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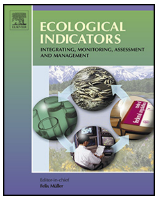

Review

Using ecological models to assess ecosystem status in support of the European Marine Strategy Framework Directive

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ABSTRACT

The European Union's Marine Strategy Framework Directive (MSFD) seeks to achieve, for all European seas, "Good Environmental Status" (GEnS), by 2020. Ecological models are currently one of the strongest approaches used to predicting and understanding the consequences of anthropogenic and climate-driven changes in the natural environment. We assess the most commonly used capabilities of the modelling community to provide information about indicators outlined in the MSFD, particularly on biodiversity, food webs, non-indigenous species and seafloor integrity descriptors. We built a catalogue of models and their derived indicators to assess which models were able to demonstrate: (1) the linkages between indicators and ecosystem structure and function and (2) the impact of pressures on ecosystem state through indicators. Our survey identified 44 ecological models being implemented in Europe, with a high prevalence of those that focus on links between hydrodynamics and biogeochemistry, followed by end-to-end, species distribution/habitat suitability, bio-optical (remote sensing) and multispecies models. Approximately 200 indicators could be derived from these models, the majority of which were biomass and physical/hydrological/chemical indicators. Biodiversity and food webs descriptors, with ~49% and ~43% respectively, were better addressed in the reviewed modelling approaches than the non-indigenous species (0.3%) and sea floor integrity (~8%) descriptors. Out of 12 criteria and 21 MSFD indicators relevant to the abovementioned descriptors, currently only three indicators were not addressed by the 44 models reviewed. Modelling approaches showed also the potential to inform on the complex, integrative ecosystem dimensions while addressing ecosystem fundamental properties, such as interactions between structural components and ecosystems services provided, despite the fact that they are not part of the MSFD indicators set. The cataloguing of models and their derived indicators presented in this study, aim at helping the planning and integration of policies like the MSFD which require the assessment of all European Seas in relation to their ecosystem status and pressures associated and the establishment of environmental targets (through the use of indicators) to achieve GEnS by 2020.

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1. Introduction

The use of robust and appropriate indicators that can assess whether an ecosystem and its services are well maintained and sustainably used (Layke, 2009; Walpole et al., 2009; TEEB, 2010) has been recognised as an essential step for the practical implementation of conservation and management policies (Rombouts et al., 2013). Several efforts have been undertaken at a European scale to evaluate marine ecosystem structure and their response to human activities, using key indicators to assess and sustain "Good Environmental Status" (GEnS; Borja et al., 2011). These initiatives have been carried out to assist the Marine Strategy Framework Directive (MSFD, 2008/56/EC; European Commission, 2008), the main European Directive that focuses on marine waters and aims at assessing the status of an ecosystem under anthropogenic pressures and the required interventions to bring the system back to its desired good status, making human activities sustainable, since this is one of the objectives of the MSFD. To achieve GEnS, 11 descriptors, 29 associated criteria and 56 indicators (from biological, physico-chemical indicators as well as pressure indicators—including hazardous substances, hydrological alterations, litter and noise, and biological disturbance such as introduction of non-indigenous species) have been identified (Cardoso et al., 2010; European Commission, 2010) (Tables 2 and 4).

Despite the fact that several attempts have been made to assess the environmental status of marine waters in an integrative manner (Borja et al., 2011; Halpern et al., 2012; Tett et al., 2013), significant gaps still exist on understanding marine ecosystem structures and functions and their response to human pressures (Katsanevakis et al., 2014; Borja et al., 2013). Currently, ecological models have been recognised as powerful tools to evaluate ecosystem structure and function and predict the impacts of human activities (Fulton and Smith, 2004; Shin et al., 2004; Christensen and Walters, 2005; Plagányi, 2007; Fulton, 2010) and climate change (Tomczak et al., 2013; Chust et al., 2014) on marine systems.

Thus, this study aims to assess the most commonly used capability of the modelling community to inform on indicators outlined in the EU MSFD (2008/56/EC), focusing particularly on biodiversity related descriptors: biological diversity (D1), non-indigenous species (D2), food webs (D4), and seafloor integrity (D6). To date, there has been no thorough evaluation of the capabilities of ecological models to provide information as explicitly outlined by the MSFD indicator structure, this task has been only partially undertaken (e.g., Reiss et al., 2014). With this work, we aim to fill in this knowledge gap by providing an inventory of models in EU regional seas that could assess MSFD indicators associated with biodiversity, non-indigenous species, food webs and seafloor integrity. For this reason, we have built a model catalogue ranging from lower to higher trophic levels, including those that successfully couple the two compartments and associated ecosystem processes. This inventory, developed as part of the DEVOTES FP7 Project (http://www.devotes-project.eu/), serves to highlight the vast potential of model-derived indicators that can be associated with MSFD descriptors and aims to provide a thorough assessment of their relevance and degree of "operationality." A detailed description of models and associated references together with the full catalogue are provided as supplementary materials (S1 and S2).

Yet, we acknowledge that this study does not aim to serve as review of all the existing models available in the literature, but instead highlight a process of exploring modelling potential to support specific European policies. Because of the nature of these issues, though, similar case studies conducted elsewhere are likely to lead to similar outcomes, conclusions, and recommendations (e.g., because of similar/same model availability and/or process understanding). Thus, this work emphasises several types of ecological modelling and derived indicators that exist at EU level stressing how such diversity of modelling approaches could be useful to support management policies and the limitations that still occur to achieve this task.

In particular, this study is divided into six sections, comprising (1) catalogue structure; (2) a general overview of model characteristics; (3) model potential to address MSFD GEnS descriptors and indicators (including the ability to address biodiversity components and habitat types); (4) geographical coverage of models; (5) ability to address pressures; and (6) gaps in models type/modelling capability and needs for further development.

2. Catalogue structure

The catalogue has been built primarily with models/areas targeted by the DEVOTES partners (which represent 23 research institutions from EU and non EU countries), yet with an effort to integrate available models/areas from other inventories (e.g., the MEECE project http://www.meece.eu/Library.aspx) and scientific literature (see S1).

The catalogue has been structured with several fields following the MSFD Commission Decision 2010/477/EU (European Commission, 2010) and grouped into six main categories:

i. Model/Indicator properties with the following sub-categories:
    a. *MSFD descriptor/indicator*, descriptor/indicator outlined in the directive

   b. *Model derived indicator (MDI)*, indicator resultant from model output
   c. *MDI type* defined as 1. *Static* (e.g., snapshot of the indicator at a precise period of time), 2. *Dynamic* (e.g., indicator which changes in time) or 3. *Spatial dynamic* (e.g., indicator which changes in time and space)
   d. *MDI status of development* defined as 1. *Operational*, when the indicator is developed, tested and validated (e.g., it could be either an indicator used by the Member States (MS) for national environmental monitoring; or in EU/International Conventions' monitoring programmes; or validated with observed/survey data although not necessarily approved by any national/international law or convention); 2. *Under development*, an indicator proposal exists, but not yet validated in field/real data (e.g., indicator not yet used for MS national environmental monitoring or for EU/International Conventions' monitoring programmes; or not yet validated with survey data); 3. *Conceptual*, an indicator idea, supported by theoretical grounds, although no practical measure/metric is yet available (e.g., indicator not yet tested)
   e. *MDI target/reference values and unit* defined as thresholds/limits representing boundaries between an acceptable and unacceptable status
   f. *Model name* referring to the label used to identify a particular model
   g. *Model type* referring to model characteristics/properties and/or to the technique used to assess specific ecosystems
   h. *Data requirements* referring to data needed to run a certain model
   i. *Confidence/uncertainty* referring to the ability of models to assess uncertainty for the input/output data and it is defined as the type of statistical analysis used to evaluate it
   j. *Source* Scientific literature and or Institutional report supporting selected MDI/models entries

ii. Model/MDI in relation to MSFD Descriptors: referring to models and MDI broad capability to address the 11 descriptors of the directive (D1–D11).

iii. Model/MDI correspondence with MSFD Biodiversity Indicators: referring to models and MDI assessed in relation to their capability to provide information for the specific indicators listed under the criteria of the four descriptors (D1/D2/D4/D6) as officially outlined in the European Commission (2010).

iv. Model/MDI correspondence with biodiversity components referring to which biodiversity components (e.g., microbes, phytoplankton and fish) the indicator was related to or was evaluated with. Categories adopted for biodiversity components followed those of the European Commission (2010) and EU Commission Staff Working Paper (CSWP, 2012).

v. Model/MDI coverage of specific habitat types and geographical range/scale referred to whether an MDI was related to certain habitats and geographical areas. Categories adopted for Habitat Types followed those of the European Commission (2010) and EU Commission Staff Working Papers (CSWP, 2011, 2012). Concerning geographical coverage, we have adopted well-established international criteria for smaller scale subdivisions or ecological assessment areas in order to increase the spatial detail on the information collected (e.g., the International Council for the Exploration of the Sea (ICES) and General Fisheries Commission for the Mediterranean (GFCM) subdivisions; see maps under S1).

vi. Model/MDI relation to specific pressures: referring to whether there was scientific evidence of a relationship between a pressure and a specific indicator. Indicators were related to pressures either as responsive/sensitive to, or affected by a given pressure (state indicators, e.g., mainly through changes in trends) or indicators were actually pressure indicators themselves. The considered pressures follow the list of pressures and impacts of Annex 3 of the MSFD (see S3).

