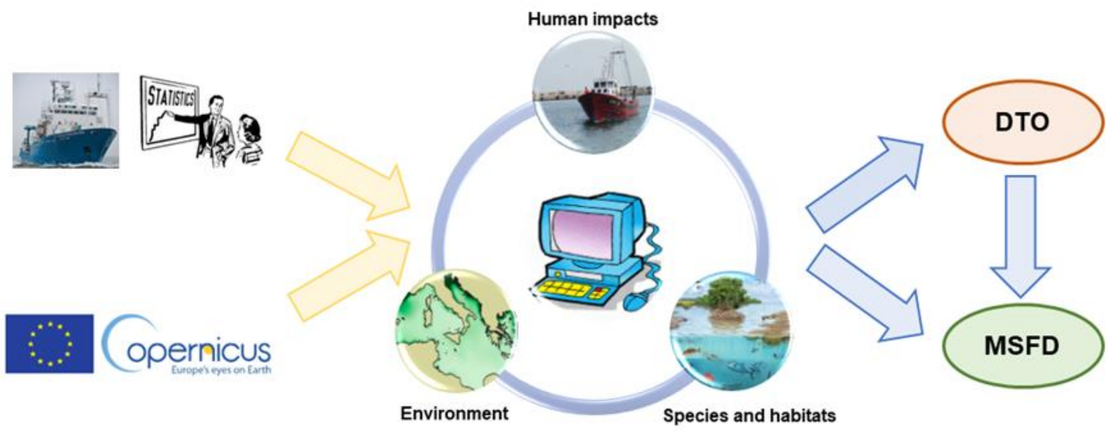


Figure 1: Relationship and flow between data, models, and policy through the Digital Twin Ocean (DTO) and the Marine Strategy Framework Directive (MSFD).

The rationale of this study is to contribute with a reference document for the implementation of the Digital Twin of the Ocean and the MFSD. To address the objectives of the study, we conducted a systematic review to identify complementary modelling approaches that have been used to analyse the past, present, and future variability of the multiple dimensions of marine biodiversity and their interaction with environmental and societal stressors. Subsequently, we catalogued available and emerging marine biodiversity/ecosystem models and developed a database recording their main characteristics. This database provided a basis to classify and identify the most representative and widely used biodiversity/ecosystem modelling approaches. We developed criteria to evaluate the potential applications of these models in the implementation of the Digital Twin Ocean and to improve the decision-making capacity under the MSFD.

2. General approach

The second phase of the project provided a more detailed assessment of the ten selected models adding information provided by the development teams of each model. Information from the previous step was revised and extended based on the responses of model developers to an extensive questionnaire designed to collect information about the main characteristics and capabilities of each model. The information was homogenized and coded to contribute to the development of a detailed database of biodiversity/ecosystem models (Database #3).

The third and fourth phase of the project account for the validation of the results of the project and for public dissemination. The third phase is a workshop with biodiversity modelers and other stakeholders to discuss and validate the identification and characterization of biodiversity models that could contribute to the implementation of the DTO. The fourth and final phase is devoted to synthesizing all information gathered during the workshop with previous developments and to the conclusion of this report.

The general approach of the project is divided in four phases (Figure 2). The first phase of the project involved an extensive literature review to identify different modelling approaches that have been used by the scientific community and marine and coastal managers to analyse marine biodiversity, and to assess their capabilities and usability. The main outputs from the first phase included two databases featuring, respectively, the results of the literature screening (Database #1) and the assessment of candidate modelling approaches identified from the literature and other sources (Database #2). Analyses on these databases led to the identification and selection of a subset of ten models based on a variety of features, especially their potential to support MSFD, and their capability to be coupled[1] with other models.

[1] The term model coupling is in general reserved for situations in which there is a two-way, interactive interchange of outputs that directly or indirectly serve as inputs of the other models. Unidirectional coupling is also common, though this situation is often referred as forcing (i.e., there is at least one model whose outputs do not serve as inputs for other model components).

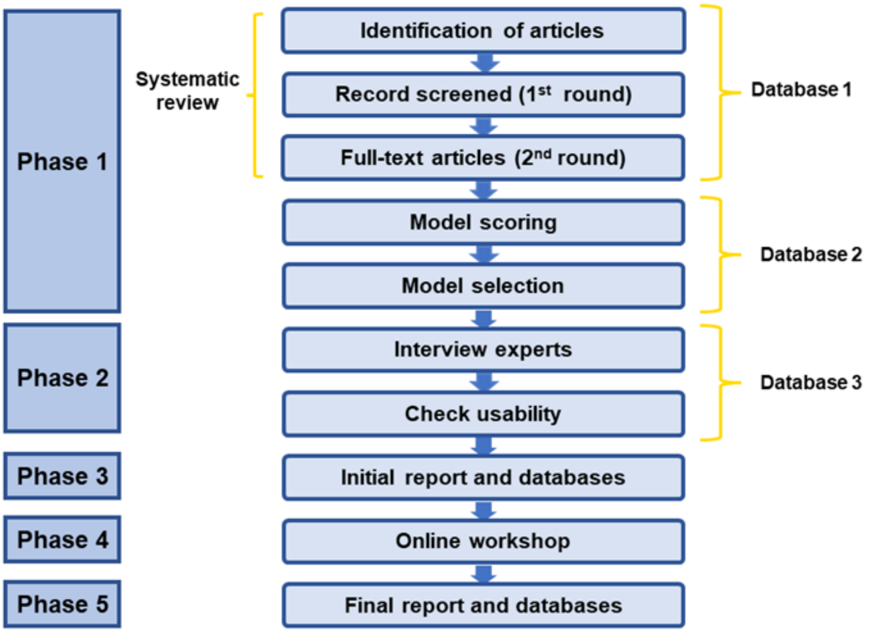


Figure 2: General approach of the project

The second phase of the project provided a more detailed assessment of the ten selected models adding information provided by the development teams of each model. Information from the previous step was revised and extended based on the responses of model developers to an extensive questionnaire designed to collect information about the main characteristics and capabilities of each model. The information was homogenized and coded to contribute to the development of a detailed database of biodiversity/ecosystem models (Database #3).

The third and fourth phase of the project account for the validation of the results of the project and for public dissemination. The third phase is a workshop with biodiversity modelers and other stakeholders to discuss and validate the identification and characterization of biodiversity models that could contribute to the implementation of the DTO. The fourth and final phase is devoted to synthesizing all information gathered during the workshop with previous developments and to the conclusion of this report

2.1. Marine biodiversity/ecosystem models

Within this project, marine biodiversity/ecosystem models were defined as any modelling approach targeting marine biodiversity and/or ecosystem components (e.g., species abundance/occurrence or traits, functional groups and habitats) and considering (1) their interactions with multiple species and/or groups of species and/or trophic levels, (2) their associations with environmental variables (e.g., temperature, salinity, light availability, oxygen levels, and water movement), and (3) the impacts from human activities (e.g., fishing, aquaculture, alien invasive species, pollution, habitat modification, anthropogenic climate change). These models enable the *in silico* simulation of a variety of aspects and emerging properties of marine ecosystems, accounting for both the impact of hydrogeochemical and habitat condition on the abundance and distribution of species and the effects of the different anthropogenic and natural pressures on the different abiotic and biotic components.

3. Identification of potential biodiversity/ecosystem models

We followed a systematic review using the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) approach (Moher et al. 2010). This approach consists of three steps: (1) systematic article selection using a search engine; (2) article screening; and (3) review of relevant articles and extraction of the information (Fig. 3).

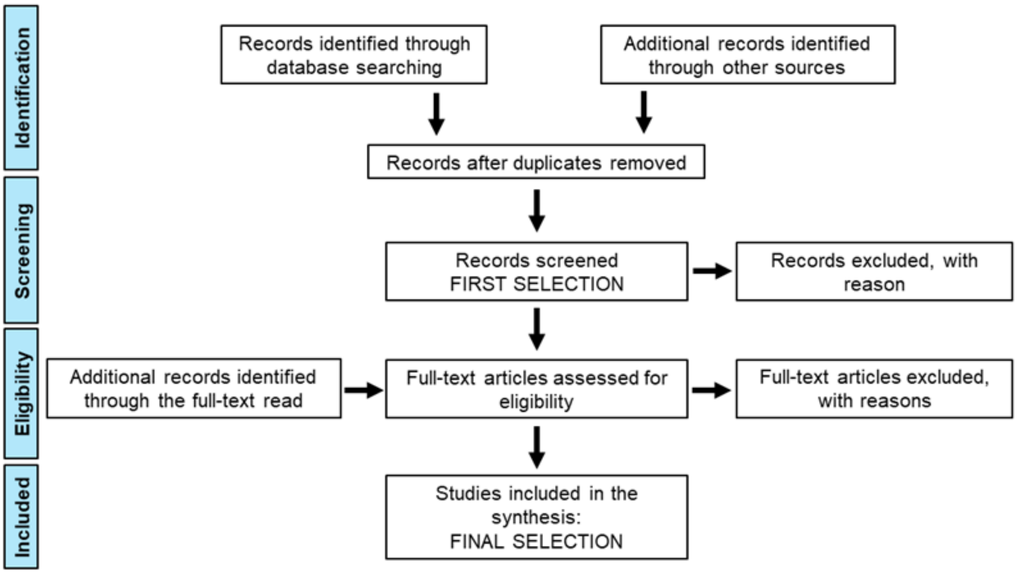


Figure 3: Flow diagram of the methodological approach (PRISMA) used in the systematic review.

3.1. Literature screening

We performed the bibliographic search using Web of Science database (www.webofscience.com). This engine allows setting eligibility criteria to include any article, review, article in press and book chapter published. We limited the search to publications from 1st January 2000 to the 16th February 2022.

With the feedback and agreement of Steering Committee (SC thereafter), we combined four groups of information: modelling, environmental conditions, human activities and pressures, and marine ecosystems. To do so, we selected the following groups of entries in the title, abstract and keywords, using "and" as the relational term:

a) Keyword group on modelling: "species model*" OR "community model*" OR "multispecies model*" OR "biodiversity model*" OR "biogeochemical model" OR "low trophic* level model*" OR "species distribution model*" OR "habitat suitability model*" OR "ecological niche-based model*" OR "minimum realistic model*" OR "model* of intermediate complexity" OR "size class model*" OR "size-class model*" OR "size structure* model*" OR "size-structure* model*" OR "size based model*" OR "size-based model*" OR "size spectrum model*" OR "size-spectrum model*" OR "individual based model*" OR "individual-based model*" OR "trophic model*" OR "food web model*" OR "food-web model*" OR "ecosystem model*" OR "ecological model*" OR "end-to-end model" OR "whole system model*" OR "management model"

b) Keyword group on environmental conditions: "environment" OR "temperature" OR "salinity" OR "oxygen" OR "pH" OR "turbidity" OR "habitat" OR "circulation" OR "current" OR "currents" OR "upwelling" OR "nutrient*" OR "chlorophyll"

c) <u>Keyword group on human activities and impacts</u>: “human impact” OR “anthropogenic impact” OR “human pressure” OR “anthropogenic pressure” OR “human stress*” OR “anthropogenic stress*” OR “human activity” OR “fishery” OR “fishing” OR “fisheries” OR “overexploitation” OR “extraction” OR “harvesting” OR “exploitation” OR “trawl*” OR “cultivation” OR “hunting” OR “aquaculture” OR “climate change” OR “ocean warming” OR “sea warming” OR “acidification” “invasive species” OR “alien species” OR “alien invasive species” OR “non-indigenous species” OR “eutrophication” OR “nutrient* enrichment” OR “organic enrichment” OR “pollution” OR “contamina*” OR “marine litter” OR “plastic*” OR “wastewater*” OR “waste water*” OR “dredging” OR “habitat degradation” OR “habitat alteration” OR “habitat change” OR “abrasion” OR “habitat loss” OR “disturbance of sediments” OR “physical loss” OR “physical damage” OR “physical disturbance” OR “wind farm” OR “offshore energy” OR “offshore wind turbines” OR “wave energy” OR “marine renewable energy” OR “tidal energy” OR “collision” OR “shipping” OR “marine transport” OR “ballast water” OR “pipeline*” OR “submarine cable*” OR “drilling” OR “underwater noise” OR “anthropogenic sound” OR “oilrig*” OR “oil exploration” OR “oil spill*” OR “oil platform” OR “offshore structure” OR “gas exploration” OR “fracking” OR “tourism” OR “hydrographic changes” OR “power plants” OR “hypoxia”

d) <u>Keyword group on marine domains</u>: “marine” OR “sea” OR “ocean*” OR “coast*” OR “coastal” OR “estuar*” OR “bay” OR “gulf” OR “ria” OR “fjord”

The search was further restricted to the following subset of relevant subject areas:

e) “Environmental Sciences Ecology” OR “Marine Freshwater Biology” OR “Zoology” OR “Mathematical Computational Biology” OR “Biodiversity Conservation” OR “Meteorology Atmospheric Sciences” OR “Life Sciences Biomedicine Other Topics” OR “Mathematics” OR “Oceanography” OR “Fisheries” OR “Water Resources” OR “Physical Sciences Other Topics” OR “Science Technology Other Topics” OR “Plant Sciences” OR “Behavioral Sciences” OR “Geography” OR “Biochemistry Molecular Biology” OR “Reproductive Biology” OR “Geochemistry Geophysics” OR “Evolutionary Biology” OR “Physiology” OR “Toxicology” OR “Engineering” OR “Genetics Heredity” OR “Computer Science” OR “Physical Geography” OR “Infectious Diseases” OR “Microbiology” OR “Chemistry” OR “Social Sciences Other Topics” OR “Parasitology” OR “Remote Sensing” OR “Social Issues” OR “Physics” OR “Biophysics” OR “Mining Mineral Processing”.

The number of papers identified with the specified keywords was 5212. The literature found during the systematic bibliographic search was complemented with relevant papers from other sources, ranging from (1) literature cited in review papers such as Piroddi et al. (2015), Lynam et al. (2016), Hyder et al. (2015) and Nielsen et al. (2018), (2) entries identified by members of the team on their personal literature databases, and (3) relevant papers found in selected articles during the third step of the systematic review (extraction of the information).

The most frequent keywords in the group of keywords *1* (on modelling) were “ecosystem model” and “biogeochemical model”, followed by individual-based model” and “ecological model” (**Annex 1**). Regarding group of keywords *2* (environmental conditions), “habitat” and “temperature” keywords were more prevalent, followed by “nutrient” and “current”. In group of keywords *3* (human activities and pressures), the most frequent keywords were “fishing” and “climate change”. Finally, in group of keywords *4* (marine ecosystems), “marine” and “sea” were the most prevalent keywords, followed by “coastal” and “ocean”. Ecological modelling was the topmost frequent journal, followed by Marine Ecology Progress Series, Frontiers in Marine Science, ICES Journal of Marine Science (Fig. 4). For further details of these analyses for each model category, see **Annex 1 and Annex 2**.

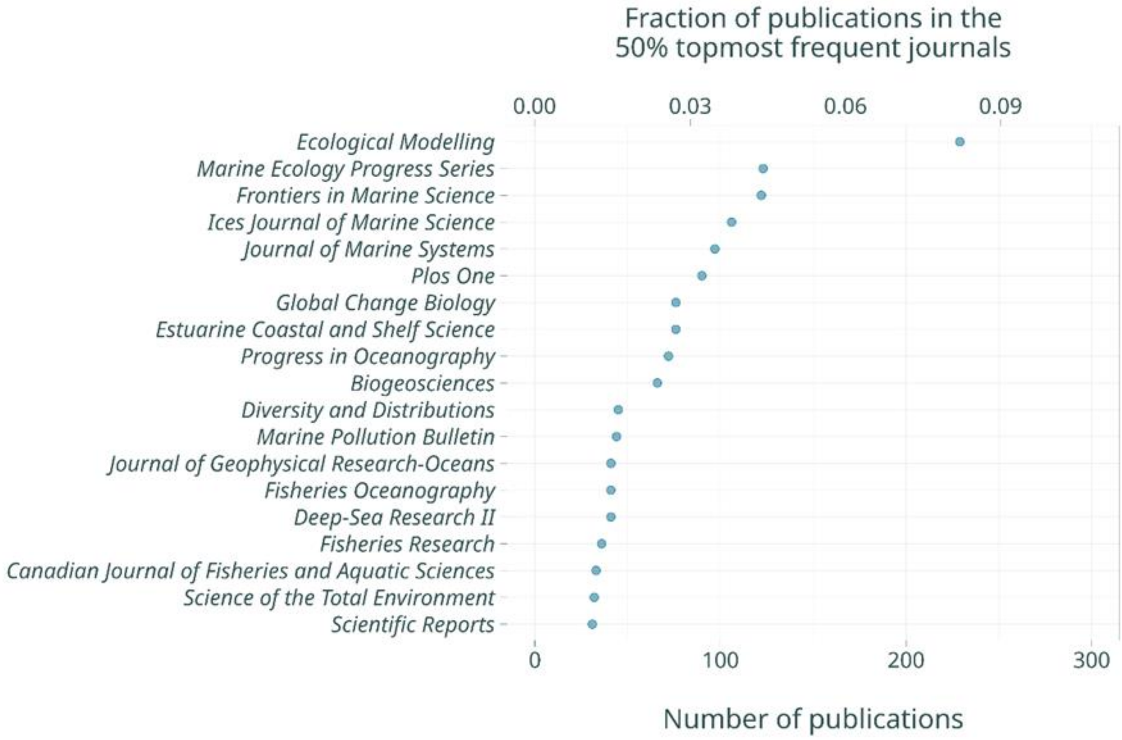


Figure 4: Fraction of publications and number of publications in the 50% topmost frequent journals.

Article screening started with these 5212 articles (Fig. 5) and consisted of a two-stage process. The first screening filtered articles based on their title and abstract, while in the second stage, articles were examined in full depth. During the first stage, articles were excluded if: (1) they did not develop/apply a model; (2) models did not evaluate the impact of human activities and/or the environment, or (3) models were related exclusively to terrestrial and/or freshwater habitat/species.

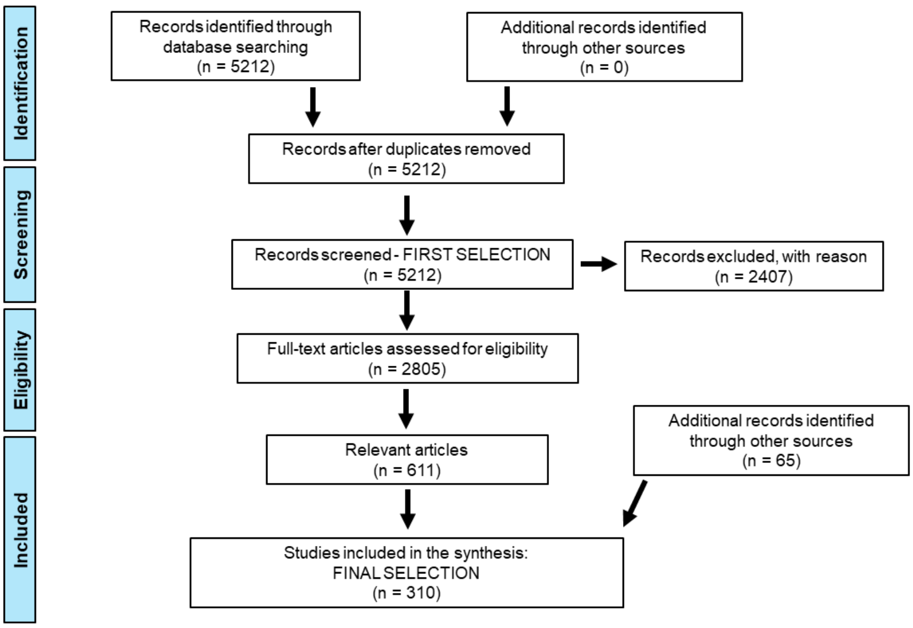


Figure 5: Flow diagram of the systematic review used in the present study

During the first stage, model category (see BOX 1 for the definition of model categories) and specific model in each article included was identified (see BOX 2 and **Annex 3** for further details of a guide we prepared for this stage)). In addition, during this first stage, relevant articles for each modelling approach were identified. Relevant articles are those with at least have one of the following attributes:

- Key reference of the modelling approach
- Review paper of the approach
- Highly cited article (i.e., more than 30 citations/year)
- New developments in recent articles (e.g., last 5 years)
- Interesting application (e.g., multiple drivers, emerging issues)

BOX 1: MODEL CATEGORY DEFINITION

1) **Single species models:** models that focus on the dynamics of a single species, featuring interactions with other species and environmental drivers but not dynamic feedbacks among them.

2) **Biogeochemical and lower trophic level models:** they describe the dynamic of lower trophic levels (phytoplankton and zooplankton) and their impact on bulk ecosystem properties in response to changes in physical (e.g., temperature, salinity, light) and chemical (e.g., nutrients, oxygen, pH) conditions. They are often coupled to hydrodynamic models to feature the impact of ocean circulation on ecosystem dynamics.

3) **Species Distribution Models (SDM)** (also called **Habitat Suitability Models (HSM)** or **Ecological Niche-Based Models**): they combine species occurrences or abundance data with environmental variables (e.g., temperature) to predict the distribution of species or potential habitat. When applied to multiple species, these models can be used to identify coexisting species and to characterize interaction networks (e.g., **Joint SDMs**).

4) **Community qualitative models:** they provide a framework for formulating qualitative relationships between variables within a particular system using signed diagraphs to represent community interactions and impacts and predict stability and perturbations (Puccia and Levins 1985, Dambacher et al. 2002, Coll et al. 2019).

5) **Minimum realistic models (MRM)** and **models of intermediate complexity (MICE):** they include a limited number of species that have important interactions with the target species of the study (Punt and Butterworth 1995, Plagányi et al. 2014). Within this category we will include models such as **GADGET** (Globally applicable Area-Disaggregated general Ecosystem Toolbox) (e.g., Andonegi et al. 2011, Pérez-Rodríguez et al. 2017), **multispecies bioenergetic models** (Koen-Alonso and Yodzis 2005) and **SMS** (Stochastic Multispecies Models) (e.g., Lewy and Vinther 2004, Kempf et al. 2010).

6) **Multispecies size-based models:** they describe energy transfer from primary producers to consumers, focussing on body size rather than species identity. Within this category we will include models such as **Mizer** (dynamic multi-species size-spectrum models) (e.g., Scott et al. 2014), **FishSUMS** (e.g., Speirs et al. 2016), **SS-DBEM** (Size-Spectra Dynamic Bioclimate Envelope Model) (e.g., Fernandes et al. 2013) and **APECOSM** (Apex Predators ECOSystem Model) (Dueri and Maury 2013).

7) **Multispecies individual-based models**: they are based on the explicit representation of individual organisms. Within this category we will include models such as **SEAPODYM** (Spatial ecosystem and population dynamic model) (e.g., Lehodey et al. 2008, Senina et al. 2016) and **OSMOSE** (Object-oriented Simulator of Marine ecOSystem Exploitation) (e.g., Shin and Cury 2004, Grüss et al. 2016).

8) **Mass based - food web models**: they represent population of dynamically interacting species or groups of species. Within this category we will include models such as the **Ecopath with Ecosim** approach (EwE) (e.g., Christensen and Walters 2004, Corrales et al. 2017) and **StrathE2E** (e.g. Heath 2012).

9) **Whole system models or end-to-end:** they attempt to represent all the ecosystem components from nutrients, biogeochemical cycling and primary producers to top predators (including human components) linked through trophic interactions and the associated abiotic environment (e.g., currents and water column properties such as temperature and salinity). Within this category, we will include models such as **Atlantis**. In addition, whole system models also include coupled models, where models were integrated (with or without dynamic feedbacks) and outputs of one model provide inputs to the other. For example, Travers-Trolet et al. (2014) **coupled** an OSMOSE model with a biophysical model (ROMS -$N_2P_2Z_2D_2$).

After the first screening process, 2804 articles (53.8% of the first identification of publications) were included. The reasons to exclude articles were as follows: they did not develop/apply a model (33.2%); (2) models did not evaluate the impact of human activities and/or the environment (11.3%), or (3) articles were related to terrestrial and freshwater habitat/species (55.5%) (Table 1).

Table 1: reasons to exclude articles

Reasons to exclude articles	n	%
Terrestrial/freshwater realm	1335	55.46
It is not a model	799	33.19
It is a model but did not evaluate the impact of human activities and/or the environment	273	11.34
Total	**2407**	**100.00**

BOX 2: SUMMARY OF THE GUIDELINES TO UNDERTAKE THE SCREENING PROCESS (see annex 1 for further details).

A guideline for the first stage of the systematic review was made to help the different members of the project team in this task. The guidelines contain the following information:

1) Definition of biodiversity/ecosystem model
2) Reasons to exclude an article
3) Classification and definition of the model category
4) Name of specific models
5) Instructions to identify relevant articles

The number of publications featuring biodiversity/ecosystem models has increased rapidly since 2000, especially after 2011 (Fig. 6). Between 2000 and 2011, the average rate of publication was 55.9 articles per year, while from 2012 and 2021 the rate increased to 209 articles per year.

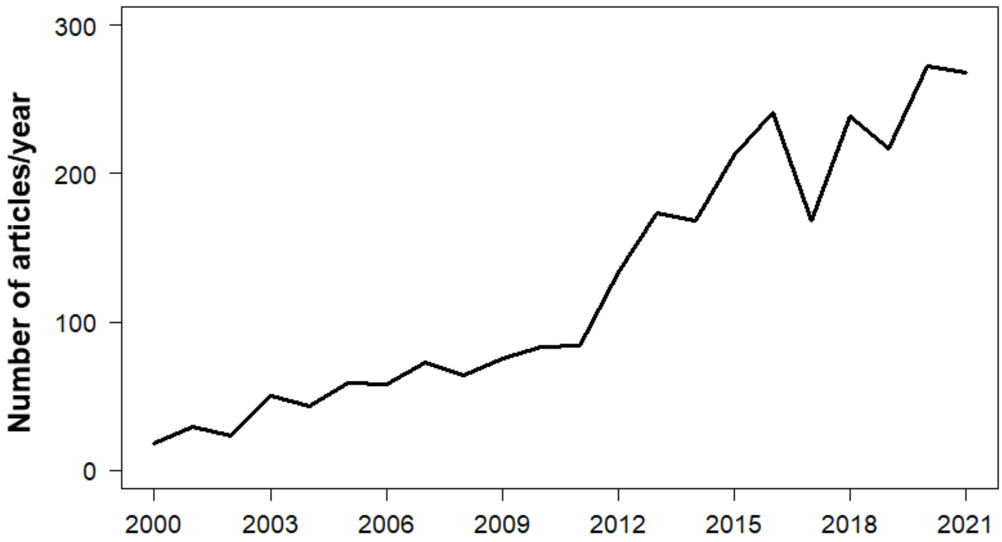


Figure 6: Cumulative number of articles that were included in the systematic review over time.

The horizon scan resulted in a total of 62 biodiversity/ecosystem models belonging to the different model categories listed in Table 2 and succinctly described in **Annex 4**. These 62 biodiversity/ecosystem models were categorized as single species models (5); biogeochemical and lower trophic level models (7); species distribution models (6); community qualitative models (1); minimum realistic models (15); multispecies size-based models (11); multispecies individual-based models (4); mass based – food web models (3); and whole system or end-to-end models (10) (Table 2). Most of the models were directly identified through literature screening, though the initial list was carefully revised and extended. About one third of the models were included based on recommendations from the project team and the Scientific Committee due to its importance through the scientific community and its potential use for the DTO (18 models highlighted in Table 2). In addition, some of the model categories were pooled together by grouping similar models or to retain just a few important representatives.

Several single species models, biogeochemical and lower trophic level models and species distribution models (SDMs) were found in the screening process. Single species models were grouped in three large groups corresponding to dynamic population models, model based on Dynamic Energy Budget (DEB) theory (Kooijman and Kooijman 2010), and Individual Based Models (IBMs) (Grimm and Railsback 2013); keeping separately recently developed Lagrangian models with a wide application scope like Ichtyopop (Lett et al. 2008) and Parcels (Lange and van Sebille 2017). In the case of biogeochemical and lower trophic level models, the screening focused on models considering their features and their potential contribution to the DTO and European Union policies. In the case of species distribution models (SDMs), the project team decided to group them into four generic categories and retained two specific applications. SDM generic categories included two widely used algorithms: MaxEnt (Phillips et al. 2017) and the ensemble modelling platform BioMod (Thuiller et al. 2009), and a hotchpotch/wildcard category for models based on the classical Hutchinsonian niche concept that included a gamut of algorithms and model approaches. The fourth generic category featured joint-SDMs (Warton et al. 2015, Wilkinson et al. 2019), which specifically include species covariation in space and/or time to improve habitat predictions. Finally, the assessment also included two specific applications; EcoCast which is a recently proposed multispecies habitat model framework designed to implement dynamic ocean management (Hazen et al. 2018), and AquaMaps which is the pioneering and reference server of species distribution maps in the marine realm, featuring standardized range maps and projections under alternative socioeconomic scenarios for more than 33,500 species (Ready et al. 2010, Kaschner et al. 2011).

Species distribution models (31.4%) and biogeochemical and lower trophic level models (30.6%) were the most frequently used modelling approaches, followed by mass based – food web models (15%) and single species models (11.3%) (Table 3). On the other hand, multispecies individual-based models (2.9%), whole system or end-to-end models (2.5%), multispecies size-based models (2.3%), minimum realistic models (2%) and community qualitative models (0.7%) were the less prevalent (Table 3). In all the model categories, the number of publications has increased since 2000 (Fig. 7). In addition, the average rate of publication between 2012 and 2021 were higher than the average rate between 2000 and 2012 in all model categories, except for community qualitative models (Fig. 8). Remarkably is the large increase of this rate between both period for species distribution models, as the rate increase from 4.2 articles per year between 2000 and 2011 to 82 articles per year between 2012 and 2021 (Fig. 7).

Table 2: List of models for each modelling category. Models highlighted in grey were included ad hoc after the initial literature screening based on expert judgement. Annex 4 provides a succinct description of each model.

Model Category	Model Abbreviation	Model Name
Single species models	DEB	Dynamic energy budget models - bioenergetic models
	Dynamic population model	Dynamic population model
	IBM	Individual based models
	Ichthyop	Ichthyop (Lagrangian tool for simulating ichthyoplankton dynamics)
	Parcels	Parcels (Probably A Really Computationally Efficient Lag rangian Simulator)
Biogeochemical and lower trophic level models	BFM	Biogeochemical Flux Model
	ECOMARS 3D	ECOMARS 3D (Ifremer)
	ERGOM	Ecological Regional Ocean Model
	ERSEM	European Regional Seas Ecosystem Model
	MEDUSA	MEDUSA
	PISCES	PISCES
	SCOBI nordic	SCOBI nordic
Species distribution models	AQUAMAPS	AQUAMAPS
	EcoCast	EcoCast
	Joint SDM	joint SDM
	SDM - BIOMOD	general SDM - BIOMOD
	SDM - Maxent	general SDM - Maxent
	SDM (habitat suitability)	general SDM (only habitat suitability - niche sensu Hutchinson) including different algorithms and tools
Community qualitative models	CEM	Conceptual ecological models (CEM)
Minimum realistic models	AGG-PROD	Multi-species production model (AGG-PROD)
	BALMAR (MICE)	BALMAR (MICE)
	Bioeconomic	Bioeconomic multispecies model (General)
	FLBEIA	FLBEIA
	GADGET	GADGET

Model Category	Model Abbreviation	Model Name
	InVest	Integrated Valuation of Ecosystem Services and Trade-offs
	ISDM-MICE	Integrative system dynamic model (MICE)
	ISIS FISH	ISIS FISH
	MEFISTO	MEFISTO
	MICE-in-space	MICE-in-space: spatio-temporal model of intermediate complexity for ecosystem assessments
	MSPM	MultiSpecies Production Model
	MSVPA	Multispecies Virtual Population Analysis
	SMOM	Spatial Multispecies Operating model
	SMS	Stochastic Multispecies Models
	TRITON	TRITON
Multispecies size-based models	APECOSM	APECOSM
	BOATS	BiOeconomic mArine Trophic Size-spectrum
	FEISTY	FEISTY: A Global Fisheries Model
	FishSUMS	FishSUMS
	LeMANS	Length-based Multi-species Analysis by Numerical Simulation
	Macroecological	Macro-ecological
	MIZER	MIZER (dynamic multi-species size-spectrum models)
	nlSSSM	Non-linear Species Size Spectrum Model
	Size-based food web model	Size-based food web model
	SS-DBEM	Size-Spectra Dynamic Bioclimate Envelope Model
	ZooMSS	Zooplankton Model of Size Spectrum
Multispecies individual-based models	DBEM	DBEM
	OSMOSE	Object-oriented Simulator of Marine ecOSystem Exploitation
	SEAPODYM	Spatial ecosystem and population dynamic model
	SPRAT	SPRAT
Mass based - food web models	ENA	ENA
	EwE	Ecopath with Ecosim
	LIEM	Linear Inverse Ecosystem Models
Whole system or end-to-end models	Atlantis	Atlantis
	BioMASS	BioMASS
	CORSET	CORSET
	ECOSMO-E2E	ECOSMO-E2E
	ECOTRAN e2e	ECOTRAN e2e
	InVitro	InVitro agent-based modelling software
	NEMURO.FISH	NEMURO.FISH
	NORWECOM.E2E	Norwegian Sea Ecosystem End-to-End Model
	POSEIDON	POSEIDON (POSEIDON/RODOS; POSEIDON-R)
	StrathE2E	StrathE2E

Table 3: Number of articles for each model category.

Model category	n	%
Single species models	318	11.34
Biogeochemical and lower trophic level models	858	30.59
Species distribution models	882	31.44
Community qualitative models	20	0.71
Minimum realistic models	57	2.03
Multispecies size-based models	64	2.28
Multispecies individual-based models	82	2.92
Mass based - food web models	422	15.04
Whole system or end-to-end models	69	2.46
Undetermined	33	1.18
Total	**2805**	**100.00**

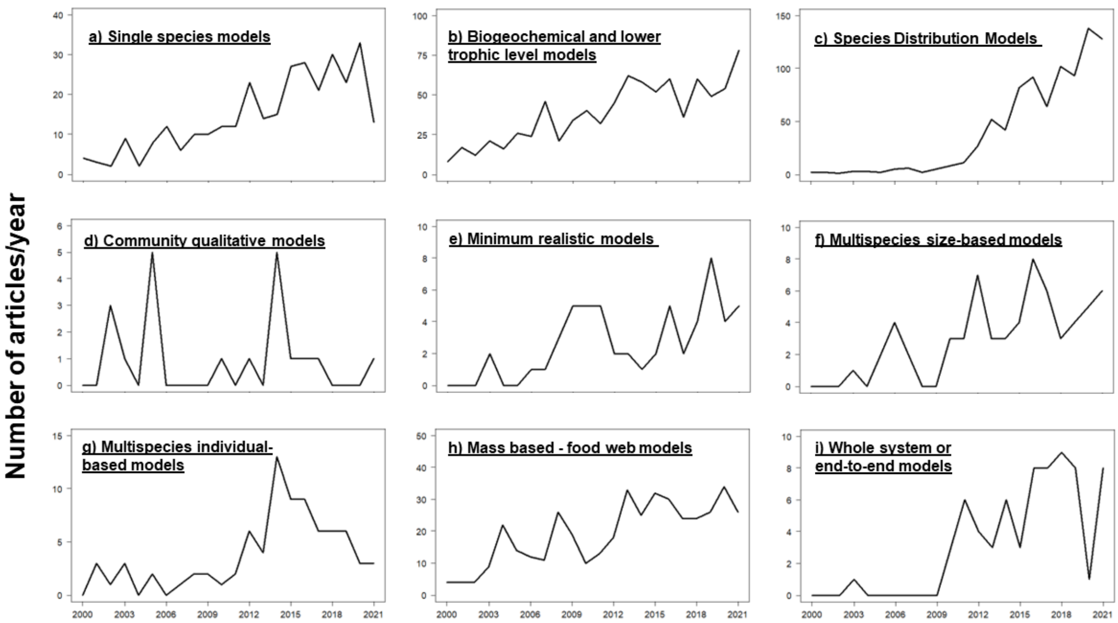


Figure 7: Number of articles per year for each model category included in the systematic review over time.

The output of the literature screening included a list of relevant scientific publications featuring major biodiversity/ecosystem model types. These relevant contributions included publications that provide the full documentation of a specific model, detailed overviews of different modelling approaches and, in many cases, relevant applications that illustrate the scope of a given model and its main use. From the 2805 articles included in the first screening process, 611 publications were considered relevant (Fig. 5). However, these relevant articles were not equally distributed through the different modelling types. Therefore, a minimum of 5 relevant contribution for each modelling approach were selected. These publications came from the list of relevant scientific publications (the 611 publications mentioned above) and from other relevant documents identified by the project team (including the Steering Committee), through independent search (key articles of the modelling approach explaining its main features, user guides, websites, new developments in recent articles), and/or from personal literature databases of project team members. At the end, 310 publications were considered for the initial characterization of the biodiversity/ecosystem models found (final selection) (Fig. 5), 245 publications came from the relevant articles found in the first screening process and 65 from additional records identified from other sources (Fig. 5).

3.2. Initial characterization of biodiversity/ecosystem models

The goal of the second screening stage was the development of a database describing the main characteristics of each model type identified during the first screening stage. Therefore, the selected articles for each modelling approach were read and relevant information of these modelling approaches was extracted. This information ranged from basic information about the model, such as the scope of the model, its strengths and weaknesses on the eyes of their authors, its capability to analyse the impact of different stressors on the marine environment, to a detailed account of more technical aspects about the development and implementation of each model. Importantly, the database featured fields detailing 1) the ability of each model to assess qualitative descriptors of the environmental status of marine waters proposed in the context of the MSFD, and 2) the possibility of using each model in combination with other models through coupling. The information collated into the database provided background for a series of analyses to rank identified models based on their suitability to support the DTO (see section 5. Analysis and ranking of biodiversity/ecosystem models).

The following information was extracted for each modelling type (see **Annex 5** for more information):

1) Information related to the model

- Model category, following the classification and definition found in Box 1.
- Type of model, following (Levins 1966) (Statistical, i.e., models do not specify relationships among variables in terms of biological processes; Mechanistic, i.e., models specify relationships among variables in terms of biological processes, and Hybrid, i.e., combining characteristics of statistical and mechanistic models).
- Important features of the model to detail those aspects defining the model, including its aims, technical advances and unique features that motivated its development, according to the developers and users of the model.
- Limitations of the model to detail the main weakness of the model, as acknowledged by the authors of the model.
- Possible data type: time (static, i.e., constant in time; dynamic, i.e., time varying; and static and dynamic models) and spatial (nonspatial, spatial and nonspatial and spatial models) frames (Jørgensen and Fath 2011).
- Ecosystem type that the model is able to represent (e.g., coastal, estuary, bay, gulf and open waters).
- Domain/domains included in the model (e.g., pelagic, demersal and benthic).
- Relevant species or groups of species considered. Relevant state variables in the context of biodiversity modelling that are able to be included in the model (e.g., single species, functional groups, size classes, ontogenic fractions of species (larvae, juveniles, adults) and target and nontarget species).
- External drivers possible to be included (e.g., fishing, climate change, aquaculture and invasive species).
- Kind of species interactions that can be included in the model (e.g., facilitation, protection, mutualism, commensalism, competition, predation, parasitism and disease).
- Levels of its maturity: the success of a model attests whether it can be easily configured and adapted to new situations by other groups independent of the original development team. Models were categorized in:
    - ✓ Recently developed models featured in a few applications and short development history (e.g., less than 5 case studies and a development history of less than 5 years).
    - ✓ Intermediate models used in moderate number applications and development history (e.g., 5-25 case studies and less than 10 years of development).

    - ✓ Advanced, mature models featured in large number of applications and long development history (e.g., more than 25 case studies and a long development history of 10 or more years).
- Minimum dataset to implement/run the model (input data) (e.g., catches, stomach content and biomass).
- Minimum dataset to evaluate the outputs (model validation) (e.g., catches and biomass).
- Data sources for the model. When available, we detail the specific databases used to develop, train, and assess the model (e.g., ICES Stock Database, OBIS and FishBase).
- Time required for model development. Models were categorized in:
    - ✓ Models that, starting de novo, require more than 24 months to move to production.
    - ✓ Models that, starting de novo can be moved to production in between 12 and 24 months.
    - ✓ Models that, starting de novo, can readily move to production in less than 12 months.

2) Information related to the software

- Computer language that has been used to code the model.
- Platforms for which the model is available (e.g., windows, linux, independent platform).
- Availability of the code of the model (i.e., yes, online; yes, upon request; no, private).
- Potential usage restrictions to the scientific community (i.e., yes; no).
- Type of license (e.g., https://en.wikipedia.org/wiki/Software_license).

3) Information related to the user community

- Number of potential users.
- Stakeholders: detail the typology of users, distinguishing major groups of stakeholders like the general public, fishermen, researchers, resource managers and decision makers and/or academic students).
- Specify the main products/services that can be obtain through the use of the model (e.g., fisheries management, impact of climate change, protected area management).
- Insights gained or decisions taken as a result of the use of the model, putting special attention to results that assess the impact of marine protected areas or recovery interventions.
- Country of model owner.
- Country main developer.
- Relevant scientific groups.
- Has the development of the model received support through EU projects?
- Name EU projects that supported the model.
- Name scientific groups that supported the model.
- Where it has been further developed?
- Next steps planned by model users.

4) **Information related to the potential use of the model for policy**

- Potential use and relationship with MSFD descriptors and criteria. Provide the number of the descriptors that the model may contribute to analyse (e.g., if the model is able to provide indicators about descriptors 1, 2 and 3, include here "1,2 and 3"):
    - ✓ Descriptor 1. Biodiversity is maintained.
    - ✓ Descriptor 2. Non-indigenous species do not adversely alter the ecosystem.
    - ✓ Descriptor 3. The population of commercial fish species is healthy.
    - ✓ Descriptor 4. Elements of food webs ensure long-term abundance and reproduction.
    - ✓ Descriptor 5. Eutrophication is minimised.
    - ✓ Descriptor 6. The sea floor integrity ensures functioning of the ecosystem.
    - ✓ Descriptor 7. Permanent alteration of hydrographical conditions does not adversely affect the ecosystem.

