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

Simone Libralato[1]

[1]Istituto Nazionale di Oceanografia e di Geofisica Sperimentale - OGS, Department of Oceanography, Trieste, Italy

Correspondence to: Simone Libralato (slibralato@ogs.it)

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 ~~and~~ 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. ~~In particular, ~~I~~i~~t 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

~~In recent decades, a~~ 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~~ies~~ 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 ~~on marine biological resources~~ (Hollowed et al., 2013; Nielsen et al., 2018).

To illustrate ~~In order to shed light on~~ 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, ~~although~~ but models can be mapped in terms of their main scope and distinguishing approaches ~~that can~~ incorporating~~e~~ age structure, environmental factors, represent trophic interactions, and spatial structure (Hollowed et al., 2000~~; Plaganyi, 2007~~). 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 ~~stock assessment~~ 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, ~~with~~ 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 ~~five~~ classes of models are reviewed in the ~~following~~ sections below, considering ~~also~~ 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. ~~The work intends to synthetically bridge across classes and examples are provided to shed light on their usage for operational coupling with lower trophic level models.~~ For this purpose, readiness and maturity of each model was subjectively elaborated ~~on the basis of~~based on its current application. The m~~M~~aturity of each example ~~were~~was assessed ~~on the basis of~~ based on the availability of code, documentation, test cases, routines for assessing model performances, diagnostics, and is~~are~~ 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 ~~on the basis of~~based on existing knowledge about~~on~~ possible connection of the model example to physical and biogeochemical spatio-temporal models. Existence of such applications, even if scarce, might ~~shed light on the~~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. ~~Readiness for operational purposes might be considered more tentative and less precise, because it is more difficult to define in a very objective way also for the potentially very sparse application.~~

For each class of models some examples are ~~reported~~ shown in Table 1., including~~and~~ their characteristics in terms of typical units, elemental structure, number of species typically represented, ~~representation of~~ eventual trophic interactions ~~are reported in Table 1~~. The table~~It~~ also contains synthetic information on primary model focus and main output, as well as ~~if each model is~~ maturity and readiness for operational ~~or not~~ 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). ~~A bioenergetic model is any mechanicistic model describing how individuals take energy from the environment and allocate it to different processes (Kooijman, 2010; Sibly et al., 2013).~~ Bioenergetic models are typically used for representing the growth of the individual~~, while accounting for respirations, excretions and other losses. Energy intake can be a model input or output, depending on whether it's modeled dynamically or derived from energy requirements (Pirotta et al., 2022). Acquisition and allocation can vary based on the individual's state and environmental conditions (e.g., Libralato and Solidoro, 2009; Nisbet et al., 2012)~~

~~Indeed, bioenergetic models~~ and can account ~~of~~ for external oceanographic conditions influencing uptakes, such as light, nutrients and temperature for autotrophs (~~e.g.,~~ Bocci et al., 1997) or food availability and temperature for heterotrophs (~~e.g.,~~ 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~~s~~ to project responses at the population and food web levels and can support other classes of approaches (Rose et al., 2024).

~~Traditional bioenergetic models describe energy intake from feeding and its allocation to maintenance, activity, growth, reproduction, and excretion. These models are advantageous due to their clear empirical interpretation and measurable units but tend to be parameter-heavy and difficult to generalize across species.~~ A widely used bioenergetic approach for fish and invertebrates is represented by the Dynamic Energy Budget (DEB~~, Koojiman, 2010~~) which is characterized by an explicit representation of energy dynamics into somatic, gonadic and storage tissues (Koojiman, 2010)~~. Dynamic Energy Budget (DEB) theory offers a more general approach by using mass-energy balance principles to link sub-organismal processes with overall organismal performance (Koojiman, 2010; Nisbet et al., 2012)~~. ~~However, this generality leads to abstract concepts that are more challenging to measure empirically (Pirotta et al., 2022).~~ Although, ~~T~~the ~~presence of the~~ storage ~~in DEB~~is challenging to be measured empirically (Pirotta et al., 2022), it allows ~~allow~~ 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)~~ and~~, 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).~~, thus it has a maturity for being used routinely and adapted to operational applications.~~