3. Model characteristics

The model catalogue revealed that currently 44 models have been applied with outputs relevant to MSFD descriptors (Table 1). These ecological models being used to describe or understand ecosystem processes can be categorised under seven types of modelling approaches described below:

3.1. Biogeochemical models

The bulk properties of biogeochemical fluxes in marine ecosystems are combined with information on physical forcing, chemical cycling and ecological structure to simulate the response of lower trophic level groups (phytoplankton and zooplankton) to environmental conditions, including climate variability and change (Gnanadesikan et al., 2011; Jørgensen and Fath, 2011). Such models typically have very simplified representations of biological organisms, and associated trophic structure (Anderson, 2005).

3.2. Multispecies models

These models represent populations of dynamically interacting species or functional groups. Some models also resolve multiple stages or size-classes within populations (Christensen and Walters, 2004; Hollowed et al., 2000; Shin and Cury, 2001). Focus of these models is on understanding the implication of the indirect interactions in ecosystems that result from the complex networks of direct predator–prey interactions in marine communities. The models aim to represent, for example, top-down or bottom-up effects along marine food chain ranging from primary producers (e.g. phytoplankton) to top predators (e.g., marine mammals), or the role of indirect competitive interactions among species (Fung et al., 2015). Effects of exploitation by fisheries and environmental change are also frequently described by these models.

3.3. Species Distribution Models (SDM)/Habitat Suitability Models (HSM)

SDM combine observations of species occurrence or abundance with environmental explanatory variables to develop ecological and evolutionary understanding and to predict distribution across selected habitats (Elith and Leathwick, 2009; Reiss et al., 2014). HSM relate field observations to a set of environmental variables (e.g., reflecting key factors of the ecological niche like climate, topography, geology) to produce spatial predictions on the suitability of locations for a target species, community or biodiversity (Hirzel et al., 2006). A new generation of SDM/HSM – i.e. dynamic bioclimatic envelope models – now provide greater links to the mechanistic understanding of niche ecology. Such models typically include additional model components that describe physiological responses of species to the environment, population dynamics and dispersal, to further constrain the distribution of suitable habitat and provide more realistic species distribution projections (Cheung et al., 2011).

3.4. Meta-community models

Meta-community is a set of interacting communities which are linked by the dispersal of multiple, potentially interacting species. In this context, meta-community models are theoretical frameworks describing specific mechanistic processes in order to predict empirical community patterns. They deal mainly with species

Table 1

Summary table of models library showing models' name, acronym, data type (SP: spatial; DY: dynamic; ST: static), number of model derived indicators and uncertainty (VOD: validated with observed data; VOD*: some of the indicators still need to be validated with observed data; NA: not available; STAT: statistical analysis; BOOT: bootstrap; PE: pedigree).

#	Model name	Model acronym	Type of the model	Coupled	Data type	Model derived indicators	Uncertainty
1	European Regional Seas Ecosystem Model (ERSEM)	ERSEM	Biogeochemical	No	SP-DY	2	VOD
2	Black Sea chlorophyll and coloured dissolved/detrital matter (Chl & CDM) model	BS-Chl & CDM	Bio-optical models (remote sensing)	No	SP-DY	4	VOD*
3	Black Sea model of downwelling radiance (BS-PAR Model)	BS-PAR	Bio-optical models (remote sensing)	No	SP-DY	1	VOD
4	Black Sea Particle Size Distribution (PSD) model	BS-PSD (PSC)	Bio-optical models (remote sensing)	No	SP-DY	3	VOD
5	Black Sea spectral Primary Production (SPP) model	BS–SPP	Bio-optical models (remote sensing)	No	SP-DY	1	VOD*
6	Black Seal Inherent Optical Properties model (IOPs)	BS-IOPs	Bio-optical models (remote sensing)	No	SP-DY	3	VOD
7	North Sea Optical Properties (NSOP)	NSOP	Bio-optical models (remote sensing)	No	DY	1	STAT
8	1D General Ocean Turbulence Model (GOTM) and European Regional Seas Ecosystem Model (ERSEM) and Ecopath with Ecosim (EwE)	GOTM-ERSEM-EwE	End to end	Yes	DY	6	NA
9	Princeton Ocean Model (POM) and Black Sea Integrated Modelling System-Ecosystem (BIMS-ECO) and Ecopath with Ecosim (EwE)	POM-BIMS-ECO-EwE	End to end	Yes	DY	3	NA
10	Regional Ocean Model System (ROMS) and Eastern Boundary Upwelling Systems (BiOEBUS) and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ROMS-BioEBUS-OSMOSE	End to end	Yes	SP-DY	5	NA
11	Regional Ocean Model System (ROMS) and $N_2P_2Z_2D_2$ biogeochemical model and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ROMS-$N_2P_2Z_2D_2$-OSMOSE	End to end	Yes	SP-DY	12	NA
12	Norwegian Sea Ecosystem, End-to-End	NORWECOM.E2E	End to end	Yes	SP-DY	6	NA
13	Ecological ReGional Ocean Model (ERGOM) and Modular Ocean Model (MOM) and Fish Model	ERGOM + MOM + Fish	End to end	Yes	DY	2	VOD
14	ECOSystem Model (ECOSMO) and Stochastic Multi-Species model (SMS)	ECOSMO-SMS	End to end	Yes	SP-DY	2	NA
15	European Regional Seas Ecosystem Model (ERSEM) and Princeton Ocean Model (POM) and Object-oriented Simulator of Marine ecOSystems Exploitation model (OSMOSE)	ERSEM-POM-OSMOSE	End to end	Yes	SP-DY	10	NA
16	Hubbell's neutral model of biodiversity (HNM)	HNM	Meta-community	No	ST	1	NA
17	Ecopath with Ecosim (EwE)	EwE	Multispecies	No	ST-DY-SP	136	PE-VOD*
18	North Sea Threshold general additive models (NS tGAM)	NS tGAM	Multispecies	No	DY	4	BOOT
19	Population-Dynamical Matching Model (PDMM)	PDMM	Multispecies	No	DY	1	VOD
20	Bay of Biscay Qualitative trophic model	BoB Qualit	Multispecies	No	ST	1	NA
21	Length-based multispecies model (LeMANS)	LeMANS	Multispecies	No	DY	2	VOD
22	Stochastic Multi-Species model (SMS)	SMS	Multispecies	No	DY	2	VOD
23	Proudman Oceanographic Laboratory Coastal Ocean Modelling System (POLCOMS) and European Regional Seas Ecosystem Model (ERSEM)	POLCOMS-ERSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA
24	3D General Estuarine Transport Model (GETM) and European Regional Seas Ecosystem Model (ERSEM)	GETM-ERSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	16	VOD*
25	Princeton Ocean Model (POM) and Black Sea Integrated Modelling System-Ecosystem (BIMS-ECO)	POM-BIMS-ECO	Physical (hydrodynamic)–biogeochemical	Yes	DY	4	NA

26	St. Petersburg Eutrophication Model (SPBEM)	SPBEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
27	European Regional Seas Ecosystem Model (ERSEM) and Princeton Ocean Model (POM)	ERSEM-POM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	11	NA
28	3D General Estuarine Transport Model (GETM) and Ecological Regional Ocean Model (ERGOM)	GETM-ERGOM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	8	VOD*
29	BAltic Sea Long-Term large-Scale Eutrophication Model (BALTSEM)	BALTSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
30	Biogeochemical Flux Model (BFM) and Princeton Ocean Model (POM)	BFM-POM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	5	NA
31	Black Sea Ecosystem Model	BSEM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	13	VOD*-STAT
32	Ecological ReGional Ocean Model (ERGOM) and Modular Ocean Model (MOM)	ERGOM + MOM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
33	ECOSystem Model (ECOSMO)	ECOSMO	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA
34	MOHID and Pelagic Biogeochemical Model (LIFE)	MOHID-LIFE	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	4	VOD*
35	Nucleus for European Modelling of the Oceans (NEMO) and Biogeochemical Flux Model (BFM)	NEMO-BFM	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	10	NA
36	Regional Ocean Model System (ROMS) and Eastern Boundary Upwelling Systems (BiOEBUS)	ROMS-BioEBUS	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	6	NA
37	Regional Ocean Model System (ROMS) and $N_2P_2Z_2D_2$ biogeochemical model	ROMS-$N_2P_2Z_2D_2$	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	12	NA
38	Swedish Coastal and Ocean Biogeochemical model (SCOBI) and Rossby Center Ocean circulation model (RCO)	RCO-SCOBI	Physical (hydrodynamic)–biogeochemical	Yes	SP-DY	7	VOD
39	Ecological Niche Factor Analysis (ENFA)	ENFA	SDM/Habitat Suitability Models	No	ST	1	NA
40	Bay of Biscay Habitat suitability based on Generalised Additive Models (GAM)	BoB GAM	SDM/Habitat Suitability Models	No	ST	1	NA
41	Bay of Biscay Habitat suitability based on Generalised Linear Models (GLM)	BoB GLM	SDM/Habitat Suitability Models	No	ST	1	NA
42	Habitat suitability based on MaxEnt (Maximum Entropy)	MaxEnt	SDM/Habitat Suitability Models	No	ST	2	NA
43	Niche-Trait Model (NTM)	NTM	SDM/Habitat Suitability Models	No	ST	1	NA
44	Process-driven habitat model	PDH	SDM/Habitat Suitability Models	No	ST	1	NA

composition and abundance and their variation within a meta-community (Hugueny et al., 2007).