  - ✓ Descriptor 8. Concentrations of contaminants give no effects.
  - ✓ Descriptor 9. Contaminants in seafood are below safe levels.
  - ✓ Descriptor 10. Marine litter does not cause harm.
  - ✓ Descriptor 11. Introduction of energy (including underwater noise) does not adversely affect the ecosystem.
- Applications supporting the MSFD policy. Provide the number of the descriptors that the model may contribute to analyse (e.g., if the model is able to provide indicators about descriptors 1, 2 and 3, include here "1,2 and 3"). See above for list of descriptors.
- Potential use and relationship with other policies (e.g., Habitats Directive, Biodiversity Convention (CBD), Common Fisheries policy (CFP), UN Sustainable Development Goals (SDGs)).

5) Information related with the model coupling and interoperability

- Coupling with lower trophic level models.
- Coupled with bioeconomic models.
- Model coupling and interoperability involves the development of dedicated codes to enable a direct interchange between the output of two or more models. The term coupling is in general reserved for situations in which there is a two-way, interactive interchange of outputs that directly or indirectly serve as inputs of the other models. Unidirectional coupling is also common, though this situation is often referred as forcing (i.e., there is at least one model whose outputs do not serve as inputs for other model components). Therefore, coupling was categorized as:
  - ✓ Models that do not accept external environmental forcing and that have not been coupled to other models (i.e., no coupling).
  - ✓ Models that accept environmental forcing and have been configured in workflows where they passively receive one-way forcing from other models (i.e., one-way coupling).
  - ✓ Models that accept environmental forcing and predict changes in environmental conditions, and which have been configured in fully coupled workflows with other models (two-way coupling).

6) **Information of available website of the model**. If there is an available website with relevant information of the model.

4. Analysis and ranking of biodiversity/ecosystem models

The second stage toward the identification of candidate biodiversity models for the DTO involved the analysis of the database describing the main characteristics of each of the model types (Database #2) identified during the first screening stage (Database #1). These analyses provided the basis to rank biodiversity/ecosystem models based on their suitability to contribute to the implementation of the DTO and boosting decision-making capacity under the Marine Strategy Framework Directive (MSFD).

4.1. Scoring criteria

The overall aim of the scoring process was to identify models featuring a specific set of characteristics that make them suitable for the assessment, monitoring and prediction of marine biodiversity and ecosystems, the implementation of the DTO and their capacity to support decision-making capacity under the MSFD. The scoring is organized about six major categories focusing on: (1) the ability of candidate models to produce outputs at different spatiotemporal scales; (2) the overall aim of each model, assessed in the context of the trade-off between generality, realism and precision proposed by Levins (1966); (3) the difficulty to setup and develop an operational version of the model; (4) the development practices followed by model development teams and their compromise with reproducible and open research; (5) the scope of the products derived from each model to support decision-making under MSFD; and (6) the potential and realized capability to couple each model to another existing models focusing either in purely physical or biogeochemical aspects of marine ecosystems, other trophic levels, or the impact of socioeconomic actors.

Table 4: Alternative used weights for the final score of each model.

Category	DTO	MSFD	Average
Model output	10	10	10
Generality and Realism	15	20	17.5
Model development and setup	15	10	12.5
Software features	20	10	15
MSFD support	10	40	25
Model coupling and interoperability	30	10	20
TOTAL	100	100	100

Within each category, the scores combine one or more of the criteria defined below. Each model received a score ranging from 0 to 3 points to flag, on the lower end, models that do not implement the feature (i.e., criteria) of interest and, in the other, a maximum score to those models that entirely fulfil the target criteria. Intermediate scores accounted for models partially fulfilling the feature of interest. Within each category, the final score was calculated as the simple average of the scores assigned to each sub-criterion, except for category on MSFD support. The final score of each model was calculated as a weighted average to reward those model features bringing a better support to the implementation of DTO and of MSFD policies (Table 4). These weights were set by the project team in agreement with the Steering Committee.

The rest of this section details the rationale behind each category and the scores assigned to each specific criterion (C):

C1 Nature of the predictions produced by the model

Biodiversity and ecosystem models target different scales, levels of organization and a variety of processes. Therefore, depending on the objectives of each model, predictions vary in extent and resolution. C1 category focused on two specific aspects that are easy to quantify; whether the models included in the assessment simulate time varying patterns, and whether they can predict spatial patterns by considering spatial processes and interactions. Therefore, models that can be configured to simulate spatio-temporal patterns received a higher score. We detail below the specific criteria followed to assign each score:

C1.1 Temporal dimension: biodiversity and ecosystem models range from zero dimensional models describing selected ecosystem properties at a single snapshot to fully dynamic models with internal feedbacks modulated by external forcing. Between these extremes, some models admit external forcing and passively produce time varying predictions, whereas other models just implement internal dynamics (the value of a state variable depends on past levels of one or more state variables). This criterion rewarded models with internal temporal dynamics capable of interacting with the external environment:

- Models predicting snapshot, static ecosystem patterns (e.g., ZooMSS): 0 pts.
- Models that do not feature temporal dynamics but simulate time varying patterns in response to external forcing (e.g., SDM): 1 pt.
- Models with internal feedbacks but do not admit external forcing: 2 pts.
- Fully dynamic models with internal feedbacks that admit modulation by external forcing variables (e.g., Ecopath with Ecosim): 3 pts.

C1.2 Spatial dimension: like in the case of temporal dynamics, the predictions of biodiversity and ecosystem models ranges from the prediction of whole ecosystem properties averages over large scales to the simulation of three-dimensional fields emerging from spatial processes like passive dispersion or direct movement. This criterion rewarded models featuring spatial interactions that are capable of simulating spatially varying predictions.

- Non spatial, adimensional models (e.g., FLBEIA): 0 pts.
- 2D spatial (horizontal dimension, e.g., most of SDMs): 2 pts.
- 3D spatial (horizontal and water-column vertical dimensions, e.g., Atlantis): 3 pts.

C2 Model generality and realism

In a landmark contribution, Levins (1966) proposed that modelers face a trade-off between generality, realism, and precision and accuracy. Therefore, model building requires a compromise among these three qualities. A general model can be applied in multiple situations; a realistic model has a structure that resembles to a large extent the real world it attempts to describe, while a precise and accurate model consistently makes predictions close to available observations. The three aspects are desirable qualities for any model. This category considered four alternative criteria to characterize model design choices made by different modelling groups. As detailed below, the criteria rewarded those models ranking higher in terms of generality and realism, though we were unable to assess their precision and accuracy.

C2.1 Generality: the number of ecosystem types where a model can be applied provides a simple metric to quantify and compare the degree of generality of alterative candidate models. The criterion considered only three potential scores and assigned a larger score to general models that consider several ecosystems and domains than to more specific models that address the dynamics of a single marine ecosystem and domain. The criteria distinguished different marine and coastal ecosystems and habitat such as coastal, estuaries, bays, gulfs, and open waters; as well as different domains such as pelagic, demersal and benthic. Models specific to a unique ecosystem received the lowest score, while models describing three or more ecosystems were considered general and received the largest score. The choice of three ecosystems might be arbitrary, but it clearly separates specific models from those targeting processes and model variables common to a variety of systems.

- Specific models describing few ecosystems and one domain: 1 pt.

- Intermediate models describing several ecosystem types and one domain or few ecosystem types and different domains: 2 pts.
- General models describing several ecosystem types and domains: 3 pts.

C2.2 Realism A: the variety of species or functional groups considered by a model attests the degree of realism pursued during model design. In the marine environment, the long tradition in the development of biodiversity and ecosystem models encompass a variety of approaches, ranging from abstract, strategic models describing the dynamics of bulk ecosystem properties, to extremely detailed descriptions of the tangled networks describing the interactions among the main species and/or functional groups in a given ecosystem. These complex models often consider different life history stages within a species or functional group. Models addressing the complexity of real ecosystems poses the advantage of enabling a direct assessment of their predictions. This criterion rewarded models featuring a large number of species and/or functional groups, especially when they covered a large fraction of the interactors involved.

- Models that consider only one species or one functional group (e.g., dynamic population models): 0 pts.
- Models that do not consider species and/or functional groups and instead focus on single ecosystem variables or traits (i.e., size groups) (e.g., MIZER): 1 pt.
- Model that considers only a limited number/small subset of the species and/or functional groups of the ecosystem (e.g., Minimum Realistic Models): 2 pts.
- Models featuring most of the species and/or functional groups of the ecosystem (e.g., Ecopath with Ecosim): 3 pts.

C2.3 Realism B: the ability of a model to predict the impact of environmental stressors on the biodiversity of an ecosystem provides a second quality to assess the degree of realism of a model. The dataset records the number of environmental and anthropogenic drivers considered by each model, with a special focus on the ability of models to assess the impact of fishing, climate change, aquaculture, and invasive species. The dataset also includes a free text field to further detail whether a model can handle one or more combinations of these stressors. The criterion rewarded models that can simultaneously consider both anthropogenic and environmental stressors. Models considering a larger number of anthropogenic stressors also received a larger score:

- Models that either consider environmental or anthropogenic stressors, independently of whether they feature one or several stressors: 1 pt.
- Models that simultaneously consider both environmental and anthropogenic stressors, but just a limited number: 2 pts.
- Models that simultaneously consider the cumulative impact of multiple environmental and anthropogenic stressors: 3 pts.

C2.4 Realism C: the scoring included a third criterion to assess model realism based on the type of biological interactions implemented by each model. This criterion considered both interactions within and between taxa and/or functional groups, including potential interactions between different life history stages or age or size classes within a species or functional group. The ability of a model to reflect actual interactions in an ecosystem is key to depict a mechanistic representation of ecosystem functioning. Thus, the criterion rewarded models considering a larger variety of biotic interactions. It assigned a higher score to models considering interactions between groups than only within groups, and to models considering other interactions besides competition and predation, as detailed below:

- Models considering no biological interactions: 0 pts.
- Models exclusively featuring interactions within groups, including interactions between life stages, size and age classes (e.g., intraspecific competition, cannibalism): 1 pt.
- Models featuring biological interactions within and between groups, but only a few types, and in general, only competition and predation: 2 pts.
- Models considering several interactions within and between groups, including for example non-trophic interactions such as facilitation and protection: 3 pts.

C3 Model development and setup

Models of marine biodiversity and ecosystems vary in the degree of difficulty to configure and run. Though some teams of modellers devoted a great effort to streamline model set up and tuning, some design choices inherently condition how easy or complex can be to run and assess alternative models. This category focused on three alternative criteria to rank candidate models according to: their degree of maturity, the data required to assess model outputs, and the time required to set up a model *de novo* by a team of experts. The three criteria rewarded models that are widely used, rely on few, well defined and readily available diagnostics for their assessment, and that can be rapidly configured.

C3.1 Maturity: the success of a model attests whether it can be easily configured and adapted to new situations by other groups independent of the original development team. This criterion ranked candidate models attending to the number of applications found during the literature review and to their degree of operationality and ease of use, distinguishing the following three reference categories:

- Recently developed models featured in a few applications and short development history (e.g., less than 5 case studies and a development history of less than 5 years): 1 pt.
- Intermediate models used in moderate number applications and development history (e.g., 5-25 case studies and less than 10 years of development): 2 pts.
- Advanced, mature models featured in large number of applications and long development history (e.g., more than 25 case studies and a long development history of 10 or more years): 3 pts.

C3.2 Dataset required for model assessment: the main advantage of realistic models is the ability to confront model outputs with real world observations. This is also a key aspect to assess the accuracy of model predictions. Lack of adequate observations due to the inherent hostility of the marine environment has historically hampered the development and assessment of biodiversity models. The growing availability of autonomous observing platforms, from ocean satellites to floats and unmanned vehicles, and the "omics" revolution both contribute to remediate this situation. These advances pose at the same time an extra challenge to modelling groups that are forced to update their assessment schemes. The gap between models and observations also fostered the development of models that purposely attempt to predict variables that cannot be otherwise estimated. This criterion considers the minimum datasets required to assess the output of a model, rewarding those models whose accuracy can be easily assessed.

- Models whose assessment requires multiple data sets and involves difficult analyses: 1 pt.
- Models whose assessment depends on multiple but readily available data sets and involves simple analyses or, on the contrary, model assessed using few data sets and a complex analysis: 2 pts.
- Models whose assessment involves few, readily available data sets and straightforward analyses: 3 pts.

C3.3 Time for model set up: the time required to set up a working model may constrain its ability to support the implementation of DTO and MSFD policies. The database of model characteristics records a subjective assessment of the time required by a team of experts to configure and set up *de novo* a model under a different architecture, including the potential coupling to another model, and the development of updated parameterizations to ensure that the new model instance keeps its original accuracy. The criterion rewarded models that can be rapidly configured and moved to production in less than a year, setting a rather arbitrary limit of two years to consider that a model might compromise the timeline of DTO and MSFD implementation:

- Models that, starting *de novo,* require more than 24 months to move to production: 1 pt.
- Models that, starting *de novo* can be moved to production in between 12 and 24 months: 2 pts.
- Models that, starting *de novo*, can readily move to production in less than 12 months: 3 pts.

C4 **Software features**

This criterion considers whether it is possible to run models in different programming languages and computer platforms, whether the computer codes are well documented and publicly available. The criterion rewarded model development teams adopting practices that align with the principles of reproducible and open research.

C4.1 Development in different programming languages: the availability of alternative implementations of a model reflects both an effort to make it available to a wider user community, as well as a test of the robustness of the model and the quality of the code. Though model codes often involve one or more programming languages, we focus here on the core code of a model. The criterion rewarded models already implemented in more than one programming language with respect to models that are only available in their original form:

- Models that keep a single main implementation using a unique programming language: 1 pt.
- Models that have been coded from scratch in a set of programming languages other than the one in which they were originally coded: 3 pts.

C4.2 Availability in different computer platforms: the choice of alternative development environments and programming languages may last the portability of a model to different platforms. This criterion rewards those models that can be run in different operating systems, either because the development team maintains alternative versions targeting major platforms (UNIX and UNIX-like systems, including Linux and iOS, Windows, and Android), or because the models were developed in a platform-independent programming languages (e.g., Java, or scripting languages like R or Python):

- Models tied to a single operating system: 1 pt.
- Platform independent models: 3 pts.

C4.3 Source code availability: the public availability of scientific codes has been identified as a key step to promote transparent and open research practices (e.g., Ince et al. 2012, Nosek et al. 2015, Mislan et al. 2016). In general, publicly available codes enjoy the benefit of careful scrutiny by a wider user community. This criterion ignored other aspects that may limit the use of candidate models to focus on the availability of their source code. The criterion rewarded development teams that opted to making their codes available through public repositories or under automatic request services. Groups requesting any kind of application or that openly opted to not share their codes received a lower score.

- Models with private codes: 0 pts.
- Models whose code is advertised as available under request: 1 pt.
- Publicly available model codes (e.g., software repositories): 3 pts.

C4.4 Potential usage restrictions: as commented above, the adoption of certain development environments and software platforms may constrain the portability and availability of a model for other users. The database recording the presence of usage restrictions like its reliance on commercial software and other potential charges. The criterion rewarded models with no usage restrictions:

- Restrictions (e.g., fees, key, proprietary software): 1 pt.
- Unrestricted usage: 3 pts.

C4.5 Type of license: model development teams can choose among a variety of software licenses that clearly divide among non-free licenses imposing restrictions on the use and redistribution of model codes, and free and open licenses that tend to request only the attribution and acknowledgement to model authors. This criterion rewarded model development teams adopting public software licenses that are more consistent with transparent and reproducible research practices.

- Models whose codes are not available: 0 pts.
- Models whose code is available, but under a non-free license: 1 pt.

- Model whose code is available under a free and open license: 3 pts.

C5 MSFD support

One of the major goals of the project is the identification of models that can contribute the boosting of decision-making processes under the MSFD. To assess the potential use and the relationship of candidate models with MSFD implementation, the database recorded whether the products and services delivered by the model relate to the 11 MSFD descriptors listed in Annex I of the Council Directive 2008/56/EC. This category considered both the potential of a model to inform decisions regarding distinct MSFD, and the explicit prior usage of candidate models in support of MSFD policies. Both criteria counted the number of potential descriptions and scaled the result using the formula $3 \cdot n / 11$, where n is the number of supported MSFD descriptors, which ranges from 0 to 11. The final score for these criteria assigns more importance to models that have supported MSFD policies (0.25 for the first subcriteria and 0.75 for the second one).

C5.1 Potential scope to support MSFD policies: the number of MSFD descriptors that a model can potentially assess.

C5.2 Applications supporting MSFD policies: the number of MSFD descriptors that have been already addressed in practical applications of a model.

C6 Model coupling and interoperability

The implementation of the DTO and of MSFD policy depends on the development of quantitative tools for ecosystem-based management. These models ideally belong to the class of end-to-end models of marine ecosystems (Rose et al. 2010) that attempt to describe entire marine food webs, from microbes to higher trophic levels. End-to-end models simultaneously feature biological responses to external variability in ocean physics and chemistry, and to anthropogenic impacts. Reaching such level of complexity usually requires the combination of models describing different components of marine systems. This category considered a single criterion to assess the potential to couple each of the candidate models to other existing models. These models may focus either in purely physical or biogeochemical aspects of marine ecosystems, higher trophic levels, or socioeconomic actors.

C6.1 Model coupling and interoperability involves the development of dedicated codes to enable a direct interchange between the outputs of two or more models. The term coupling is in general reserved for situations in which there is a two-way, interactive interchange of outputs that directly or indirectly serve as inputs of the other models. Unidirectional coupling is also common, though this situation is often referred as forcing (i.e., there is at least one model whose outputs do not serve as inputs for other model components). The criterion rewarded models that have been already coupled to other models based on the review of applications published in the scientific literature. It assigned a lower score to models that only accept external forcing or that accept no forcing at all.

- Models that do not accept external environmental forcing and that have not been coupled to other models: 0 pts.
- Models that accept environmental forcing and have been configured in workflows where they passively receive one-way forcing from other models (e.g., SDM): 2 pts.
- Models that accept environmental forcing and predict changes in environmental conditions, and which have been configured in fully coupled workflows with other models: 3 pts.

4.2. Selection of candidate models

The analysis and scoring of the 62 biodiversity and ecosystem models identified through extensive literature review resulted in a ranking that delineated the distinct potential of alternative modelling approaches to support the development of DTO and the implementation of MSFD policy (see previous section).

4.2.1. Scores by model category

The results of the scoring per model category are shown in Table 5. Three broad modelling approaches —Biogeochemical and lower trophic level models, Multispecies individual-based models, and Whole-system, end-to-end models— stand out as the model categories receiving higher average scores. Biodiversity/ecosystem models belonging to these categories provide adequate predictions for the DTO, as they have been successfully coupled to models of ocean physics or other trophic levels and components of socioeconomic marine systems. These models also stand out for their potential to contribute to support MSFD policies.

Table 5: Average score assigned to each model category according to the three alternative weighting schemes presented in Table 1. "n" is the number of modelling types per model category.

Model category	n	Average score per category		
		DTO	MSFD	Overall
Biogeochemical and lower trophic level models	7	2.53	2.15	2.34
Whole system or end-to-end models	10	2.3	2.02	2.16
Multispecies individual-based models	4	2.21	1.95	2.08
Species distribution models	6	2.07	1.64	1.85
Single species models	5	1.96	1.71	1.84
Multispecies size-based models	11	1.99	1.6	1.79
Mass based - food web models	3	1.68	1.67	1.67
Minimum realistic models	15	1.89	1.45	1.67
Community qualitative models	1	1.56	1.47	1.51
Total	**62**	**2.07**	**1.73**	**1.90**

4.2.2. Scores of each biodiversity model

Examination of individual scores assigned to each model revealed heterogeneity among and within model categories (Fig. 8). The scoring rewarded models that predict spatially and temporarily varying patterns. It also flagged models that produce static spatial patterns. The scoring highlighted the ability of a few advanced models from different categories to simultaneously embrace the complexity of marine food webs (realism) intertwined with multiple interacting environmental stressors (generalism), including the impact of human activities. This was the case of generalized modelling frameworks like Ecopath with Ecosim, OSMOSE, and Atlantis. The scoring for model generality and realism weighted down single species models and almost all SDMs (i.e., except joint SDMs). On the other hand, model complexity hinders model development and setup, so the scoring in this category rewarded computationally simple approaches. Biogeochemical models are the exception since they performed well both in terms of versatility and ease of implementation. The fourth criteria assessing software characteristics resulted in high variability in the scores within and among categories, reflecting idiosyncratic development practices of each model development group.

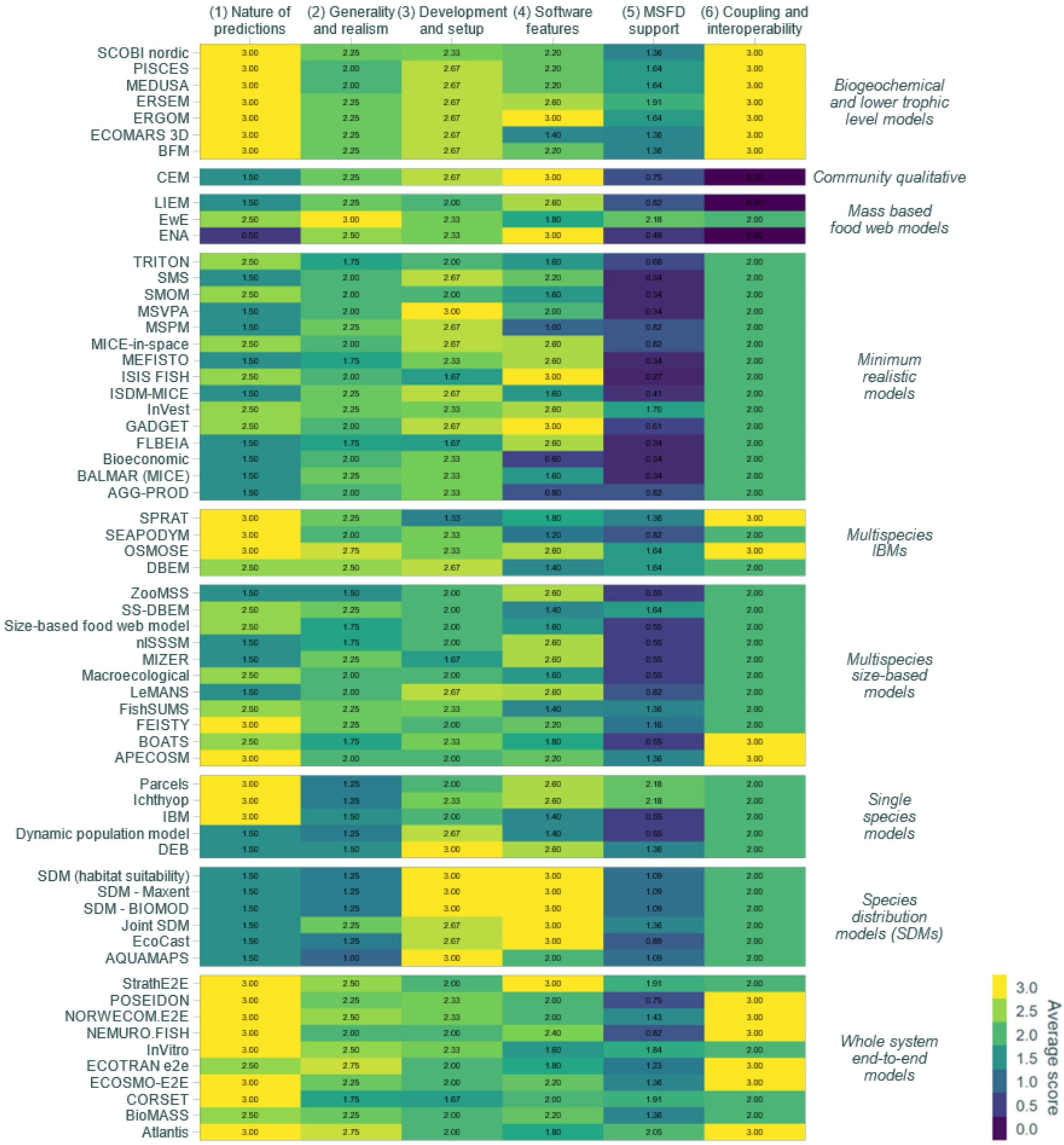


Figure 8: Average scores assigned to each biodiversity model (rows) for the broad scoring categories (columns) defined in section 2.4.1. Average scores range from zero to three. Each cell of the table includes a label with the average score and a background colour shade that maps to the scores, from a dark blue hue for lower scores to yellow for top values, through dark and pale greens. Models are grouped according to the categories defined in Box 1.

The criteria assessing the usefulness of the models to support MSFD, and its 11 descriptors, and similar environmental policies resulted in general in low scores, with only four models receiving a score above two. Most models either focused on some specific impact or lacked real world applications analysing MSFD descriptors (Fig. 9). The set of analysed biodiversity models provide good support to analysing MSFD descriptors 1 to 4, which relate to the maintenance of biodiversity, the impact of non-indigenous species, the impact of fisheries and the persistence and stability of marine food webs. There was moderate support for descriptors related to the impacts of eutrophication, alterations of the seabed and of hydrographic conditions. Few models covered other important aspects related to the impacts of marine pollution (Descriptors 8, 9 and 10), especially to anthropogenic noise and the introduction of other forms of energy into the environment (Descriptor 11). The last criteria considered whether the target biodiversity models can be coupled to other models predicting physical or biogeochemical aspects of marine ecosystems, higher trophic levels, or socioeconomic actors.

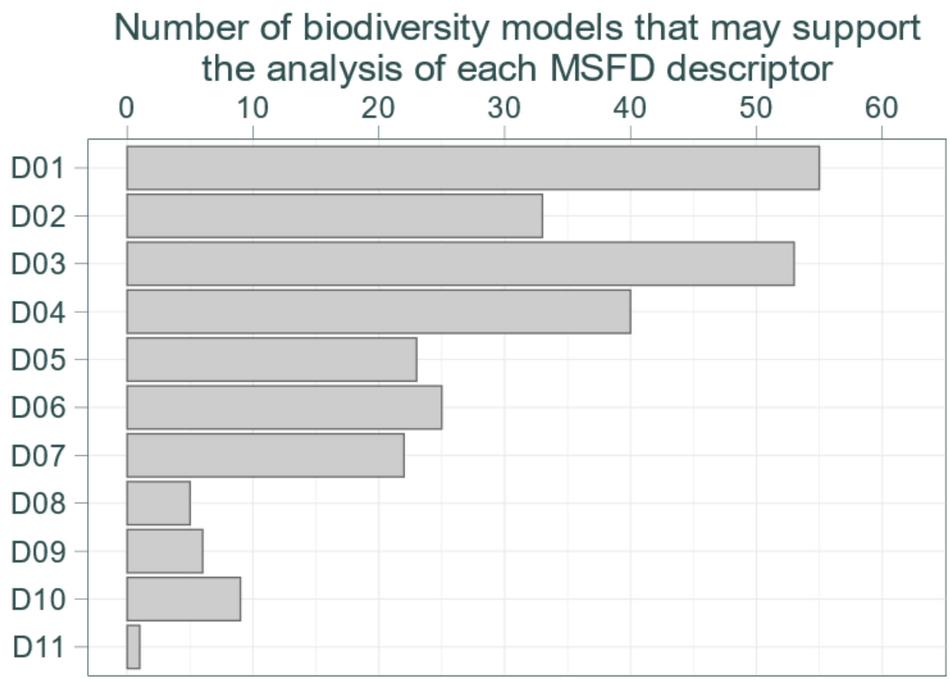


Figure 9: Histogram with the number of models that can potentially support the implementation of MSFD policies through the analyses of each of the eleven descriptors listed in Annex I of the Council Directive 2008/56/EC [http://data.europa.eu/eli/dir/2008/56/2017-06-07].

4.2.3. Initial ranking of biodiversity models

The scores assigned to each criterion were first averaged within each scoring category and then combined to rank biodiversity models according to their potential to support the development of DTO and the implementation of EU marine policies like the MSFD. The combination of average scores between categories used the weights presented in Table 4, which prioritize either the DTO, marine policies, or both simultaneously. Such ranking led to the initial selection of 15 candidate models with the best scores. These models ranked in the first quartile either in terms of their score based on the DTO or MSFD weighting schemes, and in the first tercile for any of these schemes. Almost half of the models in this initial list were biogeochemical models featuring the dynamics of nutrient cycles and lower trophic levels. Among them, models like ERSEM or ERGOM, with more than two decades of development and an extensive and varied list of applications, ranked in top positions, especially for their potential to support DTO development. The high rank of biogeochemical models indeed reflects that they are designed to be coupled with ocean circulation models, and they can thus be easily configured into coupled workflows. They also enable the assessment of multiple ecosystem health descriptors, including the dispersion of pollutants. They focus, however, on microbial processes and on the dynamics of lower trophic levels with a direct impact on bulk material cycling and energy flows, representing the impact of higher tropic levels implicitly through closure terms. In this respect, they convey an incomplete representation of marine biodiversity and ecosystems, as defined in the context of the current project.

The initial list also included models belonging to various categories that specifically target the simulation of higher trophic level dynamics and exhaustive representations of complex marine food webs. Approximately one third corresponded to whole system, end-to-end models (with five representatives), followed by a single representative of multispecies individual-based models, mass-based food web models, and multispecies size-based models. These models tended to rank higher in terms of their potential to contribute to the implementation of EU marine policies like MSFD but were also competitive in terms of previous application in coupled workflows, often involving models of ocean physical and biogeochemical dynamics proving inputs to account for physiological and trophic constraints on the performance and function of higher trophic levels.

Table 6: Topmost ranking biodiversity models according to the average score scheme (i.e., the average between scores resulting of the weighting schemes prioritizing DTO development or the support of EU policies). See Table 4 for further details about the weighting schemes

Model name	Model category	Score (rank) by weighting scheme		
		DTO	MSFD	Overall
ERSEM	Biogeochemical and lower trophic level	2.65 (2)	2.34 (2)	2.49 (1)
ERGOM	Biogeochemical and lower trophic level	2.7 (1)	2.27 (5)	2.49 (2)
OSMOSE	Multispecies individual-based	2.65 (3)	2.3 (4)	2.47 (3)
Atlantis	Whole system or end-to-end	2.48 (7)	2.35 (1)	2.41 (4)
PISCES	Biogeochemical and lower trophic level	2.5 (5.5)	2.14 (7.5)	2.32 (5.5)
MEDUSA	Biogeochemical and lower trophic level	2.5 (5.5)	2.14 (7.5)	2.32 (5.5)
StrathE2E	Whole system or end-to-end	2.37 (12)	2.26 (6)	2.31 (7)
BFM	Biogeochemical and lower trophic level	2.51 (4)	2.08 (13)	2.3 (8)
NORWECOM.E2E	Whole system or end-to-end	2.47 (8)	2.11 (11)	2.29 (9)
Ecopath with Ecosim	Mass based – food web	2.23 (18)	2.34 (3)	2.28 (10)
SCOBI nordic	Biogeochemical and lower trophic level	2.46 (9)	2.05 (15)	2.26 (11)
ECOSMO-E2E	Whole system or end-to-end	2.41 (10)	2.02 (16)	2.21 (12)
ECOMARS 3D	Biogeochemical and lower trophic level	2.35 (15)	2 (18)	2.18 (13)
APECOSM	Multispecies size-based	2.38 (11)	1.97 (21)	2.17 (14)
ECOTRAN e2e	Whole system or end-to-end	2.35 (16)	1.97 (20)	2.16 (15)

4.2.4. Proposed biodiversity models

The detailed assessment of the initial ranking and the focus of the current project on the identification of models able to complement the existing suite of monitoring and forecasting physical and biogeochemical products developed in the context of the Copernicus Marine Environment Monitoring Service (CMEMS) led to the exclusion of biogeochemical and lower trophic levels models since they are already mature and made operational in the 7 ocean forecasting centres of CMEMS, leaving eight candidate models from the initial list of 15 candidates. Instead of following precedence, the Steering Committee and the Project Team decided to complete the list through expert judgment. They selected two additional candidate models belonging to categories with a single representative in the original list: the Spatial Ecosystem And POpulation DYnamics Model (SEAPODYM, (Lehodey et al. 2008) and the Macroecological model (Jennings and Collingridge 2015).

SEAPODYM born as a multispecies individual-based model but has progressively evolved toward an end-to-end model linking the lower and mid trophic levels with an age-structured predator (fish) populations and considering the impact of fishing and environmental variability. In fact, the model has been widely used in fisheries assessment, especially of tropical fisheries of tuna and billfish in high seas areas, which are resources of high economic and conservation interest. This model is aligned with DTO/MSFD goals of supporting dynamic management of the high seas as the SPC (Secretariat of the Pacific Community) and CLS (Collecte Localisation Satellite), the main developers of the model, aims to combine the model with satellite observation and real time data collection to develop operational real time applications to monitor and manage marine resources. As such, it contributes to CMEMS and has been proposed by Mercator to be included in Copernicus as a component of the DTO. Taken together, these characteristics make SEAPODYM a suitable candidate and recommend further assessments in the context of the present project.

The Macroecological model pioneered global scale, size-spectrum modelling of the biomass of higher trophic levels. First used by Jennings and Collingridge (2015) to assess consumer biomass at the global scale, this model has been used to assess the magnitude of the impact of fisheries on total biomass and trophic flows in marine pelagic ecosystems, and to project the potential impact of climate change on future fisheries yields. Indeed, it is also one of the nine models contributing to ISIMIP assessments of global fisheries (Inter-Sectoral [Climate Change] Impact Model Intercomparison Project; see www.isimip.org).

Table 7 list the final 10 selected biodiversity models. Half of them represent whole system, end-to-end models (Atlantis, StrathE2E, NORWECOM.E2E, ECOSMO-E2E, and ECOTRAN e2e), followed by two representatives of alternative approaches to multispecies modelling based either on extending individual-based models (OSMOSE and SEAPODYM), or size-based models (APECOSM and Macroecological). The list is completed with Ecopath with Ecosim, the single representative of mass-based food web models, but one of the most versatile models in terms of its broad application to different systems and environmental stressors. All these models simulate the dynamics of multiple species or groups and their interactions, modulated by environmental variability and the impact of human activities and, therefore, aligned with DTO/MSFD goals within an EU context.

Table 7: Definitive list of selected biodiversity models to implement higher trophic levels and complex food webs in DTO and support EU policies

Model name	Model category
OSMOSE	Multispecies individual-based models
Atlantis	Whole system or end-to-end models
StrathE2E	Whole system or end-to-end models
NORWECOM.E2E	Whole system or end-to-end models
Ecopath with Ecosim	Mass based - food web models
ECOSMO-E2E	Whole system or end-to-end models
APECOSM	Multispecies size-based models
ECOTRAN e2e	Whole system or end-to-end models
SEAPODYM	Multispecies individual-based models
Macroecological	Multispecies size-based models

5. Analysis of selected biodiversity/ecosystem models

Analyses on the set of ten selected models of marine biodiversity and ecosystems rely on Database #3, which is an extended version of Database #2 featuring information to further document the capability of each proposed model to contribute to DTO implementation and to support MSFD policy. The analyses were structured in three stages. First, we prepared and sent a questionnaire to each model development teams to gather further details about the main characteristics and capabilities of each model. Then, we homogenized and coded the answers of the questionnaire to combined them with Database #2. Finally, we explored the resulting fields to synthetize the main strengths and weaknesses of each modelling approach and identify potential synergies arising from the combined use of alternative biodiversity/ecosystem models.

5.1. Questionnaire for model development teams

Database #3 extends previous Database #2 to provide a detailed account of the capability of each of the ten models selected during the second phase of the project to contribute to implement the DTO and support MSFD policy. In contrast to previous databases, Database #3 features technical details about the strategy and future development plans of each model, and a detailed account of past and current applications of the model. To gather this information, we prepared a questionnaire and ask leading scientists, from each of the model development teams, to fill them up. Some of the aspects covered in the questionnaire partially overlap with information included in the other databases, so it provided an opportunity to assess the reliability of previous efforts. The questionnaire was structured into the ten sections detailed below, each one targeting a specific aspect of model development and use:

1. General information: general characteristics and details about the model development team and about the person(s) that filled up the questionnaire.
2. Model generality and realism: model building strategy adopted by the development team, framed in terms of the trade-offs between generality, realism and precision and accuracy proposed by Levins (1966).
3. IT Transferability: accessibility of model codes and available options to compile, run and execute each model in different platforms (including special software and hardware requirements, and recommended configurations), and general development strategy (i.e., use of version control systems, and maintenance and organization of code repositories and contributors).
4. Easy of customisation: transferability of the model and possibility of applying it to different systems and by different set of users. The questions also inquire about model tuning, input data streams and how easy is to coupling it to other models.
5. Operationality: level of maturity considering its operational status, the identification of specific management applications or simulation experiments reproducing real world scenarios.
6. Spatial and temporal scalability: transferability to new spatial and temporal domains and resolutions.
7. Model tuning and assessment: calibration and assessment of the models and motivation, rationale, methods and results of this process.
8. Explicit results: applications, products or services deployed that may support MSFD implementation.
9. Potential integration with Copernicus biogeochemical models: potential to integrate each model into integrated modelling workflows and contribute to DTO implementation.
10. User community: model user community and its relationship with the model development team.

The questionnaire was coded into an online form, which enabled the project team to gather all the information remotely and provided flexibility to model development teams to answer all the questions. The questionnaire was long and included a total of 46 questions; seven of them were already answered by the project team and required the respondents to just check the answers. Most of the questions, however, were open questions, and the other third were closed questions or multiple-choice questions that do not require writing an elaborate response. Completing the questionnaire requires a considerable amount of effort and time (available responses suggest it takes about 2 hours to answer the 46 questions). At the time of writing this draft, six from a total of ten model development teams have already completed and submitted their questionnaire. Another three teams have communicated their intention to contribute to the project, and the project team is just pending on receiving a positive from one of the model development teams. **Annex 6** provides a full account of the questionnaire.

5.2. Homogenization and coding for database development

The answers to the questionnaires were combined with data about each proposed model gathered in the previous phases to generate **Database #3**. Answers to closed and multiple-choice questions were directly coded into new database fields as numbers, string or lists as appropriate (see Database #3). Answers to open questions were independently examined by at least two members of the project team before preparing a list of unique values based on all available answers. Although the database included all the free-text responses provided verbatim, the project team added new categorical, ordinal and interval variables to synthetize available information. For instance, question #28 asked about management applications, and it was translated first into a set of closed questions to reflect whether or not the model has contributed to support decision makers, resource managers or impact assessments, and if that was the case, which species, systems and regions were the target of such analyses. All data were introduced with a consistent format toward easing automatic processing during later analyses.

5.3. Analysis of proposed biodiversity/ecosystem models

The ten selected biodiversity models encompass a variety of modelling approaches and development strategies. This section provides a short overview of their main characteristics, which are coded into **Database #2** and **Database #3**. The overview is mainly based on the answers contributed by the model development teams to the online questionnaire described above, highlighting the aspects of especial interest outlined in sect 7.1.

Half of the model development teams were based within EU countries, though all of them are international teams running collaborations spanning across continents. Indeed, many of the teams based outside EU have participated at some point in EU research funding programs. Model development teams provided the URL of reference websites for each model and the contact details of a team member available to provide further information when needed.

In terms of IT transferability, the model development teams adopted no usage restriction policies, and they are open to share model source codes, which are available in most cases only under request. The teams also tended to adopt open source or freeware technologies to develop their models, with the single exception of ECOTRAN-E2E, which was originally coded in MatLab® but may be easy to adapt to Octave. Development teams also devoted considerable effort to develop simple command line interfaces to their models and to make them available into different platforms, including Linux. The degree of development and the quality of model documentation varies, however, among models. Some teams just follow the standard practice of documenting model development through articles published in scientific journals. Other teams have devoted a great effort to document their models and develop tutorials, best practice guidelines and even online courses. In this latter respect, the documentation of Atlantis, Ecopath with Ecosim, StrathE2E and OSMOSE excels. All the teams seem, however, committed to continue working to improve their documentation. They also share a common development strategy based on an open collaboration model among core model developers through a central repository to enable version control.

In terms of the ease of customization and transferability of the models to different systems, all the selected models ranked high in terms of their generality and realism. They are models that simultaneously describe the dynamics of several ecosystem types and domains and provide a detailed representation of marine food webs. They incorporate external forcing on the dynamics of marine food webs that enable assessing the impact of a great variety of environmental stressors (Table 8). External drivers include both biogeochemical variables (mainly temperature, oxygen, and oceanic currents) and anthropogenic impacts (mainly fishing effort). These drivers enable coupling to biogeochemical models outputs and the assessment of the impact of different interventions. Relatively few models use other outputs from biogeochemical models of interest for the MSFD, such as pH, salinity or the concentration of pollutants and contaminants. The models share basic ideas about the structuring of marine ecosystems, with food webs strongly linked by size dominated by predatory and competitive interactions. Fewer models (Atlantis, Ecopath with Ecosim, and ECOSMO E2E) implement positive interactions. They represent, however, complementary approaches ranging from the strategic, conceptual approach of the Macroecological model, to the highly resolved food webs implemented in Ecopath with Ecosim, which may include hundreds of species. Despite their apparent complexity, model development teams concurred in the relatively short time required to setup their models (less than 2 years), highlighting the availability of extensive sensitivity analyses that reduce the burden of developing new parameterizations and ease the application to new systems.

Table 8: Environmental and anthropogenic drivers featured by the selected models. Data extracted from the response contributed by model development teams

	Atlantis	Ecopath with Ecosim (EwE)	Macroecological	ECOSMO E2E	StrathE2E	NORWECOM. E2E	ECOTRAN E2E	OSMOSE	APECOSM	SEAPODYM	TOTAL
Temperature	X	X	X	X	X	X	X	X	X	X	**10**
Fishing effort	X	X		X	X	X	X	X		X	**8**
Oxygen	X	X		X				X	X	X	**6**
Ocean currents	X			X	X		X		X	X	**6**
Primary production		X	X						X	X	**4**
Plankton biomass		X						X	X	X	**4**
Eutrophication	X	X			X	X					**4**
Aquaculture	X	X			X	X					**4**
pH and acidification	X	X				X					**3**
Nutrients	X				X	X					**3**
Habitat heterogeneity	X	X			X						**3**
Habitat alteration	X	X		X							**3**
Salinity	X	X									**2**
Pulse perturbations		X			X						**2**
Light									X	X	**2**
Invasive species		X						X			**2**
Contaminants	X					X					**2**
Turbidity					X						**1**
Secondary production									X		**1**
Press perturbations					X						**1**
Pollutants		X									**1**
Noise and light	X										**1**
Micronekton										X	**1**
Ice cover		X									**1**
Fisheries economics									X		**1**
Detritus									X		**1**
Depth		X									**1**
Demographics									X		**1**
Atmospheric deposition					X						**1**

Model development teams consider that their models are close to an operational status or have reached a high degree of maturity. For instance, they ranked many models at levels of six or above in the Technology Readiness Level scale (TRL, which ranges from 1 to 9; level 6, for instance, corresponds to technologies demonstrated in a relevant environment). The models have been extensively used to assess environmental issues and support management decisions in the context of eutrophication, fisheries management and marine conservation, featuring both local- and large-scale applications.