3 Population and ~~stock assessment~~ 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). ~~Such s~~Stock assessment models typically represent the biomass or abundance of one ~~individual~~ species (Table 1), are routinely used by management agencies, and include probability models to incorporate various sources of observational data (Maunder and Punt, 2013). ~~In cases where stock assessments are based on limited observations, i.e., no catch by age or size, surplus production models are used. The general underlying assumption of these models is a theta-logistic function for the evolution of biomass (B; but it can also be applied to the number of individuals) over time:~~

$$\frac{dB}{dt} = \frac{r}{n-1} B_t \left(1 - \left[\frac{B_t}{K}\right]^{\Theta-1}\right) - F_t B_t \quad (Eq.1)$$

~~where F is the fishing mortality, so $F_t B_t$ corresponds to the catches Ct, while r is the population growth rate, and K is the capabilities of the system to support the population (through living space, habitat, food, etc.), and generally called as carrying capacity. The parameter Θ allows generalization of the equation (in the case of Θ=2, the classical logistic curve is obtained). Several packages use the surplus production model as principal approach, are used routinely to perform stock assessment and are including several useful diagnostics. Among them the most used are the CMSY (Froese et al., 2023) and the SPiCT (Pedersen and Berg, 2017) models. CMSY uses a time series of catch data and fishing effort to estimate parameters, reconstruct biomass and establish reference points using a Bayesian approach (Froese et al., 2023).~~ 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). ~~The model allows the inclusion of prior distributions for parameters that are difficult to estimate such as growth rate and carrying capacity.~~ SPiCT is available as an R package (R Core Team 2015) in the online GitHub repository: https://github.com/mawp/spict. ~~Surplus production models are simplistic representation of the population that is lumped with no size and/or age details.~~ More sophisticated approaches ~~(such as SS3, a4a, XSA, etc.) are used when~~ use catch ~~data~~ by age or size classes ~~are available for the exploited population~~ (catch-at-age or catch-at-length models; Maunder and Punt, 2013)~~. These stock assessment models reconstruct the number of individuals in~~ to reconstruct the cohorts ~~based on catch and~~ assuming natural mortality for each class ~~by age class~~, ~~as well as~~ and considering information on species growth, fecundity, and fisheries selectivity (Methot and Wetzel, 2013). ~~The basic dynamics are described by the number of individuals N at time t and age a, as in the following:~~

$$N = R_t + \left(N_{t-1,a=1} e^{-\frac{M}{2}} - C_{t-1,a=1}\right) e^{-\frac{M}{2}} + \left(N_{t-1,a=2} e^{-\frac{M}{2}} - C_{t-1,a=2}\right) e^{-\frac{M}{2}} + \cdots \left(N_{t-1,x-1} e^{-\frac{M}{2}} - C_{t-1,x-1}\right) e^{-\frac{M}{2}} + \left(N_{t-1,x} e^{-\frac{M}{2}} - C_{t-1,x}\right) e^{-\frac{M}{2}} \quad (Eq.2)$$

~~where each year the population comprises all age classes from the new juvenile individuals entering the population as recruits the same year (R, age 0), all age classes a, from 1 up to the oldest age modelled (age x) surviving from the year before. The number of individuals are decreasing through time on the basis of catches C at age and time, and assuming instantaneous natural mortality M.~~