3.5. Bio-optical models

The optical properties of biological materials, such as phytoplanktonic or heterotrophic unicellular organisms, are analysed and then modelled to predict distributions of biological communities over wide spatial areas (with remote sensing data) or in terms of expected depth limitations that can be inferred from modelling studies. Bio-optical models are based on various fundamental theories of optics which apply to a single particle making use of a set of equations/algorithms (Morel and Maritorena, 2001; IOCCG, 2006).

3.6. Hydrodynamic–biogeochemical Models

These are mainly coupled hydrodynamic and biogeochemical models to capture global scale patterns in physical–chemical components affecting lower trophic level groups (e.g., phytoplankton and zooplankton) (Gnanadesikan et al., 2011; Jørgensen and Fath, 2011).

3.7. End-to-end models

In recent years, hydrodynamic-biogeochemical models (or just biogeochemical models) have been coupled with multispecies models. These so called end-to-end (E2E) models combine physicochemical oceanographic processes with organisms ranging from low trophic level (LTL) to higher trophic level organisms (HTL) into a single modelling framework (Travers et al., 2009).

Of the models reported in this study, more than half were coupled ecological models (Table 1). The most common type of models currently in the catalogue were hydrodynamic-biogeochemical models (36%) followed by end-to-end (18%), species distribution/habitat suitability, bio-optical and multispecies (14% each), biogeochemical and meta-community (2% each) models (Table 1).

In the framework of ecological studies, physical–biological interactions are the main factors that can better describe ecosystem properties and the spatial and/or temporal evolution in function of relevant pressures identified, climate change or anthropogenic impacts. This is reflected in the choice of modelling approaches and in the growing need to couple different types of models within a single modelling framework (Travers et al., 2009; Rose et al., 2010). This is particularly true if the models are intended to predict changes and provide guidance in a framework of biodiversity conservation and ecosystem-based management (Travers et al., 2009; Kaplan et al., 2012).

Recent software developments, within the current (DEVOTES) and former EU projects (e.g., MEECE http://www.meece.eu/), have shown that these models (hydrodynamic-biogeochemical and multispecies models) can be coupled to run together. This represents a powerful tool for scenario testing of climate change and anthropogenic impacts simultaneously. There is a growing trend for E2E modelling, which includes anthropogenic and physical drivers behind observed changes, identifying both direct and indirect causes (Fulton, 2010; Shin et al., 2010b; Travers-Trolet et al., 2014), and so better facilitates the setting of targets and implementation of management measures (Cury et al., 2008; Kaplan et al., 2012). Fig. 1 illustrates the capacity of the seven model types to represent the different components of marine ecosystems, including or excluding, human components and/or climate impacts.

Coupled (both E2E and hydrodynamic-biogeochemical models) and bio-optical (remote sensing) models included in this catalogue were primarily spatially dynamic and 5 out of 30 models were also dynamic. The remaining models were mainly static with only 5 out of 14 models presenting dynamic and spatial modules as well (Table 1). This is an important and interesting result since spatial-dynamic models are able to provide greater capacity for forecasting of ecosystem dynamics, although they require a more data intensive calibration (e.g., the initial testing and tuning of a model) and validation (e.g., the comparison/fitting of model with a data set representing "local" field data) approaches (Jørgensen, 2008).

A total of 201 model-derived indicators (see S1 of supplementary materials) were included in this catalogue, of which more than half were considered to be "operational" (64%), while the majority of the remainder were still "under development" (33%), with only a few "conceptual" approaches (3%) presented (Table 2). We acknowledge that some indicators might have changed their status since the time of this survey (e.g., some indicators "under development" may have been assessed and now classified as "operational") but for the purpose of this work we decided to keep them in the status of development that they were reported during the survey.

Ecopath with Ecosim (EwE) was notably associated with the largest number of model-derived biodiversity indicators (Table 2). However, the majority of these biodiversity indicators were biomasses of species or groups of species at different trophic levels of the food web. For ease of characterisation/evaluation, model-derived indicators were grouped into seven major categories (see Table 3 for the detailed list). Not surprisingly, biomass indicators constituted the largest group with approximately 57% followed by diversity indices (13%) and physical, hydrological and chemical indicators (12%). Regarding targets and/or reference values associated with model-derived indicators, the catalogue highlights that only few models in few areas had assigned target or reference values, despite the fact that the majority were considered "operational" (i.e. developed, tested and validated). This is the case of fully developed models for which validated outputs exist (e.g., BSEM by Dorofeev et al., 2012), but under policy contexts such as the MSFD, lack tested and validated reference values or targets compliant with specific legal requirements.

Also, very few of the reported models have been used to clearly assess the effects of measures to meet the targets that will eventually be established. For instance, multispecies models have been applied in the Ionian Sea and in the North Sea ecosystems to assess the reduction in fishing effort as a measure to (a) bounce back common dolphin populations (e.g., EwE model by Piroddi et al., 2011); (b) assess the response of selected biodiversity indicators (e.g., PDMM by Shephard et al., 2013; Fung et al., 2013, or EwE model by Lynam and Mackinson, in press); (c) test the effect of selective fishing on community biodiversity conservation (e.g., LeMANS model by Rochet et al., 2011) and implemented in the Bay of Biscay (e.g., OSMOSE model by Chifflet et al., 2014) to evaluate the effect of different fishing scenarios on small pelagic fish stocks.

In addition, not all the models were able to address uncertainty; the majority (61%) lacked an approach to determine confidence intervals/range of uncertainty or required further validation work for indicators. This is a reflection, as mentioned above, of the type of data present in the catalogue which are more spatial-dynamic than static and for which validation is more difficult to obtain. From the models that reported addressing uncertainty (39%), data comparison and data validation (e.g., model outputs fitted to surveyed data) was the most common method reported (Table 1).

4. Model potential to address descriptors and indicators for biological descriptors

In terms of supporting the MSFD, ecological models can be the most effective means to model relationships between activities, pressures, state and thus indicators (Jørgensen, 2008; Jørgensen

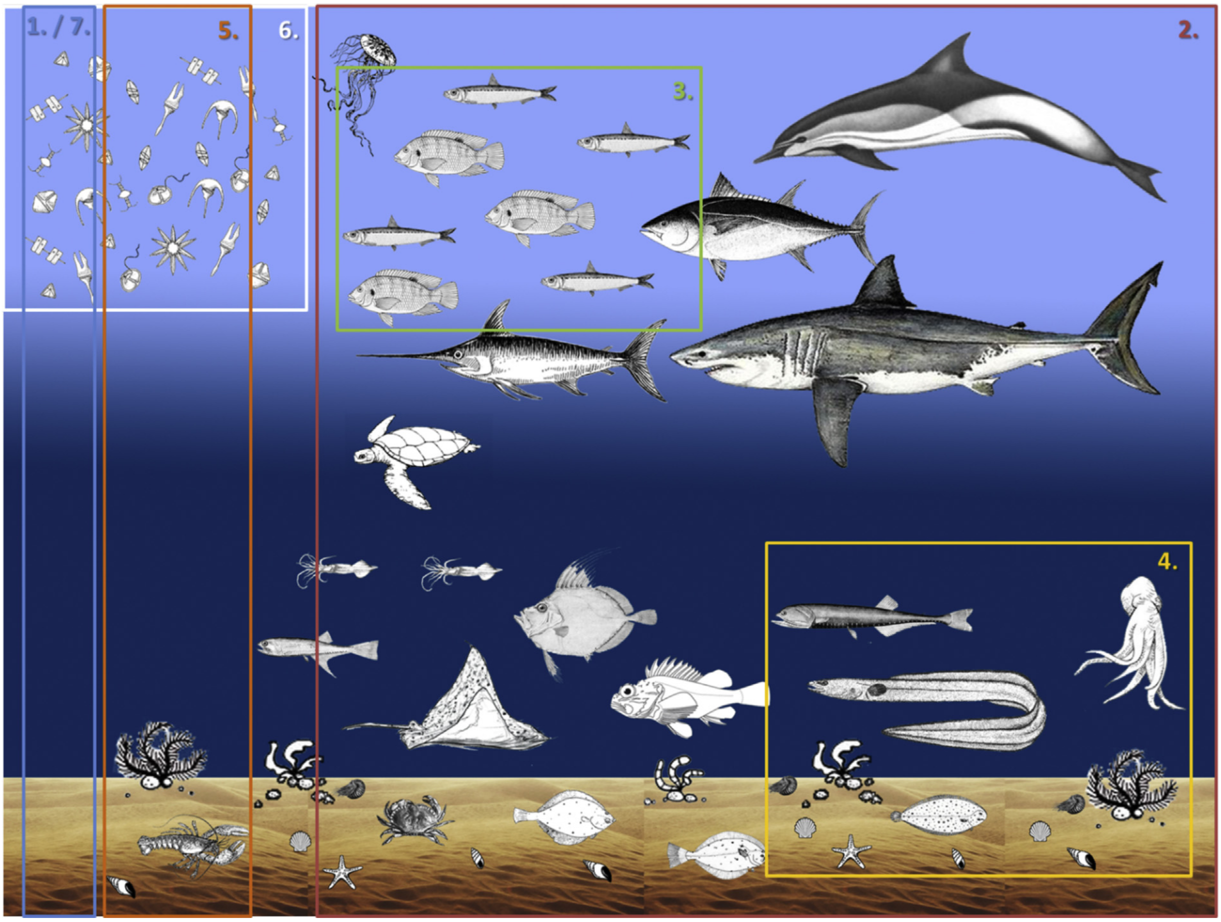

Fig. 1. Illustration of models capacity to describe the ecosystem, from specific processes integrating biological compartments and the associated abiotic environment to the entire ecosystem including, or not, human components or climate impacts. In particular, 1 and 7 – refer to biogeochemical and coupled physical–biogeochemical models; 2 and 3 – refer to multispecies models (either at species or at food web level); 4 – Species distribution/Habitat Suitability; 5 – meta-community models and 6 – bio-optical models. E2E models encompass all of them.

and Fath, 2011). This is because of the integrative character of these modelling approaches that often consider many ecosystem components from abiotic factors to biotic interactions and processes. The 44 models available in the catalogue were capable of addressing indicators in 8 of the 11 descriptors of the MSFD (Table 2) although, due to the focus of this survey which primarily dealt with the four biodiversity related descriptors, their modelling potential was stronger for two of these biodiversity descriptors: biological diversity (D1) and food webs (D4). Nevertheless, human induced eutrophication (D5), hydrographical conditions (D7) and commercial fish and shellfish (D3) were well addressed by the models in this catalogue.

