Numerical Models for Monitoring and Forecasting Ocean Ecosystems: a short description of present status

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Abstract. Understanding and managing marine ecosystems under potential stress from human activities or climate change requires the development of models with different degree of sophistication in order to be capable of predicting changes in living components in relation to human pressures and environmental variables. Recent advances in ecosystem modelling are the focus of this paper, which reviews numerical approaches to analyse the characteristics of marine conditions in terms of typical units, i.e., individuals, populations, communities and ecosystems. It specifically examines the current classification of numerical models of increasing complexity – from individuals and population and stock assessment models to models representing the whole ecosystem by covering all trophic levels – and presents examples and their operational maturity and readiness, finally demonstrating their use for supporting marine resource management, conservation, planning and mitigation actions.

1 Introduction

Understanding and managing marine ecosystems under potential stress from human activities and climate change requires the development of modelling tools able to monitor and forecast ocean ecosystem dynamics, from physics to fish (De Young et al., 2004). The challenge is to relate processes occurring at individual, population or community level with environmental variables, i.e., to connect the dynamics of marine ecosystem with the quite well established physical and biogeochemical products that exists for the ocean (Fennel et al., 2022). A large variety of numerical ecosystem models have been developed to predict the growth and dynamics of individuals and populations of marine resources. According to the scope the approaches are very diverse ranging from single- to multi-species and might include the effects of various environmental changes and human impacts (Hollowed et al., 2013; Nielsen et al., 2018).

To illustrate approaches that have the potential to become the next generation operational tools for ocean ecosystem forecast, this paper provides a structured synthesis of models applied to marine higher trophic levels (i.e., from zooplankton to fish and top predators) that can be connected with lower trophic level models (physics and biogeochemistry).

A comprehensive analysis is challenging, but models can be mapped in terms of their main scope and distinguishing approaches incorporating age structure, environmental factors, represent trophic interactions, and spatial structure (Hollowed et al., 2000). Based on the above characteristics, numerical models for marine ecosystems can be divided into six broad classes:

- Bioenergetic models representing the processes related to growth, respiration, excretion of an individual;
- population and fisheries models (typically for single species without trophic interactions and possibly age-structured);
- connectivity models (considering propagules dispersal, larval cycle, spatial structures, and environmental factors);
- species distribution models (statistical models based on representation of spatial environmental variables and biota);
- minimal realistic models (typically age-structured, representing a few species with trophic interactions);
- whole ecosystem models (typically covering all trophic levels and based on trophic interactions, which may include size structure and spatial variation).

These six classes of models are reviewed in the sections below, considering available syntheses and reviews (e.g., Plaganyi, 2007; Cowen et al., 2009; Stock et al., 2011; Hilborn and Walters, 2013; Itoh et al., 2018; Nielsen et al., 2018; Rose et al., 2024).The work does not pretend to be exhaustive and readers are referred to original reviews that are providing in depth analyses of each class of models. It aims to provide a synthetic integration across different classes, with examples provided to illustrate their application in operational coupling with lower trophic level models. For this purpose, readiness and maturity of each model was subjectively elaborated based on its current application. The maturity of each example was assessed based on the availability of code, documentation, test cases, routines for assessing model performances, diagnostics, and is used by a community of developers that can provide support, updates and advancement. Stock assessment models routinely applied for fisheries management, for example, were considered more mature because the code is publicly available and documented and input and output test cases are developed and accessible. Readiness for operational purposes was defined based on existing knowledge about possible connection of the model example to physical and biogeochemical spatio-temporal models. Existence of such applications, even if scarce, might show the difficulties in connecting (one-way or two-way) with low trophic level models. Operational readiness may be regarded as more tentative and less precise, owing to the challenges in establishing a clearly objective definition, particularly in light of its potentially limited application.

For each class of models some examples are shown in Table 1., including their characteristics in terms of typical units, elemental structure, number of species typically represented, eventual trophic interactions. The table also contains synthetic information on primary model focus and main output, as well as maturity and readiness for operational purposes.