~~Typically, these models report juvenile recruitment R as a function of a combination of fecundity by age class estimated from data (Stock et al., 2011). This class of models includes, for example, the a4a tool (assessment for all, Jadim et al., 2014), a modeling framework for fitting statistical age-structured fishery models using nonlinear statistical submodels. The submodels can include linear functions of age and year, smoothing splines with fixed degrees of freedom that vary with age and/or year and environmental indicators as covariates. The tool a4a is implemented in R Fishery Library and includes the optimization procedure.~~ Stock synthesis (SS3; Anderson et al., 2014) is ~~the most~~ an example ~~widely used~~ of catch-at-age ~~stock assessment~~ 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). ~~In all cases, p~~Projections ~~of~~ from stock assessment models are generally made for annual to decadal time periods and ~~. Catch or effort limitation scenarios can be used to~~ 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, ~~Although in most cases,~~SS3 ~~stock assessment models are~~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 ~~they are routinely used in formal assessments for management~~ and might be considered of intermediate readiness ~~as ready~~ 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 ~~behavior~~behaviour of organisms) is fundamental to explaining marine population dynamics and connectivity (for a review see Cowen et al., 2009). ~~Numerical~~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 also~~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 ~~take into account~~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). ~~: since in most of the cases living organisms have negligible influences on physical oceanographic processes parameters, modeling the biophysical~~ LTRANS is frequently applied and well documented~~, applied~~ and the code is available at (https://github.com/LTRANS/LTRANSv.2b) ~~making~~designating it as~~of~~ intermediate level of maturity. It is coupled ~~dispersion~~ offline ~~from the~~with hydrodynamic models ~~is considered a reliable strategy also considering time evolutions~~, and can ~~include~~incorporate several biological features (North et al., 2008) ~~that makes~~placing its operational readiness ~~for operational purposes of~~ at an intermediate level (Table 1). ~~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 take into account 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 [e.g., Melaku Canu et al., 2021; Paris et al., 2013; Lett et al., 2008]. Connected with oceanographic variables and spatially explicit these models however, appear less mature for operational applications.~~

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~~Brodie et al., 2020~~). Particularly useful when applied to ~~standardized,~~ spatio-temporal scientific ~~monitoring and~~ surveys of ~~biotic data~~species abundance, these approaches can also exploit ~~publicly available~~ opportunistic biological datasets~~sets~~ (e.g., ~~OBIS,~~ www.obis.org; ~~GBIF,~~ www.gbif.org). SDMs are implemented using various statistical approaches ~~approaches, including linear models (LM), generalized linear models (GLM), generalized additive models (GAM)~~ (~~Melo-Merino et al., 2020;~~ Maravelias et al., 2003; Melo-Merino et al., 2020; Brodie et al., 2020), machine learning, artificial neural networks methods ~~such as random forest (RF, Breiman et al., 2018) or artificial neural networks (ANN),~~ (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~~se classes of~~ 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~~ also~~ 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)~~and although at the moment they are not used operationally, they can be easily implemented within an operational chain~~.

6 Minimal realistic models

Dynamic multispecies models or Minimal Realistic Models (MRM~~), Punt and Butterworth, 1995)~~ 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).~~ The~~ MRMs often represent an evolution of single species stock assessment models: for example, ~~Multispecies Virtual Population Analysis (MSVPA) is an extension of virtual population analysis (Gislason, 1999), while~~ 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 (~~e.g.,~~ 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 ~~technical~~ 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~~ve~~ 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).

~~MICE ("Models of intermediate complexity for ecosystem assessment"; Plagányi et al., 2014) are developed considering the specific problem and data availability. MICE represents a limited number of populations (usually 10) exposed to fisheries or anthropogenic interactions and includes ecological processes (Angelini et al., 2016). These models have different levels of detail for the species represented: MICE can simultaneously represent focal populations in age-structured classes, while others take a surplus production approach (Morello et al., 2014). MICE can be a fairly complex but flexible tool that overcomes the many complexities of whole ecosystem models and is useful for providing tactical advice for focal species management (Plagányi et al., 2014).~~ 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~~s~~ in the Pacific (Lehodey et al., 2003). SEAPODYM includes an age-structured population model for ~~tuna species~~ top predators and a movement model based on a diffusion-advection equation ~~such that swimming behavior is modeled~~modelled as a function of habitat quality (sea surface temperature~~ (SST)~~, ocean currents, and primary production) ~~predicted~~ obtained from oceanographic models and satellites (Lehodey et al., 2015~~). This model describes spatial structures that are essential to account for the~~