Within the biodiversity related descriptors, non-indigenous species (D2) and seafloor Integrity (D6) were the most poorly addressed by the models currently in the catalogue (Table 2). However, Pinnegar et al. (2014) shows how EwE models can be useful in assessing the response of an ecosystem to the introduction of invasive species (D2). Similarly, increasing the spatial resolution of many of the current models would further improve our understanding of the direct effect of fishing and other activities (such as decommissioning of oil rigs or development of a wind farm) on seafloor integrity (D6). In several cases, models have been used to investigate the impacts of trawling and test fisheries scenarios (e.g., high resolution ERSEM-POM model, Petihakis et al. (2007)). However, most of the models considered in this catalogue do not explicitly include descriptions of these types of pressures on the marine environment, they do not link to benthic habitat layers, and their understanding of pressures and impacts is in many cases still limited by scarce empirical information (Hooper and Austen, 2014).

Typically, a single model was capable of addressing more than one MSFD descriptor and sometimes up to six, as is the case of EwE (Table 2). As a result, the same model may be noted for having indicators in multiple stages of development (e.g., operational, under developed or conceptual) either across descriptors or within the same descriptor. This is because the reported status of development relates not to the model itself but to the different indicators that can be derived from the model. The potential of the available models to address MSFD indicators specifically those within biological descriptors was evaluated by extracting the number of indicators (outlined in the European Commission (2010)) that each model can inform on (Table 2). All models could address multiple indicators, from the set of 21 MSFD indicators under these 4 descriptors. In fact, 20 models in the catalogue had the potential to address at least half of these indicators. Despite the high potential of the models to address MSFD indicators, not all of the available model-derived indicators were fully operational (see Section 2 for definition and Table 4). The mean percentage of operational model-derived indicators across all MSFD indicators was 64%. Our analysis also revealed that there were three indicators required under the biodiversity descriptors for which no model-derived indicators were available in the catalogue (Table 4): D1C3-I2: population genetic structure; D2C2-I1: Ratio between invasive non-indigenous species and native species and D2C2-I2: Impacts of non-indigenous

Table 2

Models' capability per the 11 Marine Strategy Framework Directive descriptors (D) assessed by the number of indicators provided by each model (for names, see Table 1). The development status of the indicators is indicated (op: operational, ud: under development, co: conceptual). The last column summarises the number of MSFD official indicators (European Commission, 2010) of D1, D2, D4 and D6 (check Table 4) that the model-derived indicators can inform on.

		D1 Biological diversity	D2 Non-indigenous species	D3 Commercial fish	D4 Food webs	D5 Human-induced eutrophication	D6 Seafloor integrity	D7 Hydrological alterations	D8 Contaminants	D9 Contaminants in food	D10 Marine litter	D11 Energy/ noise	# MSFD indicators addressed under D1, D2, D4, D6
1	BALTSEM	7op			5op	3op		2op					16
2	BFM-POM	5op			3op	2op		2op					14
3	BSEM	6op/7ud	1op/1ud		1op/7ud	4ud		3op					9
4	EwE	82op/82ud/7co	1ud	53op/57ud/4co	82op/82ud/7co	13op/14ud/2co	17op/25ud/4co						13 (+1[a])
5	ECOSMO	6op			3op	2op		3op					14
6	ECOSMO-SMS	2ud		2ud	2ud								8
7	ENFA	1op		1op	1op								14
8	ERGOM + MOM	7op			5op	3op		2op					16
9	ERGOM + MOM + fish	2op		2op	2op								7
10	ERSEM	2ud			2ud	1ud							12
11	ERSEM-POM	11op			6op	3op		5op					14
12	ERSEM-POM-OSMOSE	10ud		10ud	10ud								9
13	BoB GAM	1op		1op	1op								16
14	GETM-ERGOM	8ud			2ud	4ud		6ud					14
15	GETM-ERSEM	16ud			5ud	8ud	2ud	11ud					19
16	BoB GLM	1op		1op	1op								16
17	GOTM-ERSEM-EWE	6ud		4ud	6ud					3ud			8
18	HNM	1co			1co	1co	1co						16
19	BS-IOPs	3ud			2ud	3ud							8
20	LeMANS	2op		2op	2op								7
21	MaxEnt	2op	1op	1op	2op								17
22	MOHID–LIFE	4op			3op	3op		1op					10
23	NEMO-BFM	10ud			7ud	4ud		3ud					17
24	NSOP	1ud			1ud	1ud							8
25	NStGAM	4ud		2ud	4ud	1ud							10
26	NORWECOM.E2E	6op			3op	2op		3op					14
27	NTM	1ud			1ud		1ud						9
28	PDMM	1op		1op	1op								7
29	POLCOMS-ERSEM	6op			3op	2op		3op					14
30	POM-BIMS-ECO	4op			3op	2op		1op					14
31	POM-BIMS-ECO-EWE	3ud		3ud	3ud								9
32	PDH	1ud			1ud		1ud						11
33	BS-PSD (PSC)	3ud			3ud	3ud							5
34	BoB Qualit	1co		1co	1co								8 (+1[a])
35	RCO-SCOBI	7op			5op	3op		2op					16
36	BS-Chl & CDM	4ud			4ud	4ud							6
37	BS-PAR	1ud											3
38	BS-S PP	1ud			1ud	1ud							3
39	ROMS-BioEBUS	6op			3op	2op		3op					14
40	ROMS-BioEBUS-OSMOSE	5ud		5ud	5ud								9
41	ROMS-$N_2P_2Z_2D_2$	12op			8op	5op		4op					13
42	ROMS-$N_2P_2Z_2D_2$-OSMOSE	12op		12op	12op								11
43	SMS	2op		2op	2op								7
44	SPBEM	7op			5op	3op		2op					16
Number of models per descriptor		44	3	17	43	26	5	17	0	1	0	0	

[a] New proposals for Descriptor 4 *Food Webs*, not yet considered under the set of Indicators outlined in the EU Commission Decision (European Commission, 2010).

Table 3
The model-derived indicators grouped into 7 major categories, based on what the indicators inform on, with their overall percentages in the DEVOTES Catalogue of model-derived indicators.

	Type of indicators		%
1	Biomass		57
2	Diversity indicators	Biodiversity indices (e.g., Kempton diversity index, trophic level of the community) and species/habitat diversity, proportions in community	13
3	Primary or secondary production		9
4	Spatial distribution indicators	Species spatial distribution	6
5	Species life-history	Traits such as for e.g., length, weight or life span	1
6	Ecological Network Analysis (ENA) indicators	Flows, energies and efficiencies	2
7	Physical, hydrological and chemical	Describing either habitat integrity or pressures	12

invasive species at the level of (1) species, (2) habitats and (3) ecosystem.

Additionally, it is noteworthy that the potential of modelling approaches to address ecosystem fundamental properties such as D1C8I1 "Interactions between structural components" and D1C8I2 "Services provided" (Table 4) was high. These aspects, despite being clearly mentioned in the European Commission (2010), were not part of the MSFD indicators set, most probably due to the difficulty in defining them through specific indicators. Nevertheless, the majority of the model-derived indicators included in this catalogue (189 out of the 201) have the potential to inform on these complex, integrative ecosystem dimensions. In any case, although the catalogue shows the potential of models to address Ecosystem Services (ES, *sensu* Liquete et al., 2013), the survey performed cannot inform adequately on the capacity of the indicators to support policy-makers' use of these ES concepts. This is a current limitation of the MSFD set of indicators (Table 4) which does not clearly require the assessment of ecosystems services, despite the fact that in 2011, as a party of the Convention on Biological Diversity (CBD), the European Union (EU) adopted a new strategy (the Biodiversity Strategy to 2020), which integrates ES as key elements for the conservation approach to biodiversity (Maes et al., 2012). The role of ES in supporting conservation initiatives and socio-economic activities calls for action to monitor, quantify and value trends in these services, so as to ensure that they are adequately considered in decision making processes. To do so, a clear linkage needs to be established between biodiversity and ecosystem functioning and the diversity and complexity of the benefits they provide, i.e. the ecosystems services (be it provisioning, regulating or cultural), in order to allow the development of operational indicators. Yet, the indicators available are not comprehensive and are often inadequate to characterise ES; data are often either insufficient or the linkages are poorly understood to support the use of these indicators (Liquete et al., 2013).