2 Bioenergetic models

Traditional bioenergetic models describe energy intake from feeding and its allocation to maintenance, activity, growth, reproduction, and excretion (for a review see: Rose et al., 2024). Bioenergetic models are typically used for representing the growth of the individual and can account for external oceanographic conditions influencing uptakes, such as light, nutrients and temperature for autotrophs (Bocci et al., 1997) or food availability and temperature for heterotrophs (Libralato and

Solidoro, 2009), while losses are usually related to temperature and internal conditions (Koojiman, 2010). Bioenergetic models can also consider explicitly the gonadic development and egg release (Pastres et al., 2000). Because of these characteristics, bioenergetic models, other than providing realistic individual-level response to environmental conditions, permit to project responses at the population and food web levels and can support other classes of approaches (Rose et al., 2024).

A widely used bioenergetic approach for fish and invertebrates is represented by the Dynamic Energy Budget (DEB) which is characterized by an explicit representation of energy dynamics into somatic, gonadic and storage tissues (Koojiman, 2010). Although, the storage is challenging to be measured empirically (Pirotta et al., 2022), it allows representation of delayed use of energy in the individual development resulting in improved generality of the approach (Koojiman, 2010; Nisbet et al., 2012). Thus DEB has been developed into a theory for scaling the parameters for all life cycles of the individual (from eggs to larvae to juveniles and adults), provides setting parameters for a large number of marine species (see also https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/) and is well documented (Nisbet et al., 2012; Koojiman, 2020). Thus DEB is considered of high maturity for being used routinely and adapted to operational applications, and because it is seldom connected to spatiotemporal physical and biogeochemical models the readiness is considered of intermediate level (Table 1).

3 Population and fisheries models

Various types of numerical models of single populations are used worldwide to support fisheries management by determining the population at sea and the current status of exploited marine populations, thus providing insight for management in a process called stock assessment (for a review see Hilborn and Walters, 2013). Stock assessment models typically represent the biomass or abundance of one species (Table 1), are routinely used by management agencies, and include probability models to incorporate various sources of observational data (Maunder and Punt, 2013).

The Stochastic surplus Production model in Continuous Time (SPiCT), for example, provides estimates of exploitable biomass and fishing mortality at any point in time from catch and survey data collected at arbitrary and possibly irregular intervals (Pedersen and Berg, 2017). SPiCT is available as an R package (R Core Team 2015) in the online GitHub repository: https://github.com/mawp/spict.

More sophisticated approaches use catch by age or size classes (catch-at-age or catch-at-length models; Maunder and Punt, 2013) to reconstruct the cohorts assuming natural mortality for each class, and considering information on species growth, fecundity, and fisheries selectivity (Methot and Wetzel, 2013). Stock synthesis (SS3; Anderson et al., 2014) is an example of catch-at-age model that can incorporate age or length composition information from surveys, abundance indices, multi-gear effort, selectivity, and spatial data in the most recent and advanced applications (e.g., Punt, 2019; Privitera-Johnson et al., 2022). Projections from stock assessment models are generally made for annual to decadal time periods and SS3 provides estimates for biological reference points for management decisions (indicators based on maximum sustainable yield; Hilborn and Walters, 2013). As for many stock assessment fisheries models, SS3 is routinely used in formal assessments, well documented and easily accessible (https://github.com/nmfs-ost/ss3-source-code), thus it has a very high degree of maturity. Nevertheless, it is not spatially explicit and it does not consider explicitly oceanographic forcings and might be considered of intermediate readiness for operational oceanographic applications (Table 1).