~~distribution of fishing effort, swimming behavior, and environmental variations typically determined by ocean circulation models or derived from 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 ~~. Thus, WEMs typically use a very large set of~~ data collected in~~from~~ different disciplines ~~a variety of disciplines, including results from oceanographic models and stock assessments~~ (~~e.g.,~~ 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 ~~in flexible compartments representing~~ species of groups of species (Christensen and Walters, 2004; Fulton et al., 2011)~~, ecologically meaningful groups of species, or size- and age-structured populations, such as Ecopath with Ecosim (hereafter EwE, Christensen and Walters, 2004) and ATLANTIS (Fulton et al., 2005)~~; ii) through compartments that represent ~~in~~ size-structured communities, typically benthic and pelagic communities (Shin and Cury, 2004; Travers et al., 2010)~~, such as Osmose (Shin and Cury, 2001), Feisty (Petrik et al., 2019), and DBEM (Blanchard et al., 2009), for example~~; iii) in a mixture of size-structured and trophic communities ~~(typically pelagic, mesopelagic migratory, and non-migratory) and age-structured species as in Apecosm~~ (Maury, 2010); iv) using ~~the ecosystem is described by~~ dynamic spectra of trophic levels (e.g., Gashe and Gascuel, 2013) ~~as in Ecotroph (Gasche 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)~~, undoubtedly~~ is the most widely used WEM, ~~it is a~~ freely available (www.ecopath.org) and has a flexible structure~~, general~~. ~~: I~~It represents~~is~~ a suite of models developed in more than 30 years for the whole ecosystem description~~s that have been developed over 35 years (Christensen and Walters, 2004) and~~. 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 ~~a large number of~~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).

~~ATLANTIS spatially resolves the full trophic spectrum of ecosystem types, including age-structured formulations for high trophic levels, potentially in multiple vertical layers (Fulton et al., 2011). ATLANTIS includes a nutrient pool formulation that~~

~~can be used to test effects such as nutrient inputs (Audzijonyte et al., 2019). The model has been used for site-specific analyses and to examine general aspects of fishery's impacts on fish communities (Link et al., 2010).~~

~~OSMOSE (Objected-oriented Simulator of Marine ecOSystems Exploitation; Shin and Cury, 2004) is an individual-based ecosystem model that simulates size-based communities on a 2-D spatial cell grid and can be coupled with a planktonic ecosystem model (Travers et al., 2010). The model has been used to study the effects of various aspects of fisheries on the food web (e.g., Shin and Cury, 20019.~~

A large set of~~These~~ ~~models~~ WEM models (Table 1) are used increasingly ~~being used~~ to address the need for holistic ecosystem approaches, and their framework is often ~~used~~ applied to answer strategic medium-term questions related to management strategies, fisheries issues, and climate or ~~environmeental~~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 ~~therefore~~ most of the approaches in this class have a high to intermediate level of maturity and readiness (Table 1).

Conclusions

A ~~large set~~wide range of models are used~~exist that were developed~~ to~~for~~ represent~~ing~~ ocean ecosystems at different level of organisations, ~~from~~including individuals, populations, communities and ~~whole~~ entire ecosystems. Although ~~divided~~categorised into ~~in~~ 6 classes for ~~the sake of~~ clarity, some modelling approaches are not ~~esclusive~~confined to a single ~~of a~~ class. For instance, the DEB modelling approach is ~~also~~ used ~~also~~ 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 ~~objectives that embrace many issues important for society~~ societal issues, i.e., ~~from~~ effects of climate change, pollution, nutrient enrichment and~~,~~ fisheries ~~etc~~.

The numerical approaches analysed here have characteristic spatio-temporal resolutions ~~(Table 1)~~ that are generally decreasing when moving from individual species models to whole ecosystem models (Table 1). ~~Moreover, while i~~Increased represented~~ing~~ complexity with MRM and WEM classes result in ~~there is~~ a general improvement of realism ~~but also lower~~ at the cost of accuracy (generally declining from individual models to WEM)~~ies~~. Overall, the first set of approaches (bioenergetic and population models) are more adapted for tactical analyses while especially the WEM are ~~at the moment~~currently considered useful especially in strategic analyses (see Table 1). Although very few of the reviewed approaches are currently used ~~in~~ operationally (i.e., SEAPODYM), many approaches are routinely ~~used~~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 considered~~ were categorised to be at a~~of~~ 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~~they have~~ great potential~~s~~ for becoming operational,~~ly~~ and to be used for analysing~~e~~ ecosystem dynamics and ~~make useful~~ scenarios, which can be useful for~~,~~ ~~on~~ a very wide range of issues and management actions that ~~might~~ could be eventually prioritized.