4.1. *Biodiversity components and habitats*

Habitats and species are key attributes of biological diversity and their occurrence, distribution and abundance is used as criteria to assess the ecosystem status (Table 5). To attain GEnS for D1, as stated in the MSFD, "no further loss of biodiversity at ecologically relevant scale should occur, and, if it does, restoration measures should be put in place". The definition of GEnS is dependent on the ecological relevance and is approached at different scales of complexity, from species to habitats, communities and ecosystem (see Borja et al., 2013).

Biodiversity components indicated in the MSFD include microbes, phytoplankton, zooplankton, angiosperms, macroalgae, benthic invertebrates, fishes, cephalopods, marine mammals, reptiles and birds, with specific subgroups within the last four categories. Their inclusion in ecological models listed in the catalogue was highly heterogeneous. Operational model-derived indicators concerned mainly fish, phytoplankton, zooplankton, benthic and pelagic invertebrates and marine mammals (total 64, 45, 31, 23, and 17, respectively) (Fig. 3), while the remaining biodiversity components were covered with less than 10 indicators each. This reflects the traditional focus of marine ecosystem modelling, driven mainly by the wide-spread use of low trophic level models related to the bottom-up forcing of production, and in parallel, motivated by fisheries oriented policies and conservation interests in particular species (Rose et al., 2010; Shin et al., 2010b).

As expected, the various models have used similar components differently and, depending on their final goal, the resolution of the biodiversity components differed greatly: from single to multispecies models, inclusion of single or multiple functional groups and integrating both LTL and HTL key organisms (e.g., Oguz et al., 1999; Lewy and Vinther, 2004; Schrum et al., 2006; Coll et al., 2008; Rossberg et al., 2010; Lassalle et al., 2011; Mateus et al., 2012; Tsiaras et al., 2012). Of the models catalogued, only Hubbell's neutral model and the Population-Dynamical Matching Model (PDMM) resolve biodiversity at species level, and only the PDMM does so through the entire marine food chain (Fung et al., 2013). EwE model-derived indicators, either operational, conceptual or still under development, have been used to model all types of biodiversity components (excluding microbes), with fish being the most frequently assessed group (25%) followed by benthic invertebrates (15%), marine mammals (12%) and cephalopods (11%). The microbial component, as reported in the catalogue, was only evaluated by ERSEM-POM in the Aegean Sea and under development by NEMO-BFM in the Baltic Sea. When models were organised according to model type, multispecies models assessed the majority of biodiversity components with the exception of microbes that were mostly evaluated by coupled hydrodynamic–biogeochemical models (Fig. 3).

The predominant habitat types that should be assessed within the evaluation of the status under the MSFD are water-column, seabed and ice habitats, with ecological models referring to one or several of these habitats. In our catalogue, of all predominant habitats, water-column was the most comprehensively evaluated habitat, either on its own, or in relation to the other two habitats. There were only two instances where seabed habitats were evaluated on their own. Ice-associated habitats were assessed by hydrodynamic–biogeochemical and multispecies models while seabed habitats were evaluated in multispecies and SDM/Habitat suitability/Community models. Multispecies as well as coupled (both hydrodynamic–biogeochemical and E2E) models were mainly used for the assessment of species or groups of species/organisms that can be linked to water-column habitats.

Examining the intersection between model-derived indicators and habitats, the water column was the most widely covered habitat, specifically the continental shelf where all components of biodiversity were covered (Table 5). The marine oceanic water column was also widely covered; however, in this case microbes were not evaluated. In estuaries, only phytoplankton and zooplankton were assessed, which were also the main components modelled in ice-associated habitats. In the seabed habitat, shallow sublittoral mixed sediments were the most commonly evaluated with model-derived indicators assessing 7 out of the 11 biodiversity components. Invertebrates were mainly studied in relation to the water column over the continental shelf although they are also

Table 4

Model derived indicators and models available per MSFD descriptor/indicator for biodiversity related descriptors (D1, D2, D4, D6), with particular emphasis on the number of operational indicators (op) out of the indicators available for each MSFD indicator (I).

MSFD descriptor	Criteria	MSFD indicator	Model derived indicators from DEVOTES catalogue		Comments
			Operational/available indicators	Number of models	
D1	C1	I1 Distributional range	33 op/45	27	
D1	C1	I2 Distributional pattern within range	4 op/10	15	
D1	C1	I3 Area covered by the species (for sessile/benthic species)	1 op/2	5	
D1	C2	I1 Population (1) abundance and/or (2) biomass	93 op/163	37	
D1	C3	I1 Population demographic characteristics: (1) body size; (2) age class structure; (3) sex ratio; (4) fecundity rates; (5) survival/mortality rates; (6) other	14 op/37	15	
D1	C3	I2 Population genetic structure	No indicators available	No models available	*D1 Biodiversity/C3 Population condition*
D1	C4	I1 Distributional range	6 op/9	21	*The exact same indicators are proposed as suitable to address both I1 and I2 from D1C4 Com. Dec.*
D1	C4	I2 Distributional pattern	6 op/9	21	
D1	C5	I1 Area	6 op/7	20	*Nearly the same indicators as in D1C4 are also reported as suitable to address both I1 and I2 from D1C5 Com. Dec.*
D1	C5	I2 Volume	4 op/4	15	
D1	C6	I1 Condition of the typical (1) species and (2) communities	89 op/174	39	
D1	C6	I2 Relative (1) abundance and/or (2) biomass	11 op/25	7	
D1	C6	I3 (1) Physical, (2) hydrological and (3) chemical conditions	12 op/39	23	
D1	C7	I1 Composition of ecosystem components: (1) habitats and (2) species	96 op/168	39	
D1	C7	I2 Relative proportions of ecosystem components: (1) habitats and (2) species	100 op/186	43	
D1	(C8)	I1 Interactions between structural components	108 op/198	44	*Not defined under Com. Dec. list but in its text.*
D1	(C8)	I2 Services provided	105 op/183	39	
D2	C1	I1 Trends in: (1) abundance; (2) temporal occurrence; (3) spatial distribution	2 op/4	3	
D2	C2	I1 Ratio between invasive non-indigenous species and native species	No indicators available	No models available	*D2 Non-indigenous species/C2 Environmental impact of invasive non-indigenous species*
D2	C2	I2 Impacts of non-indigenous invasive species at the level of (1) species, (2) habitats and (3) ecosystem	No indicators available	No models available	
D4	C1	I1 Performance of (1) key predator species determined from their productivity; (2) other trophic group	3 op/7	19	
D4	C2	I1 (1) Large fish (by weight); (2) other species	18 op/40	10	
D4	C3	I1 Abundance trends of functionally important selected: (1) groups with fast turnover rates; (2) groups/species that are targeted by human activities or that are indirectly affected by them; (3) habitat-defining groups/species; (4) groups/species at the top of the food web; (5) long-distance anadromous and catadromous migrating species; (6) groups/species that are tightly linked to specific groups/species at another trophic level	100 op/181	42	
D4	*(C4)*[a]	*(not defined)*[a]	None operational/3	2	*D4 Food webs: new proposals*
D6	C1	I1 Biogenic substrate: (1) type; (2) abundance; (3) biomass; (4) areal extent	2 op/5	6	
D6	C1	I2 Extent of seabed significantly affect by human activities for the different substrate types	None operational/1	1	
D6	C2	I1 Presence of particularly sensitive and/or tolerant species	None operational/1	1	
D6	C2	I2 Multi-metric indexes assessing benthic community condition and functionality, such as (1) species diversity and (2) richness, (3) proportion of opportunistic to sensitive species	1 op/4	6	
D6	C2	I3 Proportion of (1) biomass or (2) number of individuals in the macrobenthos above some specified length/size	17 op/38	3	
D6	C2	I4 Parameters describing the characteristics (shape, slope and intercept) of the size spectrum of the benthic community	None operational/1	1	

[a] New proposals for Descriptor 4 Food webs, not considered under the set of indicators outlined in the Com Dec. 2010.

Table 5
Number of model-derived indicators for each biodiversity component *per* habitat type (only habitats addressed by the models are included).

Biodiversity components	Seabed			Water column				ICE
	Littoral rock and biogenic reef	Shallow sublittoral mixed sediment	Shelf sublittoral mud	Marine water: coastal	Marine water: shelf	Marine water: oceanic	Variable salinity estuarine water	Ice-associated habitats
Microbes				1	1			1
Phytoplankton		9	1	4	42	13	2	4
Zooplankton	1	10	1	3	34	12	1	2
Angiosperms					12	7		
Macroalgae	1			1	11	1		
Invertebrates	1	11	1	1	45	15		1
Fish								
Coastal fish				2				
Pelagic fish				12	18	12		1
Pelagic elasmobranchs				1	2	2		
Demersal fish				7	13			1
Demersal elasmobranchs					1	11		
Other	1	14			34	11		
Cephalopods								
Coastal/shelf pelagic		13			27	6		
Other					7	1		
Marine mammals								
Toothed whales		13		1	23	2		
Baleen whales					1	1		
Seals					3	1		1
Other	1				8	6		
Reptiles								
Sea turtles					10	1		
Birds								
Inshore pelagic feeding		13			13			
Offshore pelagic feeding				1	1			
Other					10	5		

considered in models that include a benthic component, for example, ERSEM. The least addressed biodiversity components were microbes, coastal fish, pelagic elasmobranchs, baleen whales, seals and offshore pelagic birds. When looking at habitat representation in model-derived indicators, ice associated habitats, estuarine water column and shelf sublittoral mud were seldom covered (Table 5).