The versatility of selected models results in part from their high scalability. Model development teams indicated no major constraints to run their models with different integration time steps and under different spatial domains. They have been preferentially applied using daily timesteps over relatively coarse grids, which in principle might provide an adequate match with state-of-the-art operational biogeochemical models. All selected models have been coded as complete modules independent of any spatial grid or temporal schedule. Indeed, most of them have been explicitly developed to run under irregular, adaptable spatial grids. Model developers highlighted, however, some potential constraints in the case of individual-based models, in which assumptions underlying the implementation of the model might fail in coarse grids or turn computationally expensive for very fine grids.

Model tuning and assessment is probably the greatest constraint to transfer available models to new systems and to develop widespread, local applications ready to support management decisions. Selected models range from strategic models with few parameters to complex food webs models with hundreds of parameters, which involve poorly constrained physiological and ecological flux rates (Table 9). Almost all models feature complex food webs with a static network topology but require explicit parameterization of consumption rates. Many models also require specification of rates of physiological growth and mortality. Finally, evaluation of anthropogenic impacts such as fishing require additional specification of parameters coding harvest rates or the characteristics of fishing fleets. Model development teams also reported a variety of approaches to circumvent the challenge posed by the uncertainty of model parameters. Almost all models count with some protocol for model tuning that incorporates quantitative metrics. Some teams have even implemented sophisticated automatic calibration and uncertainty assessment routines based on likelihood methods and Monte Carlo approaches. Though most models adopt a “trajectory matching” approach (i.e., they just try to match size of a subset of target compartments), some models also target emergent properties like compartment fluxes or the entire size spectra (Atlantis, APECOSM) or they feature out of sample validation (OSMOSE).

Table 9: Type of parameters featured by the selected models. Data extracted from the response contributed by model development teams.

	Atlantis	Ecopath with Ecosim (EwE)	Macroecological	ECOSMO E2E	StrathE2E	NORWECOM. E2E	ECOTRAN E2E	OSMOSE	APECOSM	SEAPODYM	TOTAL
Consumption rate	X	X		X	X		X	X	X		**7**
Mortality rate	X			X	X	X		X		X	**6**
Growth rate	X			X	X	X		X		X	**6**
Diet composition	X	X			X	X	X	X			**6**
Fish productivity	X				X			X	X	X	**5**
Harvest rate	X				X	X		X			**4**
Production rate		X	X				X				**3**
Migration rate							X		X	X	**3**
Intersection strength	X				X			X			**3**
Fecundity						X			X		**2**
Catch rate		X					X				**2**
Biomass		X					X				**2**
Trophic efficiency			X								**1**
Size structure			X								**1**
Sinking rate			X								**1**
Predator-prey ratio			X								**1**
Physiological tolerance										X	**1**
Light attenuation				X							**1**
Detection rate									X		**1**

In terms of the results of each model, we inquired model development teams to report their impressions on the potential and realized capability to support MSFD implementation. We explicitly asked for applications, products or services deployed that may contribute information related to MSFD descriptors (Table 10 and Table 11). As expected, selected models are able to inform about multiple descriptors (seven on average), but no team has deployed yet applications for all descriptors. Taken together, the models provide a balanced coverage of all MSFD descriptors, with potential to contribute ensemble assessments of eutrophication [D5], the integrity of marine food-webs [D4], and biodiversity conservation [D1]. About half of the models inform on the potential impact of invasive species [D2], fisheries [D3], alterations of the seabed [D6], and changes in hydrographic conditions [D7]. Finally, few models covered contaminants [D9], marine litter [D10], and external energy inputs [D11]. Model development teams also highlighted that their models may be helpful to support other policies such as the Common Fisheries Policy (CFP), EU Habitats Directive, Biodiversity Convention (CBD), and UN Sustainable Development Goals (SDGs), including the contribution to state-of-the-art initiatives like ISIMIP Fish-MIP.

Table 10: Descriptors of the MSFD policy that have been supported by the selected models. Data extracted from the response contributed by model development teams.

	Atlantis	Ecopath with Ecosim (EwE)	Macroecological	ECOSMO E2E	StrathE2E	NORWECOM. E2E	ECOTRAN E2E	OSMOSE	APECOSM	SEAPODYM	TOTAL
D1. Biodiversity is maintained	X	X					X	X	X		5
D2. Non-indagenous species do not adversely alter the ecosystem	X	X							X		3
D3. The population of commercial fish species is healthy	X	X			X			X	X	X	6
D4. Elements of food web ensure long-term abundance and reproduction	X	X			X		X	X	X		6
D5. Eutrophication is minimised	X	X		X		X	X				5
D6. The sea floor integrity ensures functioning of the ecosystem		X		X	X						3
D7. Permanent alteration of hydrographical conditions does not adversely affect the ecosystem	X			X		X	X		X		5
D8. Concentrations of contaminants give no effects	X	X									2
D9. Contaminants in seafood are below safe levels				X							1
D10. Marine litter does not cause harm											0
D11. Introduction of energy (including underwater noise) does not adversely affect the ecosystem	X	X		X							3

Table 11: Descriptors of the MSFD policy that could potentially be featured by the selected models. Data extracted from the response contributed by model development teams.

	Atlantis	Ecopath with Ecosim (EwE)	Macroecological	ECOSMO E2E	StrathE2E	NORWECOM. E2E	ECOTRAN E2E	OSMOSE	APECOSM	SEAPODYM	TOTAL
D1. Biodiversity is maintained	X	X			X		X	X	X		6
D2. Non-indagenous species do not adversely alter the ecosystem	X	X					X	X	X		5
D3. The population of commercial fish species is healthy	X	X			X		X	X	X	X	7
D4. Elements of food web ensure long-term abundance and reproduction	X	X			X	X	X	X	X		7
D5. Eutrophication is minimised	X	X		X	X	X	X	X			7
D6. The sea floor integrity ensures functioning of the ecosystem	X	X		X	X						4
D7. Permanent alteration of hydrographical conditions does not adversely affect the ecosystem	X			X		X	X		X		5
D8. Concentrations of contaminants give no effects	X	X			X	X		X	X		6
D9. Contaminants in seafood are below safe levels	X			X		X			X		4
D10. Marine litter does not cause harm	X				X						2
D11. Introduction of energy (including underwater noise) does not adversely affect the ecosystem	X	X		X	X						4

Model development teams also reported high prospects in terms of the potential integration with Copernicus biogeochemical models. Most models have already used monitoring and forecasting physical and biogeochemical products developed in the context of the Copernicus Marine Environment Monitoring Service (CMEMS). These applications featured mainly one-way coupling (forcing), though three models have been dynamically coupled to CMEMS biogeochemical models (two-way coupling) (ASPECOSM, ECOSMO-E2E, and NORWECOM.E2E), or to other models of similar complexity (ECOTRAN E2E, OSMOSE (ROMS), and Ecopath with Ecosim). Some groups are actively working to implement two-way coupling schemes with CMEMS models (SEAPODYM). All groups were optimistic and eager to implementing two-way coupling with CMEMS models.

Finally, in terms of efforts to interact and engage with the user community of their models, development teams reported a development path triggered by scientific research rather than meeting the needs of a target user community. Most selected models were initially designed to help answer scientific questions, and applications and interactions with users lead later to an extended focus. The interaction with users and reciprocal feedback is in most cases, however, unplanned. Development groups are in general open to adopt proactive approaches to engage and benefit from their user community.

6. Online workshop

The project team organised a workshop to boost public participation in the project and receive feedback from biodiversity modelers and other stakeholders on the identification and characterization of biodiversity models that could contribute to the implementation of the DTO. The workshop held on 15th of September 2022, as an online event with a duration of two and a half hours. Workshop participants had the opportunity to meet in small group session to foster discussion and public engagement toward the accomplishment of project goals. The workshop has been planned as an open and participatory event with the following agenda:

10:00 – 10:15	Welcome to workshop and introduction by the DG-RI: The European Digital Twin Ocean (DTO) and Marine Biodiversity	Nicolas Segebarth (DG-RI)
10:15 – 10:25	A Horizon Scan of Marine Biodiversity Modelling	Guillem Chust
10:25 – 10:40	Inventory of Ocean Biodiversity Models	Xavier Corrales
10:40 – 10:55	Proposal of Biodiversity Models for the DTO	Fernando González
10:55 – 11:05	Questions and split in groups	Meritxel González
11:05 – 11:50	Small group discussions	Chaired by AZTI
11:50 – 12:20	Open discussion	Chaired by AZTI
12:20 – 12:30	Synthesis and Next Steps	AZTI and DG-RI

A list of invited institutions is provided in **Annex 8**. A total of 66 participants have been registered covering different expertise and nationalities.

Group session

After exposition of the main findings and current state of the project, the workshop proceeded with a short session devoted to small group discussion. The aim of these small discussion groups was to ease participation from all attendants. The sessions were run in parallel. Workshop participants were randomly assigned to two discussion groups to foster interactions among participants with diverse backgrounds. The discussion was open to suggestions and questions by workshop attendants, either through direct intervention or by typing their questions on an interactive chat. The two sessions ran in parallel under the coordination of at least two members of the project team whose mission was to foster participation and to take note of all interventions. Moderators of each session attempted to cover at least the following points.

Overall approach and methodology

1. The project conducted first an extensive literature review to identify candidate models, ranked them based on its ability to support MSFD and the DTO, and concluded with a more detailed characterization of a small subset of top ranked models. Do you find the overall approach appropriate? What have you changed?

2. The literature screening sought modelling studies simultaneously analysing the effect of environmental conditions and human activities and pressures on marine ecosystems. The resulting set of models was revised and completed to result in a total of 62 models. Do you have suggestions on how to improve this horizon scanning? Do you miss important modelling tools in the initial screening?

3. After a detailed analysis of the characteristics of each model, they were ranked based on six dimensions (nature of their outputs, generality and realism, ease of development, software characteristics, and support to MSFD and DTO). Do you miss any model feature that should be included in the scoring?

4. The weights assigned to rank candidate models rewarded models able to support MSFD, DTO development and providing model generality and realism over other aspects. Do you find the scoring adequately reflects the objectives of the study? Can you suggest an alternative weighting?

Proposed models and perspectives

5. Selected models attempt to support MSFD policies and boost DTO development. Are you aware of any model that may potentially complement the list of proposed models?

6. According to the results, the set of candidate models may be able to easily adapt to other geographical domains and resolutions and inform about human interventions across European seas from the perspective of the MSFD. Do you identify any information gap? How would you further assess potential model capabilities to support MSFD and DTO?

7. There are taxonomic groups that are not well represented and human impacts that cannot be assessed by the set of selected models. Which aspects are important to further develop?

8. Which international initiatives not considered here do you think might be interested in the information generated in the present study?

Small group session 1

Twelve researchers and stakeholders participated in the session group, with Guillem Chust as moderator and Marina Chifflet as secretary. All participants introduced themselves. Discussion deal with the following issues:

- On the relevance to be careful with additional models and the need to clarify why this addition was made. It was responded that the project focus on mapping a landscape of biodiversity modelling, whilst the idea for the future now is to develop de DTO which will be a public service with new applications, where joining new initiatives for the society, for blue economy and not only for science.

- On the importance of differentiation biogeochemical models with biodiversity models. It was responded that exclusion of biogeochemical models are because they are in fact implicit in the DTO as they are more advanced and need for running the rest of biodiversity models.

Small group session 2

Ten researchers and stakeholders participated in the session group, with Xavier Corrales as moderator, and Fernando González as secretary. The chair opened the session with a short speech to introduce the rules and aims of the small group sessions. Then the participants started to review the set of guideline questions in order. The questions raised the following comments and suggestions in a fluid conversation in which almost all attendants participated to some extent:

- On the difficulty to compare different models. Citing as an example Ecospace, participants highlighted that there is always room to improve a model through the addition of new compartments or interactions to account for previously unnoticed processes or aspects of interest.

- On practices adopted in management scenarios, participants discussed standard procedures followed by ICES Working Group on Multispecies Assessments Methods

(WGSAM). This group has designed and implemented what they call "key-runs", which are a set of dedicated tests and simulation experiments to assess model quality and robustness. These runs are used for the internal assessment of models. Only those models with enough quality and passing a minimum set of standards receive a certification by the group, which is required to contribute to fisheries assessment.

- On the preliminary nature of the project. The aim of the project is to identify available approaches, and thus models that already provide an adequate description of marine ecosystems, aligned with the objectives of MSFD and the implementation of DTO. The suggestion to design and coordinate a set of “key-runs” to further assess the initial set of proposed models or to assess another candidate models if relevant, and it seems indeed a natural next step.

- On the aim of the project and its overall focus. The criticism focused on the apparent lack of a direct assessment of the theoretical foundations of alternative biodiversity models, stressing that the assumptions and conceptual view of marine ecosystem implemented by these models is the most important aspect to consider in the implementation of the DTO.

- On the artificial and sometimes inadequate application of model categories to group biodiversity models, providing as an example model like OSMOSE or APECOSM, which are E2E models, or SeaPODYM, which is a single species model.

- On the overall aim of the project team to avoid a direct judgement of the ideas behind the models given the inextricable issues associated with rank alternative theories. To avoid biases due to personal preferences, the project team focused on specific model traits, like their ability to inform MSFD policies, or records about their demonstrated ability to contribute to coupled workflows involving ocean physics of biogeochemical models.

- On the need to incorporate and discuss the representation of biodiversity on available models, and to ensure that the set of models used by the DTO represents alternative views by featuring a balance across distinct modelling approaches and philosophies. Model categories play no role on the ranking or selection of alternative models. The categories will be revised based on feedback received from model developers.

- Participants asked about the implementation of MSFD and about how models can be improved to contribute information about MSFD descriptors. They also expressed interest on receiving feedback from model users and policy makers about their information needs, recommending actions to foster this type of interactions among model developers and both direct and indirect users of model outputs.

- On the need to foster participation from marine biologists and to add biodiversity experts to these discussions in order to identify model development needs.

- Convenors reminded that the main intention of the workshop was to join marine experts with complementary backgrounds to precisely foster the kind of interactions.

- Attendants recommended the work led by Dr. Chiara Piroddi about how ecological models can contribute to support MSFD (Piroddi et al 2015, 10.1016/j.ecolind.2015.05.037), and about the potential inclusion of Gadget models in the list of candidate models potentially contributing to the DTO, providing as an example the model developed in the Baltic Sea, which includes three fish species of and seals.

- On the usefulness of Gadget models due to the combination of simplicity and ability to handle real world problems by keeping essential ecological mechanisms. The current focus of Gadget models on fisheries problems weighted them down compared to other biodiversity models that simultaneously handle other MSFD descriptors.

7. Concluding remarks

With the aim of identifying and characterizing a subset of candidate biodiversity models to contribute to the implementation of the European Digital Twin of the Ocean (DTO), we combined expert assessment and an extensive literature review of 5212 articles and technical reports from which 62 relevant biodiversity/ecosystem modelling approaches were identified. We conducted a detailed review to record the main characteristics of each model and to assess their realized and potential ability to support the implementation of DTO and EU environmental policies. Expert judgement led to the selection of the top ten candidate models. Subsequently, we undertook a detailed characterization of selected candidate models through careful review of each model and interviews with model development teams.

The selected 10 models were: APECOSM, Atlantis, EwE, ECOSMO-E2E, ECOTRAN e2e, Macroecological, NORWECOM.E2E, OSMOSE, SEAPODYM, and StrathE2E. Selected models simultaneously embrace the complexity of marine food webs intertwined with multiple interacting environmental stressors, and account for the impact of human activities on the marine environment. Development teams align with open and reproducible research practices promoted by the European Commission. These models can also be integrated into coupled workflows interacting both with physical and socioeconomic models, with the potential to contribute to the development of the DTO and boost the implementation of EU environmental policies.

All this work was disseminated to biodiversity modelers and other stakeholders and the participation of these selected experts through an online workshop on September 15th, 2022. A total of 66 participants, covering different expertise and nationalities, have attended to the workshop and participated in the session group.

The main outputs of the project include documenting and reporting of all the results and the development and curation of three online databases (DB) detailing: the output of the literature review (**Database#1**); the characterization of 62 relevant modelling approaches identified in the initial assessment (**Database #2**); and the in-depth analysis of the ten candidate models (**Database #3**).

References

Acosta, L. A., B. A. Wintle, Z. Benedek, P. B. Chhetri, S. J. Heymans, A. C. Onur, R. L. Painter, A. Razafimpahanana, and k. Shoyama. 2016. Using scenarios and models to inform decision making in policy design and implementation. Pages 43-100 *in* IPBES, editor. Methodological assessment of scenarios and models of biodiversity and ecosystem services [S. Ferrier, K. N. Ninan, P. Leadley, R. Alkemade, L. A. Acosta, H.R. Akçakaya, L. Brotons, W.W.L. Cheung, V. Christensen, K. A. Harhash, J. Kabubo-Mariara, C. Lundquist, M. Obersteiner, H. Pereira, G. Peterson, R. Pichs-Madruga, N. Ravindranath, C. Rondinini and B.A. Wintle (eds.)], Bonn, Germany.

Agardy, T., J. Alder, P. Dayton, S. Curran, A. Kitchingman, M. Wilson, A. Catenazzi, J. Restrepo, C. Birkeland, and S. Blaber. 2005. Coastal systems.

Andonegi, E., J. A. Fernandes, I. Quincoces, X. Irigoien, A. Uriarte, A. Pérez, D. Howell, and G. Stefánsson. 2011. The potential use of a Gadget model to predict stock responses to climate change in combination with Bayesian networks: the case of Bay of Biscay anchovy. ICES Journal of Marine Science **68**:1257-1269.

Barbier, E. B., S. D. Hacker, C. Kennedy, E. W. Koch, A. C. Stier, and B. R. Silliman. 2011. The value of estuarine and coastal ecosystem services. Ecological monographs **81**:169-193.

Barragán, J. M. and M. de Andrés. 2015. Analysis and trends of the world's coastal cities and agglomerations. Ocean & Coastal Management **114**:11-20.

Borja, A., M. P. White, E. Berdalet, N. Bock, C. Eatock, P. Kristensen, A. Leonard, J. Lloret, S. Pahl, and M. Parga. 2020. Moving toward an agenda on ocean health and human health in Europe. Frontiers in Marine Science **7**:37.

Coll, M., M. Albo-Puigserver, J. Navarro, I. Palomera, and J. M. Dambacher. 2019. Who is to blame? Plausible pressures on small pelagic fish population changes in the northwestern Mediterranean Sea. Marine Ecology Progress Series **617**:277-294.

Collie, J. S., L. W. Botsford, A. Hastings, I. C. Kaplan, J. L. Largier, P. A. Livingston, É. Plagányi, K. A. Rose, B. K. Wells, and F. E. Werner. 2016. Ecosystem models for fisheries management: finding the sweet spot. Fish and Fisheries **17**:101-125.

Corrales, X., M. Coll, E. Ofir, C. Piroddi, M. Goren, D. Edelist, J. Heymans, J. Steenbeek, V. Christensen, and G. Gal. 2017. Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. Marine Ecology Progress Series **580**:17-36.

Costello, M. J., M. Coll, R. Danovaro, P. Halpin, H. Ojaveer, and P. Miloslavich. 2010. A census of marine biodiversity knowledge, resources, and future challenges. PloS one **5**:e12110.

Christensen, V. and C. J. Walters. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling **172**:109-139.

Dambacher, J. M., H. W. Li, and P. A. Rossignol. 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. Ecology **83**:1372-1385.

de Oceanografia, L. d. C. M., P. A. Coelho, and M. Farol. 2019. STOMACH CONTENTS AND FEEDING HABIT OF Plagusia depressa (Fabricius, 1775)(CRUSTACEA: DECAPODA: PLAGUSIIDAE) IN SANDSTONE REEFS OF NORTHEAST BRAZIL. Revista Nordestina de Zoologia **12**:147-164.

Duarte, C. M., S. Agusti, E. Barbier, G. L. Britten, J. C. Castilla, J.-P. Gattuso, R. W. Fulweiler, T. P. Hughes, N. Knowlton, C. E. Lovelock, H. K. Lotze, M. Predragovic, E. Poloczanska, C. Roberts, and B. Worm. 2020. Rebuilding marine life. Nature **580**:39-51.

Dueri, S. and O. Maury. 2013. Modelling the effect of marine protected areas on the population of skipjack tuna in the Indian Ocean. Aquatic Living Resources **26**:171-178.

Fernandes, J. A., W. W. L. Cheung, S. Jennings, M. Butenschön, L. de Mora, T. L. Frölicher, M. Barange, and A. Grant. 2013. Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic bioclimate envelope model. Global Change Biology **19**:2596-2607.

Grimm, V. and S. F. Railsback. 2013. Individual-based modeling and ecology. Individual-Based Modeling and Ecology. Princeton university press.

Grüss, A., W. J. Harford, M. J. Schirripa, L. Velez, S. R. Sagarese, Y.-J. Shin, and P. Verley. 2016. Management strategy evaluation using the individual-based, multispecies modeling approach OSMOSE. Ecological Modelling **340**:86-105.

Halpern, B. S., M. Frazier, J. Afflerbach, J. S. Lowndes, F. Micheli, C. O'Hara, C. Scarborough, and K. A. Selkoe. 2019. Recent pace of change in human impact on the world's ocean. Scientific reports **9**:1-8.

Halpern, B. S., M. Frazier, J. Potapenko, K. S. Casey, K. Koenig, C. Longo, J. S. Lowndes, R. C. Rockwood, E. R. Selig, and K. A. Selkoe. 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications **6**.

Hazen, E. L., K. L. Scales, S. M. Maxwell, D. K. Briscoe, H. Welch, S. J. Bograd, H. Bailey, S. R. Benson, T. Eguchi, H. Dewar, S. Kohin, D. P. Costa, L. B. Crowder, and R. L. Lewison. 2018. A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. Science Advances **4**.

Heath, M. R. 2012. Ecosystem limits to food web fluxes and fisheries yields in the North Sea simulated with an end-to-end food web model. Progress in Oceanography **102**:42-66.

Heymans, J., M. Skogen, C. Schrum, and C. Solidoro. 2018. Enhancing Europe's capability in marine ecosystem modelling for societal benefit.

Hyder, K., A. G. Rossberg, J. I. Allen, M. C. Austen, R. M. Barciela, H. J. Bannister, P. G. Blackwell, J. L. Blanchard, M. T. Burrows, and E. Defriez. 2015. Making modelling count-increasing the contribution of shelf-seas community and ecosystem models to policy development and management. Marine Policy **61**:291-302.

Ince, D. C., L. Hatton, and J. Graham-Cumming. 2012. The case for open computer programs. Nature **482**:485-488.

Jennings, S. and K. Collingridge. 2015. Predicting consumer biomass, size-structure, production, catch potential, responses to fishing and associated uncertainties in the world's marine ecosystems. PloS one **10**:e0133794.

Jørgensen, S. E. and B. Fath. 2011. Fundamentals of Ecological Modelling: Application in Environmental Management and Research. 4 edition. Elsevier.

Kaschner, K., J. Ready, E. Agbayani, K. Kesner-Reyes, J. Rius-Barile, P. D. Eastwood, A. South, S. Kullander, T. Rees, R. Watson, D. Pauly, and R. Froese. 2011. Using 'Aquamaps' for representing species distribution in Regional Seas.

Kempf, A., G. E. Dingsør, G. Huse, M. Vinther, J. Floeter, and A. Temming. 2010. The importance of predator–prey overlap: predicting North Sea cod recovery with a multispecies assessment model. ICES Journal of Marine Science **67**:1989-1997.

Koen-Alonso, M. and P. Yodzis. 2005. Multispecies modelling of some components of the marine community of northern and central Patagonia, Argentina. Canadian Journal of Fisheries and Aquatic Sciences **62**:1490-1512.

Kooijman, B. and S. Kooijman. 2010. Dynamic energy budget theory for metabolic organisation. Cambridge university press.

Lange, M. and E. van Sebille. 2017. Parcels v0.9: prototyping a Lagrangian ocean analysis framework for the petascale age. Geosci. Model Dev. **10**:4175-4186.

Lehodey, P., I. Senina, and R. Murtugudde. 2008. A spatial ecosystem and populations dynamics model (SEAPODYM) - Modeling of tuna and tuna-like populations. Progress in Oceanography **78**:304-318.

Lett, C., P. Verley, C. Mullon, C. Parada, T. Brochier, P. Penven, and B. Blanke. 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. Environmental Modelling & Software **23**:1210-1214.

Levins, R. 1966. The strategy of model building in population biology. American Scientist **54**:421-431.

Lewy, P. and M. Vinther. 2004. A stochastic age-length-structured multispecies model applied to North Sea stocks. ICES CM **33**.

Lynam, C. P., L. Uusitalo, J. Patrício, C. Piroddi, A. M. Queirós, H. Teixeira, A. G. Rossberg, Y. Sagarminaga, K. Hyder, N. Niquil, C. Möllmann, C. Wilson, G. Chust, I. Galparsoro, R. Forster, H. Veríssimo, L. Tedesco, M. Revilla, and S. Neville. 2016. Uses of Innovative Modeling Tools within the Implementation of the Marine Strategy Framework Directive. Frontiers in Marine Science **3**:182.

Mislan, K., J. M. Heer, and E. P. White. 2016. Elevating the status of code in ecology. Trends in ecology & evolution **31**:4-7.

Moher, D., A. Liberati, J. Tetzlaff, and D. G. Altman. 2010. Preferred reporting items for systematic reviews and meta-analyses: The PRISMA statement. International Journal of Surgery **8**:336-341.

Nielsen, J. R., E. Thunberg, D. S. Holland, J. O. Schmidt, E. A. Fulton, F. Bastardie, A. E. Punt, I. Allen, H. Bartelings, and M. Bertignac. 2018. Integrated ecological–economic fisheries models—Evaluation, review and challenges for implementation. Fish and Fisheries **19**:1-29.

Nosek, B. A., G. Alter, G. C. Banks, D. Borsboom, S. D. Bowman, S. J. Breckler, S. Buck, C. D. Chambers, G. Chin, and G. Christensen. 2015. Promoting an open research culture. Science **348**:1422-1425.

Pendleton, L., K. Evans, and M. Visbeck. 2020. Opinion: We need a global movement to transform ocean science for a better world. Proceedings of the National Academy of Sciences **117**:9652-9655.

Pérez-Rodríguez, A., D. Howell, M. Casas, F. Saborido-Rey, and A. Avila-de Melo. 2017. Dynamic of the Flemish Cap commercial stocks: use of a Gadget multispecies model to determine the relevance and synergies among predation, recruitment, and fishing. Canadian Journal of Fisheries and Aquatic Sciences **74**:582-597.

Phillips, S. J., R. P. Anderson, M. Dudík, R. E. Schapire, and M. E. Blair. 2017. Opening the black box: An open-source release of Maxent. Ecography **40**:887-893.

Piroddi, C., H. Teixeira, C. P. Lynam, C. Smith, M. C. Alvarez, K. Mazik, E. Andonegi, T. Churilova, L. Tedesco, and M. Chifflet. 2015. Using ecological models to assess ecosystem status in support of the European Marine Strategy Framework Directive. Ecological Indicators **58**:175-191.

Plagányi, É. E. 2007. Models for an ecosystem approach to fisheries. Food & Agriculture Org.

Plagányi, É. E., A. E. Punt, R. Hillary, E. B. Morello, O. Thébaud, T. Hutton, R. D. Pillans, J. T. Thorson, E. A. Fulton, and A. D. Smith. 2014. Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish and Fisheries **15**:1-22.

Puccia, C. J. and R. Levins. 1985. Qualitative modeling of complex systems. Harvard University Press Cambridge, MA.

Punt, A. and D. Butterworth. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals Arctocephalus pusillus pusillus and the Cape hakes Merluccius capensis and M. paradoxus. South African Journal of Marine Science **16**:255-285.

Ready, J., K. Kaschner, A. B. South, P. D. Eastwood, T. Rees, J. Rius, E. Agbayani, S. Kullander, and R. Froese. 2010. Predicting the distributions of marine organisms at the global scale. Ecological Modelling **221**:467-478.

Rose, K. A., J. I. Allen, Y. Artioli, M. Barange, J. Blackford, F. Carlotti, R. Cropp, U. Daewel, K. Edwards, and K. Flynn. 2010. End-to-end models for the analysis of marine ecosystems: challenges, issues, and next steps. Marine and Coastal Fisheries **2**:115-130.

Scott, F., J. L. Blanchard, and K. H. Andersen. 2014. Mizer: An R package for multispecies, trait-based and community size spectrum ecological modelling. Methods in Ecology and Evolution **5**:1121-1125.

Senina, I., P. Lehodey, B. Calmettesa, S. Nicol, S. Caillot, J. Hampton, and P. Williams. 2016. Predicting skipjack tuna dynamics and effects of climate change using SEAPODYM with fishing and tagging data. Scientific Committee Twelfth Regular Session. Bali, Indonesia:3-11.

Shin, Y.-J. and P. Cury. 2004. Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. Canadian Journal of Fisheries and Aquatic Sciences **61**:414-431.

Speirs, D. C., S. P. Greenstreet, and M. R. Heath. 2016. Modelling the effects of fishing on the North Sea fish community size composition. Ecological Modelling **321**:35-45.

Stocker, T. F. 2015. The silent services of the world ocean. Science **350**:764-765.

Thuiller, W., B. Lafourcade, R. Engler, and M. B. Araújo. 2009. BIOMOD–a platform for ensemble forecasting of species distributions. Ecography **32**:369-373.

Tittensor, D., M. Coll, and N. D. Walker. 2018. A protocol for the intercomparison of marine fishery and ecosystem models: Fish-MIP v1. 0.

Travers-Trolet, M., Y.-J. Shin, and J. Field. 2014. An end-to-end coupled model ROMS-N2P2Z2D2-OSMOSE of the southern Benguela foodweb: parameterisation, calibration and pattern-oriented validation. African Journal of Marine Science **36**:11-29.

Vierros, M., I. D. Cresswell, P. Bridgewater, and A. D. Smith. 2015. Ecosystem approach and ocean management.

Waltham, N. J., M. Elliott, S. Y. Lee, C. Lovelock, C. M. Duarte, C. Buelow, C. Simenstad, I. Nagelkerken, L. Claassens, and C. K. Wen. 2020. UN Decade on Ecosystem Restoration 2021–2030—what chance for success in restoring coastal ecosystems? Frontiers in Marine Science **7**:71.

Warton, D. I., F. G. Blanchet, R. B. O'Hara, O. Ovaskainen, S. Taskinen, S. C. Walker, and F. K. Hui. 2015. So many variables: joint modeling in community ecology. Trends in ecology & evolution **30**:766-779.

Wilkinson, D. P., N. Golding, G. Guillera-Arroita, R. Tingley, and M. A. McCarthy. 2019. A comparison of joint species distribution models for presence–absence data. Methods in Ecology and Evolution **10**:198-211.

Worm, B., E. B. Barbier, N. Beaumont, J. E. Duffy, C. Folke, B. S. Halpern, J. B. Jackson, H. K. Lotze, F. Micheli, and S. R. Palumbi. 2006. Impacts of biodiversity loss on ocean ecosystem services. Science **314**:787-790.

ANNEXES

Annex 1. Analysis of the keyword for each model category

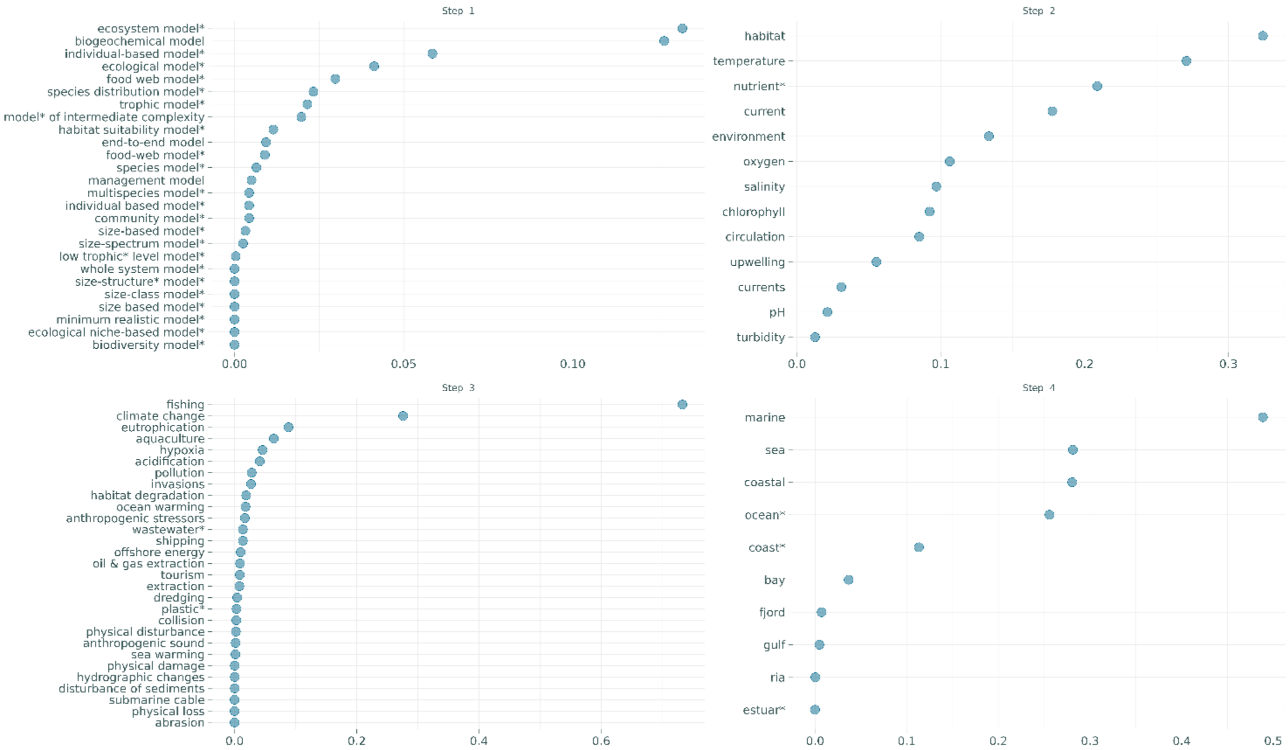


Fig. 1. Fraction of publications of biodiversity/ecosystem models containing each search term in each step.

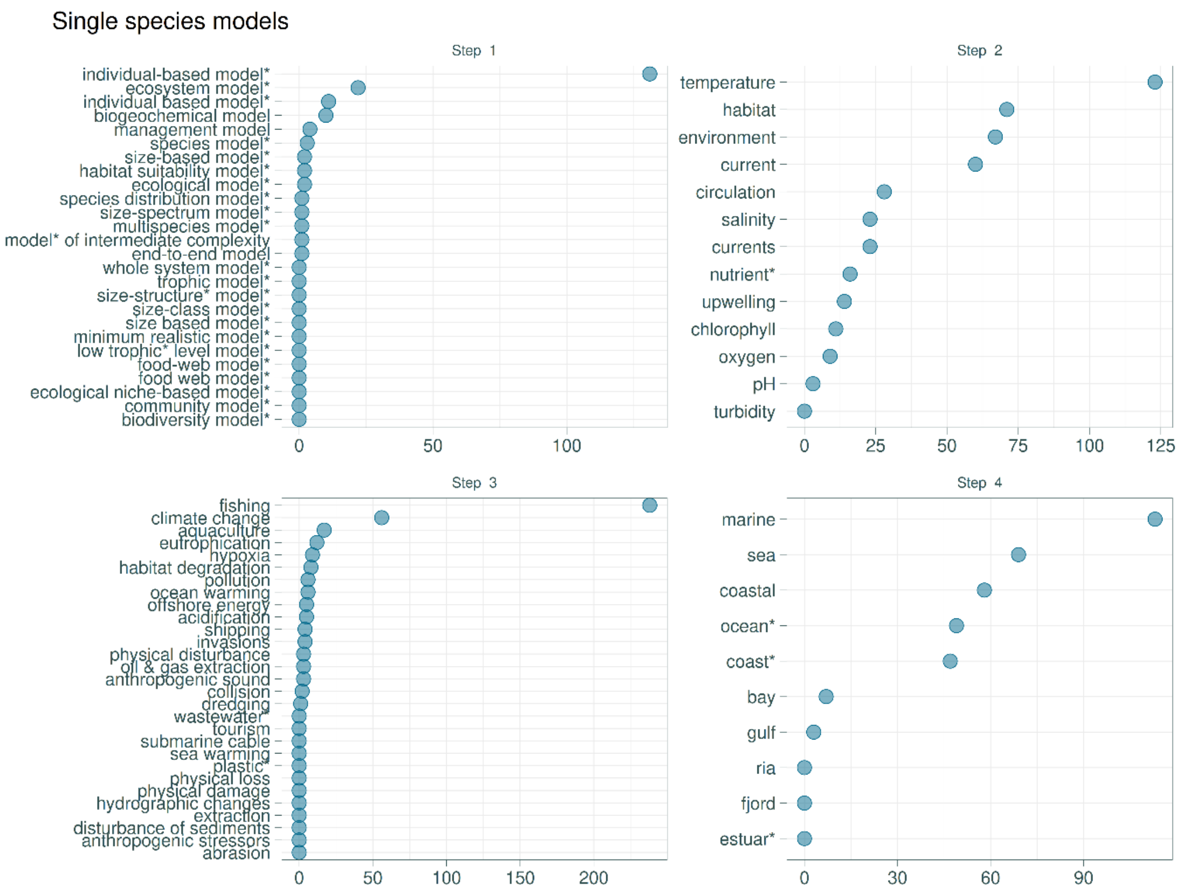


Fig. 2. Number of publications of single species models containing each search term in each step.

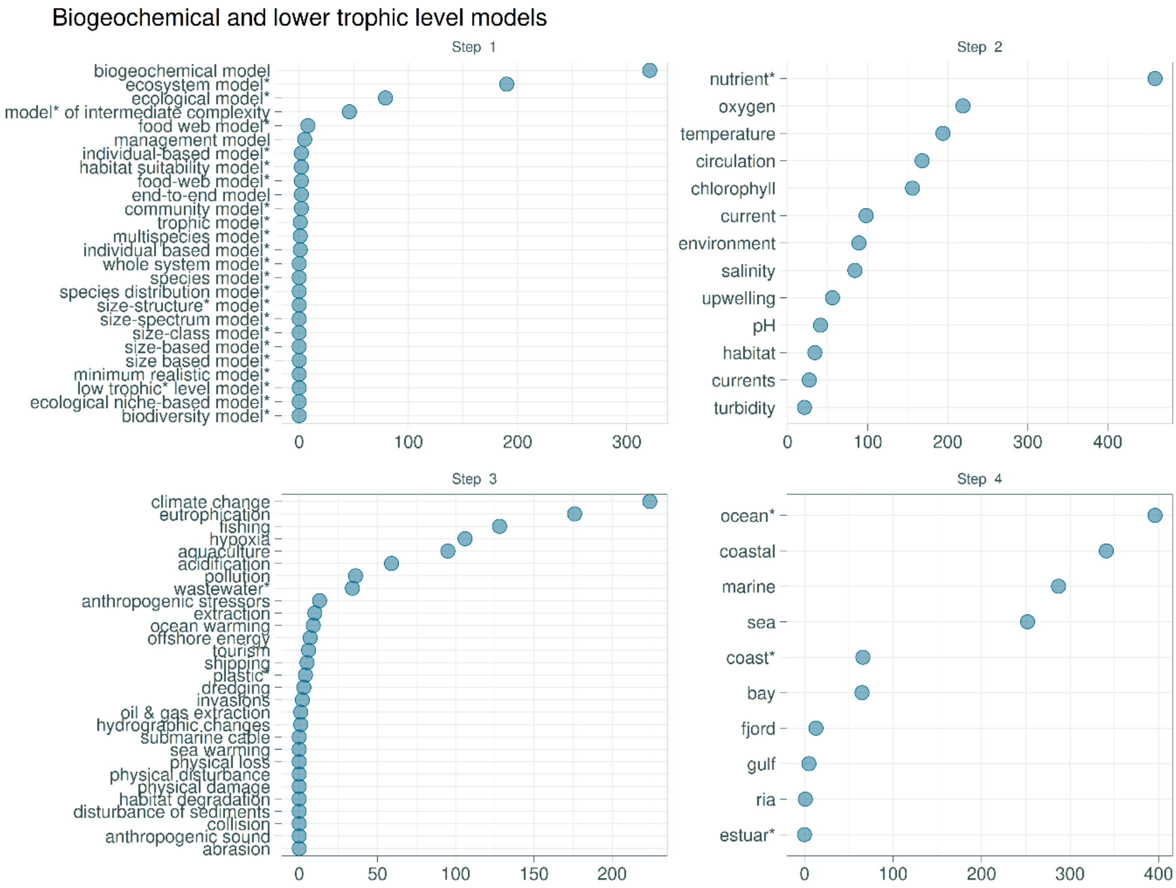


Fig. 3. Number of publications of biogeochemical models containing each search term in each step.