4 Connectivity models

The distribution and survival of small eggs and larvae of marine fishes and invertebrates, as well as propagules of algae and seagrass' seeds are advected and thus are strongly influenced by currents, which can disperse individuals both near spawning sites and in distant areas (Cowen et al., 2007). Therefore, biophysical dispersal (advection, diffusion, and migratory behaviour of organisms) is fundamental to explaining marine population dynamics and connectivity (for a review see Cowen et al., 2009). Connectivity models are used to quantitatively integrate the large spatial and temporal variability of oceanographic processes (physical connectivity) with processes inherent in the biology of marine organisms (life history traits) to investigate connectivity between and within populations and across larval stages (Gawarkiewicz et al., 2007; Melaku Canu et al., 2021). Connectivity models such as Larval TRANSport Lagrangian model (LTRANS, North et al., 2008) typically uses offline physical parameters (velocity, density, temperature, and salinity) obtained from hydrodynamic models and estimate the distribution of organisms. The advection–diffusion–reaction equation is typically used for biomass distribution (e.g., Sibert et al., 1999; Faugeras and Maury, 2005), while Lagrangian approaches are used to track particles and thus distribute individuals (e.g., Laurent et al., 2020). These approaches consider life history traits such as growth, mortality and the behavior of target organisms in terms of seasonal variability, spawning sites, vertical movement and settlement preferences (Melaku Canu et al., 2021; Paris et al., 2013; Lett et al., 2008). LTRANS is frequently applied and well documented, and the code is available at (https://github.com/LTRANS/LTRANSv.2b) designating it as intermediate level of maturity. It is coupled offline with hydrodynamic models, and can incorporate several biological features (North et al., 2008) placing its operational readiness at an intermediate level (Table 1).

5 Species distribution models

Species distribution models (SDM, also called habitat suitability models) are statistical models that predict the occurrence, abundance, or biomass of organisms using geoposition, biotic and environmental data (for a review see: Elith and Leathwick, 2009). Particularly useful when applied to spatio-temporal scientific surveys of species abundance, these approaches can also exploit opportunistic biological data (e.g., www.obis.org; www.gbif.org). SDMs are implemented using various statistical approaches (Maravelias et al., 2003; Melo-Merino et al., 2020; Brodie et al., 2020), machine learning, artificial neural networks methods (Catucci et al., 2025) and maximum entropy (Jones et al., 2012; Pittman and Brown, 2011; Reiss et al., 2011). The inclusion of physical and biogeochemical oceanographic covariates, which can have direct and indirect effects on species distributions, can improve the capabilities of SDMs to explain observed biotic data compared to using only geopositional variables (Panzeri et al., 2021; Thorson et al., 2015). Recent advances include combining the approaches into an ensemble (Jones et al., 2012; Panzeri et al., 2024) and including multiple species as covariates into the so called Joint-Species Distribution Models (JSDM, Pollock et al., 2015; Thorson et al., 2016). The SDMs are increasingly being used to describe current and future distributions of exploited and endangered species, identify hotspots, map essential fish habitat, support conservation development, and feed other ecosystem models (Jones et al., 2012; Colloca et al., 2015; Grüss et al., 2014; Dolder et al., 2018). The Dynamic Bioclimate Envelope Model (DBEM) estimates species distributions based on environmental preferences and considers population dynamics and dispersal (Cheung et al., 2009). The DBEM makes predictions of future envelopes using physical and biogeochemical data from oceanographic models and considers the response of organisms to natural/anthropogenic environmental changes such as growth, mortality, larval dispersal, and migration (Cheung et al., 2013). In general SDMs are widely applied, well documented and available (see for example: https://github.com/helixcn/sdm_r_packages) thus have an intermediate level of maturity but giving their direct integration with physical-biogeochemical models they have a good readiness level for operational use (Table 1).

6 Minimal realistic models

Dynamic multispecies models or Minimal Realistic Models (MRM) are approaches that represent a limited number of species (usually less than 10 species) that have important interactions with a target species (for a review see Plaganyi, 2007). MRMs often represent an evolution of single species stock assessment models: for example, GADGET (Globally applicable Area-Disaggregated General Ecosystem Toolbox) is an extension of stock synthesis in the multispecies framework, where populations can be partitioned by species, size classes, age groups, areas, and time steps (Andonegi et al., 2011). In particular, GADGET is flexible, allowing easy addition/replacement of alternative model components for biological processes such as growth, maturation, and predator-prey interactions representing some species in age classes. GADGET provides estimates of population dynamics under fisheries and biological interactions with the ability to use different growth functions and fitness functions (Plaganyi, 2007). Although well documented (see https://gadget-framework.github.io/gadget2/userguide/) its fitting is quite complex and thus has few applications: for these reasons maturity is considered intermediate and readiness for operational purposes is low because of lack of interactions with physical and biogeochemical models (Table 1).
An example of minimum realistic model is the Spatial Environmental POpulation Dynamics Model (SEAPODYM), which is a two-dimensional coupled physical-biological model originally developed for tropical tuna in the Pacific (Lehodey et al., 2003). SEAPODYM includes an age-structured population model for top predators and a movement model based on a diffusion-advection equation modelled as a function of habitat quality (sea surface temperature, ocean currents, and primary production) obtained from oceanographic models and satellites (Lehodey et al., 2015; Senina et al., 2020). SEAPODYM is well documented and already used for operational global projections (https://github.com/PacificCommunity/seapodym-codebase) thus can be considered to have a high degree of maturity and readiness for operational purposes (Table 1).