References

Agnetta, D., Badalamenti, F., Colloca, F., Cossarini, G., Fiorentino, F., Garofalo, G., Patti, B., Pipitone, C., Russo, T., Solidoro, C. and Libralato, S.: Interactive effects of fishing effort reduction and climate change in a central Mediterranean fishing area: Insights from bio-economic indices derived from a dynamic food-web model. Frontiers in Marine Science, 8. https://doi.org/10.3389/fmars.2022.909164, 2022.

Anderson, S.C., Monnahan, C.C., Johnson, K.F., Ono, K. and Valero, J.L.: ss3sim: an R package for fisheries stock assessment simulation with Stock Synthesis. PLoS One, 9(4), e92725. https://doi.org/10.1371/journal.pone.0092725, 2014.

Andonegi, E., Fernandes, J.A., Quincoces, I., Irigoien, X., Uriarte, A., Pérez, A., Howell, D. and Stefánsson, G.: The potential use of a Gadget model to predict stock responses to climate change in combination with Bayesian networks: the case of Bay of Biscay anchovy. ICES Journal of Marine Science, 68(6), 1257-1269. https://doi.org/10.1093/icesjms/fsr087, 2011.

~~Angelini, S., Hillary, R., Morello, E.B., Plagányi, É.E., Martinelli, M., Manfredi, C., Isajlović, I. and Santojanni, A.: An Ecosystem Model of Intermediate Complexity to test management options for fisheries: A case study. Ecological Modelling, 319, 218-232. https://doi.org/10.1016/j.ecolmodel.2015.07.031, 2016.~~

~~Audzijonyte, A., Pethybridge, H., Porobic, J., Gorton, R., Kaplan, I. and Fulton, E.A.: Atlantis: A spatially explicit end-to-end marine ecosystem model with dynamically integrated physics, ecology and socio-economic modules. Methods in Ecology and Evolution, 10(10), 1814-1819. https://doi.org/10.1111/2041-210X.13272, 2019.~~

Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.J. and Benoît, E.: How does abundance scale with body size in coupled size-structured food webs? Journal of Animal Ecology, 78(1), 270-280. https://doi.org/10.1111/j.1365-2656.2008.01466.x, 2009.

Bocci, M., Coffaro, G. & Bendoricchio, G.: Modelling biomass and nutrient dynamics in eelgrass (*Zostera marina L.*): applications to the Lagoon of Venice (Italy) and Øresund (Denmark). Ecological modelling, 102(1), pp.67-80. https://doi.org/10.1016/S0304-3800(97)00095-1, 1997.

~~Breiman, L., Cutler, A., Liaw, A., & Wiener, M.: Package 'randomForest.' Annals of Operations Research, 97(1-4), 131-141. https://doi.org/10.1023/A, 2018.~~

Brodie, S. J., Thorson, J. T., Carroll, G., Hazen, E. L., Bograd, S., Haltuch, M. A., Holsman, K. K., Kotwicki, S., Samhouri, J. F., Willis-Norton, E., & Selden, R. L.: Trade-offs in covariate selection for species distribution models: a methodological comparison. Ecography, 43(1), 11–24. https://doi.org/10.1111/ecog.04707, 2020.

Butenschön, M., Clark, J., Aldridge, J.N., Allen, J.I., Artioli, Y., Blackford, J., Bruggeman, J., Cazenave, P., Ciavatta, S., Kay, S., Lessin, G., van Leeuwen, S., van der Molen, J., de Mora, L., Polimene, L., Sailley, S., Stephens, N., Torres, R.: ERSEM 15.06: a generic model for marine biogeochemistry and the ecosystem dynamics of the lower trophic levels. Geoscientific Model Development, 9(4), 1293–1339. doi: 10.5194/gmd-9-1293-2016, 2016.

Catucci, E., Panzeri, D., Libralato, S., Cossarini, G., Garofalo, G., Maina, I., Kavadas, S., Quattrocchi, F., Cipriano, G., Carlucci, R. and Vitale, S.: Modeling the spatial distribution and abundance of deep-water red shrimps in the Mediterranean Sea: a machine learning approach. Fisheries Research, 281, p.107257. https://doi.org/10.1016/j.fishres.2024.107257, 2025.