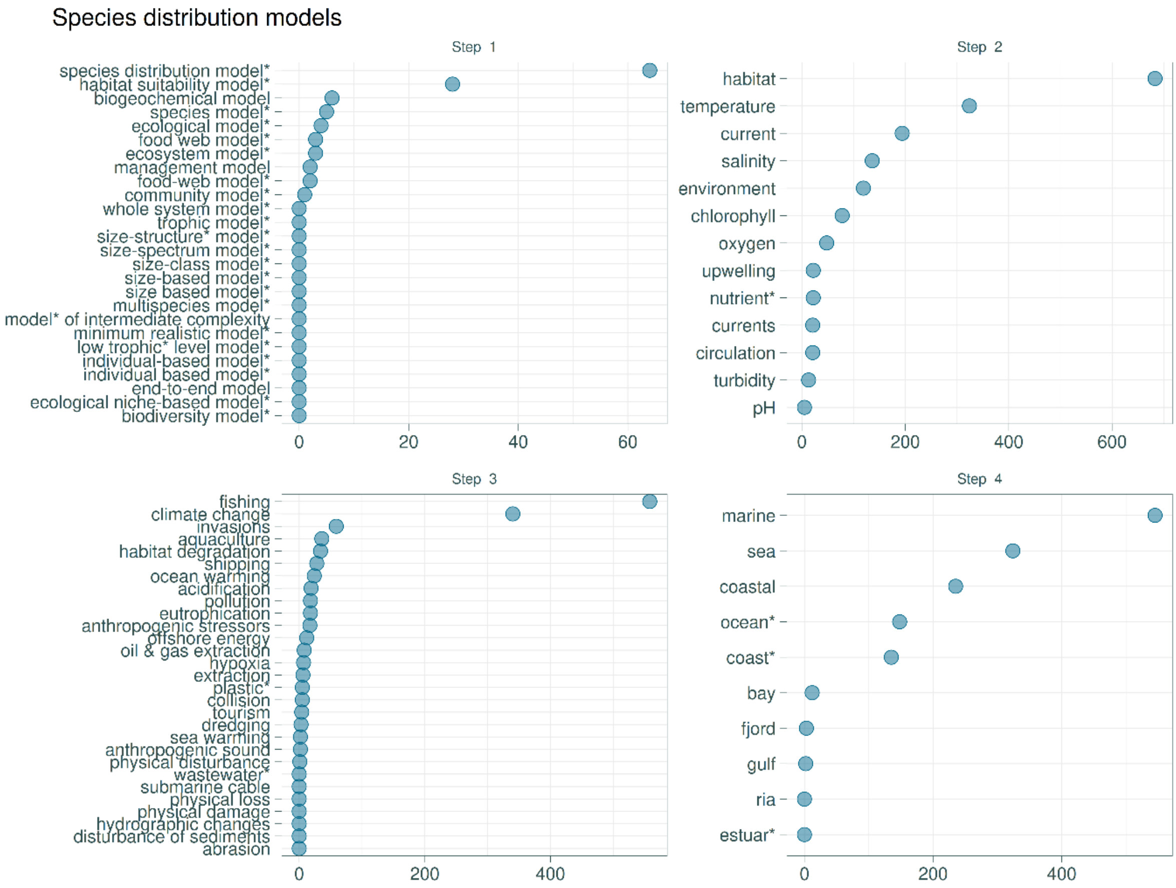


Fig. 4. Number of publications of species distribution models containing each search term in each step.

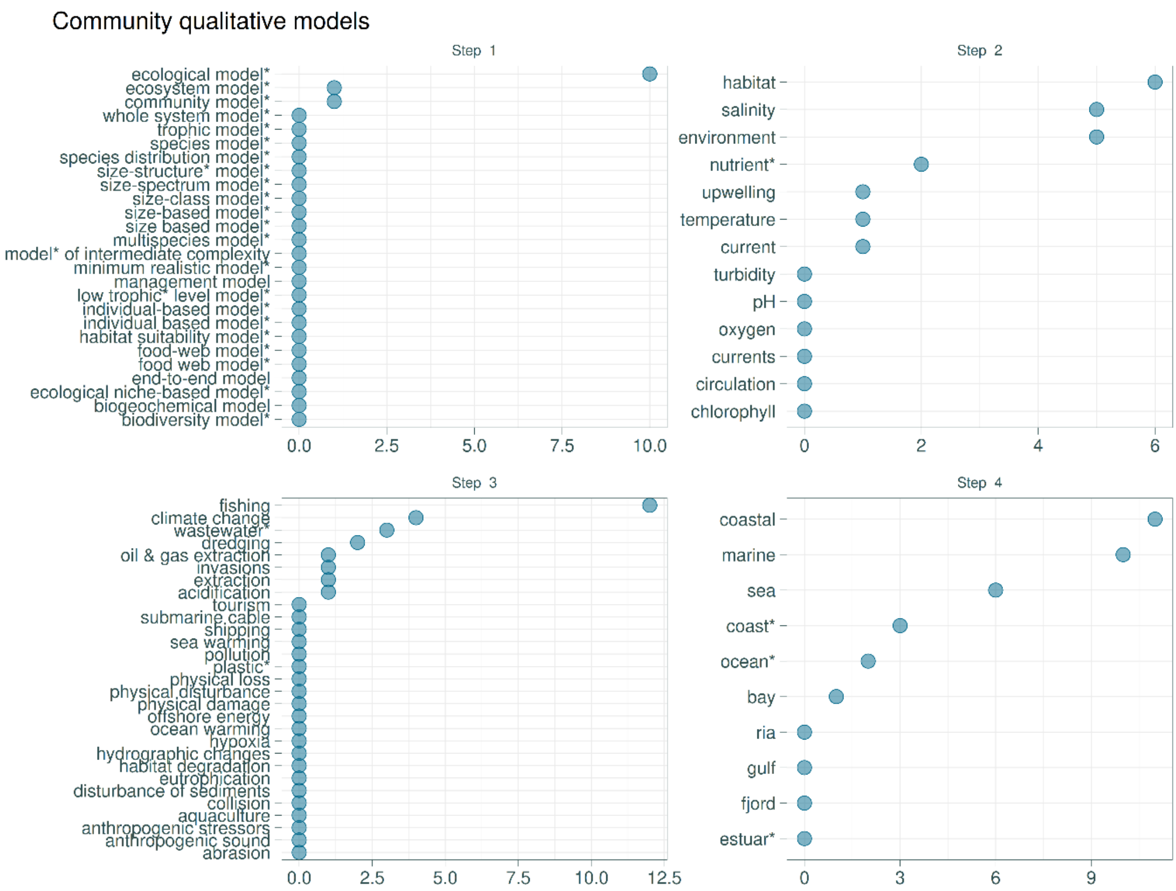


Fig. 5. Number of publications of community qualitative models containing each search term in each step.

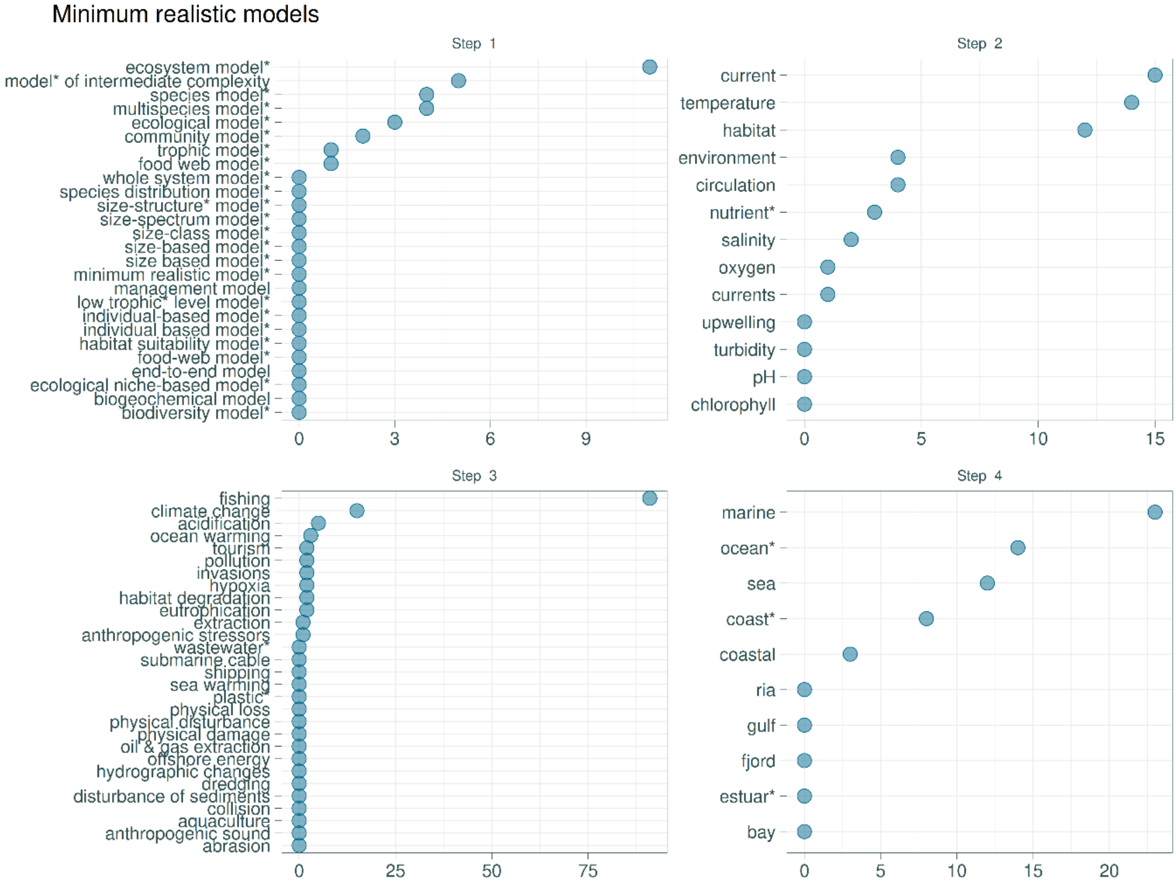


Fig. 6. Number of publications of minimum realistic models containing each search term in each step.

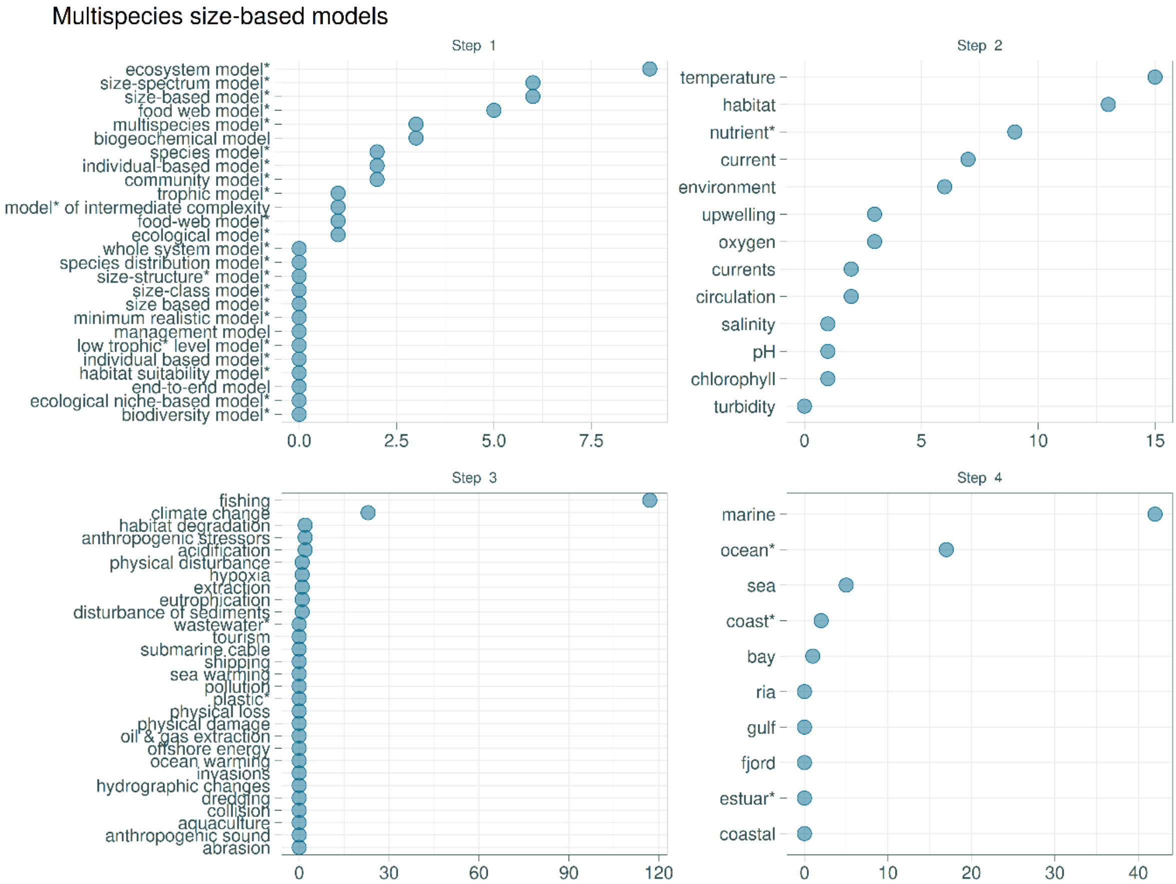


Fig. 7. Number of publications of multispecies size-based models containing each search term in each step.

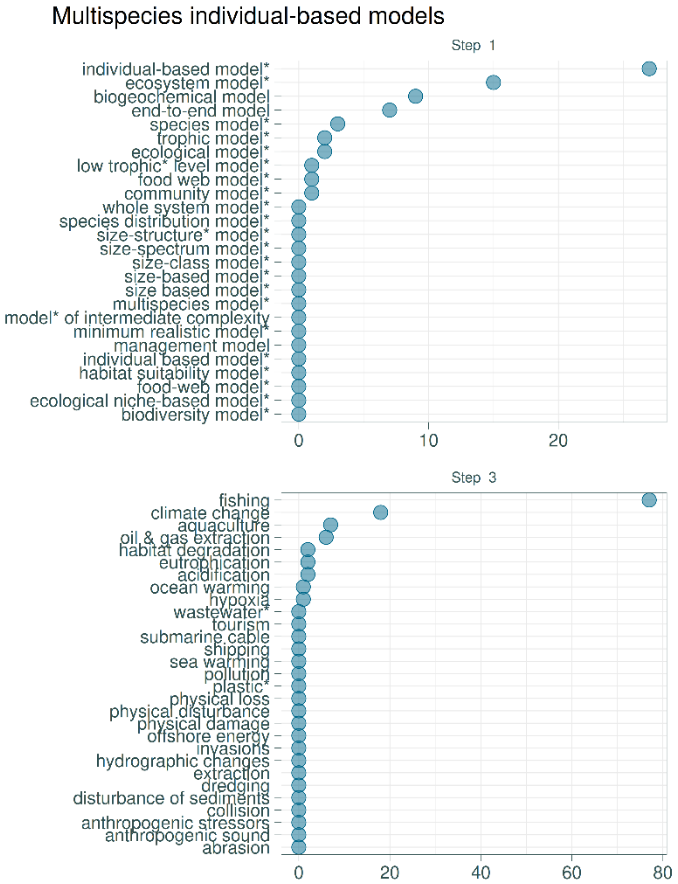


Fig. 8. Number of publications of multispecies individual-based models containing each search term in each step.

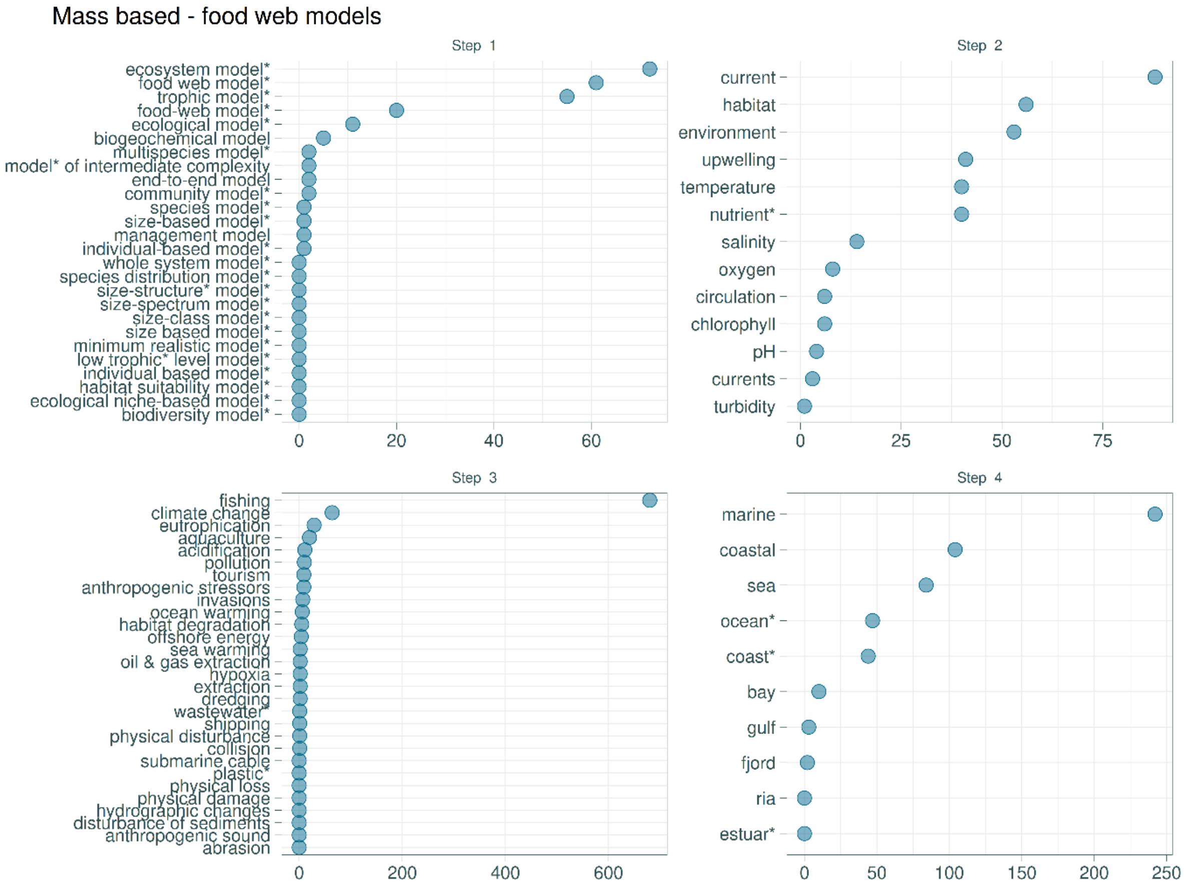


Fig. 9. Number of publications of mass based – food web models containing each search term in each step.

Whole system or end-to-end models

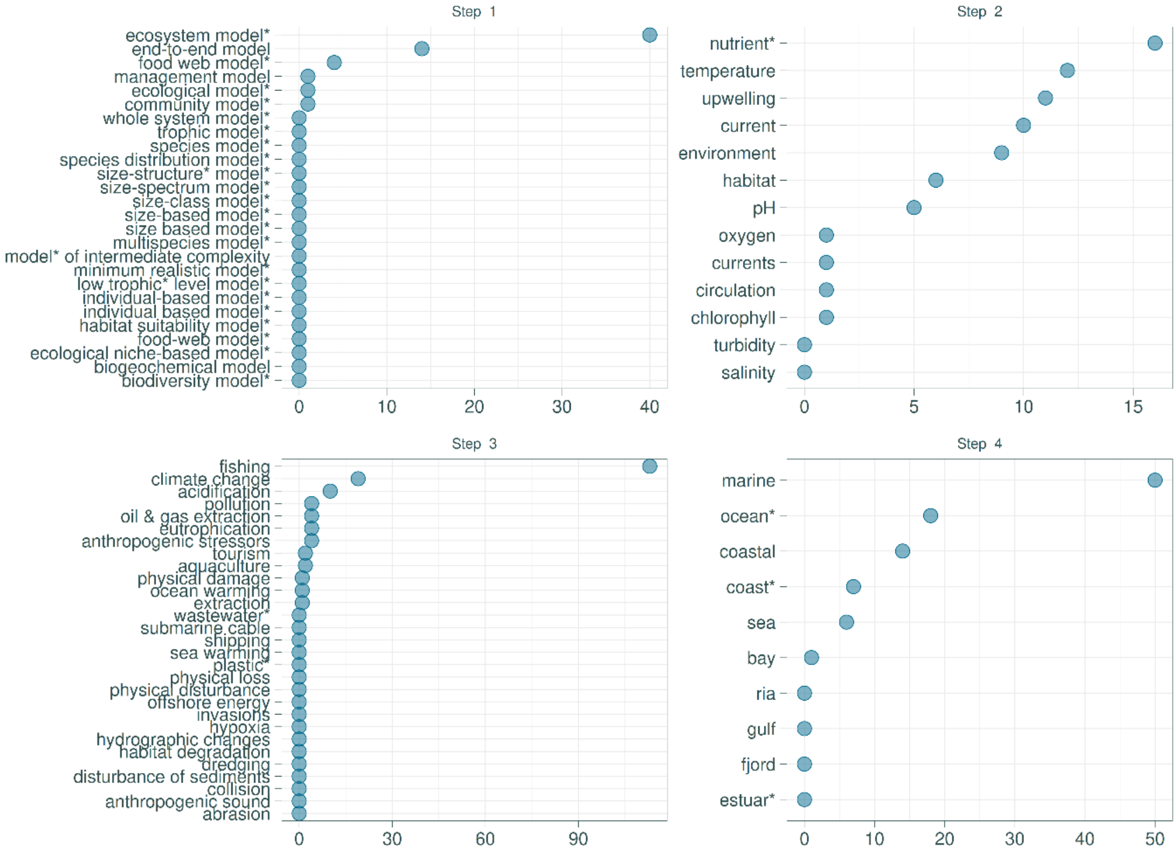


Fig. 10. Number of publications of whole system or end-to-end models containing each search term in each step.

Annex 2. Analysis of the journals for each model category

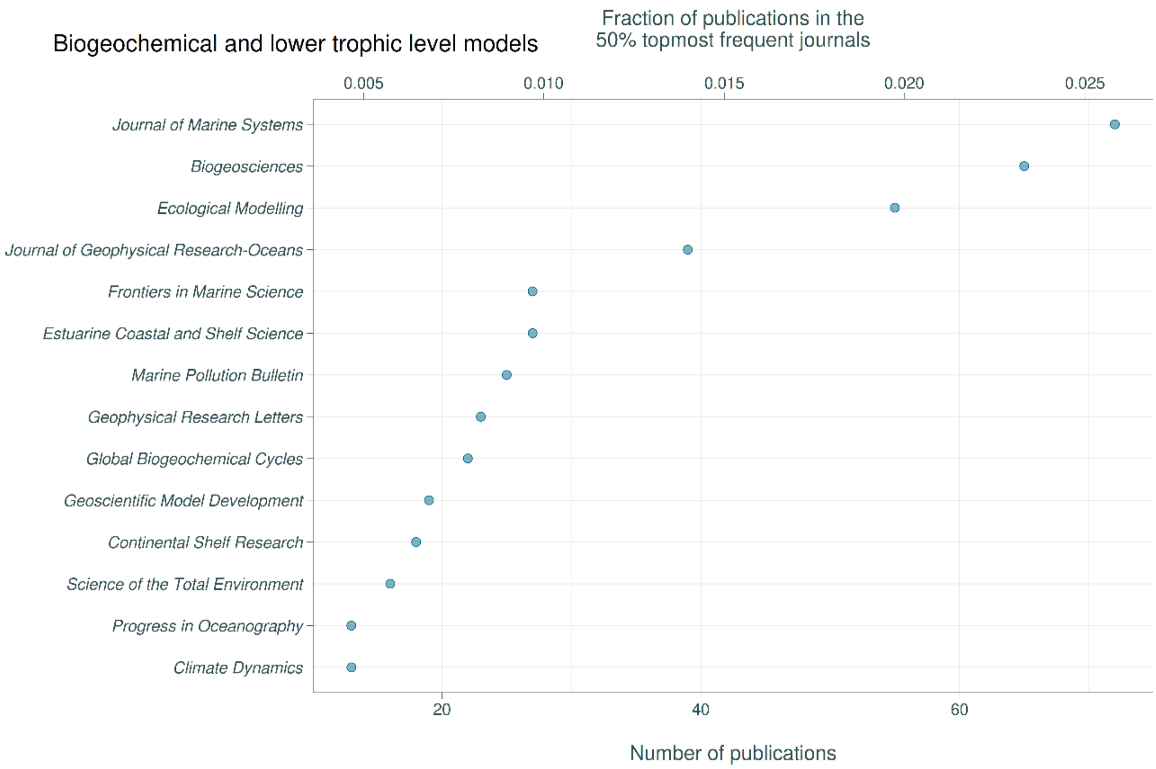


Fig. 1. Fraction of publications and number of publications of biogeochemical and lower trophic level models in the 50% topmost frequent journals.

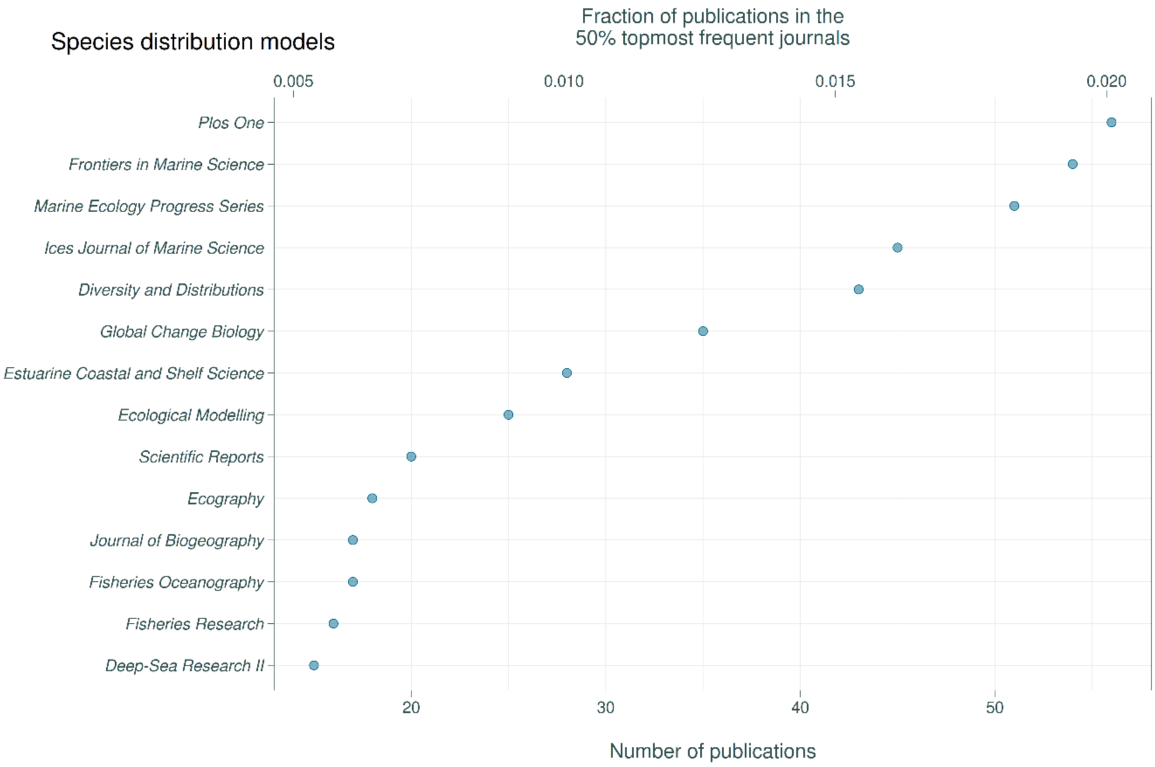


Fig. 2. Fraction of publications and number of publication of species distribution models in the 50% topmost frequent journals.

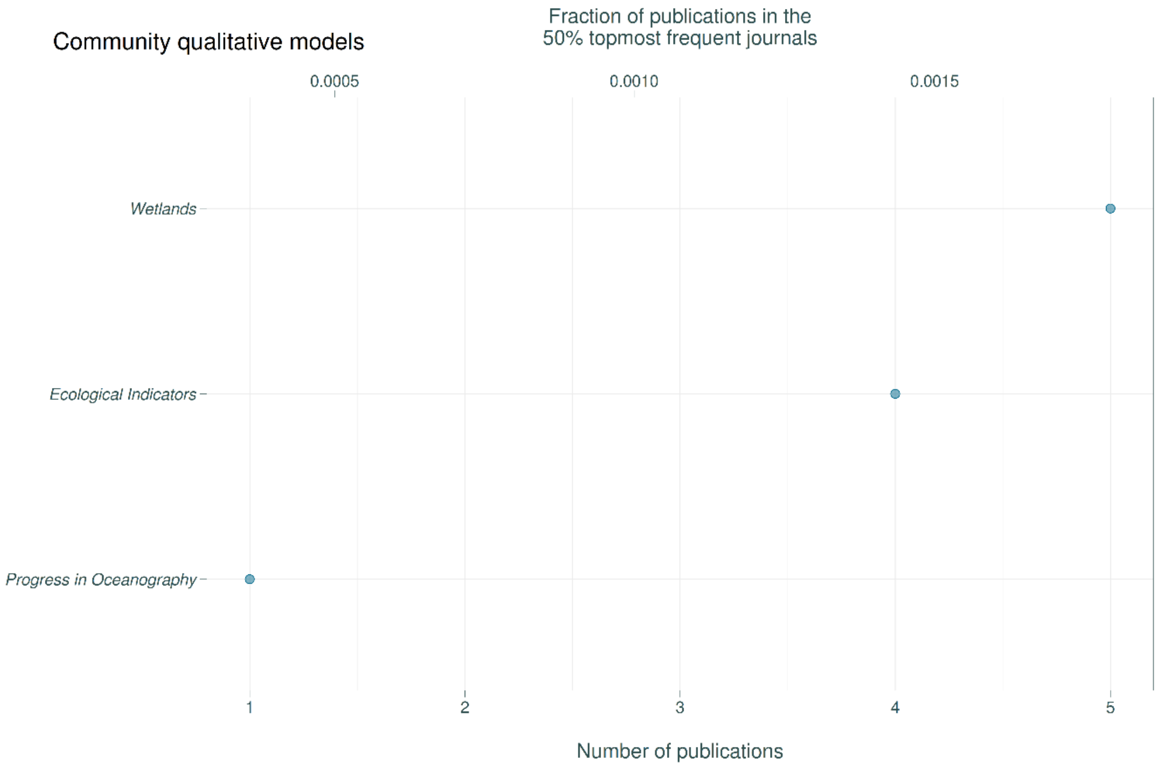


Fig. 3. Fraction of publications and number of publications of community qualitative models in the 50% topmost frequent journals.

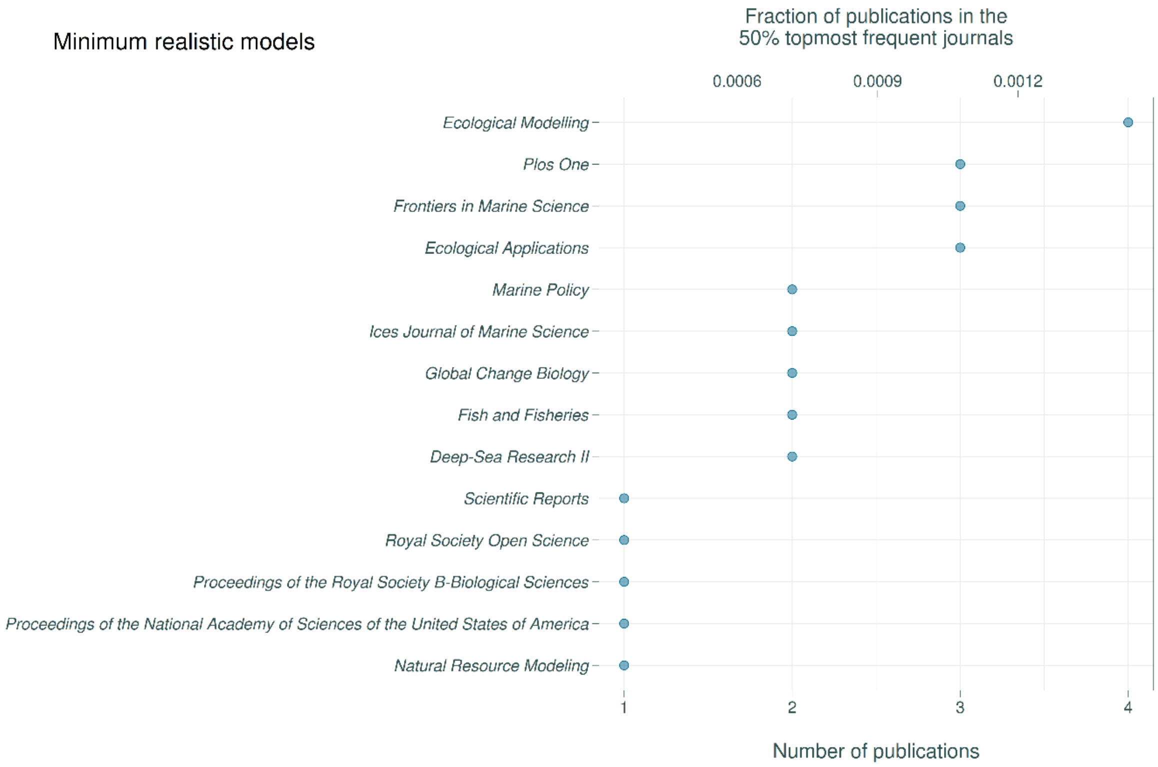


Fig. 4. Fraction of publications and number of publications of minimum realistic models in the 50% topmost frequent journals.

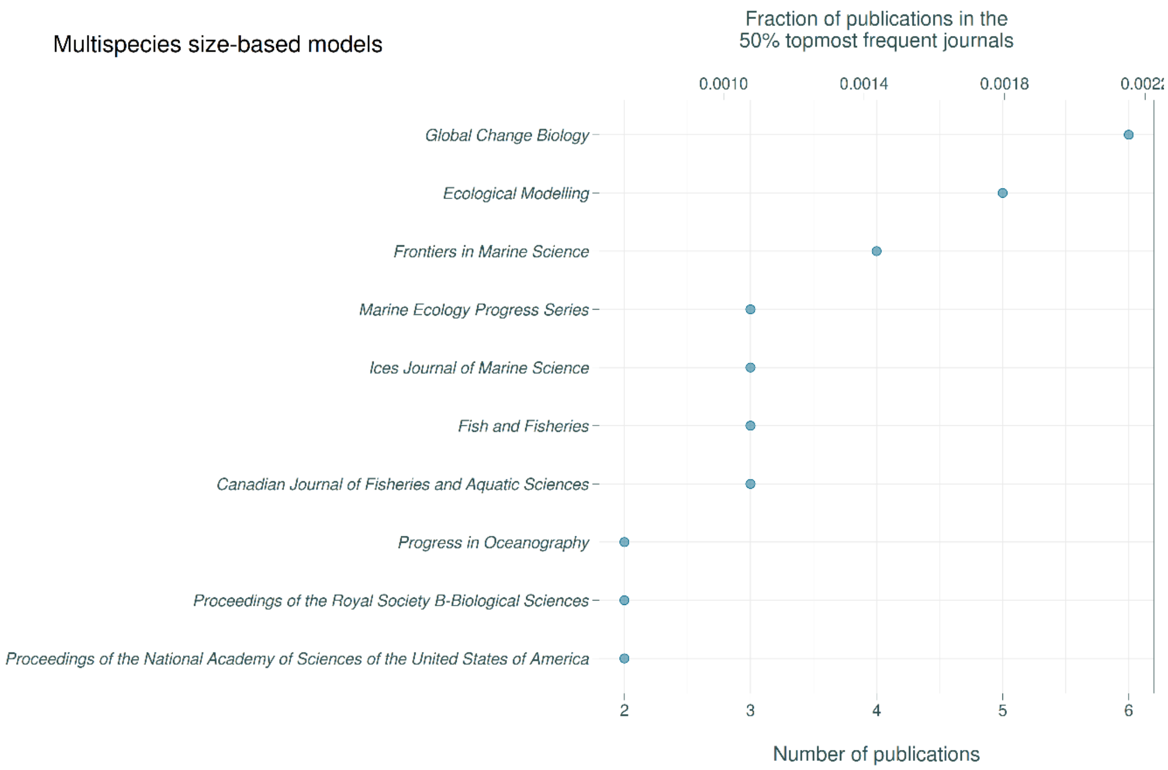


Fig. 5. Fraction of publications and number of publications of multispecies size-based models in the 50% topmost frequent journals.

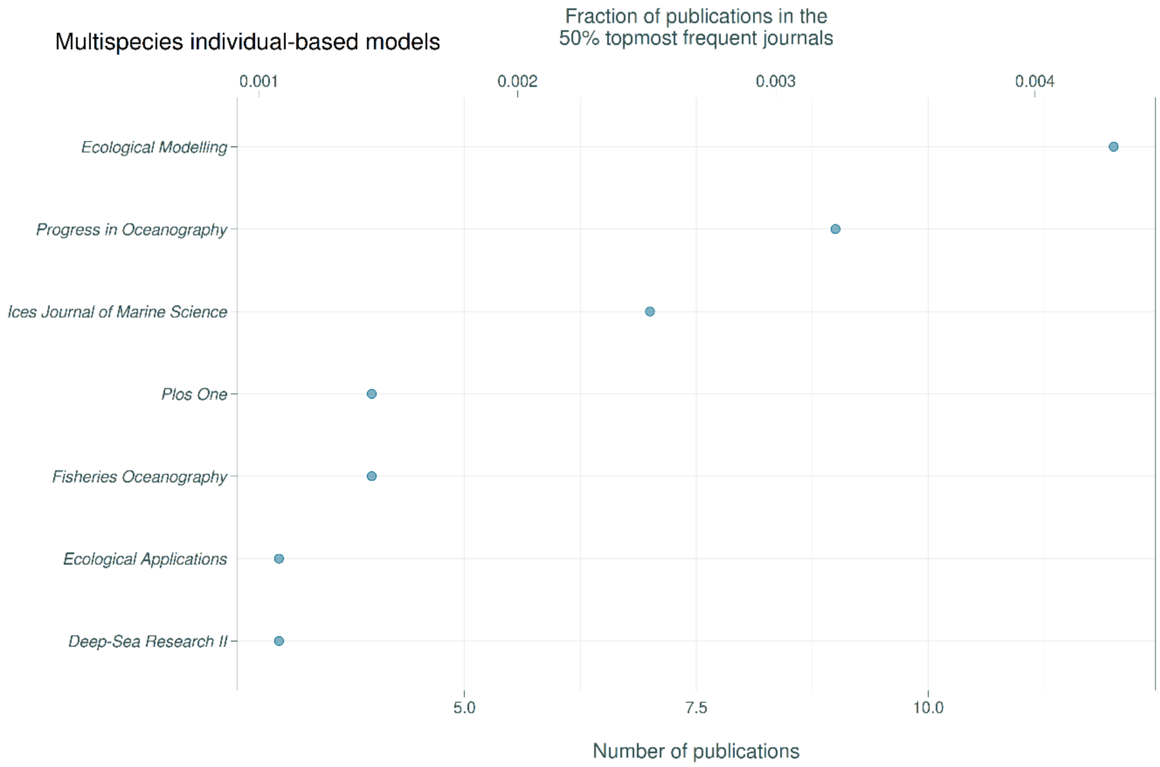


Fig. 6. Fraction of publications and number of publications of multispecies individual-based models in the 50% topmost frequent journals.

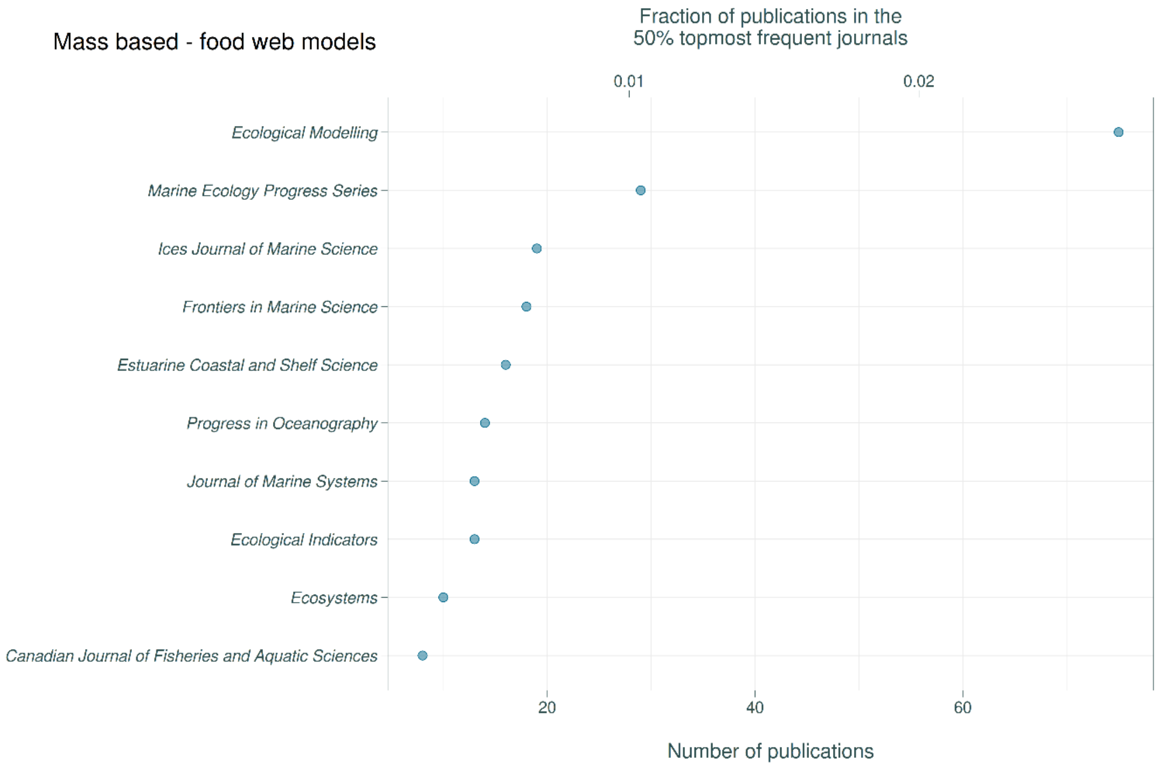


Fig. 7. Fraction of publications and number of publications of mass balance – food web models in the 50% topmost frequent journals.