7 Whole ecosystem models

Whole ecosystem models (WEM) are designed to represent all trophic levels in an ecosystem, from primary producers to top predators and take advantage of data collected in different disciplines (Agnetta et al., 2022). The main distinguishing feature between the different WEM is the way in which the ecosystem is described: i) through compartments representing species of groups of species (Christensen and Walters, 2004; Fulton et al., 2011); ii) through compartments that represent size-structured communities, typically benthic and pelagic communities (Shin and Cury, 2004; Travers et al., 2010); iii) in a mixture of size-structured and trophic communities(Maury, 2010); iv) using dynamic spectra of trophic levels (e.g., Gashe and Gascuel, 2013). All these models are based on biomass and consider rules such as biomass conservation (Table 1; for a review see Plaganyi, 2007).

Ecopath with Ecosim (EwE; Christensen and Walters, 2004) is the most widely used WEM, freely available (www.ecopath.org) and has a flexible structure. It represents a suite of models developed in more than 30 years for the whole ecosystem description. EwE has been used to analyze past and future impacts of fisheries, nutrient inputs, invasive species, and climate change (e.g., Heymans et al., 2014; Libralato et al., 2015; Serpetti et al., 2017; Piroddi et al., 2021). It consists of three different interconnected main modules, i) a static mass-balanced ecosystem network (Ecopath, Christensen and Pauly, 1992), ii) a temporally dynamic simulation module (Ecosim, Walters et al., 2000), and iii) a spatially and temporally dynamic module (Ecospace, Walters et al., 1999). EwE contains many additional modules for calibration, uncertainty analysis, calculation of indicators, and simulation of pollutant dynamics (Steenbeek et al., 2016). Recent advances allow the direct embedding of two-dimensional monthly results from oceanographic physical-biogeochemical models (Steenbeek et al., 2013). EwE can be considered an approach of high maturity and intermediate degree of readiness for operational applications (Table 1). A large set of WEM models (Table 1) are used increasingly to address the need for holistic ecosystem approaches, and their framework is often applied to answer strategic medium-term questions related to management strategies, fisheries issues, and climate or environmental change (e.g., Tittensor et al., 2021). Notably, WEM can be coupled with other classes of models (population dynamic, SDM, connectivity models), as well as with biogeochemical models, which is why most of the approaches in this class have a high to intermediate level of maturity and readiness (Table 1).

Conclusions

A wide range of models are used to represent ocean ecosystems at different level of organisations, including individuals, populations, communities and entire ecosystems. Although categorised into 6 classes for clarity, some modelling approaches are not confined to a single class. For instance, the DEB modelling approach is used to also represent the growth of individuals in Connectivity models and MRM classes (see for example Maury 2010). Conversely MICE ("Models of intermediate complexity for ecosystem assessment"; Plagányi et al., 2014) of the MRM class, are developed using different levels of detail for the species represented by combining for example age-structured and surplus production approaches (Morello et al., 2014).

These models have been developed for specific societal issues, i.e., effects of climate change, pollution, nutrient enrichment and fisheries.

The numerical approaches analysed here have characteristic spatio-temporal resolutions that are generally decreasing when moving from individual species models to whole ecosystem models (Table 1). Increased represented complexity with MRM and WEM classes result in a general improvement of realism at the cost of accuracy (generally declining from individual models to WEM). Overall, the first set of approaches (bioenergetic and population models) are more adapted for tactical analyses while especially the WEM are currently considered useful especially in strategic analyses (see Table 1). Although very few of the reviewed approaches are currently used operationally (i.e., SEAPODYM), many approaches are routinely applied for supporting management (e.g., fisheries stock assessment models). Most of the approaches reviewed have repository for documentation, code and testing cases, thus have high degree of maturity (Table 1). Conversely, approaches under the MRM class are not widely applied, are often quite complex to fit and therefore were categorised to be at a poor level of readiness for operational purposes (Table 1). Nevertheless, all the tools have some degree of coupling (mainly off-line) with physical and biogeochemical variables, thus have a great potential for becoming operational, and to be used for analysing ecosystem dynamics and scenarios, which can be useful for a very wide range of issues and management actions that could be eventually prioritized.