Cheung, W.W., Lam, V.W., Sarmiento, J.L., Kearney, K., Watson, R. and Pauly, D.: Projecting global marine biodiversity impacts under climate change scenarios. Fish and Fisheries, 10(3), 235-251. https://doi.org/10.1111/j.1467-2979.2008.00315.x, 2009.

Cheung, W.W., Sarmiento, J.L., Dunne, J., Frölicher, T.L., Lam, V.W., Deng Palomares, M.L., Watson, R. and Pauly, D.: Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Climate Change, 3(3), 254-258. https://doi.org/10.1038/nclimate1691, 2013.

Christensen, V. and Pauly, D.: ECOPATH II—a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling, 61(3-4), 169-185. https://doi.org/10.1016/0304-3800(92)90016-8, 1992.

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

Colloca, F., Garofalo, G., Bitetto, I., Facchini, M. T., Grati, F., Martiradonna, A., Mastrantonio, G., Nikolioudakis, N., Ordinas, F., Scarcella, G., Tserpes, G., Tugores, M. P., Valavanis, V., Carlucci, R., Fiorentino, F., Follesa, M. C., Iglesias, M., Knittweis, L., Lefkaditou, E., … Spedicato, M. T.: The seascape of demersal fish nursery areas in the North Mediterranean Sea, a first step towards the implementation of spatial planning for trawl fisheries. PLoS ONE, 10(3), 1-25. https://doi.org/10.1371/journal.pone.0119590, 2015.

Cowen, R.K. and Sponaugle, S.: Larval dispersal and marine population connectivity. Annual review of marine science, 1, 443-466. https://doi.org/10.1146/annurev.marine.010908.163757, 2009.

Cowen, R.K., Gawarkiewicz, G., Pineda, J., Thorrold, S.R. and Werner, F.E.: Population connectivity in marine systems an overview. Oceanography, 20(3), 14-21. https://doi.org/10.5670/oceanog.2007.26, 2007.

Dolder, P. J., Thorson, J. T., and Minto, C.: Spatial separation of catches in highly mixed fisheries. Scientific Reports, 8(1). https://doi.org/10.1038/s41598-018-31881-w, 2018.

Elith, J. and Leathwick, J.R.: Species distribution models: ecological explanation and prediction across space and time. Annual review of ecology, evolution, and systematics, 40(1), pp.677-697. https://doi.org/10.1146/annurev.ecolsys.110308.120159, 2009.

Codice campo modificato

Fennel, K., Mattern, J.P., Doney, S.C., Bopp, L., Moore, A.M., Wang, B. and Yu, L.,: Ocean biogeochemical modelling. Nature Reviews Methods Primers, 2(1), p.76. http://dx.doi.org/10.1038/s43586-022-00154-2, 2022.

Faugeras, B. and Maury, O.: An advection-diffusion-reaction size-structured fish population dynamics model combined with a statistical parameter estimation procedure: application to the Indian Ocean skipjack tuna fishery. Mathematical Biosciences and Engineering, 2(4), pp.719-741. DOI: 10.3934/mbe.2005.2.719, https://doi.org/10.3934/mbe.2005.2.719, 2005.

Froese, R., Winker, H., Coro, G., Palomares, M.L., Tsikliras, A.C., Dimarchopoulou, D., Touloumis, K., Demirel, N., Vianna, G., Scarcella, G. and Schijns, R. .: New developments in the analysis of catch time series as the basis for fish stock assessments: The CMSY++ method. Acta Ichthyologica et Piscatoria, 53, 173-189, https://doi.org/10.3897/aiep.53.105910, 2023.

Fulton, E.A., Link, J.S., Kaplan, I.C., Savina-Rolland, M., Johnson, P., Ainsworth, C., Horne, P., Gorton, R., Gamble, R.J., Smith, A.D. and Smith, D.C.: Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries, 12(2), 171-188. https://doi.org/10.1111/j.1467-2979.2011.00412.x, 2011.

~~Fulton, E.A., Smith, A.D. and Punt, A.E.: Which ecological indicators can robustly detect effects of fishing? ICES Journal of Marine Science, 62(3), 540-551. https://doi.org/10.1016/j.icesjms.2004.12.012, 2005.~~

Gasche, L. and Gascuel, D.: EcoTroph: a simple model to assess fishery interactions and their impacts on ecosystems. ICES Journal of Marine Science, 70(3), 498-510. https://doi.org/10.1093/icesjms/fst016, 2013.