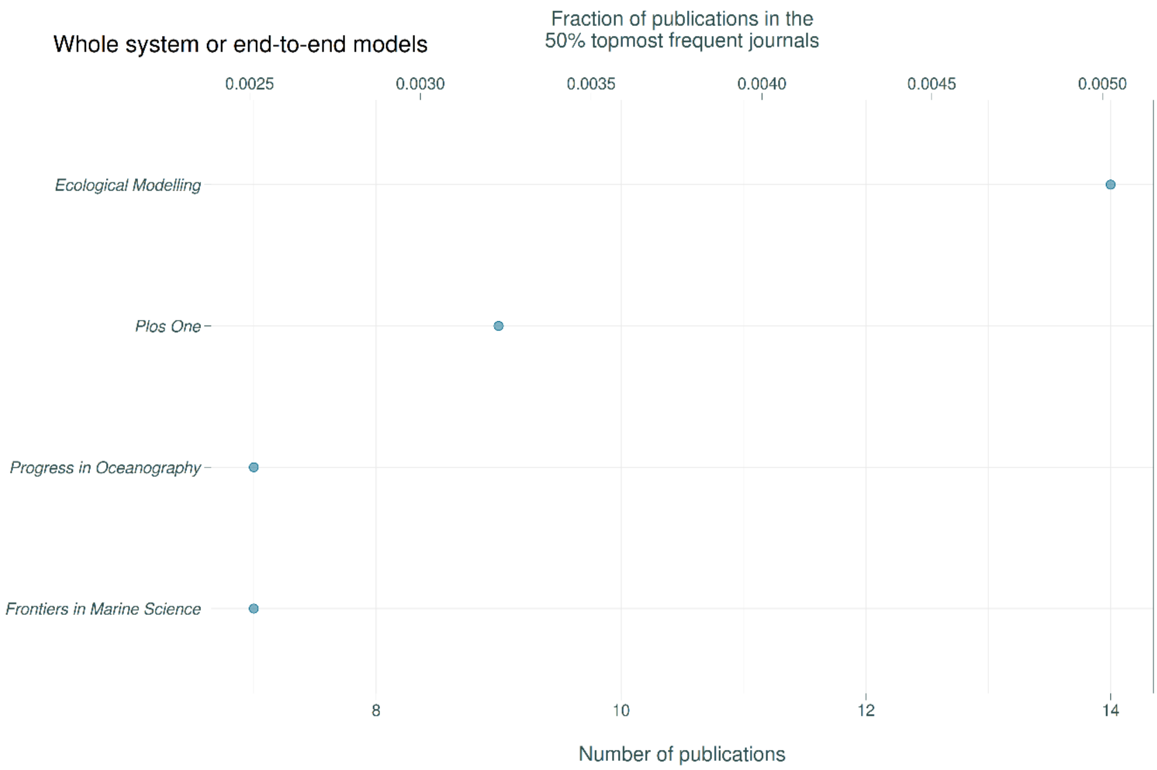


Fig. 8. Fraction of publications and number of publications of whole system or end-to-end models in the 50% topmost frequent journals.

Annex 3. First screening stage: Guidelines to undertake the screening

Once you have your list of papers, for each of them read the title and the abstract and try to answer the questions below following the rules. Fill the columns H, I, J, K, L, M, N and O.

Question: Does the paper develop/apply a biodiversity/ecosystem model in the marine realm?

We define marine biodiversity/ecosystem models as any modelling approach targeting ecosystem components (e.g., species abundance/occurrence or traits, functional groups and habitats) and considering:

1. their interactions with multiple species and/or groups of species and/or trophic levels,

2. their associations with environmental variables (e.g., temperature, salinity, light availability, oxygen levels, and water movement),

3. the impacts from human activities (e.g., fishing, aquaculture, alien invasive species, pollution, habitat modification, anthropogenic climate change).

These models enable the *in silico* simulation of a variety of aspects and emerging properties of marine ecosystems, accounting for both the impact of hydrogeochemical and habitat condition on the abundance and distribution of species and the effects of the different anthropogenic and natural pressures on the different abiotic and biotic components. Note that a model that fulfils the three requirements (species interactions, environmental associations, and impact of human activities) will be prioritized (i.e., higher score) than another that only include one or two, but this condition (addressing all of three requirements) should not be a criteria to exclude a model from the analysis. If **NOT**: exclude the paper (column H) and fill column I (reasons to justify exclusion).

Reasons to justify exclusion:

a. Study focusing on the terrestrial/freshwater realm

b. Observational or experimental study (i.e., it is not a model)

c. Modelling studies that do not focus on ecosystem components or do not evaluate the impact of human activities and/or the environment

In case you have doubts, highlight the row in orange, and discuss with other members of the team.

IMPORTANT: If the paper does not develop a model but is a review paper of models (attached an abstract as an example), exclude the paper (column H) but download the paper and put the paper in folder “3. Relevant review paper”.

- If **YES**, include the paper (column H) and fill columns J (model category), K (type of model), maybe L (type of model) and M and L (relevant article). **THEN**

    - Try to identify the model category:

1) **Single species models:** models that focus on the dynamics of a single species, featuring interactions with other species and environmental drivers but not dynamic feedbacks among them.

2) **Biogeochemical and lower trophic level models:** they describe the dynamic of lower trophic levels (phytoplankton and zooplankton) and their impact on bulk ecosystem properties in response to changes in physical (e.g., temperature, salinity. light) and chemical (e.g., nutrients, oxygen, pH) conditions. They are often coupled to hydrodynamic models to feature the impact of ocean circulation on ecosystem dynamics. These models are expected to be identified in the systematic review because they can include trophic interactions, the impact of environmental variability and human impacts. However, they will not be considered in the final selection because specifically one of the objectives of the study is to assess the possibility to couple biodiversity/ecosystem models with physics and/or biogeochemical models.

3) **Species Distribution Models (SDM)** (also called **Habitat Suitability Models (HSM)** or **Ecological Niche-Based Models**): they combine species occurrences or abundance data with environmental variables (e.g., temperature) to predict the distribution of species or potential habitat. When applied to multiple species, these models can be used to identify coexisting species and to characterize interaction networks (e.g., **Joint SDMs**).

4) **Community qualitative models:** they provide a framework for formulating qualitative relationships between variables within a particular system using signed diagraphs to represent community interactions and impacts and predict stability and perturbations (Puccia and Levins 1985, Dambacher et al. 2002, Coll et al. 2019). Keywords: sign directed graphs.

5) **Minimum realistic models (MRM)** and **models of intermediate complexity (MICE):** they include a limited number of species that have important interactions with the target species of the study (Punt and Butterworth 1995, Plagányi et al. 2014). Within this category we will include models such as **GADGET** (Globally applicable Area-Disaggregated general Ecosystem Toolbox) (e.g., Andonegi et al. 2011, Pérez-Rodríguez et al. 2017), **multispecies bioenergetic models** (Koen-Alonso and Yodzis 2005) and **SMS** (Stochastic Multispecies Models) (e.g., Lewy and Vinther 2004, Kempf et al. 2010).

6) **Multispecies size-based models:** they describe energy transfer from primary producers to consumers, focussing on body size rather than species identity. Within this category we will include models such as **Mizer** (dynamic multi-species size-spectrum models) (e.g., Scott et al. 2014), **FishSUMS** (e.g., Speirs et al. 2016), **SS-DBEM** (Size-Spectra Dynamic Bioclimate Envelope Model) (e.g., Fernandes et al. 2013) and **APECOSM** (Apex Predators ECOSystem Model) (Dueri and Maury 2013).

7) **Multispecies individual-based models**: they are based on the explicit representation of individual organisms. Within this category we will include models such as **SEAPODYM** (Spatial ecosystem and population dynamic model) (Lehodey et al. 2008, Senina et al. 2016) and **OSMOSE** (Object-oriented Simulator of Marine ecOSystem Exploitation) (e.g., Shin and Cury 2004, Grüss et al. 2016).

8) **Mass based - food web models**: they represent population of dynamically interacting species or groups of species. Within this category we will include models such as the **Ecopath with Ecosim** approach (EwE) (e.g., Christensen and Walters 2004, Corrales et al. 2017) and **StrathE2E** (e.g. Heath 2012).

9) **Whole system models or end-to-end:** they attempt to represent all the ecosystem components from nutrients, biogeochemical cycling and primary producers to top predators (including human components) linked through trophic interactions and the associated abiotic environment (e.g., currents and water column properties such as temperature and salinity). Within this category we will include models such as **Atlantis**. In addition, whole system models also include coupled models, where models were integrated (with or without dynamic feedbacks) and outputs of one model provide inputs to the other. For example, Travers-Trolet et al. (2014) **coupled** an OSMOSE model with a biophysical model (ROMS -$N_2P_2Z_2D_2$).

   - Try to identify the specific model (for coupled end-to-end models, preference to the high TL model):

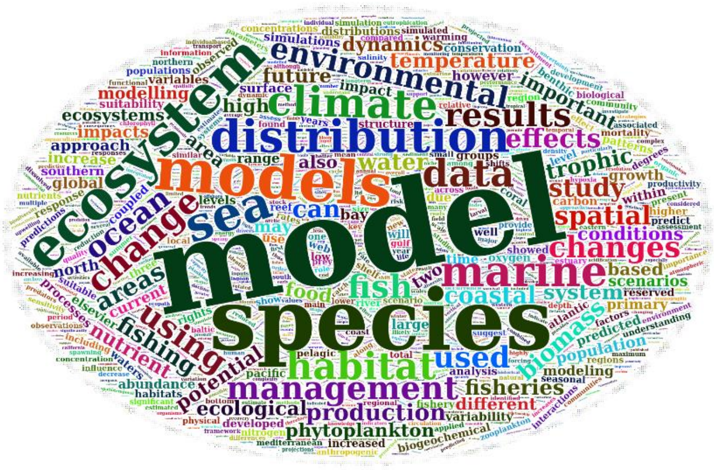
- List of models names: e.g., ERSEM (NEMO-ERSEM and others), Biogeochemical flux model (BFM), MEDUSA, SDM, StrathE2E, Ecopath with Ecosim (EwE), OSMOSE, Atlantis, StrathSPACE, MIZER, FishSUMS, SS-DBEM (Size-Spectra Dynamic Bioclimate Envelope Model), APECOSM (Apex Predators ECOSystem Model), SEAPODYM (Spatial ecosystem and population dynamic model), LeMANS, Gadget, SMS (Stochastic Multispecies Models), SEAPODYM (Spatial ecosystem and population dynamic model), InVitro, MSVPA (Multispecies Virtual Population Analysis) and SMOM (Spatial Multispecies Operating model). - **If you find another model**, select "Other model" and fill column L (Type of model2)

- Identify relevant article, which are considered if they conform with at least one of the following attributes:

    - Key reference of the modelling approach
    - Review paper of the approach
    - Highly cited article (i.e., more than 30 citations/year)
    - New developments in recent articles (e.g., last 5 years)
    - Interesting application (e.g., a lot of drivers)

Annex 4. Model description

This Annex provides a succinct description of each model category and of each of the 62 biodiversity/ecosystem models identified and analysed in this project. The main features of each model are further detailed in Database#2. Each section of the Annex starts with a short description of each category and a word cloud based on the abstracts of the publications analysed during the literature screening like the one below, which is based on all screened abstracts.



A4.1 Single species models

A4.2 Biogeochemical and lower trophic level models

A4.3 Species distribution models

A4.4 Community qualitative models

A4.5 Minimum realistic models

A4.6 Multispecies size-based models

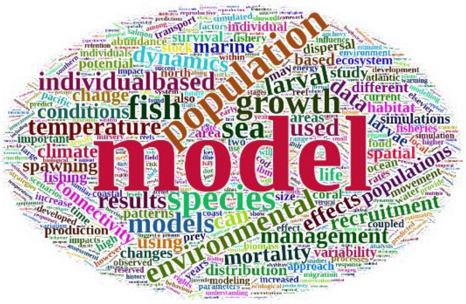
A4.7 Multispecies individual-based models

A4.8 Mass based - food web models

A4.9 Whole system or end-to-end models

A4.1 Single species models

Models that focus on the dynamics of a single species, featuring interactions with other species and environmental drivers but not dynamical feedbacks among them.



A4.1.1 Dynamic energy budget (DEB) and bioenergetic models

The Dynamic Energy Budget [*DEB*] proposes a general bioenergetic theory that provides a quantitative framework to describe the dynamics of individual metabolism (energy and mass budgets). The models developed under this theory are extensively used as the building block of complex models of marine ecosystems. The framework is used to model individual growth, energy acquisition, reproduction, and excretion. It can handle complex life cycles, changes in diet, stoichiometric constraints, toxicants, and evolutionary dynamics, to name some of the multiple variations allowed by this versatile approach. The framework has been widely used, especially to analyze and predict the dynamics of animal species. Parameterizations are largely based on literature reviews of physiological rates and allometric exponents, but there is a large database collecting data for hundreds of species. These data have been used to parameterize biophysical models used to assess the response of species to climate change.

Website: https://www.bio.vu.nl/thb/deb

http://bioforecasts.science.unimelb.edu.au/app_direct/deb_sea,

https://www.bio.vu.nl/deb/deblab/add_my_pet/index_main.html

Key references

Kearney MR, Porter, WP. 2020. NicheMapR – an R package for biophysical modelling: the ectotherm and Dynamic Energy Budget models. *Ecography* 43: 85-96. doi: 10.1111/ecog.04680.

Kooijman, SALM. 2010. *Dynamic Energy Budget Theory for Metabolic Organisation [3rd ed]*. Cambridge University Press. 490 pp.

Marques GM, Augustine S, Lika K, Pecquerie L, Domingos T, Kooijman SALM. 2018. The AmP project: Comparing species on the basis of dynamic energy budget parameters. *PLoS Computational Biology* 14(5): e1006100. 10.1371/journal.pcbi.1006100.

Nisbet RM, Muller EB, Lika K, Kooijman SALM. 2000. From molecules to ecosystems through dynamic energy budget models. *Journal of Animal Ecology* 69: 913-926. doi: 10.1111/j.1365-2656.2000.00448.x.

van der Meer J, Klok M, Kearney MR, Wijsman JWM, Kooijman SALM. 2014. 35 years of DEB research. *Journal of Sea Research* 94: 1-4. doi: 10.1016/j.seares.2014.09.004.

A4.1.2 Dynamic population models

Dynamic population models describe the change along time of a single population. The main processes involved are new individuals, growth, mortality, and migration, which can sometimes depend on environmental conditions. This type of models is mainly applied to commercially exploited fish species for stock assessment and management purposes. They encompass a large variety of models that differ in the level of complexity and the amount of data. Often, the results of these models are used as input for more general models, such as ecosystem end-to-end models.

Key references

Hilborn, R. and Walters, C.J. (1992) Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty. Chapman and Hall, Boston.

Quinn, T.J. II and Deriso, R.B. (1999) Quantitative fish dynamics. Oxford University Press, Oxford.

Punt, A. E., Dunn, A., Elvarsson, B. ó., Hampton, J., Hoyle, S. D., Maunder, M. N., Methot, R. D., et al. 2020. Essential features of the next-generation integrated fisheries stock assessment package: A perspective. Fisheries Research, 229: 105617.

Maunder, M. N., and Punt, A. E. 2013. A review of integrated analysis in fisheries stock assessment. Fisheries Research, 142: 61-74.

A4.1.3 Individual-based models (IBMs)

IBM, also called agent-based models, are a population and community modelling approach that allows for a high degree of complexity of individuals and of interactions among individuals. IBMs simulate populations or systems of populations as being composed of discrete individual organisms. Each individual has a set of state variables or attributes and behaviors. State variables can include spatial location, physiological traits and behavioral traits. These attributes vary among the individuals and can change through time. Behaviors can include growth, reproduction, habitat selection, foraging, and dispersal. IBMs provide an adaptable framework for simulating complex ecological and evolutionary processes, with trait variation, dispersal, genetic structure, and demographic stochasticity modelled at the individual level (Xuereb et al. 2021). High computational demands. Toolkits: SLiM.

Website: https://facultyopinions.com/prime/reports/b/6/39/

Key references

DeAngelis, D. L. and V. Grimm. 2014. Individual-based models in ecology after four decades. F1000prime reports 6:39-39.

Xuereb, A., Q. Rougemont, P. Tiffin, H. Xue, and M. Phifer-Rixey. 2021. Individual-based eco-evolutionary models for understanding adaptation in changing seas. Proceedings of the Royal Society B-Biological Sciences 288.

Van Winkle, W., K. A. Rose, and R. C. Chambers. 1993. Individual-Based Approach to Fish Population Dynamics: An Overview. Transactions of the American Fisheries Society 122:397-403.

A4.1.4 Lagrangian tool for simulating ichthyoplankton dynamics (Ichthyop)

Ichthyop is an individual-based model (IBM) designed to study the effects of physical (e.g., ocean currents, temperature) and biological (e.g., growth, mortality) factors on the dynamics of fish eggs and larvae[1]. It is a free java tool that incorporates the most important processes involved in fish early life: spawning, movement, growth, mortality, and recruitment. In ichthyop, individuals are characterized by the state variables: age, length, stage (egg, yolk-sac larva or feeding larva), location, depth, and status (alive or dead). The physical environment is determined by ocean state variables including current velocities, temperature, and salinity. The environment state variables are provided on a discrete three-dimensional grid by archived simulations of the “Regional Oceanic Modelling System” (ROMS)[2], the “Model for Applications at Regional Scale’’ (MARS)[3], the "Nucleus for European Modelling of the Ocean" (NEMO)[4] or SYMPHONIE[5]. It also enables to track virtual drifters and the ocean properties (temperature, salinity) that they experience.

Ichthyop offers two functioning modes. The first mode provides a user-friendly GUI for setting-up and running the simulation and visualizing the transport of virtual eggs and larvae, either creating animated GIF or exporting the trajectories to KMZ format (Google Earth). The second one is a batch mode that gives full power to computation. Both modes produce NetCDF output files that store information about the simulated dynamics of individuals (time, longitude, latitude, depth, length, etc.). Using Ichthyop for other species in other systems may imply a few changes in the source code (e.g., changing the growth function, implementing a specific larval vertical migration scheme, etc.).

Website: https://ichthyop.org

Key references

Lett, C. *et al.* A Lagrangian tool for modelling ichthyoplankton dynamics. *Environ. Model. Softw.* **23**, 1210–1214 (2008).

Shchepetkin, A. F. & McWilliams, J. C. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Model.* **9**, 347–404 (2005).

Lazure, P. & Dumas, F. An external-internal mode coupling for a 3D hydrodynamical model for applications at regional scale (MARS). doi:10.1016/j.advwatres.2007.06.010.

Gurvan, M. *et al.* NEMO ocean engine. (2019) doi:10.5281/ZENODO.3878122.

Marsaleix, P., Auclair, F. & Estournel, C. Considerations on Open Boundary Conditions for Regional and Coastal Ocean Models. *J. Atmos. Ocean. Technol.* **23**, 1604–1613 (2006).

A4.1.5 Probably A Really Computationally Efficient Lagrangian Simulator (Parcels)

Parcels (“Probably A Really Computationally Efficient Lagrangian Simulator”) is a novel framework for computing Lagrangian particle trajectories[1,2]. It is a set of Python classes and methods to create customisable particle tracking simulations using output from Ocean General Circulation Models (OGCM). Parcels focusses on tracking of passive water parcels, as well as active particulates such as plankton, plastic and fish. The code is licensed under an open source MIT license and can be downloaded from github.com/OceanParcels/parcels or installed via anaconda.org/conda-forge/parcels. Parcels aim to process the continuously increasing number of data generated by the contemporary and future generations of ocean general circulation models (OGCMs). This requires two important features of the model: (1) not to be dependent on one single format of fields and (2) to be able to scale up efficiently to cope with up to petabytes of external data produced by OGCMs. While development efforts of Parcels focus on oceanographic applications, the Parcels framework is expected to be adaptable to atmospheric particle tracking simulations.

Website: https://oceanparcels.org

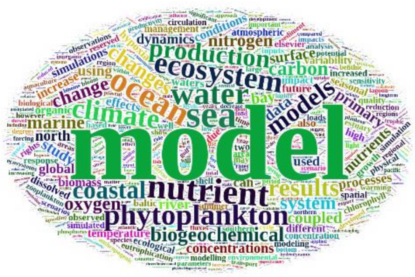
Key references

Lange, M. & Sebille, E. Van. Parcels v0.9: Prototyping a Lagrangian ocean analysis framework for the petascale age. Geosci. Model Dev. 10, 4175–4186 (2017).

Delandmeter, P. & Van Sebille, E. The Parcels v2.0 Lagrangian framework: New field interpolation schemes. Geosci. Model Dev. 12, 3571–3584 (2019).

A4.2 Biogeochemical and lower trophic level models

Models describing the uptake, cycling, and transformations of carbon and nutrients by lower trophic levels (phytoplankton and zooplankton) and their impact on bulk ecosystem properties in response to changes in physical (e.g., temperature, salinity, light) and chemical (e.g., oxygen, pH) conditions. They are often coupled to hydrodynamic models to feature the impact of ocean circulation on ecosystem dynamics.



A4.2.1 Biogeochemical Flux Model (BFM)

The Biogeochemical Flux Model (BFM) is a general numerical modelling framework to simulate the dynamics and functioning of lower trophic levels in marine ecosystems. The model is a direct descendant of early versions of the European Regional Seas Ecosystem Model (ERSEM I and II) but focuses mainly on biogeochemical processes in the water column and sediments. BFM default configuration features a pelagic ecosystem with bacterioplankton (one variable for both aerobic and anaerobic bacteria), four phytoplankton groups (picophytoplankton, autotrophic nanoflagellates, diatoms, and a wide group of large, slow-growing phytoplankton), and four zooplankton groups (heterotrophic nanoflagellates, microzooplankton, and carnivorous and omnivorous mesozooplankton). The biomass of each of these living components are defined and simulated in terms of C, N and P. The default configuration also features non-living components like dissolved and particulate organic matter, and several chemical tracers (C, O, N, P, Si by construction, and optionally, Fe and the carbonate system). Besides the water column, the model features a benthic closure model to account for biogeochemical remineralization in the sediments; and a sea ice module that includes one group of algae growing on ice. The code is advanced and versatile, enabling users to easily customize and extend the default formulation and parameterization of BFM. The detailed simulation of the chemical composition of lower trophic levels and of the availability of nutrients in the environment enable the simulation of multiple nutrient limitation and stoichiometric constraints. Similarly, the detailed simulation of air-sea gas exchanges, and of production and decomposition processes in the water column and in the sediments, enable the prediction of changes in ambient oxygen, pH and alkalinity.

Website: https://bfm-community.github.io, www.bfm-community.eu

Key references

Vichi M, Lovato T, Butenschön M, Tedesco L, Lazzari P, Cossarini G, Masina S, Pinardi N, Solidoro C, Zavatarelli M. 2020. *The Biogeochemical Flux Model (BFM): Equation Description and User Manual*. BFM version 5.2. BFM Report series N. 1, Release1.2, June 2020, Bologna, Italy, http://bfm-community.eu, pp. 104.

Vichi M, Pinardi N, Masina S. 2007a. A generalized model of pelagic biogeochemistry for the global ocean ecosystem. Part I: theory. *Journal of Marine Systems* 64: 89-109. doi: 10.1016/j.jmarsys.2006.03.006.

Vichi M, Masina S, Navarra A. 2007b. A generalized model of pelagic biogeochemistry for the global ocean ecosystem. Part II: numerical simulations. *Journal of Marine Systems* 64: 110-134. doi: 10.1016/j.jmarsys.2006.03.014.

A.4.2.2 Ecosystem Model for Application at Regional Scales (ECO-MARS3D)

The model Ecosystem Model for Application at Regional Scales ECO-MARS3D is a general numerical modelling framework to simulate the dynamics and functioning of lower trophic levels in marine ecosystems. ECO-MARS3D describes the seasonal evolution of primary production by diatoms, dinoflagellates and pico-nanoplankton, with limitations by nitrates, ammonium, phosphates and silicates. Phosphates can be adsorbed to and desorbed from Suspended Particulate Inorganic Matter (SPIM) and may be a limiting factor for production in some coastal locations during certain period of the year. All elements are present in the detritus under particulate matter form. The model simulates two zooplankton compartments: microzooplankton and mesozooplankton, the latter being the closure term of the model. All biogeochemical tracers are coupled to the hydrodynamics model MARS through the advection–diffusion equation. The model is forced by realistic meteorological model results (ERA and ARPEGE models) and rivers runoff data.

Website: https://mars3d.ifremer.fr/docs/doc.basic.intro.html

Key reference

Huret M., Sourisseau M., Petitgas P., Struski C., Léger F. and Lazure P. 2013. A multi-decadal hindcast of a physical–biogeochemical model and derived oceanographic indices in the Bay of Biscay. *Journal of Marine Systemes*, 109-110, supplement, S77-S94. https://doi.org/10.1016/j.jmarsys.2012.02.009

A4.2.3 Ecological Regional Ocean Model (ERGOM)

The Ecological Regional Ocean Model (ERGOM) is a biogeochemical modelling framework that enables the development of complex models of coupled marine pelagic and benthic ecosystems. The model can be extended but its basic structure features the simulation of the biogeochemical cycles of carbon, nitrogen and phosphorus. The model has a detailed implementation of processes related to eutrophication and anoxia (including sediment processes like sulfate reduction). The default configuration features a pelagic model with three phytoplankton groups (small, large and nitrogen-fixing cyanobacteria), one zooplankton group and several chemical tracers [C,N,P] that, importantly, allow the simulation of non-Redfield stoichiometry. The model also simulates detrital dynamics in the water column and in the sediments, where it further simulates chemical tracers related to sulfide hydrogen production, and phosphate mobilization. Model code is very well documented and versatile, enabling users to easily customize and extend the default formulation and parameterization.

Website: https://ergom.net

Key references

Neumann T. 2000. Towards a 3D-ecosystem model of the Baltic Sea. *Journal of Marine Systems* 25, 405-419. doi: 10.1016/S0924-7963(00)00030-0.

Fennel W, Neumann T. 2001. Coupling biology and oceanography in models. *AMBIO* 30, 232-236. doi: 10.1579/0044-7447-30.4.232.

Fennel W, Neumann T. 2015. *Introduction to the Modelling of Marine Ecosystems*. [2nd ed.]. Elsevier, Amsterdam, 371 pp.

A4.2.4 European Regional Seas Ecosystem Model (ERSEM)

The European Regional Seas Ecosystem Model (ERSEM) is an ecosystem model for marine biogeochemistry. Despite its name, current versions of ERSEM provide a framework to create complex models of coupled marine pelagic and benthic ecosystems from distinct regional settings to applications at the global scale. The model adopts a functional approach to marine ecosystems by simulating the dynamics of ataxonomic groups and non-living compartments (including particulate and dissolved organic matter pools). The model features variable stoichiometry, the microbial loop food web, and major biogeochemical cycles (carbon, nitrogen, phosphorus, and silicate), including oxygen dynamics through the water column and in the benthos. Recent versions include iron cycle, calcifiers, and complex light and microbial loop models. The default configuration features a pelagic model with bacterioplankton, four phytoplankton groups (pico-, nano- and micro- phytoplankton, and diatoms), three zooplankton groups (heterotrpohic flagellates, micro- and meso- zooplankton); a benthic model with three types of infauna (meiobenthos and suspension and deposit feeders) and two types of bacteria (aerobic and anaerobic), and multiple chemical tracers and dissolved and particulate organic matter types. The code is advanced, well documented, and versatile, enabling users to easily customize and extend the default formulation and parameterization of ERSEM.

Website: https://ersem.readthedocs.io

Key references

Blackford JC, Radford PJ. 1995. A structure and methodology for marine ecosystem modelling. *Netherlands Journal of Sea Research* 33(3-4):247-260. doi: 10.1016/0077-7579(95)90048-9.

Butenschön M, Clark J, Aldridge JN, Allen JI, 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, 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(4): 1293-1339. doi: 10.5194/gmd-9-1293-2016.

A4.2.5 Model of Ecosystem Dynamics, nutrient Utilisation, Sequestration and Acidification (MEDUSA)

MEDUSA is a Model of Ecosystem Dynamics, nutrient Utilisation, Sequestration and Acidification. Developed as an “intermediate complexity” plankton ecosystem model to study the biogeochemical response, and the “biological pump” to anthropogenically driven change in the World Ocean. MEDUSA is coupled with NEMO circulation model. NEMO-MEDUSA has been developed for global applications, and validation has naturally focused at the large scale, such as basins, ahead of fine-scale regions like the UK shelf.

Website:

https://noc.ac.uk/science/research-areas/marine-systems-modelling

http://imarnet.org/Models/MEDUSA

https://gmd.copernicus.org/articles/6/1767/2013/gmd-6-1767-2013.html

code available in SuppMat of Yool et al. 2013:
https://gmd.copernicus.org/articles/6/1767/2013/gmd-6-1767-2013-supplement.zip

Key references

Yool, A., E. E. Popova, and T. R. Anderson. 2013. MEDUSA-2.0: an intermediate complexity biogeochemical model of the marine carbon cycle for climate change and ocean acidification studies. Geosci. Model Dev. 6:1767-1811.

Yool, A., E. E. Popova, A. C. Coward, D. Bernie, and T. R. Anderson. 2013. Climate change and ocean acidification impacts on lower trophic levels and the export of organic carbon to the deep ocean. Biogeosciences 10:5831-5854.

A4.2.6 Pelagic Interactions Scheme for Carbon and Ecosystem Studies (PISCES)

PISCES is a biogeochemical model which simulates the marine biological productivity and describes the biogeochemical cycles of carbon and of the main nutrients (P, N, Si, Fe). PISCES takes into account twenty-four state variables. There are five modelled limiting nutrients for phytoplankton growth: Nitrate and Ammonium, Phosphate, Silicate and Iron. Four living compartments are represented: two phytoplankton size-classes/groups corresponding to nanophytoplankton and diatoms, and two zooplankton size classes which are microzooplankton and mesozooplankton. For phytoplankton, prognostic variables are total biomass, the iron, chlorophyll and silicon contents. This means that the Fe/C, Chl/C and Si/C ratios of both phytoplankton groups are fully predicted by the model. For zooplankton, only the total biomass is modelled. For all species, the C/N/P/O2 ratios are supposed constant and are not allowed to vary. In PISCES, the Redfield ratios C/N/P are set to 122/16/1 and the O/C ratio is set to 1.34. In addition, the Fe/C ratio of both zooplankton groups is kept constant. No silicified zooplankton is assumed. The bacterial pool is not yet explicitly modelled. There are three non-living compartments: semi-labile dissolved organic matter, small and big sinking particles. As for the living compartments, the C, N and P pools are not distinctly modelled. Thus, constant Redfield ratios are imposed for C/N/P. However, the iron, silicon and calcite pools of the particles are explicitly modelled. As a consequence, their ratios are allowed to vary. The sinking speed of the particles is not altered by their content in calcite and biogenic silicate. The latter particles are assumed to sink at the same speed than big organic matter particles. All the non-living compartments experience aggregation due to turbulence and differential settling. In addition to the ecosystem model, PISCES also simulates dissolved inorganic carbon, total alkalinity and dissolved oxygen. The latter tracer is also used to define the regions where oxic or anoxic remineralization takes place.

PISCES has been coupled to the Nucleus for European Modelling of the Ocean (NEMO) and Regional Ocean Modeling System (ROMS) systems. Ultimately, PISCES was assumed to be suited for a wide range of spatial and temporal scales, including, typically, several thousand year-long simulations on the global scale.

Website: https://www.pisces-community.org

Key references

Aumont, O., Belviso, S., and Monfray, P.: Dimethylsulfoniopropionate (DMSP) and dimethylsulfide (DMS) sea surface distributions simulated from a global 3-D ocean carbon cycle model, J. Geophys. Res., 107, 4.1–4.19, doi:10.1029/1999JC000111, 2002.

Aumont, O., Maier-Reimer, E., Blain, S., and Monfray, P.: An ecosystem model of the global ocean including Fe, Si, P co-limitation, Global Biogeochem. Cy., 17, 1060, doi:10.1029/2001GB001745, 2003.

Aumont, O. and Bopp, L.: Globalizing results from ocean in-situ iron fertilization studies, Global Biogeochem. Cy., 20, GB2017, doi:10.1029/2005GB002591, 2006.

Aumont, O., Ethé, C., Tagliabue, A., Bopp, L., and Gehlen, M.: PISCES-v2: an ocean biogeochemical model for carbon and ecosystem studies, Geosci. Model Dev., 8, 2465–2513, https://doi.org/10.5194/gmd-8-2465-2015, 2015.

Ayata, S. D., Lévy, M., Aumont, O., Sciandra, A., SainteMarie, J., Tagliabue, A., and Bernard, O.: Phytoplankton growth formulation in marine ecosystem models: should we take into account photo-acclimation and variable stoichiometry in oligotrophic areas? J. Marine Syst., 125, 29–40, doi:10.1016/j.jmarsys.2012.12.010, 2013.

Bopp, L., Aumont, O., Cadule, P., Alvain, S., and Gehlen, M.: Response of diatoms distribution to global warming and potential implications: a global model study, Geophys. Res. Lett., 32, L19606, doi:10.1029/2005GL023653, 2005.

Bopp, L., Aumont, O., Belviso, S., and Blain, S.: Modelling the effect of iron fertilization on dimethylsulphide emissions in the Southern Ocean, Deep-Sea Res. Pt. II, 55, 901–912, doi:10.1016/j.dsr2.2007.12.002, 2008.

Bopp, L., Resplandy, L., Orr, J. C., Doney, S. C., Dunne, J. P., Gehlen, M., Halloran, P., Heinze, C., Ilyina, T., Séférian, R., Tjiputra, J., and Vichi, M.: Multiple stressors of ocean ecosystems in the 21st century: projections with CMIP5 models, Biogeosciences, 10, 6225–6245, doi:10.5194/bg-10-6225-2013, 2013.

Gehlen, M., Bopp, L., Emprin, N., Aumont, O., Heinze, C., and Ragueneau, O.: Reconciling surface ocean productivity, export fluxes and sediment composition in a global biogeochemical ocean model, Biogeosciences, 3, 521–537, https://doi.org/10.5194/bg-3-521-2006,

A4.2.7 Swedish Coastal and Ocean BIogeochemical model (SCOBI Nordic)

The model Swedish Coastal and Ocean BIogeochemical model (SCOBI) developed by SMHI is used to study the influence of climate changes and human activities on biological and chemical processes and the cycling of nutrients in the seas surrounding Sweden. The aim is to develop a model system tool to support decision makers for the marine environmental conservation. The SCOBI model handle dynamics of nitrogen, oxygen and phosphorus, including inorganic nutrients (nitrate, ammonia and phosphate) and particulate organic matter consisting of phytoplankton (autotrophs), dead organic matter detritus and zooplankton. Primary production assimilates the inorganic nutrients by three functional groups of phytoplankton, diatoms, flagellates and cyanobacteria. The SCOBI model may provide information of for example: nutrients, oxygen conditions and production of biomass; fluxes, transports, sources and sinks; water quality and sedimentation of organic matter; development and spreading of algal blooms; occurrence of harmful algal blooms (*e.g.*, cyanobacteria). SCOBI has been developed for Baltic and North Seas and it is also coupled to a high resolution 3-D ocean circulation climate model (Rossby Centre Ocean model, RCO).

Website: https://www.smhi.se/en/research/research-departments/oceanography/scobi-1.8680

Key references

Almroth-Rosell, E., K. Eilola, I. Kuznetsov, P. O. J. Hall, and H. E. M. Meier. 2015. A new approach to model oxygen dependent benthic phosphate fluxes in the Baltic Sea. Journal of Marine Systems 144:127-141.

A4.3 Species distribution models

Species Distribution Models (SDM) (also called Habitat Suitability Models (HSM) or Ecological Niche-Based Models) combine species occurrences or abundance data with environmental variables (e.g., temperature) to predict the distribution of species or potential habitat. When applied to multiple species, these models can be used to identify coexisting species and to characterize interaction networks (e.g., Joint SDMs).

A4.3.1 AQUAMAPS

AquaMaps is an approach to generating model-based, large-scale predictions of currently known natural occurrence of marine species. Models are constructed from estimates of the environmental tolerance of a given species with respect to depth, salinity, temperature, primary productivity, and its association with sea ice or coastal areas. The modelling approach (Kaschner et al. 2006) is based on statistical fitting of occurrences along each environmental variable assuming a trapezoidal response curve. Environmental envelopes are derived from large sets of occurrence data available from online collection databases such as GBIF, OBIS, FishBase. PRODUCT ONLINE: https://www.aquamaps.org/, also FishBase maps use Aquamaps algorithm: https://www.fishbase.se/. GIS software package (SimMap 3.1).

Website: https://www.aquamaps.org

Key references

Kaschner, K., R. Watson, A. W. Trites, and D. Pauly. 2006. Mapping world-wide distributions of marine mammal species using a relative environmental suitability (RES) model. Marine Ecology Progress Series 316:285-310.

A4.3.2 EcoCast

EcoCast is a data-driven, multispecies predictive habitat modelling framework. Based on a dynamic ocean management approach, the model can respond to changing species management priorities at scales relevant for animal movement and human use, in contrast to the static fishery closures often ineffective to manage species shift in a warming ocean. To do so, EcoCast couples high-resolution Earth Observation data with fisheries observer and fisheries-independent data sets and predicts daily relative catch and bycatch probabilities at previously unachievable spatial and temporal scales in near real time. This information is key as it helps fishers and managers evaluate how to allocate fishing effort to maintain target fish catch while minimizing bycatch of protected or threatened species.

The Dynamic Ocean management in general, and EcoCast in particular, can use diverse analytical approaches (simple to complex), supports climate-resilient fisheries, and is already implemented in many oceans around the world. For example, EcoCast has already been applied to the California drift gillnet (DGN) fishery which targets the broadbill swordfish, and the bycatch species including blue shark, California sea lion, and leatherback turtle. The results of this work suggest that, by tracking daily oceanographic conditions, the California swordfish DGN fishery could access currently closed fishing areas while still protecting leatherback turtles. These highlights the opportunity to implement near real-time management strategies that support economically viable fisheries and meet mandated conservation objectives in the face of changing ocean conditions

EcoCast is a consortium of scientists, managers, and members of the fishing industry. The EcoCast team is made up of scientists from several universities (San Diego State University, University of California Santa Cruz, University of Maryland, Old Dominion University, Stanford University) and NOAA Environmental Resource Division, working in direct collaboration with resource managers, fishing industry, and other stakeholders.

Website: https://coastwatch.pfeg.noaa.gov/ecocast

Key references

Hazen, E. L. *et al.* A dynamic ocean management tool to reduce bycatch and support sustainable fisheries. *Sci. Adv.* **4**, (2018).

A4.3.3 Joint Species Distribution Models

Joint SDMs are species distribution models that can be used to identify coexisting species and to characterize interaction networks. Main approach is based on hierarchical Bayesian models. At least there are two main implemented softwares/packages: 1) Hierarchical Modelling of Species Communities (HMSC) is a general and flexible framework for fitting JSDMs (Tikhonov et al. 2017, 2020). HMSC allows the integration of community ecology data with data on environmental covariates, species traits, phylogenetic relationships and the spatio-temporal context of the study, providing predictive insights into community assembly processes. 2) BORAL (Hui, 2016), which is based on the analysis of multivariate abundance data, with estimation performed using Bayesian Markov chain Monte Carlo methods.

Website: https://www.helsinki.fi/en/researchgroups/statistical-ecology/software/hmsc

Key references

Tikhonov, G., N. Abrego, D. Dunson, and O. Ovaskainen. 2017. Using joint species distribution models for evaluating how species-to-species associations depend on the environmental context. Methods in Ecology and Evolution 8:443-452.

Tikhonov, G., Ø. H. Opedal, N. Abrego, A. Lehikoinen, M. M. J. de Jonge, J. Oksanen, and O. Ovaskainen. 2020. Joint species distribution modelling with the r-package Hmsc. Methods in Ecology and Evolution 11:442-447.

Hui, F. K. C. 2016. boral – Bayesian Ordination and Regression Analysis of Multivariate Abundance Data in r. Methods in Ecology and Evolution 7:744-750.

A4.3.4 BioMod

BioMod is a computer platform for ensemble forecasting of species distributions[1,2]. It offers the possibility to run 10 state-of-the-art modelling techniques to describe and model the relationships between a given species and its environment, assess species temporal turnover, plot species response curves, and test the strength of species interactions with predictor variables. The models included in the BIOMOD ensemble are: GLMs (Generalized Linear Model), GAMs (Generalized Additive Models), GBM (Generalized Boosting Model or usually called Boosted Regression Trees), CTA (Classification Tree Analysis), ANN (Artificial Neural Network), SRE (Surface Range Envelop or usually called BIOCLIM), FDA (Flexible Discriminant Analysis), MARS (Multiple Adaptive Regression Splines), RF (Random Forest, and MAXENT (Maximum Entropy). Although it has been mostly developed for ecologists that aim to predict species distribution, BIOMOD can also be used to model any binomial data (for instance, gene, markers, ecosystem...) in function of any explanatory variables. BIOMOD is implemented in R and is a freeware, open source, package.

Website: https://cran.r-project.org/web/packages/biomod2/index.html

Key references

Thuiller, W. BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. Glob. Chang. Biol. 9, 1353–1362 (2003).

Thuiller, W., Lafourcade, B., Engler, R. & Araújo, M. B. BIOMOD – a platform for ensemble forecasting of species distributions. Ecography (Cop.). 32, 369–373 (2009).

A4.3.5 Maxent software for modelling species niches and distributions

Maxent is a species distribution modelling technique based on the maximum entropy method (Maxent) for modelling species geographic distributions with presence-only data (Phillips et al 2006). The idea of Maxent is to estimate a target probability distribution by finding the probability distribution of maximum entropy (i.e., that is most spread out, or closest to uniform), subject to a set of constraints that represent our incomplete information about the target distribution. In MaxEnt we assume that the data available to the modeller are presence-only, i.e., a set of locations within L, the landscape of interest, where the species has been observed. Let $y = 1$ denote presence, $y = 0$ denote absence, z denotes a vector of environmental covariates, and background be defined as all locations within L (or a random sample thereof). The information available about the target distribution often presents itself as a set of real-valued variables, called “features”, and the constraints are that the expected value of each feature should match its empirical average (average value for a set of sample points taken from the target distribution; Phillips et al 2006). MaxEnt’s model output gives insight about what features are important and estimates the relative suitability of one place vs. another for a species to occur. MaxEnt, from a statistical viewpoint, minimizes the relative entropy between two probability densities, one estimated from the presence data and one from the landscape, defined in feature space (Elith et al 2011).