5. Models geographical coverage

Ecological models can be applied to many different areas with adequate customization (Henry et al., 2012; Mateus et al., 2012). The models in the catalogue have not been applied with the same spatial scale in all European regional seas (Fig. 2). The majority of reported indicators related to the Mediterranean Sea, representing more than half of the indicators entered in the catalogue (137), followed by the North-East Atlantic Ocean (78), Black Sea (29), Baltic Sea (18), non-EU regional seas (11) and EU scale (2). The EwE software was the most widely used model and has been applied in each EU regional sea area and most sub-regions; the second most commonly used model was ECOSMO, which has been implemented for the Baltic Sea, the North-East Atlantic Ocean and one non-EU regional sea (Barents Sea). In most regional seas, the proportion of model-derived indicators considered operational was high (ranging between 60 and 80%), except for the Black Sea where a suite of ecological models had been developed but using model-derived indicators still under development (about 70%) at the time of the assessment. Conceptual models were mainly reported for the North-East Atlantic region.

As stated by the MSFD, Member States (MS) need to cooperate to ensure a coordinated effort in the study and development of management strategies for the different marine regions and sub-regions. This is the case for ecological models developed for understanding and forecasting the marine ecosystem response to pressures. This catalogue demonstrates that the geographical coverage of ecological models in European marine waters is extensive and that the assessment of the environmental status can benefit considerably from greater use of ecological modelling. However, the use of differing models in different regions constrains the possibility of comparisons and inference of robust conclusions on causalities and scenarios (Chust et al., 2014).

6. Addressing pressures with models

Models are powerful tools for scenario testing of climate and anthropogenic impacts both separately and simultaneously (Jørgensen and Fath, 2011). All 44 available models included in the present catalogue, have been used to address at least one pressure or its impact on state of the ecosystem or its components. Most of the model-derived indicators compiled in the catalogue are state indicators (91%; S1), meaning that they inform on the condition of the ecosystem, its components or its functioning, while reflecting the impacts of single or multiple pressures in the environment. The majority do not provide a direct measure of the pressure(s) affecting the system, so they can only indirectly be associated to the pressures mentioned above. And despite strong scientific evidence for the overall cause–effect relationships between many of these pressures and the state of the ecosystem (Shin et al., 2005, 2010a; Fulton, 2011), the identification and quantification of the pressure(s) cannot be achieved through these indicators. On the other hand, a few of the indicators produced by the models are actually pressure indicators (9%; S1), which means that they act as proxies for relevant pressures. For instance, temperature or pH can act as a proxies for climate change; nutrients concentration and oxygen levels as proxies for eutrophication; biomass of an invasive species (e.g., *Mnemiopsis leidyi*, Dorofeev et al., 2012) as a proxy for non-indigenous species pressure; and also 'Inverse fishing pressure' which measures the total fishing pressure on an ecosystem

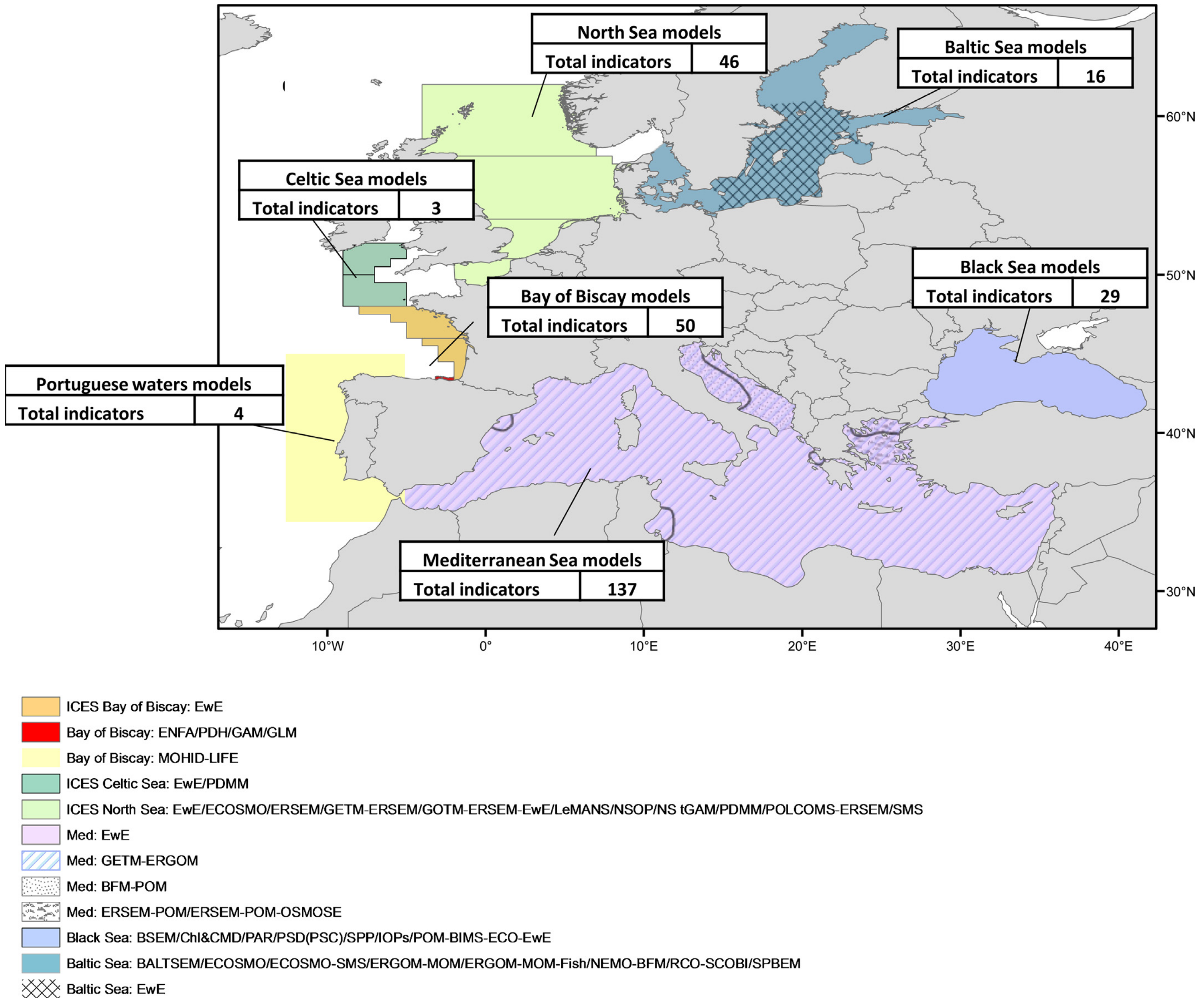

Fig. 2. Geographical distribution and spatial coverage of the models in the catalogue, when applicable. ECOSMO, ROMS-BioEBUS and ROMS-BioEBUS-OSMOSE are not displayed since are occurring in areas (Barents Sea and Benguela) outside the European Seas. EU Hubbell's neutral model and Maxent since they are applied to all EU regional seas are not represented.

using landings over biomass, could be considered as a proxy for exploitation rate and therefore a potential pressure indicator (Shin et al., 2010a).

The survey showed that, collectively, these models had the capacity to address (i.e. respond to, in most cases) all pressures except two ('*Contamination by radio-nuclides*' and '*Microbial pathogens*') of those outlined in the Directive (S3) and summarised in Fig. 4. The potential for the models to inform on the effects of pressures on the ecosystem was heterogeneous and whilst the majority addressed at most five pressures, a few models, mainly represented by multispecies and E2E models, were reported as capable of addressing up to fifteen different pressures (see S1 for a detailed list of pressures addressed by each model). Often pressures were of very different nature: from physical disturbance, to contamination by hazardous substances, nutrient and organic matter enrichment, biological disturbance and climate change (Fig. 4).

Of all the pressures listed in the MSFD, '*Interference with the hydrological regime*' was the most frequently addressed (in terms of numbers of models), with all 44 models reported and currently being used in monitoring or research associated with this pressure (Fig. 4). The '*Input of nutrients and organic material*' and '*Marine acidification*' (pH change) followed as pressures that could be addressed by more than half of the models. On the other hand, '*Non-indigenous species*', '*Marine litter*' and '*Underwater noise*' were the least addressed pressures by the type of models included in our survey, with just four models able to inform on the responses to one, or maximum two, of these pressures.

The pressures '*Physical loss of marine habitat*' and '*Physical damage to marine habitats*' (combined as '*sum of Physical damage*' in Fig. 4), could primarily be addressed using E2E, multispecies and SDM/Habitat suitability types of models (S1). The Metacommunity model could also produce indicators related to these pressures. A total of 20 models provided 114 indicators to address these pressures, with EwE able to provide 95 of these indicators. Such indicators were mostly state indicators, primarily related to biomass of different trophic levels, with a small number also relating to species distribution, primary and secondary production. Two physico-chemical indicators from the GETM-ERSEM model were the only pressure indicators reported (S1): denitrification layer depth and oxygen penetration depth.