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

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Table 1: Main characteristics of some widely used numerical models of marine biological resources divided into the six classes

	Bioenergetic models												**Rose et al., 2024**
Acronym	**Model**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use**	**Physical/biogeochemical processes**	**Repository (if open access)**	**Reference**
DEB	Dynamic Energy Budget	Individual	Individual weight (gww, gC or others) or length	day	No	1	No	growth	High	Good	Yes used as forcings (temperature, light, food, nutrients)	https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/	Koojiman, 2020
	Population and fisheries models												**Hilborn and Walters, 2013**
Acronym	**Model**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use**	**Physical/biogeochemical processes**	**Repository (if open access)**	
SPICT	Stochastic surplus Production model In Continuous Time	Surplus prodution	Biomass	Year	No	1	No	Biological reference points for fisheries	High	Poor	No	https://github.com/mawp/spict.	Pedersen and Berg, 2017
CMSY	Catches at Maximum sustainable Yield	Surplus prodution	(tonn)	Year	No	1	No	Biological reference points for fisheries	Intermediate	Poor	No	https://github.com/SISTA16/cmsy	Froese et al., 2023
A4a	All for all	Catch-at-age	Biomass (tonn)	Year	No	1	No	Biological reference points for fisheries	Intermediate	Intermediate	No	https://github.com/a4a	Jardim et al., 2014
SS3	Stock Synthesis	Catch-at-age	Number of Individuals; biomass (ton)	Year	Potentially yes	1	No	Biological reference points for fisheries	High	Intermediate	Potentially yes	https://github.com/nmfs-ost/ss3-source-code	Anderson et al., 2014
VPA	Virtual population analysis	Catch-at-age	Number of Individuals; biomass (ton)	Year	no	1	No	Biological reference points for fisheries	Poor	Poor	No	https://noaa-fisheries-integrated-toolbox.github.io/VPA	Gislason, 1999
	Connectivity models												**Cowen et al., 2009**
Acronym	**Model**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use**	**Physical/biogeochemical processes**	**Repository (if open access)**	
LTRANS	Lagrangian Transport	Agents (super individuals)	Number of individuals	days	Yes	Typically one species	No	Distribution of species and connectivity among sites	Intermediate	Intermediate	Yes (physical processes)	https://github.com/LTRANS/LTRANSv.2b	North et al., 2008
Ichthyop	Lagrangian tool for simulating ichthyoplankton dynamics	Individuals (early life stages)	Number of individuals	days	Yes	Typically one species	No	Study effects of physical and biological factors on ichthyoplankton dynamics	Intermediate	Intermediate	Yes (physical processes)	https://ichthyop.org/	Lett et al., 2008
IBM/ABM	Individual-based and Agent Based Models	Individual	Biomass	days	Yes	Typically a few species	Efficient predator	Ecosystem effects on target population and connectivity	Poor	Poor (computationally complex)	Yes	NA	Rose et al., 2015