Since becoming available in 2004, it has been utilized extensively for modelling species distributions. Published examples cover diverse aims (finding correlates of species occurrences, mapping current distributions, and predicting to new times and places) across many ecological, evolutionary, conservation and biosecurity applications. Government and non-government organizations have also adopted MaxEnt for large-scale, real-world biodiversity mapping applications.

Website: https://biodiversityinformatics.amnh.org/open_source/maxent

Key references

Phillips, S. J., Anderson, R. P. & Schapire, R. E. Maximum entropy modeling of species geographic distributions. Ecol. Modell. 190, 231–259 (2006).

Elith, J. et *al.* A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**, 43–57 (2011).

A4.3.6 General Species Distribution Models (SDMs)

Species distribution models (SDMs) are numerical tools that combine observations of species occurrence or abundance with environmental correlates based on statistically or theoretically derived response surfaces (Elith & Leathwick 2009; Guisan & Zimmermann 2000). They rely on the environmental niche concept of Hutchinson (1957), in which a multi-dimensional hypervolume is defined by the combination of multiple environmental conditions required by a species population to survive and reproduce. Species data can be simple presence, presence–absence or abundance observations based on random or stratified field sampling, or observations obtained opportunistically. Environmental predictors can exert direct or indirect effects on species, arranged along a gradient from proximal to distal predictors and are optimally chosen to reflect the habitat suitability of the species (Guisan & thuiller 2005). Since species' responses to environmental predictors tend to be complex, it is usually desirable to fit nonlinear functions by means of correlative approaches including GAMs and GLM, or Artificial Neural Network and Machine Learning (Austin, 2002).

SDMs are used to gain ecological and evolutionary insights and to predict distributions across landscapes, often requiring extrapolation in space and time (Elith & Leathwick 2009). *Predictive mapping*, or geographical extrapolation using the model, results in a spatially explicit "wall-to-wall" prediction of species distribution or habitat suitability (Franklin 2010). SDMs are widely used across terrestrial, freshwater, and marine realms. SDMs have been widely used to project how species ranges might change in the future. Then, using projections from the Intergovernmental Panel on Climate Change (IPCC), one can investigate how environmental changes will affect future species distributions[4]. Alternatively, SDMs can also be used to reconstruct historical changes in species distributions.

Website: https://damariszurell.github.io/SDM-Intro/

Key references

Elith, J. & Leathwick, J. R. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697 (2009).

Guisan, A. & Zimmermann, N. E. Predictive habitat distribution models in ecology. Ecol. Modell. 135, 147–186 (2000).

Hutchinson, G. E. Concluding remarks. Cold Spring Harb. Symp. Quant. Bilogy 22, 415–427 (1957).

Guisan, A. & Thuiller, W. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8, 993–1009 (2005).

Franklin, J. *Mapping Species Distributions: Spatial Inference and Prediction*. (Cambridge University Press, 2010). doi:10.1017/cbo9780511810602.

A4.4 Community qualitative models

Qualitative models are based on a general understanding of the relationships of the ecosystem variables and can be represented by equation, matrices, or graphs (Puccia and Levins, 1985, Dambacher et al., 2009). Qualitative models provide a framework for formulating alternative hypothesis about the structure and function of ecosystem (Puccia and Levins, 1985, Dambacher et al., 2002).

A4.4.1 Conceptual ecological models (CEM)

Conceptual ecological models or qualitative models are mainly developed using sign directed graphs or signed digraphs methodology, where the links between variables describe positive or negative direct effects (i.e., the sign +, -, 0) (Puccia and Levins, 1985, Dambacher et al., 2009). Therefore, this modelling approach requires only qualitative understanding of how species and variables composing a system interact. Therefore, these types of models offer an alternative or complementary method that could be very useful in data-limited systems, as they did not require excessive data requirements typical of many ecosystem models (Puccia and Levins, 1985).

Key references

Coll, M., M. Albo-Puigserver, J. Navarro, I. Palomera, and J. M. Dambacher. 2019. Who is to blame? Plausible pressures on small pelagic fish population changes in the northwestern Mediterranean Sea. Marine Ecology Progress Series **617**:277-294.

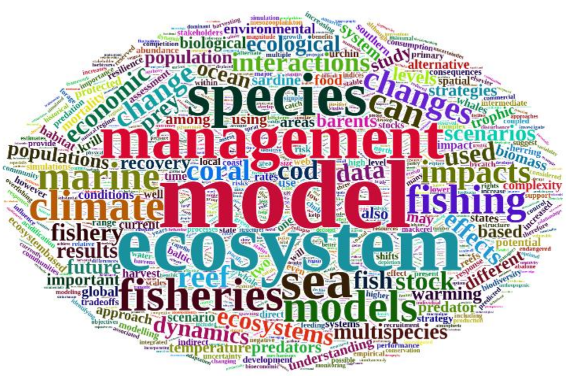
Dambacher, J. M., H. W. Li, and P. A. Rossignol. 2002. Relevance of community structure in assessing indeterminacy of ecological predictions. Ecology **83**:1372-1385.

Puccia, C. J. and R. Levins. 1985. Qualitative modeling of complex systems. Harvard University Press Cambridge, MA.

Dambacher JM, Gaughan DJ, Rochet MJ, Rossignol PA, Trenkel VM (2009) Qualitative modelling and indicators of exploited ecosystems. Fish Fish 10: 305−322

A4.5 Minimum realistic models

Minimum realistic models (MRM) and models of intermediate complexity (MICE) include a limited number of species that have important interactions with the target species of the study (Punt and Butterworth 1995, Plagányi et al. 2014). Within this category we will include models such as GADGET (Globally applicable Area-Disaggregated general Ecosystem Toolbox) (e.g., Andonegi et al. 2011, Pérez-Rodríguez et al. 2017), multispecies bioenergetic models (Koen-Alonso and Yodzis 2005) and SMS (Stochastic Multispecies Models) (e.g., Lewy and Vinther 2004, Kempf et al. 2010).



A4.5.1 Multi-species production model (AGG-PROD)

The Multi-species Production Model [AGG-PROD] is a minimum realistic model designed to simulate upper trophic level dynamics in the Northeast USA large marine ecosystem (NEUS LME). It is a food web model based on Schaeffer surplus porduction model but includes also competition and predation. The model was parameterized to describe the dynamics of commercially exploited species in the NEUS LME and focuses mainly on biotic interactions. The model simulates the dynamics of the main fish groups and marine mammals of NEUS LME (Gadids, Flatfish, Small pelagics, Mysticetes, Odontocetes, Pinnipeds), and provides a useful tool to implement ecosystem-based management.

Key references

Gamble RJ, Link JS. 2009. Analyzing the tradeoffs among ecological and fishing effects on an example fish community: A multispecies (fisheries) production model. *Ecological Modeling* 220(19): 2570-2582. doi: 10.1016/j.ecolmodel.2009.06.022.

Gamble RJ, Link JS. 2012. Using an aggregate production simulation model with ecological interactions to explore effects of fishing and climate on a fish community. *Marine Ecology Progress Series* 459: 259-274. doi: 10.3354/meps09745.

Smith L, Gamble R, Gaichas S, Link J. 2015. Simulations to evaluate management trade-offs among marine mammal consumption needs, commercial fishing fleets and finfish biomass. *Marine Ecology Progress Series* 523: 215-232. doi: 10.3354/meps11129.

A4.5.2 BALMAR (MICE)

The BALMAR model is a food web model coupled with a climate model and a simplified bioeconomic model (Tunca et al., 2019). The food web model includes 3 species (sprat, herring and cod) and accounts for their species interactions, as well as the impact of climate, zooplankton and fisheries on their recruitment and survival (Lindegren et al., 2009). This food web model is based on a multivariate autoregressive model (MAR), which applies a statistical framework for modelling food web interactions at multiple trophic levels (Ives et al., 2003). The climate model is based on the outputs from the BALTEX Assessment on Climate Change for the Baltic Sea Region (BACC, 2006). The outputs of this climate model are used to force the food web model

Key references

BACC 2006 Assessment of climate change for the Baltic Sea Basin: the BALTEX assessment of climate change for the Baltic Sea region (BACC) Project. Geesthacht, Germany: GKSS.

Ives, A. R., Dennis, B., Cottingham, K. L. & Carpenter, S. R. 2003 Community interaction webs and zooplankton responses to planktivory manipulations. Ecol. Monogr. 73, 301–330.

Lindegren, M., Möllmann, C., Nielsen, A., and Stenseth, N. C. (2009). Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. Proc. Natl. Acad. Sci. U.S.A. 106, 14722–14727.

Tunca, S.; Lindergren, M.; Ravn-Jonsen, L.; Lindroos, M. 2019. Cooperative fisheries outperform non-cooperative ones in the Baltic Sea under different climate scenarios."Frontiers in Marine Science 6 (2019): 622.

A4.5.3 Bioeconomic multispecies model (General)

A bio-economic model (BEM) is a mathematical representation of biological and economic systems, which typically links economic and biological components and parameters together. The biological component represents the natural resource, whilst the economic component characterises resource users, e.g. the fishermen (Prellezo et al.,2012). Therefore, bioeconomic multispecies models consist of multispecies models in which the biological and economic dynamics interact, allowing integrated analyses of the exploitation of natural resources. Some of these models can also include environmental influences and trophic interactions.

Key references

Prellezo, R., Accadia, P., Andersen, J. L., Andersen, B. S., Buisman, E., Little, A., Nielsen, J. R., et al. 2012. A review of EU bio-economic models for fisheries: The value of a diversity of models. Marine Policy, 36: 423-431.

Clark C. Mathematical bioeconomics: the optimal management of renewable resources, 2nd ed.; 1976. 404 pp.

FAO, Fisheries bioeconomics—theory, modelling and management. Rome; 1998. 108 p.

Nieminen, E., Lindross, M., Heikinheimo, O. 2012. Optimal bioeconomic multispecies fisheries management: a Baltic Sea case study. Marine Resource Economics 27: 115-136.

A4.5.4 FLBEIA

FLBEIA is a simulation toolbox implemented as an R library which facilitates the development of bio-economic impact assessments of fisheries management strategies. It is built under a management strategy evaluation framework using FLR libraries. The simulation is divided in two worlds, the operating model (OM, the real world) and the management procedure model (MPM, the perceived world). The model is seasonal, and the number of seasons as well as the season length, are selected by the user. Stochasticity is introduced into the model via Montecarlo simulation. The model has no limitation in the number of the stocks, the number of fleets, the number of seasons or the number of iterations in the Montecarlo simulation, the limitation is marked by the computer. The configuration of the current toolbox presents several limitations that could be solved with additional coding; for example, trophic interactions among stocks, effort-based harvest control rules. FLBEIA has been built in a modular and extensible way to simplify the incorporation of new models if necessary.

Website: https://flbeia.azti.es

Key references

Garcia, D., S. Sánchez, R. Prellezo, A. Urtizberea, and M. Andrés. 2017. FLBEIA: A simulation model to conduct Bio-Economic evaluation of fisheries management strategies. SoftwareX 6:141-147.

A4.5.5 GADGET

Gadget is the Globally Applicable Area Disaggregated General Ecosystem Toolbox. Gadget is a flexible and powerful software tool that has been developed to model marine ecosystems, including both the impact of the interactions between species and the impact of fisheries harvesting the species. Gadget simulates these processes in a biologically realistic manner and uses a framework to test the development of the modelled ecosystem in a statistically rigorous manner. It can run complicated statistical models which take many features of the ecosystem into account. Gadget works by running an internal forward projection model based on many parameters describing the ecosystem, and then comparing the output from this model to observed measurements to get a likelihood score. The model ecosystem parameters can then be adjusted, and the model re-run, until an optimum is found, which corresponds to the model with the lowest likelihood score. This iterative, computationally intensive process is handled within Gadget, using a robust minimisation algorithm.

Website: https://github.com/gadget-framework

Key references

Howell, D. and B. Bogstad. 2010. A combined Gadget/FLR model for management strategy evaluations of the Barents Sea fisheries. ICES Journal of Marine Science 67:1998-2004.

A4.5.6 Integrated Valuation of Ecosystem Services and Trade-offs (InVest)

InVest is a modelling suite used to map and value the goods and services from nature that sustain and fulfill human life. To do that it combines models of different nature, from static look up tables with the economic value of different types of ecosystems to strategic models to simulate the dynamics of simple food webs. As such, it can be classified either as a bioeconomic model or as a minimum realistic model in the context of the current project. *InVest* helps to explore how changes in ecosystems can lead to changes in the flows of many different benefits to people. It was originally developed in land, taking advantage of abundant geographical information systems (GIS). For this reason, the main focus are modelling the services provided distinct ecosystem types defined through areal extent maps, although *InVest* can also handle individual species (e.g. fisheries) or aggregate metrics like species richness. In the marine realm available applications focus mainly on coastal services and spatial planning. There is a coastal blue carbon model tuned to calculate carbon storage potential. There have been also implementations featuring spatial fisheries dynamics (age structured models with migration, recruitment and growth).

Websites:

https://github.com/natcap

https://naturalcapitalproject.stanford.edu,

https://naturalcapitalproject.stanford.edu/software/invest,

http://marineapps.naturalcapitalproject.org

Key references

Arkema KK, Verutes GM, Wood SA, Clarke-Samuels C, Rosado S, Canto M, Rosenthal A, Ruckelshaus M, Guannel G, Toft J, Faries J, Silver JM, Griffin R, Guerry AD. 2015. Embedding ecosystem services in coastal planning leads to better outcomes for people and nature. *Proceedings of the National Academy of Sciences USA* 112(24): 7390-7395. doi: 10.1073/pnas.1406483112.

Hamel P, Chaplin-Kramer R, Sim S, Mueller C. 2015. A new approach to modeling the sediment retention service (InVEST 3.0): Case study of the Cape Fear catchment, North Carolina, USA. *Science of the Total Environment* 524-525: 166-177. doi: 10.1016/j.scitotenv.2015.04.027.

Khoukh M, Maynou F. 2018. Spatial management of the European hake *Merluccius merluccius* fishery in the Catalan Mediterranean: Simulation of management alternatives with the InVEST model. *Scientia Marina*. 82S1: 175-188. doi: 10.3989/scimar.04748.18A.

Sharp R, Douglass J, Wolny S, Arkema K, Bernhardt J, Bierbower W, Chaumont N, Denu D, Fisher D, Glowinski K, Griffin R, Guannel G, Guerry A, Johnson J, Hamel P, Kennedy C, Kim

CK, Lacayo M, Lonsdorf E, Mandle L, Rogers L, Silver J, Toft J, Verutes G, Vogl AL, Wood S, Wyatt K. 2020, *InVEST 3.10.2.post34+ug.ga66060d User's Guide*. The Natural Capital Project, Stanford University, University of Minnesota, The Nature Conservancy, and World Wildlife Fund.

A4.5.7 Integrative system dynamic model (ISDM-MICE)

Is a system dynamic model developed in the software STELLA (Costanza and Ruth, 1988), which can make it in a powerful tool with a clear graphic user interface. The model structure includes the more important species for various stakeholders' groups and their interactions (Koenigstein et al., 2016). The model includes low trophic level species (e.g., phytoplankton) up to high trophic levels such as seals and tooth whales. To reduce model complexity, ecologically similar species can be aggregated into groups. On the other hand, the model includes reproduction and recruitment processes within fish species. In addition, fishing, ocean warming, acidification, primary production and tourism and recreation services were incorporated. The model includes calibration and validation processes. Finally, the model integrates stakeholder perceptions about ecological processes (e.g., interactions between species and impact of ocean warming.

Key references

Costanza, R., Ruth, M. (1998). Using dynamic modeling to scope environmental problems and build consensus. Environmental management, 22(2), 183-195.

Koenigstein, S., Ruth, M., Gößling-Reisemann, S. (2016). Stakeholder-informed ecosystem modeling of ocean warming and acidification impacts in the Barents Sea region. Frontiers in Marine Science, 3, 93.

A4.5.8 ISIS FISH

Model to assess mixed fisheries issues. ISIS-Fish is a complex fishery simulator. The simulation model is generic in order to be used for different types of fisheries. Existing knowledge about each fishery is stored in a database included in the software, and may be easily modified. This includes the parameters describing each population and each fishing activity. Both management measures and behaviour of fishermen in reaction to these measures may be interactively designed through a Script language. The simulation tool enables one to compare the respective impacts of conventional management measures like catch and effort controls, and measures more recently advocated like marine protected areas. It is not multispecies since it does not include species interactions but considers fleet dynamics. It is entirely written in Java. In the second version, ECMAScript was used as the scripting language, since version 3, Java is used directly. This provides syntax verification, colour coding and identification of lines with errors.

Website:

http://isis-fish.org

https://gitlab.nuiton.org/ifremer/isis-fish

Key references

Mahévas, S. & D. Pelletier, 2004. 'ISIS-Fish, a generic and spatially-explicit simulation tool for evaluating the impact of management measures on fisheries dynamics.' Ecological Modelling 171, 65-84.

Pelletier, D. , Mahévas, S., Drouineau, H., Vermard, Y., Thebaud, O., Guyader,O. & Poussin, B., 2009. 'Evaluation of the bioeconomic sustainability of multi-species multi-fleet fisheries under a wide range of policy options using ISIS-Fish.' Ecological Modelling 220 (7): pp. 1013-1033.

A4.5.9 MEFISTO

MEFISTO is a model to reproduce the bio-economic conditions in which the fisheries occur. The model is, perforce, multispecific and multigear and multifleet. Management based on effort (developed for Mediterranean fisheries). The model has 3 boxes: stock box (simulates dynamic of a particular stock), market box (converts catch into money) and fisherman box (simulates fishermen economic behavior). It has some specificities related to the Mediterranean fisheries sector: based on fishing effort (instead of TACs) (the way to increase effort is increasing the fishing catchability because time is limited) and the economic part follows the "share" retribution system. Biological box is based on an age-structured population model.

Website:

http://webco.faocopemed.org/old_copemed/en/activ/infodif/mefisto.htm

https://mefisto2017.com

Key references

Lleonart J, Maynou F, Recasens L, Franquesa R. 2003. A bioeconomic model for Mediterranean Fisheries, the hake off Catalonia (Western Mediterranean) as a case study. Scientia Marina, 67(suppl. 1), 337–351.

A4.5.10 Spatio-temporal model of intermediate complexity for ecosystem assessments (MICE-in-Space)

The spatio-temporal Model of Intermediate Complexity for Ecosystem assessments [MICE-in-space] is a multispecies model that reconstructs spatial and temporal variability in species abundances taking into account species interactions, fishing mortality and statistical estimates of species-specific biological reference points commonly used for fisheries management. MICE-in-space extends previous developments focusing on the analysis of single stocks using Vector Autoregressive Spatio-Temporal (VAST) models to take advantage of potential covariation in the abundance of coexisting species. The model reconstructs the abundance and distribution of a set of coexisting species from noisy, irregular survey data, and estimates the strength of density dependent effects vs species interactions. Although initially focusing on species interactions, the model can be extended to account for the impact of environmental variables.

Website: https://github.com/James-Thorson-NOAA/VAST/wiki/MICE-in-space

Key references

Thorson, JT, Adams G, Holsman K. 2019. Spatio-temporal models of intermediate complexity for ecosystem assessments: A new tool for spatial fisheries management. *Fish & Fisheries* 20: 1083-1099. doi: 10.1111/faf.12398.

Thorson JT, Barnett LAK. 2017. Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. *ICES Journal of Marine Science* 74: 1311-1321. 10.1093/icesjms/fsw193.

A4.5.11 MultiSpecies Production Model (MSPM)

The Multi-Species Production Model [MSPM] is a minimum realistic model developed to assess the dynamics of cod, herring and sprat stocks in the central Baltic Sea. It has certain resemblance with Multi-Species Virtual Population Analysis (MSVPA) models, but is a parsimonious approach that takes advantage of biological knowledge about the target ecosystem. As a coarse, macroscale strategic model, it attempts to capture the essential ecological processes that determine the dynamics of the main fish stocks in the Baltic by considering key abiotic effects (e.g. the salinity on herring growth and of the volume of hypoxic waters on cod growth) interactions between species (predation and competition).

Website:

https://mir.gdynia.pl/dzialalnosc-naukowa/zaklady-naukowe/zaklad-zasobow-rybackich/?lang=en

Key references

Horbowy J. 1996. The dynamics of Baltic fish stocks on the basis of a multispecies stock-production model. *Canadian Journal of Fisheries and Aquatic Sciences* 53(9): 2115-2125*.* doi: 10.1139/f96-128.

Horbowy J. 2005. The dynamics of Baltic fish stocks based on a multispecies stock production model. *Journal of Applied Ichthyology* 21: 198-204. doi: 10.1111/j.1439-0426.2005.00596.x.

Bauer B, Horbowy J, Rahikainen M, Kulatska N, Müller-Karulis B, Tomczak MT, Bartolino V. 2019. Model uncertainty and simulated multispecies fisheries management advice in the Baltic Sea. *PLoS One* 14(1): e0211320. doi: 10.1371/journal.pone.0211320

A4.5.12 Multispecies Virtual Population Analysis (MSVPA)

Multispecies Virtual Population Analysis (MSVPA) generalizes the single species virtual population analysis developed by Gulland (1965) to several fish stocks by including predator-prey interactions. In contrast to single species VPA, in which natural mortality is assumed to be known, in MSVPA natural mortality is split into two components: predation mortality due to all predators included in the model and residual natural mortality (i.e., due to all other causes). While residuals natural mortality is assumed to be known, predation mortality is estimated inside.

Key references

Garrison, L. P., Link, J. S., Kilduff, D. P., Cieri, M. D., Muffley, B., Vaughan, D. S., Sharov, A., Mahmoudi, B. and Latour, R. J. 2010. An expansion of the MSVPA approach for quantifying predator-prey interactions in exploited fish communities. ICES Journal of Marine Science, 267: 856-870.

Gislason, H. and Helgason, T. 1985. Species interaction in assessment of fish stocks with special application to the North Sea. Dana 5, 1-44.

Magnusson, K. G. 1995. An overview of the multispecies VPA-theory and applications. Reviews in Fish Biology and Fisheries 5, 195-212.

Vinther, M. 2001. Ad hoc multispecies VPA tuning applied for the Baltic and North Sea fish stocks. ICES Journal of Marine Science 58: 311-320.

A4.5.13 Spatial Multispecies Operating model (SMOM)

The Spatial Multi-species Operating Model (SMOM) simulates krill-predator-fishery interaction dynamics. SMOM was developed for scientific advice regarding the subdivision of the precautionary catch limit for krill among 15 small-scale management units (SSMUs) in the Scotia Sea to reduce the potential impact of fishing on land-based predators. The model includes 15 SSMUs and uses an annual timestep to update the abundance of krill and predators in each of these areas. The model includes two predator groups (penguins and seals). The initial reference set used comprises 12 alternative combinations that try to bound the uncertainty in the choice of survival estimates and the breeding success relationship. The model is coded in AD Model Builder.

Key references

Plagányi, É., & Butterworth, D.S (2006). A Spatial Multi-species Operating Model (SMOM) of krill–predator interactions in small-scale management units in the Scotia Sea. http://137.158.44.66/maram/pub/2006/emm-06-12.pdf

A4.5.14 Stochastic Multispecies Models (SMS)

The Stochastic Multi Species (SMS) model is a seasonal stochastic multispecies model for which fishery mortality is described using catch-at-age data while predation mortality and food preference are based on stomach contents data by size (Lewy and Vinther, 2004). It uses the same data sources as MSVPA. It is used in the North Sea and in the Baltic Sea to provide natural mortality estimates by age and year as input to single species assessments.

Website: https://github.com/MortenVinther/Stochastic-Multispecies-Models

Key references

Lewy, P., & Vinther, M. 2004. A stochastic age-length-structured multispecies model applied to North Sea stocks. ICES CM 2004/FF: 20.

A4.5.15 TRITON

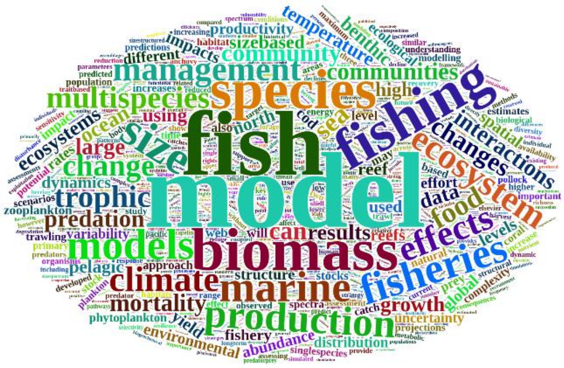
TRITON (Temperate Reefs in Tasmania with lObsters and urchiNs) is a simulation model (Minimum realistic model) with three functional groups that includes grazing of sea urchins on seaweeds, predation of lobsters on sea urchins and dependency of lobster dynamics on the seawed bed (abalone was indirectly included in later applications). Used for decision-making, linked to MSE.

Key references

Marzloff, M. P., C. R. Johnson, L. R. Little, J.-C. Soulié, S. D. Ling, and S. D. Frusher. 2013. Sensitivity analysis and pattern-oriented validation of TRITON, a model with alternative community states: Insights on temperate rocky reefs dynamics. Ecological Modelling 258:16-32. https://doi.org/10.1016/j.ecolmodel.2013.02.022

A4.6 Multispecies size-based models

Multispecies size-based models describe energy transfer from primary producers to consumers, focussing on body size rather than species identity. Within this category we will include models such as Mizer (dynamic multi-species size-spectrum models) (e.g., Scott et al. 2014), FishSUMS (e.g., Speirs et al. 2016), SS-DBEM (Size-Spectra Dynamic Bioclimate Envelope Model) (e.g., Fernandes et al. 2013) and APECOSM (Apex Predators ECOSystem Model) (Dueri and Maury 2013).



A4.6.1 Apex Predators ECOSystem Model (APECOSM)

APECOSM model aims to represent the spatialized dynamics of open ocean pelagic ecosystems in the global ocean. Physical forcings (winds, temperature and currents from the OPA circulation model), biogeochemical forcings (primary production and oxygen from the PISCES biogeochemical model) as well as the effects of fishing are explicitely taken into account in the model (Figure). The model represents the energy flow through the Open Ocean Pelagic Ecosystem (OOPE) with a size-structured energy flux equation in 5 explicit dimensions (space, time, community and weight).

The epipelagic community is distinguished from the mesopelagic migratory community. The energy input at the basis of the OOPE comes from the PISCES biogeochemical model (*cf*. Paragraph "Biogeochemical Models"). The tuna species under interest (yellowfin, skipjack, bigeye, albacore) belongs to the OOPE (*i.e.* interact trophically with it) but have a finer structure. Tuna population dynamics are indeed represented with a DEB-based (Dynamic Energy Budget) physiologicaly structured advection-diffusion flux equation which transports individuals through a 6-dimensional space (space, time, reserves, structure, gonads).

Behaviour of fish is related to their physiological status. A sub-model enables to take into account the small-scale vertical movements of tunas into the larger scale ecosystem dynamics model and drives the interactions between tunas and OOPE.

Website: https://apecosm.org

Key References

Aumont O, Maury O., Lefort S., and Bopp L. "Evaluating the potential impacts of the diurnal vertical migration by marine organisms on marine biogeochemistry," *Global biogeochemical cycles*, vol. 32, pp. 1622-1643, 2018.

Guiet J., Aumont O., Poggiale J., and Maury O, "Effects of lower trophic level biomass and water temperature on fish communities: a modelling study," *Progress in oceanography*, vol. 146, pp. 22-37, 2016.

Guiet J., Bianchi D., Maury O., Barrier N. and Kessouri F., “Movement shapes the structure of fish communities along a cross-shore section in the california current,” *Frontiers in marine science*, vol. 9, 2022.

Heneghan R.F., Galbraith E., Blanchard J. L., Harrison C., Barrier N., Bulman C., Cheung W., Coll M., Eddy T.D., Erauskin-Extramiana M., Everett J.D., Fernandes-Salvador J.A., Gascuel D., Guiet J., Maury O., Palacios-Abrantes J., Petrik C.M., du Pontavice H., Richardson A.J., Steenbeek J., Tai T.C., Volkholz J., Woodworth-Jefcoats P. A., and Tittensor D. P. “Disentangling diverse responses to climate change among global marine ecosystem models,” *Progress in oceanography*, p. 102659, 2021.

Lotze H. K., Tittensor D. P., Bryndum-Buchholz A., Eddy T. D., Cheung W. W. L., Galbraith E. D., Barange M., Barrier N., Bianchi D., Blanchard J. L., Bopp L., Büchner M., Bulman C. M., Carozza D. A., Christensen V., Coll M., Dunne J. P., Fulton E. A., Jennings S., Jones M. C., Mackinson S., Maury O., Niiranen S., Oliveros-Ramos R., Roy T., Fernandes J. A., Schewe J., Shin Y., Silva T. A. M., Steenbeek J., Stock C. A., Verley P., Volkholz J., Walker N. D., and Worm B. “Global ensemble projections reveal trophic amplification of ocean biomass declines with climate change,” *Proceedings of the national academy of sciences*, vol. 116, p. 12907(de Oceanografia et al.)12912, 2019.

Maury O., Faugeras B., Shin Y., Poggiale J., Ari T. B. and Marsac F. “Modeling environmental effects on the size-structured energy flow through marine ecosystems. part 1: the model,” *Progress in oceanography*, vol. 74, pp. 479-499, 2007.

Maury O., Shin Y., Faugeras B., Ari T.B. and Marsac F., “Modeling environmental effects on the size-structured energy flow through marine ecosystems. part 2: simulations,” *Progress in oceanography*, vol. 74, pp. 500-514, 2007.

Maury O. “An overview of apecosm, a spatialized mass balanced “apex predators ecosystem model” to study physiologically structured tuna population dynamics in their ecosystem,” *Progress in oceanography*, vol. 84, pp. 113-117, 2010.

Tittensor D. P., Novaglio C., Harrison C. S., Heneghan R. F., Barrier N., Bianchi D., Bopp L., Bryndum-Buchholz A., Britten G. L., Büchner M., Cheung W. W. L., Christensen V., Coll M., Dunne J. P., Eddy T. D., Everett J. D., Fernandes-Salvador J. A., Fulton E. A., Galbraith E. D., Gascuel D., Guiet J., John J. G., Link J. S., Lotze H. K., Maury O., Ortega-Cisneros K., Palacios-Abrantes J., Petrik C. M., du Pontavice H., Rault J., Richardson A.J., Shannon L., Shin Y., Steenbeek J., Stock C. A., and Blanchard J. L. “Next-generation ensemble projections reveal higher climate risks for marine ecosystems,” *Nature climate change*, 2021.

A4.6.2 BiOeconomic mArine Trophic Size-spectrum (BOATS)

The BiOeconomic mArine Trophic Size-spectrum [BOATS] is an upper trophic levels model designed to study global fisheries. It includes an economic module based on the classical Gordon-Schaeffer model, which enables the interactive simulation of open fisheries. The model code is specifically designed for use in gridded global ocean models. BOATS predicts the biomass spectra for fish sizes from 10 g to 100 kg by simultaneously simulating the size spectra of three fish groups (small, medium and large). The model uses as input forcing gridded fields of net primary productivity, temperature, and phytoplankton, and additional settings that enable the assessment of alternative economic scenarios.

Website:

https://zenodo.org/record/27700#.YkGNOOdBxD8

https://earthsystemdynamics.org

Key references

Carozza DA, Bianchi D, Galbraith ED. 2016. The ecological module of BOATS-1.0: a bioenergetically constrained model of marine upper trophic levels suitable for studies of fisheries and ocean biogeochemistry. *Geoscientific Model Development* 9: 1545-1565. doi: 10.5194/gmd-9-1545-2016.

Carozza DA, Bianchi D, Galbraith ED. 2017. Formulation, general features and global calibration of a bioenergetically-constrained fishery model. *PLoS ONE* 12(1): e0169763. doi: 10.1371/journal.pone.0169763.

Galbraith E, Carozza D, Bianchi D. 2017. A coupled human-Earth model perspective on long-term trends in the global marine fishery. *Nature Communications* 8: 14884. doi: 10.1038/ncomms14884.

A4.6.3 FEISTY: A Global Fisheries Model

Fisheries Size and Functional Type model (FEISTY) is a temporally dynamic, spatially explicit, mechanistic model of size-structured forage, large pelagic, and demersal fish functional types and an unstructured benthic invertebrate biomass pool[1,2]. The model quantifies and predicts global fish biomass and yield globally. Fish functional types are defined by their maximum size, habitat, and prey preference. It is based on allometric scaling principles, includes basic life cycle transitions, as well as the competitive and predatory trophic interactions between the fishes and with their pelagic and benthic food resources. It also includes a simple representation of fishing with constant mortality rates in time and space. FEISTY uses outputs from GFDL's ESM2.6 high-resolution Earth System Model to provide physical and plankton food web forcing. ESM2.6 is constructed integrating carbon and plankton food web dynamics from GFDL's Carbon, Ocean Biogeochemistry and Lower Trophics (COBALT) ecosystem model[3] with a high-resolution physical climate simulation[4]. COBALT is linked to FEISTY in an "offline" fashion. That is, COBALT outputs drive the fish model, but there are no feedbacks of the fish on the plankton.

FEISTY has already been applied to understand the bottom-up drivers of spatial catch patterns globally, capturing relatively well the main drivers and processes that structure marine communities at high trophic levels. Specifically, FEISTY reveals similar estimates to the total fish biomass as size-based models without functional types and reproduces well the underlying mechanism involved in structuring large pelagic vs. demersal environment. It is also able to represent observed trends in fisheries catches and environmental variability in trophodynamics. In addition, the fact that it is a temporally dynamic model makes it capable of capturing trends forced by climate change, as well as nonlinear tipping points and regime shifts.

Website: https://scripps.ucsd.edu/profiles/cpetrik

Key references

Petrik, C. M., Stock, C. A., Andersen, K. H., van Denderen, P. D. & Watson, J. R. Bottom-up drivers of global patterns of demersal, forage, and pelagic fishes. *Prog. Oceanogr.* **176**, 102124 (2019).

Petrik, C. M., Stock, C. A., Andersen, K. H., van Denderen, P. D. & Watson, J. R. Large Pelagic Fish Are Most Sensitive to Climate Change Despite Pelagification of Ocean Food Webs. *Front. Mar. Sci.* **7**, 1–19 (2020).

Stock, C. A., Dunne, J. P. & John, J. G. Global-scale carbon and energy flows through the marine planktonic food web: An analysis with a coupled physical–biological model. *Prog. Oceanogr.* **120**, 1–28 (2014).

Delworth, T. L. *et al.* Simulated Climate and Climate Change in the GFDL CM2.5 High-Resolution Coupled Climate Model. *J. Clim.* **25**, 2755–2781 (2012).

A4.6.4 FishSUMS

FishSUMS is a partial ecosystem model which simulates in detail a cadre of 10-15 focal species, each of whose populations is represented by a series of discrete length classes representing the full life-history from egg to adult. Predation between species is specified by a generic distribution of the prey-predator size ratio, so that the length classes of all species form an integrated food web. The focal species are selected from those that are commercially or ecologically important in a given ecosystem, together with others that are important as predators or prey. In addition, in order to represent basal and alternative sources of food for the cadre focal species, the rest of the ecosystem is subdivided into zooplankton, benthic invertebrates and `other fish', each of which is modelled by a simple biomass length spectrum divided into bins of equal width on a log scale of organism weight. The length-based structure of the cadre of focal species is a key feature which sets FishSUMS apart from other multi-species food web models based on age-classes. In the latter, predator-prey links between species age classes must be parameterised explicitly from data, whilst in FishSUMS diet composition is a simulated output and observed data become a validation or fitting resource rather than a necessity for parameterisation. The model outputs are times series of total stock biomass (TSB), recruits and fisheries landings and discards, diet composition, and the population length distributions, for each of the cadre of focal species.

FishSUMS is designed to simulate cascade dynamics – e.g. the propagation through the focal species food web of the effects of changes in harvesting rates, or climate-driven changes in recruitment performance. The model has been thoroughly parameterised for the North Sea and intensively compared with observed diet and survey species abundance and length distribution data. Model implementations are in progress for regions of the west of Scotland supported by NERC and Marine Scotland research grant and DTG funding. The model is available as a package for the R statistical environment from a sharepoint site at the University of Strathclyde and is supported by professional documentation and version control.

Key reference

Speirs, D.C., Guirey, E.J., Gurney, W.S.C. and Heath, M.R. (2010). A length structured partial ecosystem model for cod in the North Sea. Fisheries Research 106, 474-494.

A4.6.5 Length-based Multi-species Analysis by Numerical Simulation (LeMANS)

The Length-based Multi-species Analysis by Numerical Simulation[LeMANS] is a size-based model that is mainly used to analyze and simulate the coupled dynamics of upper trophic level species, especially communities of commercially exploited marine fish species. The main feature of the model, especially when compared to other size-spectra models, is that it simultaneously keeps track of changes in community size structure while accounting for other species-specific traits. Such approach enables the model to take into account species differences in recruitment, mortality, individual growth, diet preferences, or susceptibility to fishing. It has been successfully applied to provide advice toward implementing ecosystem based management in the Nort Sea and in the Irish Sea. *LeMANS* also enables the production of probabilistic ensemble forecasts and the simulation of fleet behavior according to different bioeconomic strategies like Nash equilibrium.

Website: https://cran.r-project.org/web/packages/LeMaRns/vignettes/lemarns.html

Key references

Hall SJ, Collie JS, Duplisea DE, Jennings S, Bravington M, Link J. 2006. A length-based multispecies model for evaluating community responses to fishing. *Canadian Journal of Fisheries and Aquatic Sciences* 63(6): 1344-1359. doi: 10.1139/f06-039.

Rochet MJ, Collie JS, Jennings S, Hall SJ. 2011. Does selective fishing conserve community biodiversity? Predictions from a length-based multispecies model. *Canadian Journal of Fisheries and Aquatic Sciences* 68(3): 469-486. doi: 10.1139/F10-159.

Spence MA, Bannister HJ, Ball JE, Dolder PJ, Griffiths CA, Thorpe RB. 2020. LeMaRns: A Length-based Multi-species analysis by numerical simulation in R. *PloS ONE* 15(2): e0227767. doi: 10.1371/journal.pone.0227767.

Thorpe RB, Le Quesne WJF, Luxford F, Collie JS, Jennings S. 2015. Evaluation and management implications of uncertainty in a multispecies size-structured model of population and community responses to fishing. *Methods in Ecology & Evolution* 6: 49-58. doi: 10.1111/2041-210X.12292.

A4.6.6 Macroecological model

The macroecological model is a size-spectra model designed to assess uncertainty in total consumer biomass and the impact of fishing in marine ecosystems through the implementation of simple assumptions about consumer resource dynamics, and energy and material fluxes in the sea. It produces steady-state predictions of the size-spectra of consumers using as input surface fields for temperature, chlorophyll and primary production. The model considers size classes from 0.001 g to 1000 kg for 13 species with increasing asymptotic size. The macroecological model has been used to estimate global consumer biomass, biogeochemical fluxes, and the impact of fishing on marine ecosystems.

Website: https://www.isimip.org/impactmodels/details/87/

Key reference

Jennings S, Collingridge K. 2015. Predicting consumer biomass, size-structure, production, catch potential, responses to fishing and associated uncertainties in the world's marine ecosystems. *PLoS One* 10(7): e0133794. Doi: 10.1371/journal.pone.0133794.

A4.6.7 MIZER (Dynamic Multi-Species Size-Spectrum Models)

The model was developed to represent the size and abundance of organism from phytoplankton to large fish predators in a size-structured food web. Organisms are represented by body size (Blanchard et al., 2012), and in some species by specific traits (Blanchard et al., 2014). The development and use of the model has focused on North Sea (Blanchard et al., 2014), and Bering Sea (Reum et al., 2019). The code is published as an R package (Scott et al., 2014) with the name of Mizer which is based on: 1) an individual can be characterized by its and the model calculates the size and trait spectrum which is the density of individuals at a particular size; and, 2) food preference is determined partly by species preference and partly by individual weight combined with a prey weight preference, described by a lognormal selection model in terms of the ratio between the weight of predators and prey. Fishing mortality, F, is a product of the gear selectivity function, fishing effort and catchability. Fishing effort can vary through time allowing dynamic harvest patterns to be simulated.

Website: https://sizespectrum.org/mizer

Key references

Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., Holt, J., et al. 2012. Potential consequences of climate change for primary production and fish production in large marine ecosystems. Philosophical Transactions of the Royal Society B, 367: 2979–2989.

Blanchard, J. L., Andersen, K. H., Scott, F., Hintzen, N. T., Piet, G., & Jennings, S. (2014). Evaluating targets and trade-offs among fisheries and conservation objectives using a multispecies size spectrum model. Journal of Applied Ecology, 51(3), 612-622.

Reum, J. C., Blanchard, J. L., Holsman, K. K., Aydin, K., Hollowed, A. B., Hermann, A. J., ... & Punt, A. E. (2020). Ensemble projections of future climate change impacts on the Eastern Bering Sea food web using a multispecies size spectrum model. Frontiers in Marine Science, 7, 124.

Scott, F., Blanchard, J. L., & Andersen, K. H. (2014). Mizer: An R package for multispecies, trait-based and community size spectrum ecological modelling. Methods in Ecology and Evolution, 5(10), 1121-1125.

Woodworth-Jefcoats, P. A., Blanchard, J. L., & Drazen, J. C. (2019). Relative impacts of simultaneous stressors on a pelagic marine ecosystem. Frontiers in Marine Science, 383.

A4.6.8 Non-linear Species Size Spectrum Model (nlSSSM)

The Non-linear Species Size Spectrum Model [*Non-linear SSSM*] is a recently developed model that admits deviations from the power law size-spectra predicted by most theoretical models of the pelagic size-spectrum. Such approach enables *Non-linear SSSM* to capture the characteristic domes and troughs that are observed in the real world data. The model is able to reproduce these patterns by assuming perturbations of the spectra arising from top-down trophic cascades. The default parameterization of the model produces steady-state predictions of the size-spectra for size classes ranging from 20 pg to 10 kg. The model has been successfully used to reproduce large scale geographical variation in the size spectra of pelagic communities across marine and freshwater ecosystems.