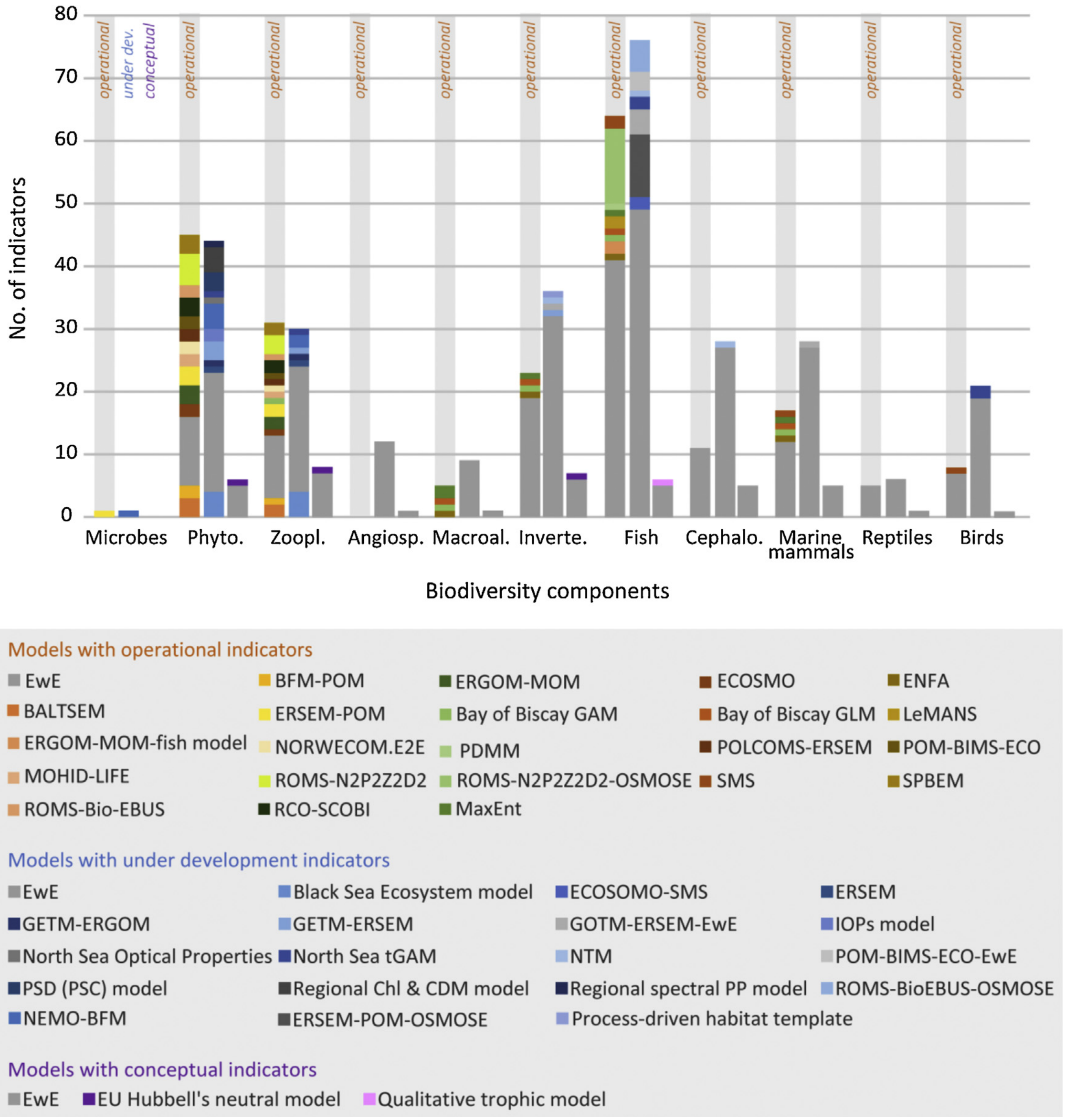

Fig. 3. Number of model-derived indicators available per biodiversity component. For each biological group the indicators are organised by columns according to their development status: operational, under development and conceptual. The different colours and patterns identify the models providing the indicators.

'*Underwater noise*' and '*Marine litter*' were both addressed by the same two models (GOTM-ERSEM-EwE and EwE), and through a similar set of model-derived indicators (in a total of 19 state indicators; S1), all relating to top predator biomass such as large fish, marine mammals, reptiles and seabirds. This is a common thread for many of the pressures acting particularly on higher trophic groups and therefore their impacts are better evidenced by models encompassing such trophic levels.

The pressure '*Interference with the hydrological processes*' could be addressed by 190 indicators from all models in our catalogue. Such changes in hydrological regime (namely thermal and salinity), were perceived as pressures related closely to climate change, although climate change is also accounted for by other pressures such as '*Marine acidification*'. In this sense, the large majority of the state indicators in the catalogue (S1) were reported as able to reflect the impact of these regime-shifts with strong ecological implications throughout the food web. Only 19 are pressure indicators, essentially physical–chemical indicators derived from coupled models with physical (hydrodynamic)–biogeochemical modules. The EwE food web and the BS-PAR bio-optical (remote sensing) were the other type of models providing two of these pressures indicators (respectively, '1/(landings/biomass) – Inverse fishing pressure' and 'Habitat condition – water transparency').

The pressures 'Contamination by synthetic compounds', 'Contamination by non-synthetic substances & compounds' and 'Acute pollution' (represented as 'Sum of contamination Pressures' in Fig. 4) were addressed by a total of 17 models of different types (multispecies, meta-community, SDM/habitat suitability and coupled models). Up to 132 model-derived indicators were identified, with the EwE model able to provide the highest number (S1). The majority of these were indicators of biomass with a small proportion of indicators relating to energy flow and primary/secondary production. One pressure indicator '1/(landings/biomass) – Inverse fishing pressure' has also been reported under this pressure type.

The majority of the 25 models assessing '*Inputs of nutrients and organic matter*' (Fig. 4) were spatial-dynamic coupled models (both E2E and hydrodynamic–biogeochemical) and, less frequently, biogeochemical, multispecies and bio-optical models. The total number of indicators that could address this pressure is 42, focusing on various measures of primary production and

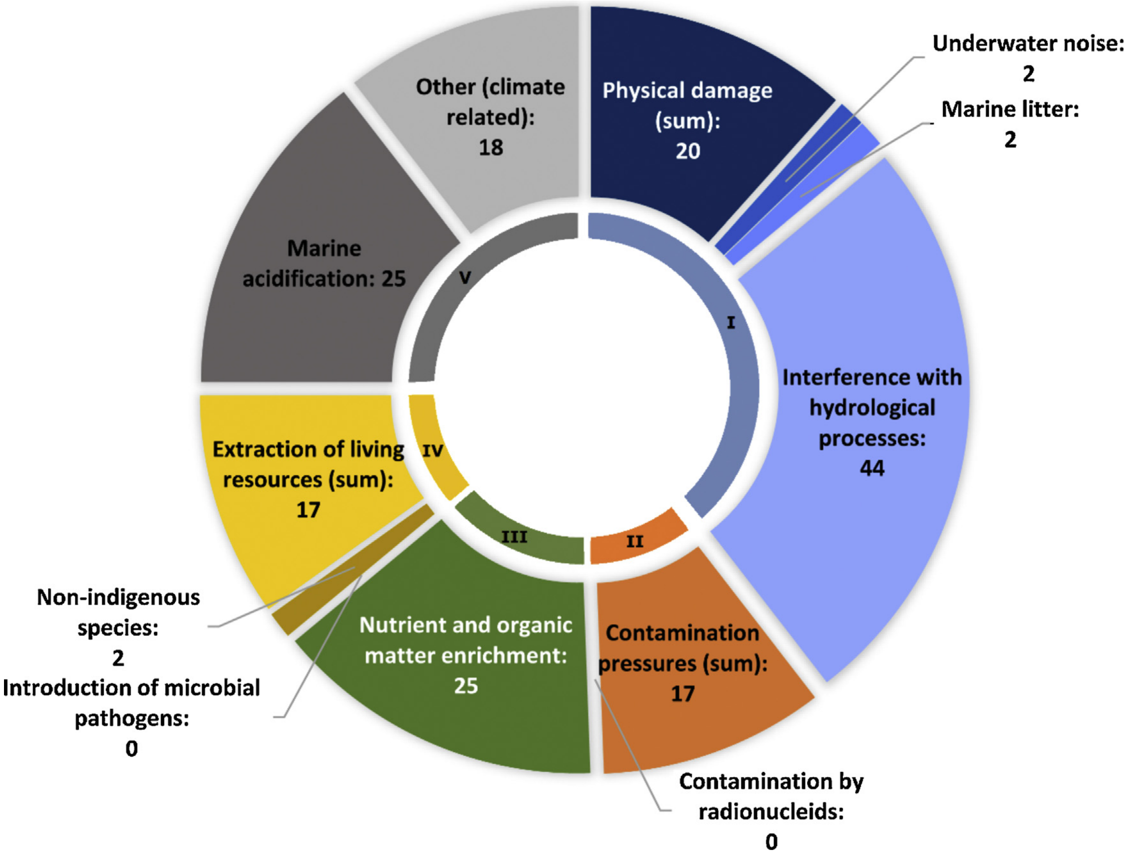

Fig. 4. Capability of models in the DEVOTES catalogue to address pressures outlined in the Marine Strategy Framework Directive (Annex III; see S3); the number of models available per major type of pressure is indicated: I – physical disturbance type of pressures; II – contamination by hazardous substances; III – nutrient and organic matter enrichment; IV – biological disturbance; and V – climate related pressures.

parameters relating to zooplankton. Only two of them are pressure indicators: 'Population size (as biomass) of a non-indigenous species – *Mnemiopsis leidyi*' and 'Habitat condition as water transparency'.