	Species Distribution Models												**Elith and Leathwick, 2009**
Acronym	**Model**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use**	**Physical/biogeochemical processes**	**Repository (if open access)**	
Enseamble of SDM	Ensamble of Species Distribution models	Species adundance, presence or biomass	Number of individuals or weight per unit surface or presence/absence	Month, year, climatology	Yes	1	No	Species distribution; essential fish habitats	Good	Good	Environmental factors can be included	https://github.com/helixcn/sdm_r_packages	Panzeri et al., 2024
Joint-SDM	Joint Species Distribution models	Species adundance, presence or biomass	Number of individuals or weight per unit surface	Month, year	Yes	A few species	implicit	Distribution of target species	Intermediate	Poor (computationally intensive)	Environmental factors can be included	https://github.com/James-Thorson/spatial_DFA	Thorson et al., 2016
DEBM	Dynamic Bioclimate Envelope Model	Species biomass	biomass	year	Yes	Several species	No	Distribution of multiple species	Intermediate	Good	Yes included for developing the bioenvelope	NA	Cheung et al., 2013
	Minimal Realistic models												**Plagányi 2007**
Acronym	**Model**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use**	**Physical/biogeochemical processes**	**Repository (if open access)**	
GADGET	Globally applicable Area Disaggregated General Ecosystem Toolbox	Population in age structure	Biomass derived from population size structure	Year	Yes, can be included	Typically 3-4 species	Yes, suitability-based, flexible	Ecosystem effects on target population; yearly biomass	Intermediate	low	Can be coupled with physical-biogeochemical model	https://gadget-framework.github.io/gadget2/userguide/	Andonegi et al., 2011
MSVPA and MSFOR	Multi-species Virtual population Analysis and multi-species Forecasting Model	Populations in age structure	Numbers at age; Biomass	Year	No	Typically 3-4 species	Yes; Suitability-based; Efficient predator	Ecosystem effects on target population; yearly biomass	Poor	Poor (seldom applied)	Not usually included	https://noaa-fisheries-integrated-toolbox.github.io/MSVPA_X2	Gislason, 1999
MICE	Model of Intermediate Complexity for Ecosystem assessments	Populations in surplus production and age structure	Numbers at age, Biomass	Year	No	Typically 6-7 species	Efficient predator	Dynamics of focal species and their predators or preys	Difficult to establish: programmed on purpose	Poor (only few applications)	Environmental effects can be included	NA	Plagányi et al., 2014
SEAPODYM	Spatial Ecosystem, and population Dynamics Model	Populations in age structure	Biomass	Year	Yes	Typically 3-4 species	Efficient predator	Ecosystem effects on target population	High	High (already applied for top predators, i.e., tunas)	Can be coupled with physical-biogeochemical model	https://github.com/PacificCommunity/seapodym-codebase	Lehodey et al., 2015
ERSEM II	Commission for the Conservation of Antarctic Marine Living Resources	Functional group approach	Nutrient	month	Yes	Limited number of HTL groups	Type II	Effects in both directions	Intermediate	Too complex	Yes, detailed	https://github.com/pmlmodelling/ersem	Butenschön et al., 2018
Apecosm	Apex Predators ECOSystem Model	Size spectra approach	Biomass	month	Yes	Few species	Few top predators	Top predator group dynamics	Poor (few applications)	Poor (model complexity)	Tes, included	https://github.com/apecosm/python-apecosm	Maury, 2010
	Whole Ecosystem Models												**Plagányi 2007**
Acronym	**Model**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use**	**Physical/biogeochemical processes**	**Repository (if open access)**	

ATLANTIS	Atlantis	Functional group approach; Populations in age structure	Nutrient	month	Yes	Can be a very large number; typically order 40	Flexible, Type II, type III or other	Effects of ecosystem and fisheries in both directions; yearly outputs	High	poor (model complexity)	Yes, detailed	https://github.com/runatlantis/atlantis	Fulton et al., 2011
EwE	Ecopath with Ecosim	Functional group approach; Populations also in age structure	Biomass, Nutrient	month	Yes (ECOSPACE)	Can be a very large number; typically order 40	Foraging arena, flexible approach	Effects of ecosystem and fisheries in both directions; yearly outputs	High	Poor (model complexity)	Included as off-line coupling	https://ecopath.org/	Christensen and Walters, 2004
OSMOSE	Object-oriented Simulator of marine ecosystem Exploitation	Size spectra approach	Biomass at different levels of aggregation	year	Yes	Large number of species	Efficient predator but can starve	Multispecies dynamics	Intermediate	Intermediate (model complexity)	Included as off-line coupling	https://osmose-model.org/	Shin and Cury, 2004;
FEISTY	FishErIes Size and functional TYpe model	Size spectra approach	Biomass at different levels of aggregation	year	Yes	Large number of species	Flexible approach	Multispecies dynamics	Intermediate	Intermediate	Included as off-line coupling	https://github.com/Kenhasteandersen/FEISTY	Blanchard et al., 2009