Website: http://axel.rossberg.net, https://doi.org/10.1038/s41467-019-12289-0

Key references

Rossberg AG. 2012. A complete analytic theory for structure and dynamics of populations and communities spanning wide ranges in body size. *Advances in Ecological Research* 46: 429-522. doi: 10.1016/B978-0-12-396992-7.00008-3.

Rossberg AG, Gaedke U, Kratina P. 2019. Dome patterns in pelagic size spectra reveal strong trophic cascades. *Nature Communications* 10: 4396. 10.1038/s41467-019-12289-0.

A4.6.9 Size-based food web model

Size-based methods capture the properties of foodwebs that describe energy flux and production at a particular size, independent of species' ecology (Barange et al., 2014). There are multiple models based on size-spectrum where some have been used at global scales (Jennings et al., 2008; Blanchard et al., 2012). In Jennings et al. (2008) fish productivity is estimated based on temperature and primary production considering the ocean as a single layer. This model is one of the bases for SS-DBEM model explained below. A reconsideration of transfer efficiency and dealing with its uncertainty is published in Jennings and Collingridge (2015). Similarly, a model estimates potential for fish production by size class, considering temperature effects on the feeding and intrinsic mortality rates of organisms in Blanchard et al., (2012), but dividing fish productivity in bottom and pelagic layers. This model is the base for MIZER model explained below.

Key references

Barange, M., Merino, G., Blanchard, J. L., Scholtens, J., Harle, J., Allison, E. H., ... & Jennings, S. (2014). Impacts of climate change on marine ecosystem production in societies dependent on fisheries. Nature Climate Change, 4(3), 211-216.

Blanchard, J. L., Jennings, S., Holmes, R., Harle, J., Merino, G., Allen, J. I., ... & Barange, M. (2012). Potential consequences of climate change for primary production and fish production in large marine ecosystems. Philosophical Transactions of the Royal Society B: Biological Sciences, 367(1605), 2979-2989.

Jennings, S., Mélin, F., Blanchard, J. L., Forster, R. M., Dulvy, N. K., & Wilson, R. W. (2008). Global-scale predictions of community and ecosystem properties from simple ecological theory. Proceedings of the Royal Society B: Biological Sciences, 275(1641), 1375-1383.

Jennings, S., & Collingridge, K. (2015). Predicting consumer biomass, size-structure, production, catch potential, responses to fishing and associated uncertainties in the world's marine ecosystems. PloS one, 10(7), e0133794.

A4.6.10 Size-Spectra Dynamic Bioclimate Envelope Model (SS-DBEM)

SS-DBEM (Fernandes et al., 2013; Fernandes et al., 2021a), based on the Dynamic Bioclimate Envelope Model (DBEM), is a combined mechanistic-statistical approach that has been applied to a large number of marine species globally (Fernandes et al., 2013; Mullon et al., 2016; Fernandes et al., 2017; Fernandes et al., 2021b; Erauskin-Extramiana et al., 2022), regionally (Jones et al., 2013; Fernandes et al., 2016; Fernandes et al., 2017), to consider size impacts of climate change (Queirós et la., 2018;) and for spatial planning under climate change (Queirós et al., 2016; Queirós eta al., 2021). The DBEM model projects changes in species distribution and abundance with explicit consideration of mechanisms of population dynamics, dispersal (larval and adult) and ecophysiology (see Table I), under changes in ocean temperature, salinity, upwelling, sea-ice extent and habitats (Cheung et al., 2011; Cheung et al., 2016) considering all the species distribution (not specific stocks of each species separately). Specifically, the multi-species version of the model (SS-DBEM) incorporates species interactions based on size-spectrum (SS) theory and habitat suitability. Therefore, the model considers predation and food availability through size-spectrum energy transfer from primary producers to consumers of progressively larger body size (Fernandes et al., 2013). Despite yearly outputs, pelagic species have two internal time steps to account for interannual seasonality and both, bottom and surface environmental drivers are considered since these species have pelagic and demersal life stages.

SS-DBEM has been used for Copernicus Climate Change Indicators services:

https://climate.copernicus.eu/marine-coastal-and-fisheries-project

Website: http://azti.es

Key references

Cheung, W. W. L., Lam, V. W. Y., & Pauly, D. (2008). Modelling Present and Climate-Shifted Distribution of Marine Fishes and Invertebrates. Fisheries Centre Research Report 16 (3), University of British Columbia, Vancouver.

Cheung, W. W., Dunne, J., Sarmiento, J. L., & Pauly, D. (2011). Integrating ecophysiology and plankton dynamics into projected maximum fisheries catch potential under climate change in the Northeast Atlantic. ICES Journal of Marine Science, 68(6), 1008-1018.

Cheung, W. W., Jones, M. C., Reygondeau, G., Stock, C. A., Lam, V. W., & Frölicher, T. L. (2016). Structural uncertainty in projecting global fisheries catches under climate change. Ecological Modelling, 325, 57-66.

Erauskin-Extramiana, M., Chust, G., Arrizabalaga, H., Cheung, W. W., Santiago, J., Merino, G., & Fernandes-Salvador, J. A. (2022) Implications for Global Tuna Fishing Industry of Climate Change-Driven Alterations in Productivity and Body Sizes. Available at SSRN 4059543.

Fernandes, J. A., Cheung, W. W., Jennings, S., Butenschön, M., Mora, L., Frölicher, T. L, Barange M., & Grant, A. (2013). Modelling the effects of climate change on the distribution and production of marine fishes: accounting for trophic interactions in a dynamic bioclimate envelope model. Global change biology, 19, 2596-2607.

Fernandes, J. A., Kay, S., Hossain, M. A., Ahmed, M., Cheung, W. W., Lazar, A. N., & Barange, M. (2016). Projecting marine fish production and catch potential in Bangladesh in the 21st century under long-term environmental change and management scenarios. ICES Journal of Marine Science, 73(5), 1357-1369.

Fernandes, J. A., Papathanasopoulou, E., Hattam, C., Queirós, A. M., Cheung, W. W., Yool, A., ... & Calosi, P. (2017). Estimating the ecological, economic and social impacts of ocean acidification and warming on UK fisheries. Fish and Fisheries, 18(3), 389-411.

Fernandes, J. A., Rutterford, L., Simpson, S. D., Butenschön, M., Frölicher, T. L., Yool, A., ... & Grant, A. (2020a). Can we project changes in fish abundance and distribution in response to climate?. Global change biology, 26(7), 3891-3905.

Fernandes, J. A., Frölicher, T. L., Rutterford, L. A., Erauskin-Extramiana, M., & Cheung, W. W. (2020b). Changes of potential catches for North-East Atlantic small pelagic fisheries under climate change scenarios. Regional environmental change, 20(4), 1-16.

A4.6.11 Zooplankton Model of Size Spectrum (ZooMSS)

The Zooplankton Model of Size Spectrum [*ZooMSS*] is a functional size-spectrum model of marine pelagic ecosystems that resolves the steady-state biomass density of several zooplankton functional types. It considers nine major zooplankton functional groups: heterotrophic flagellates, heterotrophic ciliates, larvaceans, omnivorous copepods, carnivorous copepods, chaetognaths, euphausiids, salps and jellyfish, and three groupds of fish. The model can be considered a zooplankton extension of MIZER, but it is unique in its approach to the analysis of zooplankton biomass patterns at the global scale. The model uses sea surface temperature and chlorophyll *a* concentration fields as inputs.

Website: https://github.com/MathMarEcol/ZoopModelSizeSpectra

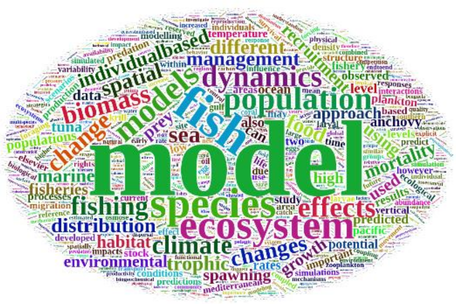
Key references

Heneghan RF, Everett JD, Blanchard JL, Richardson AJ. 2016. Zooplankton are not fish: Improving zooplankton realism in size-spectrum models mediates energy transfer in food webs. *Frontiers in Marine Science* 3, 1-15. doi: 10.3389/fmars.2016.00201.

Heneghan RF, Everett JD, Sykes P, Batten SD, Edwards M, Takahashi K, Suthers IM, Blanchard JL, Richardson AJ. 2020. A global size-spectrum model of the marine ecosystem that resolves zooplankton composition. *Ecological Modelling* 435, 109265. doi: 10.1016/j.ecolmodel.2020.109265.

A4.7 Multispecies individual-based models

Multispecies individual-based models are based on the explicit representation of individual organisms. Within this category we will include models such as SEAPODYM (Spatial ecosystem and population dynamic model) (e.g., Lehodey et al. 2008, Senina et al. 2016) and OSMOSE (Object-oriented Simulator of Marine ecOSystem Exploitation) (e.g., Shin and Cury 2004, Grüss et al. 2016).



A4.7.1 DBEM

See SS-DBEM model description.

A4.7.2 Object-oriented Simulator of Marine ecOSystem Exploitation (OSMOSE)

OSMOSE is a multispecies and Individual-based model (IBM) which focuses on fish species (Shin and Cury 2001, 2004; Shin *et al.*, 2004). The central hypothesis of the model is that fish predation is opportunistic, based on spatial co-occurrence and size adequacy between a predator and its prey (size-based opportunistic predation). It represents fish individuals grouped into schools, which are characterized by their size, weight, age, taxonomy and geographical location (2D model), and which undergo major processes of fish life cycle (growth, reproduction, recruitment, migration and mortality from predation, natural and starvation) and a fishing mortality distinct for each species. The model takes a wide parameterisation for each fish species and is area specific according to local populations. The species parameterized depend on their local importance related to their biomass, catch and consumption (predator/prey). The model is overall constrained by carrying capacity, with each species governed by its explicit life cycle (standard von Bertalanffy growth, mortality (starvation and fishing) and reproduction equations: see Shin and Cury, 2001), but with interactions through predation modelling involving foraging, min/maximum thresholds for predator/prey size ratios, spatio-temporal co-occurrence and maximum ingestion rates. The model needs basic parameters that are often available for a wide range of species, and which can be found in FishBase. In output, a variety of size-based and species-based ecological indicators can be simulated and converted to in situ data (surveys and catch data) at different levels of aggregation: at the species level (mean size, mean size-at-age, max size, trophic level), and at the community level (slope and intercept of size spectrum, Shannon diversity index). The model can be calibrated to observed biomass, using genetic algorithms. The coupling process used to link OSMOSE to LTL (low trophic level) models (*e.g.* NPZD, BFM, ERSEM) is the predation process (Travers et al., 2009). The LTL model is used as a prey field for the HTL model (concentration of nitrogen/carbon converted into wet biomass) and the HTL model provides a predation mortality field for the LTL model.

Website: https://www.osmose-model.org

Key references

Shin, Y-J., Cury P. 2001. Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquat. Living Resour. 14: 65–80.

Shin, Y-J., Cury P. 2004. Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. Can. J. Fish. Aquat. Sci. 61: 414–431.

Shin, Y.-J., Shannon L.J., Cury, P.M. 2004. Simulations of fishing effects on the southern Benguela fish community using an individual-based model: learning from a comparison with ECOSIM. In Ecosystem Approaches to Fisheries in the Southern Benguela. Shannon, L.J., Cochrane, K.L. and S.C. Pillar (Eds). African Journal of marine Science 26: 95-114.

Travers M., Shin Y.-J., Jennings S., Machu E., Huggett J.A., Field J., Cury P. 2009. Two-way coupling versus one-way forcing of plankton and fish models to predict ecosystem changes in the Benguela. Ecological Modelling, 220: 3089-3099.

A4.7.3 Spatial ecosystem and population dynamic model (SEAPODYM)

Spatial ecosystem and population dynamics model of tuna and tuna-like species in the Pacific and Atlantic Ocean. SEAPODYM has been initiated in the mid 1990s by the Oceanic Fisheries Programme of the Secretariat of the Pacific Community (SPC) and developed under several European development projects. The objective was to propose new management tools taking into account both the fishing impact and environmental variability. Since 2006, in partnership with SPC, its development has continued with the Marine Ecosystem Modelling team of CLS (Collecte Localisation Satellite). The main features of SEAPODYM modelling framework are: 1) Prediction of the temporal and spatial distributions of functional lower and mid-trophic level groups (Lehodey et al. 2010; 2015), 2) Prediction of the temporal and spatial distributions of age-structured predator (fish) populations (Lehodey et al. 2008); 3) Prediction of the total catch and the size-frequency of catch by fishing fleet; 4) Parameter optimization based on data assimilation techniques (Senina et al., 2008).

Website: http://www.seapodym.eu/

Key references

Lehodey, P., I. Senina, and R. Murtugudde. 2008. A spatial ecosystem and populations dynamics model (SEAPODYM) – Modeling of tuna and tuna-like populations. Progress in Oceanography 78:304-318.

Senina, I., J. Sibert, and P. Lehodey. 2008. Parameter estimation for basin-scale ecosystem-linked population models of large pelagic predators: Application to skipjack tuna. Progress in Oceanography 78:319-335.

A4.7.4 SPRAT

SPRAT is a spatially explicit fish stock model for end-to-end ecosystem modelling based on population balance equations (PBEs; Johanson et al. 2017). It relies on the mathematical theory of Partial Differential Equations (PDEs) integrating biogeochemical models while still being formulated from the perspective of the individual fish with a dynamic food web structure. Thus, SPRAT combines the advantages of Individual Based Models (IBMs) and Advection Diffusion Reaction (ADR) models. The main limitations of SPRAT are the following: (i) Since it represents fish as density distributions, it cannot track fish and their interactions down to the level of single individuals. (ii) On the other hand, in comparison to ADR models, the SPRAT model is associated with increased computational costs. SPRAT has been already applied and validated in the eastern Scotian Shelf ecosystem. Specifically, SPRAT was used to explore a well-documented regime shift observed on the eastern Scotian Shelf in the 1990s from a cod-dominated to a herring-dominated ecosystem. Model results are coherent with the observed multitrophic dynamics including changes in both fishing pressure and water temperature, followed by a predator–prey reversal that may have impeded recovery of depleted cod stocks. Thus, SPRAT can be potentially applied to an array of marine systems addressing spatially interacting fish populations, and their joint responses to both environmental and fisheries forcing.

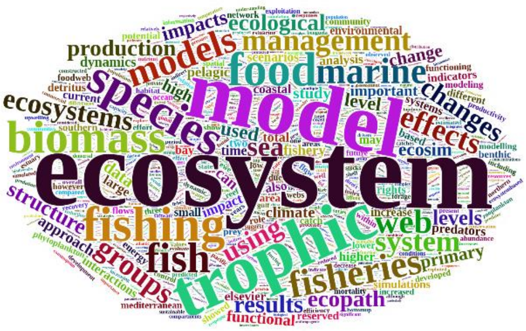
Website: https://oceanrep.geomar.de

Key references

Johanson, A. N., Oschlies, A., Hasselbring, W. & Worm, B. SPRAT: A spatially-explicit marine ecosystem model based on population balance equations. *Ecol. Modell.* **349**, 11–25 (2017).

A4.8 Mass based - food web models

Mass based - food web models represent population of dynamically interacting species or groups of species. Within this category we will include models such as the Ecopath with Ecosim approach (EwE) (e.g., Christensen and Walters 2004, Corrales et al. 2017) and StrathE2E (e.g. Heath 2012).



A4.8.1 Ecological Network Analysis (ENA)

Ecological Network Analysis (ENA) is a set of algorithms to evaluate the flow of energy and material through natural ecosystems from which a suite of systems properties can be derived. Ecological Network Analysis (ENA) combines modelling and analysis used to investigate the structure, function, and evolution of ecosystems and other complex systems. ENA is applied to network models that trace the movement of thermodynamically conserved energy or matter through the system. ENA include a number of software programs that can be used for analytical, predictive and balancing of ecosystem flow models.

Key references

Fath, B. D., U. M. Scharler, R. E. Ulanowicz, and B. Hannon. 2007. Ecological network analysis: network construction. Ecological Modelling 208:49-55.

Chaalali, A., B. Saint-Béat, G. Lassalle, F. Le Loc'h, S. Tecchio, G. Safi, C. Savenkoff, J. Lobry, and N. Niquil. 2015. A new modeling approach to define marine ecosystems food-web status with uncertainty assessment. Progress in Oceanography 135:37-47.

Baird, D., H. Asmus, R. Asmus, S. Horn, and C. de la Vega. 2019. Ecosystem response to increasing ambient water temperatures due to climate warming in the Sylt- Romo Bight, northern Wadden Sea, Germany. Estuarine Coastal and Shelf Science 228.

A4.8.2 Ecopath with Ecosim (EwE)

The Ecopath with Ecosim approach (EwE) consiste of three main linked modules: the mass-balance routine Ecopath, the time dynamic routine Ecosim and the spatial-temporal dynamic module Ecospace. For an extensive review of EwE principles, basic concepts, capabilities, limitations, and challenges of the approach, see Walters et al. (1997), Walters et al. (1999), Christensen and Walters (2004), Christensen et al. (2008), Ainsworth and Walters (2015) and Heymans et al. (2016).

Ecopath models provide a quantitative representation of the studied ecosystem, or a "snapshot", in terms of trophic flows, for a defined period of time. The key principle of the Ecopath model is the mass balance: for each functional group represented in the model, the energy removed from that group, for example by predation or fishing, must be balanced by the energy consumed, i.e., consumption, and the energy incorporated to the system, i.e., through migration. This principle is achieved through the two master equations: one describing the biological production and the other describing the consumption for each functional group or "box" in the model. Ecopath parametrizes the model by describing a system of linear equations for all the functional groups in the model. A functional group in the EwE approach consists of an onthogenic fractions of a species, a single species or a group of species that share common biological and ecological traits such as habitat, feeding and depth distribution (Christensen and Walters, 2004, Christensen et al., 2008).

Ecosim is the time-varying expression of the Ecopath model and consists of the analysis of biomass dynamics expressed through a series of differential equations (Walters et al., 1997, Christensen and Walters, 2004). Ecosim uses the initial parameters of Ecopath and the predator-prey dynamics are based on the foraging arena theory, which assumes that preys are not 100% available for predators in aquatic systems (Walters et al., 1997; Ahrens et al., 2012).

Ecospace is the spatial-temporal component of the EwE approach and considers all the key parameters of Ecosim (Walters et al. 1999). It is graphically represented by a grid of equally square cells (i.e., same size but different propierties). Ecospace applies the Ecosim equations, and the habitat foraging capacity model (HFCM) and distributes the biomass of the functional groups over the grid of cells. The HFCM calculates the suitability of each cell for all the functional groups based on the preferences of the groups for substrate type and environmental parameters (e.g., depth, sea surface and bottom temperature, oxygen) (Christensen et al., 2014). The spatial distribution of fisheries is usually driven by potential yields vs. the cost of fishing in specific locations. The movement between cells is constrained to vertices of adjacent cells (movement cannot occur diagonally).

Website: https://ecopath.org

Key references

Ahrens, R. N., Walters, C. J., & Christensen, V. (2012). Foraging arena theory. *Fish and fisheries, 13*(1), 41-59.

Ainsworth, C. H., & Walters, C. (2015). Ten common mistakes made in Ecopath with Ecosim modelling. *Ecological Modelling*(308), 14-17.

Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., & Walters, C. J. (2014). Representing Variable Habitat Quality in a Spatial Food Web Model. *Ecosystems, 17*(8), 1397-1412. doi: 10.1007/s10021-014-9803-3

Christensen, V., & Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling, 172*(2-4), 109-139. doi: 10.1016/j.ecolmodel.2003.09.003

Christensen, V., Walters, C. J., & Pauly, D. (2008). Ecopath with Ecosim version 6 user guide *Fisheries Centre, University of British Columbia, Vancouver* (Vol. 154, pp. 31).

Heymans, J. J., Coll, M., Link, J. S., Mackinson, S., Steenbeek, J., Walters, C., & Christensen, V. (2016). Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecological Modelling, 331*, 173-184.

Walters, C., Christensen, V., & Pauly, D. (1997). Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Reviews in fish biology and fisheries, 7*(2), 139-172.

Walters, C., Pauly, D., & Christensen, V. (1999). Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. *Ecosystems, 2*(6), 539-554.

A4.8.3 Linear Inverse Ecosystem Models (LIEM)

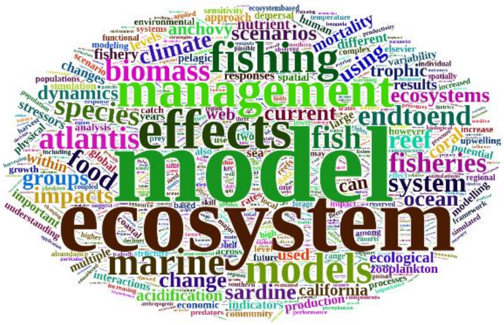
Linear inverse model uses a Monte Carlo method coupled with a Markov Chain (LIM-MCMC) to characterize the system's trophic food-web status and its associated structural and functional properties. By taking into account the natural variability of ecosystems (and their associated flows) and the lack of data on targeted environment, LIEM quantifies uncertainties for both estimated flows and derived food-web indices.

Key references

Chaalali, A., B. Saint-Béat, G. Lassalle, F. Le Loc'h, S. Tecchio, G. Safi, C. Savenkoff, J. Lobry, and N. Niquil. 2015. A new modeling approach to define marine ecosystems food-web status with uncertainty assessment. Progress in Oceanography 135:37-47.

A4.9 Whole system or end-to-end models

Whole system models or end-to-end models attempt to represent all the ecosystem components from nutrients, biogeochemical cycling and primary producers to top predators (including human components) linked through trophic interactions and the associated abiotic environment (e.g., currents and water column properties such as temperature and salinity). Within this category, we will include models such as Atlantis. In addition, whole system models also include coupled models, where models were integrated (with or without dynamic feedbacks) and outputs of one model provide inputs to the other. For example, Travers-Trolet et al. (2014) coupled an OSMOSE model with a biophysical model (ROMS -$N_2P_2Z_2D_2$).



A4.9.1 Atlantis

Atlantis is an ecosystem model that considers all parts of marine ecosystems – biophysical, economic and social. Originally focused on the biophysical world and then fisheries it has grown to begin to be used for multiple use and climate questions. Atlantis is a deterministic biogeochemical whole of ecosystem model. Its overall structure is based around the Management Strategy Evaluation (MSE) approach, where there is a sub-model (or module) for each of the major steps in the adaptive management cycle. Atlantis is 3-dimensional, age-structured (juvenile and adult) model that includes all the components of an adaptive management strategy. Considers growth, size-weight, predation, fishing mortality, recruitment, nutrient inputs, oceanographic features (option to force the model), and different human activities (mainly fishing).

Website: *http://atlantis.cmar.csiro.au*

Key references

Audzijonyte, A., Gorton, R., Kaplan, I. and Fulton, E.A. 2017. Atlantis User's Guide Part I: General Overview, Physics & Ecology. CSIRO living document.

Audzijonyte, A., Gorton, R., Kaplan, I. and Fulton, E.A. 2017. Atlantis User's Guide Part II: Socio-Economics. CSIRO living document.

Link, J.S., Fulton, E.A. and Gamble, R.J. 2010. The Northeast US Application of ATLANTIS: An full system model exploring marine ecosystem dynamics in a living marine resource management context. Progress in Oceanography 87: 214–234.

A4.9.2 BioMASS

BioMASS (Biological Multi-Agent Simulation System) is a modelling framework that unifies behaviorbehaviour and ecosystem models within a single simulation (Sansores et al., 2016). More specifically, it is an IBM framework that is able of handling and unifying the behavioural and ecosystem experimental categories with a comprehensive biological and behavioural model that strictly adheres to the physiological functions of ingestion, growth, and metabolism of organisms. In addition, the model incorporates the exchange and transfer of mass and energy through local interactions at all trophic levels (lower to higher), the physical environment and anthropogenic activity. It is implemented as a Java library and it has a graphical user interface (GUI) that facilitates its use.

Key references

Sansores, C. E., Reyes-Ramírez, F., Calderon-Aguilera, L. E. and Gómez, H. F. 2016. A novel modelling approach for the "end-to-end" analysis of marine ecosystems. Ecological informatics 32: 39-52.

Sansores-Pérez, C. E., Trejo-Sánchez, J. A. 2020. BioMASS, a spatial model for situated multiagent systems that optimizes neighborhood search. IEEE Access, vol. 8, pp. 120282-120294.

A4.9.3 CORSET

The Coral Reef Scenario Evaluation Tool (Melbourne-Thomas, 2010a, 2010b) is a stochastic model of coral reefs ecosystems that couples ecological dynamics from local (10^2m) to regional (10^6m) scales and incorporates larval dispersal models and anthropogenic (e.g., fishing) and environmental forcing (e.g., nutrification). It is graphically represented by a gridded based-map (e.g., 1x1 km or 2x2 km) and includes the interactions between five benthic functional groups (brooding corals, spawning corals, macroalgae, turf and epilithic algal communities) and four consumer groups (urchins, herbivorous fish and small and large piscivorous fish). Functional groups interact through spatial patterns of recruitment, dispersal, foraging and competition. The model has been used to assess impacts fishing and coral bleaching (Rowland et al., 2020) and inform management decisions (Melbourne-Thomas et al., 2011a) and ecosystem risk assessment (Bland et al., 2017).

Key references

Melbourne-Thomas, J., 2010a. CORSET Documentation: How to Access and Use the Coral Reef Scenario Evaluation Tool via the Reef Scenarios Portal 96.

Melbourne-Thomas, J., 2010b. Decision Support Tools for Visualising Coral Reef Futures at Regional Scales. (Ph.D. Thesis).

Rowland, J.; Lee, C.; Blansd, L.; Nicholson, E. 2020. Testing the performance of ecosystem indices for biodiversity monitoring. Ecological indicators.

A4.9.4 ECOSMO-E2E

ECOSMO (ECOSystem MOdel) is a coupled physical-biogeochemical model, with the hydrodynamics based on HAMSON model. Based on availability of nutrients (nitrogen, phosphorous and silica) and light availability, ECOSMO simulates the dynamics of three functional groups of phytoplankton (diatoms, flagellates and cyanobacteria), with the dynamics of each group simulated based on their respective physiological characteristics. The fate of two zooplankton functional groups, microzooplankton and mesozooplankton, are estimated, with the dynamics based on their specific feeding behaviour. ECOSMO E2E is NPZD-Fish modelling that represents both fish and macrobenthos as functional groups that are linked to the lower trophic levels via predator-prey relationships. The model allows investigating bottom-up impacts on primary and secondary production and cumulative fish biomass dynamics, but also bottom-up mechanisms on the lower trophic level production. In addition, ECOSMO has been coupled with spatial IBM for sprat.

Website:
https://hereon.de/institutes/coastal_systems_analysis_modeling/matter_transport_ecosystem_dynamics/models/

Key references

Schrum, C., I. Alekseeva, and M. St. John. 2006. Development of a coupled physical-biological ecosystem model ECOSMO - Part I: Model description and validation for the North Sea. Journal of Marine Systems 61:79-99.

Daewel, U., C. Schrum, and J. I. Macdonald. 2019. Towards end-to-end (E2E) modelling in a consistent NPZD-F modelling framework (ECOSMO E2E_v1.0): application to the North Sea and Baltic Sea. Geoscientific Model Development 12:1765-1789.

A4.9.5 ECOTRAN e2e

Version from EwE: transform a top–down linear solution (ECOPATH) into a bottom–up model called ECOTRAN. The end-to-end production matrix partitions the fate of biomass flowing into each functional group box between egestion losses (faeces detritus), metabolic costs (ammonium production), predation by each consumer group, removal by fisheries, and unconsumed production (“surplus” production detritus).

Key references

Robinson, K. L., J. J. Ruzicka, F. J. Hernandez, W. M. Graham, M. B. Decker, R. D. Brodeur, and M. Sutor. 2015. Evaluating energy flows through jellyfish and gulf menhaden (*Brevoortia patronus*) and the effects of fishing on the northern Gulf of Mexico ecosystem. ICES Journal of Marine Science 72:2301-2312.

Steele, J. H. and J. J. Ruzicka. 2011. Constructing end-to-end models using ECOPATH data. Journal of Marine Systems 87:227-238.

Ruzicka, J. J., K. H. Brink, D. J. Gifford, and F. Bahr. 2016. A physically coupled end-to-end model platform for coastal ecosystems: Simulating the effects of climate change and changing upwelling characteristics on the Northern California Current ecosystem. Ecological Modelling 331:86-99.

A4.9.6 InVitro agent-based modelling software

InVitro is an end-to-end model initially designed to assess alternative management strategies in the North West Australian Shelf ecosystem. Its main strength is the extremely detailed representation of the dynamics of tropical shelf ecosystems, including the impact of human stressors. To do that, *InVitro* adopts a hybrid modelling approach that combines computationally intensive agent-based modelling with less demanding numerical models based on ordinary differential equations. Agent-based modelling enables the representation of complex behaviours and interactions in space and time. For instance, *InVitro* implements interactive agents to model the dynamics of top predators and species of interest like turtles, and human activities like coastal agriculture, fisheries, and tourism. In the latter case, the model even features interactive learning and the accumulation of experience by fishermen. On the other hand, the dynamics of lower trophic levels, or the impacts of human activities with a diffuse impact like pollution or terrestrial development are represented using aggregated compartments. The model represents a variety of benthic habitats, from coral reefs to mangroves, through sponge reefs, seagrass meadows and macroalgae beds. As an end to end model, it also considers several tropic levels, from a compartmentalized lower trophic levels food web to several groups of fish (from prawns to forage fish and target and non-target finfish, large fish and elasmobranchs) and charismatic species of sea turtle, seabirds and marine mammals.

Key references

Fulton, E. A., Gray, R., Sporcic, M., Scott, R., and Hepburn, M. 2009.Challenges of crossing scales and drivers in modelling marinesystems. Proceedings of the 18th World IMACS/MODSIMCongress, Cairns, Australia, 13–17 July 2009.

Gray, R., E. Fulton, R. Little, R. Scott. 2006. *Ecosystem Model Specification with an Agent Based Framework.* North West Shelf Joint Management Study (NWSJEMS) Technical Report No. 16, 140 pp.

McDonald, A.D., E. Fulton, L.R. Little, R. Gray, K.J. Sainsbury, V.D. Lyne. 2006. *Multiple-Use Management Strategy Evaluation for Coastal MarineEcosystems Using InVitro,* pp. 283-298 *in* P. Perez & D. Baten (eds.), *Complex Science for a Complex World. Exploring Human Ecosystems with Agents.* The Australian National University (ANU) Press.

McDonald, A.D., L.R. Little, R. Gray, E. Fulton, K.J. Sainsbury, V.D. Lyne. 2008. An agent-based modelling approach to evaluation of multiple-use management strategies for coastal marine ecosystems. *Mathematics and Computers in Simulation* 78: 401-411.

4.9.7 NEMURO.FISH

NEMURO.FISH (NEMURO For Including Saury and Herring) is a fish growth bioenergetics model that uses as input the plankton densities generated by the NEMURO (North Pacific Ecosystem Model for Understanding Regional Oceanography) lower trophic model. It can be run in uncoupled and coupled modes to NEMURO. In the uncoupled mode, the growth and weight of an individual fish is computed using plankton densities simulated by NEMURO, but there is no feedback between fish consumption and plankton mortality, whereas the coupled mode includes total consumption by the fish of prey. Kishi et al. (2011) provides a review of the developments and applications of this model.

Website: https://meetings.pices.int/members/task-teams/disbanded/TT-MODELb

Key references

Kishi, M.J., Ito, Si., Megrey, B.A. et al. A review of the NEMURO and NEMURO.FISH models and their application to marine ecosystem investigations. J Oceanogr 67, 3–16 (2011).

Megrey, B. A., Rose, K. A., Klumb, R. A., Hay, D. E., Werner, F. E., Eslinger D. L., Smith S. L. 2007. A bioenergetics-based population dynamics model of Pacific herring (Clupea harengus pallasi) coupled to a lower trophic level nutrient-phytoplankton-zooplankton model: description, calibration and sensitivity analysis. Ecological modelling 2002: 144-164.

Rose, K. A., Megrey, B. A., Hay, D., Werner, F., Schweigert, J. 2008. Climate regime effects on Pacific herring growth using coupled nutrient-phytoplankton-zooplankton and bioenergetics models. Transactions of the American Fisheries Society 137:278–297.

Rose, K. A., Fiechter, J., Curchitser, E. N., Hedstrom, K., Bernal, M., Creekmore, S., Haynie, A., Ito, S., Lluch-Cota, S., Megrey, B. A., Edwards, C. A., Checkley, D., Koslow, T., McClatchie, S., Werner, F., MacCall, A., Agostini, V. 2015. Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current, Progress in Oceanography 138 (Part B): 348-380.

A4.9.8 Norwegian Sea Ecosystem End-to-End Model (NORWECOM.E2E)

The Norwegian Sea Ecosystem End-to-End Model [NORWECOM.E2E] is a whole system or end-to-end model of the Norwegian Sea ecosystem. The model features a lower trophic level biogeochemical model with functional groups for phytoplankton (flagellates and diatoms) and microzooplankton, and detailed individual-based models for dominant zooplankton species, e.g. *Calanus finmarchicus*, and for commercial fish and mammals. The model has been used to assess the impact of global change in Nordic seas, from ocean warming and acidification to the impact of fishing and pollutants. The model has been extensively evaluated using net primary productivity fields and zooplankton survey data.

Website: https://bio.uib.no/te/research/norwecom.php

Key references

Aksnes DL, Ulvestad KB, Baliño BM, Berntsen J, Egge JK, Svendsen E. 1995. Ecological modelling in coastal waters: Towards predictive physical-chemical-biological simulation models. *Ophelia* 41(1): 5-36. doi: 10.1080/00785236.1995.10422035.

Hansen C, van der Meeren GI, Loeng H, Skogen MD. 2021. Assessing the state of the Barents Sea using indicators: how, when, and where? *ICES Journal of Marine Science* 78: 2983–2998. doi: 10.1093/icesjms/fsab053.

Huse G, NORWECOM Team. 2012. *Strategic plan for development of the NORWECOM.E2E model.* Internal Strategy Document. 13 pp. URL: https://bio.uib.no/te/papers/NORWECOMstrategy.pdf [Accessed on Jun 16, 2022].

Skogen MD, Søiland H. 1998. *A User's guide to NORWECOM v2.0*. Institute of Marine Research. 42 pp. URL: http://hdl.handle.net/11250/113623 [Accessed on Jun 16, 2022]..

Skogen MD, Budgell WP, Rey F. 2007. Interannual variability in Nordic seas primary production. *ICES Journal of Marine Science* 64: 889-898. doi: 10.1093/icesjms/fsm063.

Skogen MD, Olsen A, Børsheim KY, Sandø AB, Skjelvan I. 2014. Modelling ocean acidification in the Nordic and Barents Seas in present and future climate. *Journal of Marine Systems* 131: 10-20. doi: 10.1016/j.jmarsys.2013.10.005.

Utne KR, Hjøllo S, Huse G, Skogen M. 2012. Estimating the consumption of *Calanus finmarchicus* by planktivorous fish in the Norwegian Sea using a fully coupled 3D model system. *Marine Biology Research* 8(5-6): 527-547. doi: 10.1080/17451000.2011.642804.

A4.9.9 POSEIDON (POSEIDON/RODOS; POSEIDON-R)

Model to assess the radiological consequences of radioactive releases into marine environment; adapted to cope with emergency conditions, in situations of radioactive discharges into the oceans from direct deposition from the atmosphere, sunken ships and containers, from discharges of rivers and estuaries and from coastal runoff. A dynamic food chain model was implemented to deal with the short-term dynamical uptake of radioactivity by specific marine plants and organisms.

Website: https://resy5.iket.kit.edu/RODOS/

Key references

Lepicard, S., R. Heling, and V. Maderich. 2004. POSEIDON/RODOS models for radiological assessment of marine environment after accidental releases: application to coastal areas of the Baltic, Black and North Seas. Journal of Environmental Radioactivity 72:153-161.

Maderich, V., K. O. Kim, R. Bezhenar, K. T. Jung, V. Martazinova, and I. Brovchenko. 2021. Transport and Fate of Cs-137 Released From Multiple Sources in the North Atlantic and Arctic Oceans. Frontiers in Marine Science 8.

Maderich, V., R. Bezhenar, Y. Tateda, M. Aoyama, and D. Tsumune. 2018. Similarities and differences of Cs-137 distributions in the marine environments of the Baltic and Black seas and off the Fukushima Dai-ichi nuclear power plant in model assessments. Marine Pollution Bulletin 135:895-906.

A4.9.10 StrathE2E

StrathE2E comprises two parts – a model of the marine ecology, and a model of fishing fleets. The ecology model is a network of coupled ordinary differential equations representing the rates of change in nitrogen mass of organic detritus, dissolved inorganic nutrient and coarse guilds of living biomass spanning microbes to megafauna. The equations include representations of feeding, metabolism, reproduction, active migrations, advection and mixing. Environmental driving data include temperature, irradiance, hydrodynamics and nutrient inputs from rivers, atmosphere and ocean boundaries. To make this feasible, we simplify the ecology - all the plants and animals in the sea are grouped together into what we call 'guilds' of species that have similar properties. Fisheries in StrathE2E are represented by a separate sub-model which is connected to the ecology part. In the sub-model, all of fishing gears used in a region are grouped together into up to 12 different types defined by their effectiveness at catching each of the ecology guilds, the spatial distribution of their activity, seabed abrasion rates, and discarding patterns.

Website:
https://www.strath.ac.uk/science/mathematicsstatistics/smart/marineresourcemodelling/researchtools/strathe2e

https://outreach.mathstat.strath.ac.uk/apps/StrathE2EApp/

Key references

Heath, M. R., D. C. Speirs, I. Thurlbeck, and R. J. Wilson. 2021. StrathE2E2: An R package for modelling the dynamics of marine food webs and fisheries. Methods in Ecology and Evolution 12:280-287.