'*Non-indigenous species*' were only addressed by two models, the BSEM physical (hydrodynamic)–biogeochemical coupled model and the EwE food web model, through the indicators 'Population size (as biomass) of a non-indigenous species – *Mnemiopsis leidyi*' and 'Alien shrimps biomass", respectively.

A total of 17 models, essentially food web and coupled models, have been applied in the context of '*Selective extraction of living resources*' (encompassing extraction of fish and shellfish through direct catch, by-catch and discards and extraction of maërl, seaweed harvesting and the extraction of any other species) (Fig. 4). Overall, 143 indicators were associated collectively with these models (S1). The majority of these were indicators of biomass, being associated with the EwE model. Only one pressure indicator was reported ('1/(landings/biomass) – Inverse fishing pressure') from EwE.

'*Marine acidification (pH change)*' was currently addressed by 25 models (Fig. 4), essentially coupled models (both E2E and hydrodynamic–biogeochemical) with a dynamic or spatial-dynamic nature, but also multispecies, bio-optical models, and biogeochemical models. A total of 56 indicators capable of assessing the effects of this pressure, relating also to climate change, could be derived by these models. These indicators are predominantly related to biomass of lower trophic groups and primary production.

Finally, other pressures not listed in the MSFD Annex III, related to climate and inter-annual meteorology, were also mentioned by the modellers, reporting 18 models that could provide 30 indicators responsive to such pressures. The majority were state indicators, such as low trophic groups biomass, but also some production, diversity or species life-history indicators. As pressure indicators, six physical–chemical proxies of climate pressures were mentioned (S1).

7. Gaps and development needs

This work summarises the current capabilities of the modelling community to provide information about indicators outlined in the MSFD, particularly on biodiversity, food webs, non-indigenous species and seafloor integrity. The cataloguing of models and their derived indicators presented in this study aim to help the planning and the implementation of objectives defined in the MSFD particularly in relation to which models and indicators exist and the missing components to support such policy. This is particularly important in the MSFD framework that requires the assessment of all European Seas in relation to their ecosystem status and pressures associated, and the establishment of environmental targets (through the use of indicators) to achieve GEnS by 2020.

Overall it was evident from the analysis of the model catalogue that some descriptors (and their requirements) within the MSFD (Table 4) are best assessed by modelling (e.g., D4 food webs), while other indicators are better assessed by "traditional" empirically derived ecological indices. For instance, many models potentially addressing D6 (seafloor integrity) lacked specific indicators of substrate type or seabed extent (Table 4) mainly because of their inability to express benthic habitat as some form of component. D2 (non-indigenous species) is currently poorly addressed by the models even though some of them would have the capability to provide useful indicators for this descriptor. Similarly indicators for D8 (contaminants), D9 (contaminants in food), D10 (marine litter), D11 (underwater noise) outlined by the European Commission (2010) are not currently addressed by any of the models reported here; however, these descriptors were not the target of our survey. Three indicators related to the four biodiversity related descriptors (D1, D2, D4, D6) had no model-derived indicator in the catalogue (Table 4):

- D1 Biodiversity/C3 Population condition.
  - o I2 Population genetic structure
- D2 Non-indigenous species/C2 Environmental impact of invasive non-indigenous species
  - o I1 Ratio between invasive non-indigenous species and native species
  - o I2 Impacts of non-indigenous invasive species at the level of (1) species, (2) habitats and (3) ecosystem.

With respect to the gaps addressed to pressures, the majority of models require further work to show how sensitive and specific to pressures they are. Underwater noise, marine litter and contamination by microbial pathogens are poorly addressed by existing models and those that have been reported to produce indicators that are sensitive to these pressures require further development. It is emphasised that this summary of model use does not reflect model adequacy, data quality or the overall quality and effectiveness of the monitoring and research programmes under which the models are applied.

Focusing on model features, two main gaps were identified that require further development: one related to the setting of targets, and the other to uncertainty associated with model results. Targets exist when objectives have been clearly identified and their translation into operational performance metrics agreed to, which involves a socio-political decision process that occurs independently of model-development. If the models have been developed independently of such processes, which is the case for most of the models listed in the study, targets for selected variables may not be available (despite the indicator being operational) reflecting the context in which they have been developed. Thus, because the models in the catalogue were not developed with the aim of supporting MSFD, and because the MSFD does not set clear targets or aims, it is not surprising that model developers often reported difficulties in setting targets and/or reference values for their models. Two main barriers were identified. First, the process of association of ecologically meaningful targets to model outputs (derived indicators) without a clear vision of where and what the model would be used for in a specific MSFD context. Second, the level of demand required by the targets: should thresholds and/or reference values reflect the good condition of the assessed component in isolation (for e.g., for each indicator used) or reflect a compromise between ecological integrity and the use of the marine environment, as implicit in the MSFD GEnS definition? The level at which GEnS should be defined, either at indicator or at the descriptor level, or even for all eleven descriptors together, will influence the way thresholds setting is perceived and established (Borja et al., 2013). This will ultimately affect the final assessment as discussed in depth in Claussen et al. (2011) and Borja et al. (2013). For the last point, it can be argued that there is not enough information at this stage for model developers to set meaningful targets for MSFD purpose. Therefore, threshold setting should be guided by clear objectives and end goals as achievable targets and these are not known at present.

In this context, several initiatives have been created to support and address, at least partly, most of the issues arise above; for example FP7 projects such as MEECE (completed) and DEVOTES (in progress) have been developed to explore the use of ecological models in assessing ecosystem status and in support of decision making and EU policy. More recently, MIDAS, a modelling inventory database with models currently in use by the European Commission, allows the assessment of how models are used and/or support impact assessments at EU level.

In addition, not all the models were able to address uncertainty; the majority lacked confidence intervals or an approach to evaluate uncertainty of the model outputs. Marine system models are indeed becoming increasingly complex and sophisticated, but far too little attention has been paid to model errors and the extent to which model outputs actually relate to ecosystem processes (Allen et al., 2007). Further developments on this would produce more robust assessments and forecasts and therefore more reliable indicators.

European geographical coverage is also very heterogeneous with several identified marine areas with enormous potential for improvement. Also certain habitats (e.g., ice-associated habitats or continental shelf sublittoral mud) and biodiversity components (e.g., microbes) are underrepresented in the modelling approaches presently in the catalogue. As mentioned before, this is mostly due to the emphasis that has been given historically to particular flag species, commercially important organisms or particularly endangered species/habitats. However, the relative importance of modelling such components can change according to the system studied. Current gaps should, therefore, be evaluated on a regional scale basis. Looking at current modelling gaps from a regional seas perspective, one of the limitations observed is the focus of the participants in the review process that may have shown a bias in the selection of models/model types. An example of this is Atlantis, a E2E model not currently operational in Europe, or the Bioenergetics and Dynamic Energy Budget (DEB) type of models currently not included in this catalogue but widely used in the regions covered by DEVOTES (Teal et al., 2012). These models describe how individuals acquire and utilise energy, in addition to how physiological performance is influenced by environmental variables, and can serve as a link between different levels of biological organisation (Nisbet et al., 2000, 2012). Considering them would thus increase the potential to address MSFD Descriptors/Indicators that focus particularly on properties at the individual level and physiological level, usually responding to pressures whose impacts operate or can primarily be detected at that scale (e.g., biological disturbance, such as food resource depletion; contamination; or effects of climate change, namely marine acidification). In addition, regional model runs identified the need to improve the existing models with regards to species diversity (e.g., adding certain species or refining subgroups), spatial resolution for selected species and for better description of the direct effect of anthropogenic pressures on ecosystems. Model response towards the impact of certain pressures still requires further testing.

Relevance of certain pressures differs across regional marine areas. Broadly speaking, those that could benefit from further research are for physical damage to marine habitats, underwater noise, marine litter, contamination by radio-nuclides, introduction of microbial pathogens, extraction of species (maërl, seaweed and others), marine acidification, acute pollution events and nutrient and organic matter enrichment.

Data availability is also a constraint. This could partially explain why the number of 'under development' indicators is still quite high suggesting that this requires particular efforts to increase the potential to address MSFD descriptors. To assess the environmental status descriptors adequately, the gap analysis conducted here highlights that further refining of the current models and their associated indicators as well as the adoption of new modelling techniques are needed.

The information (data) needs for model development and the results provided (outputs), is very heterogeneous. Two main modelling approaches can be distinguished: statistical (i.e. SDMs) and mechanistic (i.e. multispecies and biogeochemical models)

(Kendall et al., 1999). In general terms, spatial mechanistic models require large amounts of computational resources, and can only be applied when demographical, physiological, and life traits of species are well known. On the other hand, statistical (i.e. SDMs) modelling studies often neglect dispersal-limitation and advection, although they can play an important role on spatial distribution, while spatial dynamical models minimise the role of environmental factors on species distribution (Robinson et al., 2011). Taking a balanced view between the importance of dispersal-limitation and of niche partitioning on the species spatial distribution, we suggest that research efforts should focus on integrating the two mechanisms into ecological modelling.

Finally, in some instances, the gaps identified may not need to be filled. This is the case for component(s) and/or pressure(s) considered 'un-manageable' (e.g., the target for zooplankton biomass or distribution). However, given the complex interactions within ecosystems, management of some components may have unexpected effects on 'unmanageable' components. Thus, ecological models should be developed to encompass all components, to the extent that they are known, wherever possible.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2015.05.037

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