Annex 5. Second screening stage: Database 2 fields

The following table lists the fields included in Database #2, which is available at URL. Fields highlighted with a yellow background correspond to homogenized fields used to score and rank the set of models.

label	Field	Description [including allowed values]
A	[Blank]	[Subroup]
B	Specific model name	[Already filled] Model name.
C	Model category	[Already filled] Choosing among one of the following # categories (see the Appendix for further details); • Biogeochemical and lower trophic level models • Species Distribution Models (SDM) (also called Habitat Suitability Models (HSM) or Ecological Niche-Based Models) • Community qualitative models • Minimum realistic models (MRM) and models of intermediate complexity (MICE) • Multispecies size-based models • Multispecies individual-based models • Mass based – food web models • Whole system models or end-to-end
D	Type of model	Following Levins (1966): • *Statistical*: models do not specify relationships among variables in terms of biological processes • *Mechanistic*: models specify relationships among variables in terms of biological processes. • *Hybrid*: combining characteristics of statistical and mechanistic models
E	Important features of the model (if relevant) (free text)	Free text to detail those aspects defining the model, including its aims, technical advances and unique features that motivated its development, according to the developers and users of the model.
F	Limitations of the model (free text)	Free text to detail the main weakness of the model, as acknowledged by the authors of the model.
G	Possible data type-Time frame	• *Static*: constant in time • *Dynamic:* time varying • Static and dynamic: both options
H	Possible data type-Spatial frame	• nonspatial • spatial • nonspatial and spatial
I	Temporal dimension	First of the two fields describing the nature of the predictions produced by the model' • Snapshot [0]: models predicting snapshot, static ecosystem patterns (e.g., ZooMSS). • External forcing [1]: models that do not feature temporal dynamics but simulate time varying patterns in response to external forcing (e.g., SDM). • Internal feedbacks [2]: models with internal feedbacks but do not admit external forcing, • Dynamic [3]: fully dynamic models with internal feedbacks that admit modulation by external forcing variables (e.g., Ecopath with Ecosim).
J	Spatial dimension	Second field describing the nature of the predictions produced by the model' • 0D [0]: non spatial, a-dimensional models (e.g., FLBEIA). • 2D [2]: two dimensional spatial models (horizontal dimension, e.g., most of SDMs). • 3D [3]: 3D spatial model (horizontal and water-column vertical dimensions, like e.g., Atlantis).

label	Field	Description [including allowed values]
		• External forcing [1]: models that do not feature temporal dynamics but simulate time varying patterns in response to external forcing (e.g., SDM). • Internal feedbacks [2]: models with internal feedbacks but do not admit external forcing, Dynamic [3]: fully dynamic models with internal feedbacks that admit modulation by external forcing variables (e.g., Ecopath with Ecosim).
K	Ecosystem type	Specify the ecosystem types that the model is able to represent: • Coastal • Estuary • Bay • Gulf • Open waters • Many
l	Ecosystem type (in case many, which (free text)	Free text to further detail the type of ecosystems that the model may describe.
M	Domain/domains included in the model	• Pelagic • Demersal • Benthic • Pelagic and Demersal • Pelagic and Benthic • Benthic and Demersal • All
N	# Ecosystem types and domains	Number (as a simple count) of the ecosystem types and domains simulated by the model.
O	Model generality	First of the four fields describing model generality and realism; taking the following values to grade model generality; • Specific [1]: specific models describing a single ecosystem or domain. • Intermediate [2]: intermediate models describing two different ecosystems and domains. • General [3]: general models describing three or more ecosystem types and domains.
P	Relevant species or groups of species considered	Relevant state variables in the context of biodiversity modelling that are able to be included in the model [free text; example entries include single species, functional groups, size classes, ontogenic fractions of species (larvae, juveniles, adults)// target and nontarget species etc.]
Q	Realism A	Second of the four fields describing model generality and realism; taking the following values to assess model realism based on structural model complexity; • Single species [0]: models that consider only one species or one functional group (e.g., dynamic population models). • Single ecosystem variable or trait [1]: models that do not consider species and/or functional groups and instead focus on single ecosystem variables or traits (i.e., size groups) (e.g., MIZER). • Limited number [2]: models that consider only a limited number/small subset of the species and/or functional groups of the ecosystem (e.g., Minimum Realistic Models). • Detailed [3]: models featuring most of the species and/or functional groups of the ecosystem (e.g., Ecopath with Ecosim).
R	External drivers possible to be included	• Fishing • Climate change • Aquaculture • Invasive species • Fishing and climate change

label	Field	Description [including allowed values]
		• Fishing and invasive species • Fishing, climate change and invasive species • Other combinations
S	External drivers possible to be included (in case you select "others", please specify) (free text)	Free text to complete previous field if necessary
T	Realism B	Third of the four fields describing model generality and realism; taking the following values to assess model realism based on the type and variety of environmental drivers considered; • Environmental or anthropogenic stressors [1]: models that either consider environmental or anthropogenic stressors, independently of whether they feature one or several stressors. • Both types, but a limited number of stressors [2]: models that simultaneously consider both environmental and anthropogenic stressors, but just a limited number. • Both types and several stressors [3]: models that simultaneously consider the cumulative impact of multiple environmental and anthropogenic stressors.
U	Kind of species interactions	Enumerate both positive (e.g., mutualism and commensalism) and negative (e.g., competition, predation, parasitism and disease) interactions that can be included in the model. There are different options: • Predation • Competition • Predation and competition • Parasitism • Disease • Mutualism • Commensalism • Facilitation • Protection • Other combinations
V	Kind of species interactions (in case other combination, which?) (free text)	In case in the previous cell you select “other combination”, please write all the species interactions that can be included in the model
W	Realism C	Fourth and last field describing model generality and realism; taking the following values to assess model realism based on the type and variety of species interactions considered; • No interactions [0]: models considering no biological interactions. • Within-group interactions [1]: models exclusively featuring interactions within groups, including interactions between life stages, size and age classes (e.g., intraspecific competition, cannibalism). • Few interactions [2]: models featuring biological interactions within and between groups, but only a few types, and in general, only competition and predation. • Several interactions [3]: models considering several interactions within and between groups, including for example non-trophic interactions such as facilitation and protection.
X	Levels of its maturity	Prime models with a more varied and prolonged history of applications: • Not advanced (less than 5 applications and less than 5 years of development) • Intermediate (between 5 and 25 applications and less than 10 years of development)

label	Field	Description [including allowed values]
		• Advanced (more than 25 applications and more than 10 years of development)
Y	Maturity	First of the three fields used to rank models according to their development and setup; • Recent [1]: Recently developed models featured in a few applications and development history (e.g., less than 5 case studies and a development history of less than 5 years). • Intermediate [2]: Intermediate models used in moderate number applications and development history (e.g., 5-25 case studies and less than 10 years of development). • Advanced [3]: Advanced, mature models featured in large number of applications and development history (e.g., more than 25 case studies and a long development history of 10 or more years).
Z	Minimum dataset to implement/run the model (input data): catches, stomach content, biomass, …	Please, specify the minimum datasets that are needed to implement/run the model
AA	Minimum dataset to evaluate the outputs	Please, specify the minimum datasets that are needed to evaluate the outputs
AB	Data sources for the model	When available, please detail the specific databases used to develop, train, and assess the model. [e.g. ICES Stock Database, OBIS, FishBase]
AC	Assessment	Second of the three fields used to rank models according to their development and setup; specifically in relation to the datasets required for model assessment; • Not possible [0]: models whose output cannot be assessed because their predictions are not directly comparable or can be constrained by real world observations (e.g., MEFISTO). • Difficult [1]: models whose assessment requires multiple data sets and involves difficult analyses. • Intermediate [2]: models whose assessment depends on multiple but readily available data sets and involves simple analyses or, on the contrary, model assessed using few data sets and a complex analyses. • Available [3]: models whose assessment involves few, readily available data sets and straightforward analyses.
AD	Time required for model development	Please select one of the following options: • within one year • within 2 years • more than 2 years
AE	Time for model setup	Third and last field used to rank models according to their development and setup; considering here the time required to configure and run the model; • Long [1]: models that, starting de novo, require more than 24 months to move to production. • Intermediate [2]: models that, starting de novo can be moved to production in between 12 and 24 months. • Short [3]: models that, starting de novo, can readily move to production in less than 12 months.
AF	Software features: computer language	Free text; specify the computer language that has been used to code the model
AG	Development in different programming languages	First of the five fields used to rank models according to software features; here focusing on availability of alternative implementations; • Single [1]: models that keep a single main implementation using a unique programming language. • Multiple [3]: models that have been coded from scratch in a set of programming languages other than the one in which they

label	Field	Description [including allowed values]
		were originally coded.
AH	Software features: available platforms? (linux, windows, …) (free text)	Specify platforms for which the model is available (windows, linux, …)
AI	Availability in different computer platforms	Second of the five fields used to rank models according to software features; here focusing on availability on different computing platforms; • Specific [1]: models tied to a single operating system. • Independent [3]: platform independent models.
AJ	Software features: code of the model is available?	Specify if the code of the model is publicly available to the scientific community • Yes, online • Yes, upon request • No, private
AK	Source code availability	Third of the five fields used to rank models according to software features; here focusing on the adoption of FAIR research practices; • Private [0]; models with private codes. • Request [1]; models whose code is advertised as available under request. • Public [3]: publicly available model codes (e.g., software repositories).
AL	Software features: Are there potential usage restrictions?	Specify if there are potential usage restrictions to the scientific community: • Yes • No
AM	Potential usage restrictions	Fourth of the five fields used to rank models according to software features; again focusing on the adoption of FAIR research practices; • Restricted [1]: restrictions (e.g., fees, key, proprietary software). • Unrestricted [3]: unrestricted usage.
AN	Software features: type of license	Free text, see e.g. https://en.wikipedia.org/wiki/Software_license
AO	Type of license	Fifth and last of the five fields used to rank models according to software features; again focusing on the adoption of FAIR research practices; • Unavailable [0]: models whose codes are not available. • Non-free [1]: models whose code is available, but under a non-free license/. • Open and free [3]: model whose code is available under a free and open license.
AP	Number of users (NOT necessary now)	Number of potential users. [Not necessary to fill up now.]
AQ	Stakeholders (e.g., general public, fishermen, researchers, resource managers and decision makers) (free text)	Free text to detail the typology of users, distinguishing major groups of stakeholders like the general public, fishermen, researchers and/or academic students, resource managers and decision makers.
AR	Products/services (e.g., fisheries management, impact of climate change, protected area management)	Specify the main products/services that can be obtain through the use of the model
AS	Insights gained or decisions taken as a result of the use of the model (NOT NOW)	Specify insights gained or decisions taken as a result of the use of the model. Put special attention to results that assess the impact of marine protected areas or recovery interventions [Not necessary to fill up now.]
AT	Country of model owner	List the country or countries of the owner(s) of the model, separated by

label	Field	Description [including allowed values]
		commas.
AU	Country main developer	List the country or countries of the main developers of the model, separated by commas.
AV	Relevant scientific group	List the names of the leading researchers or research groups that lead the development of the model.
AW	Has the development of the model received support through EU projects	• Yes • No
AX	Name EU projects that supported the model	List separated by commas the name and code of any EU funded project acknowledged in the relevant contributions. (NOT necessary now).
AY	Name scientific groups that supported the model	List separated by commas the names of the leading researchers or research groups that have adopted the model among those in the relevant applications
AZ	Where it has been further developed?	Please list other countries, separated by commas, where the models have been further developed.
BA	Next steps planned by model users	Free text to summarize. (NOT necessary now)
BB	Potential use and relationship with MSFD descriptors and criteria (see list and specify the number of the descriptors)	Provide the number of the descriptors that the model may contribute to analyse (e.g., if the model is able to provide indicators about descriptors 1, 2 and 3, include here "1,2 and 3"): • Descriptor 1. Biodiversity is maintained • Descriptor 2. Non-indigenous species do not adversely alter the ecosystem • Descriptor 3. The population of commercial fish species is healthy • Descriptor 4. Elements of food webs ensure long-term abundance and reproduction • Descriptor 5. Eutrophication is minimised • Descriptor 6. The sea floor integrity ensures functioning of the ecosystem • Descriptor 7. Permanent alteration of hydrographical conditions does not adversely affect the ecosystem • Descriptor 8. Concentrations of contaminants give no effects • Descriptor 9. Contaminants in seafood are below safe levels • Descriptor 10. Marine litter does not cause harm • Descriptor 11. Introduction of energy (including underwater noise) does not adversely affect the ecosystem
BC	count	Number of MSFD descriptors that a model can potentially assess.
BD	Potential scope to support MSFD policies	First of the two fields used to rank models according to their potential to support MSFD policies and similar efforts; calculated using the following formula: • 3 x n / 11: where n is the number of MSFD descriptors that a model can potentially assess.
BE	Applications supporting the MSFD policies (see list and specify the number of the descriptors - e.g., if the model is able to provide indicators about descriptors 1, 2 and 3, include here "1,2 and 3")	Provides the number of the descriptors that the model has contributed to analyse (e.g., if the model is able to provide indicators about descriptors 1, 2 and 3, include here "1,2 and 3"): • Descriptor 1. Biodiversity is maintained • Descriptor 2. Non-indigenous species do not adversely alter the ecosystem • Descriptor 3. The population of commercial fish species is healthy • Descriptor 4. Elements of food webs ensure long-term abundance and reproduction • Descriptor 5. Eutrophication is minimised • Descriptor 6. The sea floor integrity ensures functioning of the ecosystem • Descriptor 7. Permanent alteration of hydrographical conditions

label	Field	Description [including allowed values]
		does not adversely affect the ecosystem • Descriptor 8. Concentrations of contaminants give no effects • Descriptor 9. Contaminants in seafood are below safe levels • Descriptor 10. Marine litter does not cause harm • Descriptor 11. Introduction of energy (including underwater noise) does not adversely affect the ecosystem
BF	count	Number of MSFD descriptors that a model has assessed.
BG	Applications supporting MSFD policies	Second of the two fields used to rank models according to their potential to support MSFD policies and similar efforts; calculated using the following formula: • 3 x n / 11: where n is the number of MSFD descriptors that a model has contributed to assess.
BH	Potential use and relationship with other policies (e.g. Habitats Directive, Biodiversity Convention (CBD), Common Fisheries policy (CFP), UN Sustainable Development Goals (SDGs)).	Free text, please provide a comma separated list of other policies that the model may contribute to implement. Feel free to use abbreviations like Natura2000, CBD, CFP, SDGs. [Not necessary to fill up now.]
BI	Coupled with lower trophic levels	Yes/Not
BJ	Coupled with bioeconomic models	Yes/Not
BK	Comments about coupling	Free text
BL	Model coupling and interoperability	Single field summarizing the potential to use a given model within coupled and interoperable workflows: • No coupling [0]: models that do not accept external environmental forcing and that have not been coupled to other models. • One-way [2]: models that accept environmental forcing and have been configured in workflows where they passively receive one-way forcing from other models (e.g., SDM). • Two-way [3]: Models that accept environmental forcing and predict changes in environmental conditions, and which have been configured in fully coupled workflows with other models.
BM	Website	URL of any webpage devoted to the model (in particular, code repositories)
BN	Comments	Free text, anything relevant information not included in the other fields, including extra information to refine the responses

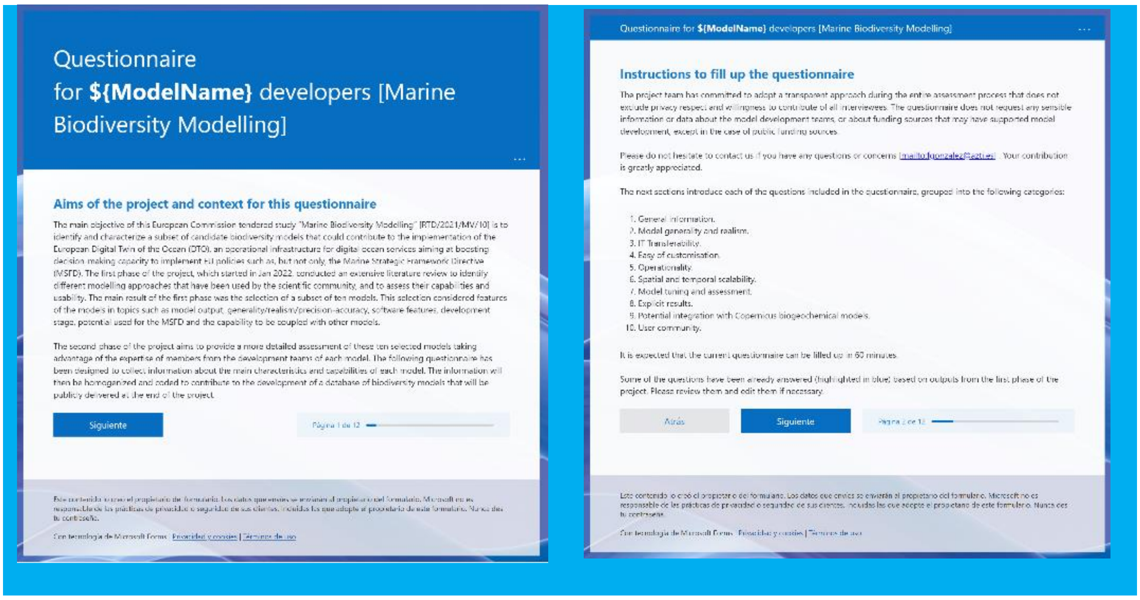
Annex 6. Questionnaire for model development teams

Leaders of the model development teams for each of the ten biodiversity models selected in Task II were invited to fill up a questionnaire online prepared using Microsoft Forms®. The template questionnaire is available through the following URL: https://forms.office.com/Pages/DesignPageV2.aspx?subpage=design&FormId=GfEZYnk-f06s3qV1CAjNm3xXOdBJQIBCnmDcFvIBwf5UN0FBU0lTRFlROFhQUUVCSzAzMVdYMDNVTi4u&Token=d3f173543345422da84a7dc167e9b881 .

The questionnaire was sent to the corresponding modelling teams:

Model name	Model category
OSMOSE	Multispecies individual-based
Atlantis	Whole system or end-to-end
StrathE2E	Whole system or end-to-end
NORWECOM.E2E	Whole system or end-to-end
Ecopath with Ecosim	Mass based - food web
ECOSMO-E2E	Whole system or end-to-end
APECOSM	Multispecies size-based
ECOTRAN e2e	Whole system or end-to-end
SEAPODYM	Multispecies individual-based
Macro-ecological	Multispecies size-based

The screenshots below (Fig. 1) provide an idea of the questionnaire, though its text is included below for the shake of completeness.



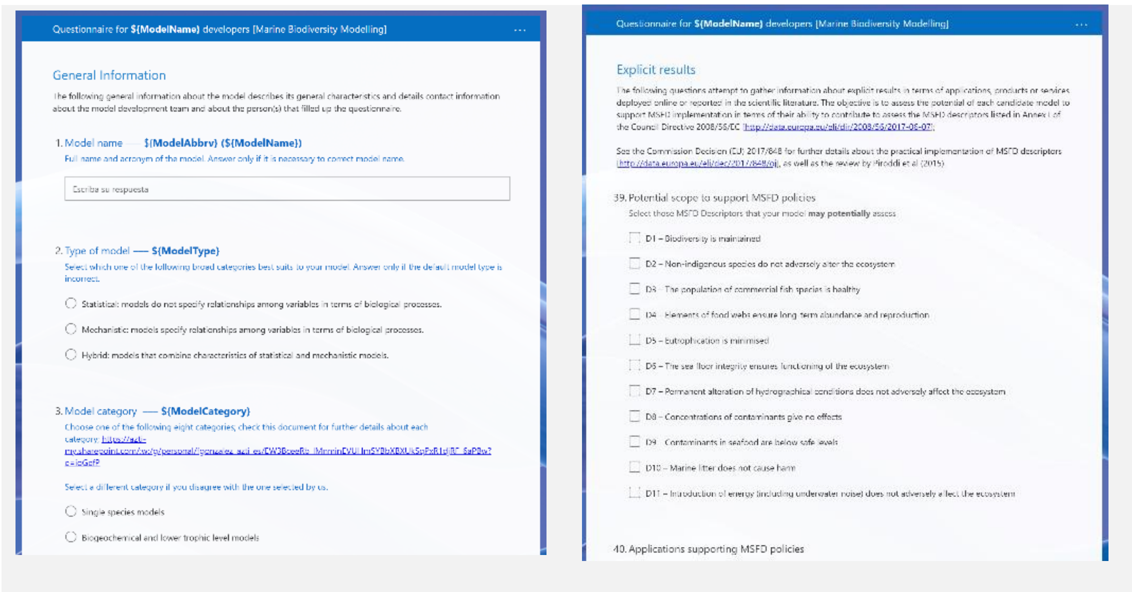


Fig. 1. Screenshots of the questionnaire sent to selected model development team leaders to retrieve further information about the ten models selected in Task II (see $).

Questionnaire for model development teams

Aims of the project and context for this questionnaire

The main objective of this European Commission tendered study "Marine Biodiversity Modelling" [RTD/2021/MV/10] is to identify and characterize a subset of candidate biodiversity models that could contribute to the implementation of the Digital Twin Ocean (DTO)[2], an operational infrastructure for digital ocean services aiming at boosting decision-making capacity to implement EU policies such as, but not only, the Marine Strategic Framework Directive (MSFD). The first phase of the project, which started in Jan 2022, conducted an extensive literature review to identify different modelling approaches that have been used by the scientific community, and to assess their capabilities and usability. The main result of the first phase was the selection of a subset of ten models. This selection considered features of the models in topics such as model output, generality/realism/precision-accuracy, software features, development stage, potential used for the MSFD and the capability to be coupled with other models.

The second phase of the project aims to provide a more detailed assessment of these ten selected models taking advantage of the expertise of members from the development teams of each model. The following questionnaire has been designed to collect information about the main characteristics and capabilities of each model. The information will then be homogenized and coded to contribute to the development of a database of biodiversity models that will be publicly delivered at the end of the project.

The project team has committed to adopt a transparent approach during the entire assessment process that does not exclude privacy respect and willingness to contribute of all interviewees. The questionnaire does not request any sensible information or data about the model development teams, or about funding sources that may have supported model development, except in the case of public funding sources. Please do not hesitate to contact us if you have any questions or concerns. Your contribution is greatly appreciated.

The next sections introduce each of the questions included in the questionnaire, grouped into the following categories:

a) General information.
b) Model generality and realism.
c) IT Transferability.
d) Easy of customisation.
e) Operationality.
f) Spatial and temporal scalability.
g) Model tuning and assessment.
h) Explicit results.
i) Potential integration with Copernicus biogeochemical models.
j) User community.

[2] European Digital Twin of the Ocean (European DTO) | European Commission (europa.eu)

It is expected that the current questionnaire can be filled up in 60 minutes. Some of the questions have been already answered (highlighted in blue) based on outputs from the first phase of the project. **Please review them and edit them if necessary.**

a) General Information

The following general information about the model describes its general characteristics and details contact information about the model development team and about the person(s) that filled up the questionnaire.

1) Model name – full name and acronym of the model.

Answer – [Already filled]

2) Type of model – indicate which of the following broad categories best suits to your model [check the box that better reflects your model]:

☐ Statistical: models do not specify relationships among variables in terms of biological processes.

☐ Mechanistic: models specify relationships among variables in terms of biological processes.

☐ Hybrid: models that combine characteristics of statistical and mechanistic models.

3) Model category – choose among one of the following eight categories;

☐ Single species models

☐ Biogeochemical and lower trophic level models.

☐ Species Distribution Models (SDM) (Habitat Suitability Models (HSM) or Ecological Niche-Based Models).

☐ Community qualitative models.

☐ Minimum realistic models (MRM) and models of intermediate complexity (MICE).

☐ Multispecies size-based models.

☐ Multispecies individual-based models.

☐ Mass based - food web models.

☐ Whole system or end-to-end models.

See supplementary material for the definition of each category.

4) Model development team – list the names of the research group(s) and/or individual researchers that lead and coordinate model development.

Answer – [Already filled]

5) Country of model owner (if applicable).

Answer – [Already filled]

6) Country(ies) main developer.

Answer – [Already filled]

7) Has the development of the model received support through EU projects? In case yes, could you provide the name of these projects?

Answer – [Already filled]

8) Website – write out the URL of any webpage devoted to the model (in particular, code repositories).

Answer – [Already filled]

9) Contact person – provide the name, email address and/or telephone number of a member of the development team wiling to serve as a contact person in the context of this questionnaire and future activities of this project.

Answer –

10) Respondent – provide the name, email address and/or telephone number of the person(s) who answered the questionnaire. If it is the same person(s) set as contact, just answer "Same as contact person".

Answer –

b) Model generality and realism

The second set of questions explores the model building strategy of the development team in terms of the trade-offs between generality, realism and precision and accuracy (Levins (1966)).).

11) Realism A: provide the name of environmental and anthropogenic drivers that can be considered by the model (e.g., fishing, aquaculture, invasive species and temperature).

Answer –

12) Realism B: provide the name of the biological interactions that can be implemented by the model. This criterion considered both interactions within and between taxa and/or functional groups, including potential interactions between different life history stages or age or size classes within a species or functional group (e.g., intraspecific competition, cannibalism, interspecific competition, predation, facilitation and protection).

Answer –

c) IT Transferability

13) Computer language: specify the computer language that has been used to code the model.

Answer –

14) Usage restrictions: Specify if there are potential usage restrictions to some specific community and, in case yes, which constraints for which kind of community.

Answer –

15) Available platforms: Specify platforms for which the model is available (windows, linux, …).

Answer –

16) Documentation (e.g., user guide, best practices): please specify if there is a document that provide to user's (1) information of how to use the software and/or run the model (e.g., user guide); (2) guidelines about best practices in developing and using models, and (3) tutorial materials targeting new users.

Answer –

17) Hardware requirements and minimum settings recommended by the model developers: specify the hardware requirements and the minimum settings for a normal functioning of the software and/or platform or a normal model run.

Answer –

18) Other software requirements: specify the software requirements for a normal functioning of the software or platform and/or a normal model run.

Answer –

19) Estimate of computer capacity. Please, indicate if your model requires extensive computational resources. Please indicate any bottlenecks that compromise model performance (large number of variables, running iterative optimization algorithms on each step, etc.).

Answer –

20) Model development strategy: please specify if there is a development team that coordinates through a central reference repository or if, instead, there are multiple coexisting and unrelated versions of the model. Has the model teams follows configuration management practices[3]?

Answer –

d) Ease of customization

This batch of questions gathers again information about the transferability of the model, but now in terms of its versatility and the possibility of applying the model in different systems and by different set of users. The questions retrieve information about how easy and how much time it takes to tune the model while developing a new application, like updating the input data streams of the model or coupling it to another model.

21) Software license – detail the license adopted to distribute model codes. [See e.g., https://en.wikipedia.org/wiki/Software_license].

Answer –

[3] https://en.wikipedia.org/wiki/Software_configuration_management

22) User interface – briefly describe the user interface of the model (menu-driver, command line, etc.) and whether the development team has any future plans to improve it.

Answer –

23) Set up time – please provide an educated guess of the time that a team of experts would require configuring and set up de novo your model under a different architecture, including the potential coupling to another model, and the development of updated parameterizations to ensure that the new model instance keeps its original accuracy. If possible, discuss potential bottlenecks and actions that may contribute to avoid them.

☐ within 1 year

☐ within 2 years

☐ within 3 years

☐ more than 3 years

24) Ancillary data – enumerate the physical, chemical, and biological data —including human stressors— required to run the model and assess its performance. Please detail for each listed item whether it is a model input or a target output to validate the model.

Answer – For example:

Data	Input/output
Temperature	Input
Biomass	Input

25) Model sensitivities and uncertainty – detail whether the model team or expert users have completed (and documented) a sensitivity analysis of the model, and whether it is possible or not to routinely assess model uncertainty (i.e., do model codes include any procedure to automatically do so?).

Answer –

e) Operationality

This batch of questions try to assess the level of maturity of the model and whether it has reached operational status through the identification of specific management applications or simulation experiments reproducing real world scenarios. The questions also attempt to gather information about the reliability of model codes and the adoption of test-driven development practices by the model development team.

26) TRL (Technology Readiness Level)[4]:

☐ TRL 1 – basic principles observed.

[4] https://en.wikipedia.org/wiki/Technology_readiness_level

☐ TRL 2 – technology concept formulated.

☐ TRL 3 – experimental proof of concept

☐ TRL 4 – technology validated in lab.

☐ TRL 5 – technology validated in relevant environment (industrially relevant environment in the case of key enabling technologies).

☐ TRL 6 – technology demonstrated in relevant environment (industrially relevant environment in the case of key enabling technologies).

☐ TRL 7 – system prototype demonstration in operational environment.

☐ TRL 8 – system complete and qualified.

☐ TRL 9 – actual system proven in operational environment (competitive manufacturing in the case of key enabling technologies; or in space).

27) Management applications – detail whether any applications, products or services based on the model are currently used or have been used in the past to support decision makers in the context of environmental resource management issues or as part of environmental impact assessments. If possible, please also detail the specific management context in which the model has been used (e.g., species, region).

Answer –

28) Learned lessons – describe the insights gained and the decisions made as a result of the use of the model to solve practical environmental problems. Please detail what kind of recommendations has been based on the model.

Answer –

29) Code robustness – detail the strategy followed by the development team to test the reliability of the model code and its results, including the potential adoption of test-driven development practices to prevent bugs.

Answer –

30) Customer validation – please detail whether the development team has implemented or plans to implement any kind of customer validation procedures like beta testing, pools and interviews, active request of user feedback, and collation and analysis of usage data and bugs to improve the code.

Answer –

f) Spatial and temporal scalability

The questions in this section explore the transferability of the model to spatial and temporal domains and resolutions different from that originally targeted by the model development team, and whether these aspects are part of the model development strategy.

31) Temporal dimension – please detail the time step of the model and the target range of temporal frequencies for each of the main patterns and processes predicted by the model.

Answer –

32) Spatial dimension – please detail the spatial resolution of the model (grain) and the target range of spatial resolutions resolved for each of the main patterns and processes predicted by the model.

Answer –

33) Transferability – please detail any potential limitations to applying the model under different spatial and temporal physical domains and resolutions.

Answer –

34) Adaptation – please comment whether the model can be easily adapted to overcome potential constraints when applied in a different domain, and whether the model development team took into account the potential use of the model under different domains while developing model code.

Answer –

g) Model tuning and assessment

This section inquiries about the process of model calibration and assessment and, more specifically, about whether the model development team keeps a detailed documentation accounting for the motivation, rationale, methods and results of this process. We encourage respondents to cite any documentation that the model development team or the model user community has developed in support of these activities.

35) Model parameters – enumerate and define the parameters that are routinely used to tune the model. Please detail if there are free parameters set using some kind of optimization routine, or if they correspond to barely known or uncertain quantities that can only be guessed based on currently available information.

Answer –

36) Tuning – please describe any optimization procedure adopted by the model development team to tune model parameters, especially if the model already incorporates itself an optimization procedure. Please indicate also if model parameters were set based on a direct calculation (e.g., solving for a target equilibrium level, etc.).

Answer –

37) Diagnostics and performance metrics– please detail which model diagnostics are routinely used to assess model performance and which performance metrics can be calculated to rank alternative model realizations, including competing parameterizations. Please detail how these metrics can be used to constrain emergent model behaviours and to compare model predictions to real world patterns.

Answer –

h) Explicit results

The following questions attempt to gather information about explicit results in terms of applications, products or services deployed online or reported in the scientific literature. The objective is to assess the potential of each candidate model to support MSFD implementation in terms of their ability to contribute to assess the MSFD descriptors listed in Annex I of the Council Directive 2008/56/EC [http://data.europa.eu/eli/dir/2008/56/2017-06-07];

See the Commission Decision (EU) 2017/848 for further details about the practical implementation of MSFD descriptors [http://data.europa.eu/eli/dec/2017/848/oj], as well as the review by Piroddi et al (2015).

38) Potential scope to support MSFD policies – please enumerate the MSFD descriptors that your model can potentially assess.

☐ Descriptor 1. Biodiversity is maintained.

☐ Descriptor 2. Non-indigenous species do not adversely alter the ecosystem.

☐ Descriptor 3. The population of commercial fish species is healthy.

☐ Descriptor 4. Elements of food webs ensure long-term abundance and reproduction.

☐ Descriptor 5. Eutrophication is minimised.

☐ Descriptor 6. The sea floor integrity ensures functioning of the ecosystem.

☐ Descriptor 7. Permanent alteration of hydrographical conditions does not adversely affect the ecosystem.

☐ Descriptor 8. Concentrations of contaminants give no effects.

☐ Descriptor 9. Contaminants in seafood are below safe levels.

☐ Descriptor 10. Marine litter does not cause harm.

☐ Descriptor 11. Introduction of energy (including underwater noise) does not adversely affect the ecosystem.

39) Applications supporting MSFD policies – please enumerate the MSFD descriptors that have been already addressed in practical applications of your model, whether or not they have been incorporated or not into management decision systems (but please indicate if that is the case).

☐ Descriptor 1. Biodiversity is maintained.

☐ Descriptor 2. Non-indigenous species do not adversely alter the ecosystem.

☐ Descriptor 3. The population of commercial fish species is healthy.

☐ Descriptor 4. Elements of food webs ensure long-term abundance and reproduction.

☐ Descriptor 5. Eutrophication is minimised.

☐ Descriptor 6. The sea floor integrity ensures functioning of the ecosystem.

☐ Descriptor 7. Permanent alteration of hydrographical conditions does not adversely affect the ecosystem.

☐ Descriptor 8. Concentrations of contaminants give no effects.

☐ Descriptor 9. Contaminants in seafood are below safe levels.

☐ Descriptor 10. Marine litter does not cause harm.

☐ Descriptor 11. Introduction of energy (including underwater noise) does not adversely affect the ecosystem.

40) Potential use and relationship with other policies (e.g., Common Fisheries Policy (CFP), Habitats Directive, Biodiversity Convention (CBD), UN Sustainable Development Goals (SDGs)).

Answer –

i) Potential integration with Copernicus biogeochemical models

The next questions explore the potential to integrate your model into integrated modelling workflows contributing to the implementation of the Digital Twin Ocean (DTO).

41) Model coupling – please detail if the model has been already coupled successfully with monitoring and forecasting physical and biogeochemical products developed in the context of the Copernicus Marine Environment Monitoring Service (CMEMS, see https://marine.copernicus.eu, Le Traon et al 2019) [for a complete list of marine products, please visit https://resources.marine.copernicus.eu/products]. Please also indicate whether your model has been successfully coupled within other integrated modelling frameworks.

Answer –

42) Development strategy – please indicate if the development team are currently involved or planning to pursue in the near future the improvement of the interoperability of the model with CMEMS physical and biogeochemical products or with similar models of ocean physics and/or biogeochemistry.

Answer –

43) Potential integration – please provide a brief assessment of how easy would be, in your opinion, to integrate your model into CMEMS workflows.

Answer –

j) User community

The last batch of questions gathers information about the user community and their relationship with the model development team.

44) Target users – please detail if the model was initially designed to address the specific needs of a group of users, providing the characteristics of that set of users and how the model development team has monitored the success of the model to accomplish their initial objectives.

Answer –

45) User needs – please indicate if the model development team actively seeks receiving feedback from their user base and their evolving needs through any kind of communication channel.

Answer –

Annex 7. Homogenized fields for Database 3

The following table lists fields included in Database #3 homogenized from the answers to the questionnaire (

Annex 6). Note that, in this spreadsheet, columns correspond to each of the selected models, and the rows to the fields of interest, whose label is also available through column A. Entries with multiple answers are grouped in a single cell and separated by a semicolon ‘;’.

Row #	Field	Description [including allowed values]
1	[Blank]	[Header row]
2	ID	Arbitrary ID assigned to each questionnaire [1-10].
3	Start time	Time when the respondent started to answer the questionnaire [dd/mm/yyyy HH:MM:SS].
4	Completion time	Questionnaire submission time [dd/mm/yyyy HH:MM:SS],
5	Email	Public email of the respondent, automatically gathered by the questionnaire platform but set to anonymous.
6	Name	Short model name.
7	Model name	Full model name.
8	Type of model	Statistical, Mechanistic or Hybrid.
9	Model category	See Box 1.
10	Model development team	Name(s) of the model development team(s).
11	Lead developers	Name(s) of the lead developer(s).
12	Country of model owner (if applicable)	Name(s) of the country(ies) of the model owner,
13	Country(ies) main developer	Name(s) of the country(ies) of the model main developer(s),
14	Funding	Projects supporting model development, highlighting if they were funded by the EU [prefix EU].
15	Website	URL(s) of the model website.
16	Contact person	Name(s) and email(s) of a contact person(s) from the model development team.
17	Respondent	Name(s) and email(s) of the questionnaire respondent.
18	Environmental and anthropogenic drivers [model realism]:	List of drivers considered by the model [aquaculture; atmospheric deposition; contaminants; demographics; depth; detritus; eutrophication; fisheries economics; fishing effort; habitat alteration; habitat heterogeneity; ice cover; invasive species; light; micronekton; noise and light; nutrients; ocean currents; oxygen; pH and acidification; plankton biomass;

		pollutants; press perturbations; primary production; pulse perturbations; salinity; secondary production; temperature; turbidity].
19	Biological interactions [model realism B]	List of biological interactions implemented on each model [size and age structure; size structure; predation; competition; mutualism].
20	Computer language	Names of the computer languages used to code the model.
21	Code availability	Text detailing whether model source codes are publicly available or, otherwise, the conditions that apply to access the and use the code.
22	Usage restrictions	Potential restrictions to use the model.
23	Platform	Operating systems under which the model runs
24	Documentation	Description of available documentation and their URL, and details about conditions to access the documentation if any.
25	Hardware requirements and minimum settings recommended by the model developers	Description of recommended and minimum hardware required to run the model.
26	Other software requirements	Libraries and compilers required to compile from source and/or run the model.
27	Estimate of computer capacity	Two possibilities {Non computer intensive, HPC} depending on whether or not running the model requires a high-performance computing platform.
28	Model development strategy	Detail whether there is {Central reference repository; No formal development; Version control}.
29	Software license	Detail whether the development team adopted a license and which one.
30	User interface	Description of the user interface, whether the model is available through a graphical user interface or just through the command line, pre-processing options, etc.
31	Set-up time	Time required to setup the model {Less than a year; Between one and two years; More than two years}.
32	Inputs	Model inputs among {atmospheric deposition; demographics; detritus; fisheries economics; fishing effort; light; mass-balanced food web; micronekton; nutrients; ocean currents; oxygen; phytoplankton; primary production; rivers; salinity; secondary production; temperature; waves; winds; zooplankton}.

33	Outputs	Model outputs among {energy and material fluxes; fish biomass; fish growth; fisheries catch; fisheries yields; fishing effort; macrobenthos biomass; metabolism; phytoplankton biomass; size structure; species abundance; species biomass; species specific size structure; trophic transfer; zooplankton biomass}.
34	Sensitivity analysis	Availability or possibility to easily perform a sensitivity analysis: {yes; no}.
35	Technology Readiness Level [TRL]	Classification in the TRL scale {TRL1 to TRL9}.
36	Management support	Detail whether the model has been directly used in management applications {yes,no}.
37	Management species/groups	Detail which species or functional groups have been the target of management applications of the model.
38	Management regions	Detail in which region the model has been used in management applications.
39	Code tests	Practices implemented to assure code robustness {beta testing; bug reporting; unit testing}.
40	Customer feedback	Practices implemented to receive feedback from customers in management applications {annual meetings; beta testing; bug reporting; user requests}.
41	Time step	Recommended or typical time step.
42	Spatial mesh	Recommended or typical spatial grid, its dimensions and whether it is adaptable (i.e. whether the model automatically adapts to variable resolutions).
43	Transferability constraints	Detail if the model can be easily setup and run into a different domain or system {yes, no}.
44	Easy to adapt	Judgement about how easy is to adapt the model to a new domain {yes, no}.
45	Parameters	Non-exhaustive list of model parameters { biomass; catch rate; consumption rate; detection rate; diet composition; fecundity; fish productivity; growth rate; harvest rate; interaction strength; light attenuation ; migration rate; physiological tolerance; predator-prey ratio; production rate; sinking rate; size structure; trophic efficiency}.
46	Automatic calibration	Availability of automatic calibration procedures {yes,no}.
47	Quantitative diagnostic metrics	Detail whether model calibration is based on a reliable set of quantitative diagnostics {yes,no}.

48	Potential scope to support MSFD policies	List of MSFD descriptors for which the model may be able to contribute valuable information.
49	Applications supporting MSFD policies	List of MSFD descriptors for which the model can contribute valuable information.
50	Other policies	Other policies that the model may help to implement: {Common Fisheries Policy [CFP]; Convention on Biological Diversity [CBD]; Ecosystem based Management Approach [EBM]; European Green Deal [EGP]; Habitats Directive [HD]; Sustainable Development Goals [SDGs]; Pacific Community [SPC]}
51	Coupling	{One-way forcing, Two-way coupling}
52	Planning CMEMS integration	Detail if the model team is planning to integrate CMEMS productions {yes,no} and the name of undergoing project(s) toward such objective.
53	Potential integration CMEMS	Assess the potential/willingness to integrate CMEMS products and workflows {yes; no}.
54	Target users	Primary target users of the model { fisheries managers; scientists}.
55	User community	Detail if the model team actively works to maintain close interactions and receive feedback from the model user community: {active engagement; not developed}.

Annex 8. Invitation to the online workshop

An online workshop was organised with modelling developers and users with the aim to obtain their feedback on the mentioned analysis and public report. Invitees included representatives of at least the following organisations: the Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP – ISIMIP), Food and Agriculture Organization (FAO), International Council for the Exploration of the Sea (ICES - working group to be identified), Baltic Marine Environment Protection Commission (Helsinki Commission – HELCOM), Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR), Barcelona Convention (UNEP-MAP), Bucharest Convention (Black Sea Commission), Global Ocean Observing System (GOOS - Bio-eco panel), Marine Ecosystem Analysis and Prediction (MEAP-TT – OceanView), MBON – Marine Biodiversity Observation Network (MBON), Integrated Marine Biosphere Research Project (IMBeR), Copernicus marine service, DG JRC, European Marine Board (EMB working group), consortium members from relevant EU research projects starting from FP7, and possible other contacts given by the contracting authority. The final list of invited institutions and organizations was agreed upon by the contracting authority.

The workshop logistics were managed by the Communication team from AZTI.

Date: 15th September 2022.

Invited institutions and organizations:

- Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP – ISIMIP):
- Food and Agriculture Organization (FAO)
- International Council for the Exploration of the Sea (ICES - working group to be identified)
- Baltic Marine Environment Protection Commission (Helsinki Commission – HELCOM)
- Convention for the Protection of the Marine Environment of the North-East Atlantic (OSPAR)
- Global Ocean Observing System (GOOS - Bio-eco panel)
- Marine Ecosystem Analysis and Prediction (MEAP-TT – OceanView)
- Marine Biodiversity Observation Network (MBON)
- Integrated Marine Biosphere Research Project (IMBeR)
- Copernicus marine service
- DG JRC
- European Marine Board (EMB working group)

Other organizations or initiatives

- Scientific, Technical and Economic Committee for Fisheries (STECF)
- Barcelona Convention (UNEP-MAP)
- Bucarest Convention (Black Sea Commission)
- European Topic Centre
- European Environment Agency
- IRD (MARBEC)
- ODYSSEA

- DTU
- NOAA
- ICCAT

Consortium members from relevant EU research projects starting from FP7

- MacoBios (Marine Coastal Ecosystem Biodiversity and Services in a Changing World)
- DEVOTES (Development of innovative tools for understanding marine biodiversity and assessing Good Environmental Status)
- MERCES (Marine Ecosystem Restoration in Changing European Seas)
- ATLAS (A Trans-Atlantic Assessment and deep-water ecosystem-based Spatial management plan for Europe)
- IATLANTIC (Integrated Assessment of Atlantic Marine ecosystems in space and time)
- Mistic Seas (Developing a coordinated approach for assessing Descriptor 4 via its linkages with D1 and other relevant descriptors in the Macaronesian sub-region)
- Helcom Action (Actions to evaluate and identify effective measures to reach GES in the Baltic Sea marine region)
- MEDRegion (Support Mediterranean member states towards implementation of the MSFD new GES decision and programmes of measures and contribute to regional/subregional cooperation)
- Future Mares
- CERES
- CLIMEFISH
- SEAwise
- Mission Atlantic
- TRIATLAS

GETTING IN TOUCH WITH THE EU

In person

All over the European Union there are hundreds of Europe Direct centres. You can find the address of the centre nearest you online (european-union.europa.eu/contact-eu/meet-us_en).

On the phone or in writing

Europe Direct is a service that answers your questions about the European Union.
You can contact this service:

- by freephone: 00 800 6 7 8 9 10 11 (certain operators may charge for these calls),
- at the following standard number: +32 22999696,
- via the following form: european-union.europa.eu/contact-eu/write-us_en.

FINDING INFORMATION ABOUT THE EU

Online

Information about the European Union in all the official languages of the EU is available on the Europa website (european-union.europa.eu).

EU publications

You can view or order EU publications at op.europa.eu/en/publications. Multiple copies of free publications can be obtained by contacting Europe Direct or your local documentation centre (european-union.europa.eu/contact-eu/meet-us_en).

EU law and related documents

For access to legal information from the EU, including all EU law since 1951 in all the official language versions, go to EUR-Lex (eur-lex.europa.eu).

EU open data

The portal data.europa.eu provides access to open datasets from the EU institutions, bodies and agencies. These can be downloaded and reused for free, for both commercial and non-commercial purposes. The portal also provides access to a wealth of datasets from European countries.

This study reviews the status of Marine Biodiversity Monitoring in the European Commission tendered the study “Marine Biodiversity Modelling” [RTD/2021/MV/10] to pursue the identification and characterization of a subset of candidate biodiversity models that could contribute to the implementation of the European Digital Twin of the Ocean (EU DTO). The EU DTO will be an operational infrastructure for digital ocean services that aims to support decision-making capabilities by authorities to implement EU policies like the Marine Strategy Framework Directive (MSFD) but also by citizens and businesses operating at sea. Specific objectives of the project were:

1. Conduct a horizon scan to identify and map available modelling approaches used to hindcast, nowcast;
2. Develop a comprehensive catalogue to classify available modelling approaches according to their characteristics;
3. Propose a subset of the most meaningful models among major model typologies;
4. Assess whether these models can be used in the implementation of the Digital Twin Ocean and can improve the decision-making capacity under the MFSD.

Studies and reports

Publications Office
of the European Union