Gawarkiewicz, G., Monismith, S. and Largier, J.: Observing larval transport processes affecting population connectivity: progress and challenges. Oceanography, 20(3), 40-53. https://doi.org/10.5670/oceanog.2007.28, 2007.

Gislason, H.: Single and multispecies reference points for Baltic fish stocks. ICES Journal of Marine Science, 56(5), 571-583. https://doi.org/10.1006/jmsc.1999.0492, 1999.

Grüss, A., Drexler, M., and Ainsworth, C. H.: Using delta generalized additive models to produce distribution maps for spatially explicit ecosystem models. Fisheries Research, 159, 11-24. https://doi.org/10.1016/j.fishres.2014.05.005, 2014.

Heymans, J.J., Coll, M., Libralato, S., Morissette, L. and Christensen, V.: Global patterns in ecological indicators of marine food webs: a modelling approach. PloS one, 9(4), e95845. https://doi.org/10.1371/journal.pone.0095845, 2014.

Hilborn, R. and Walters, C.J. eds., *Quantitative fisheries stock assessment: choice, dynamics and uncertainty*. Springer Science & Business Media. 2013.

Hollowed, A.B., Barange, M., Beamish, R.J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M.G., Hare, J.A., Holt, J., Ito, S.I. and Kim, S.,: Projected impacts of climate change on marine fish and fisheries. *ICES Journal of Marine Science*, *70*(5), pp.1023-1037. https://doi.org/10.1093/icesjms/fst081, 2013.

Hollowed, A.B., Bax, N., Beamish, R., Collie, J., Fogarty, M., Livingston, P., Pope, J. and Rice, J.C.: Are multispecies models an improvement on single-species models for measuring fishing impacts on marine ecosystems? ICES Journal of Marine Science, 57(3), 707-719. https://doi.org/10.1006/jmsc.2000.0734, 2020.

Itoh, S., Takeshige, A., Kasai, A. and Kimura, S.: Modeling the coastal ecosystem complex: present situation and challenges. Fisheries science, 84, 293-307. https://doi.org/10.1007/s12562-018-1181-x, 2018.

ha formattato: Inglese (Stati Uniti)

ha formattato: Inglese (Stati Uniti)

ha formattato: Inglese (Stati Uniti)

Jardim, E., Millar, C.P., Mosqueira, I., Scott, F., Osio, G.C., Ferretti, M., Alzorriz, N. and Orio, A.: What if stock assessment is as simple as a linear model? The a4a initiative. ICES Journal of Marine Science, 72(1), 232-236. https://doi.org/10.1093/icesjms/fsu050, 2014.

Jones, M. C., Dye, S. R., Pinnegar, J. K., Warren, R., & Cheung, W. W.: Modelling commercial fish distributions: Prediction and assessment using different approaches. Ecological Modelling, 225, 133-145. https://doi.org/10.1016/j.ecolmodel.2011.11.003, 2012.

Kooijman, S.A.L.M.: Dynamic energy budget theory for metabolic organisation. Cambridge university press. 2010.

Kooijman, S., The standard dynamic energy budget model has no plausible alternatives. *Ecological Modelling* 428, p. 109106. 2020.

Laurent, C., Querin, S., Solidoro, C., and Melaku Canu, D.: Modelling marine particle dynamics with LTRANS-Zlev: Implementation and validation. Environmental Modelling & Software, 125, 104621. https://doi.org/10.1016/j.envsoft.2020.104621, 2020.

Lehodey, P., Chai, F. and Hampton, J.: Modelling climate-related variability of tuna populations from a coupled ocean–biogeochemical-populations dynamics model. Fisheries Oceanography, 12(4-5), 483-494. https://doi.org/10.1046/j.1365-2419.2003.00244.x, 2003.

Lehodey, P., Senina, I., Nicol, S. and Hampton, J.: Modelling the impact of climate change on South Pacific albacore tuna. Deep Sea Research Part II: Topical Studies in Oceanography, 113, 246-259. https://doi.org/10.1016/j.dsr2.2014.10.028, 2015.

Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P. and Blanke, B.: A Lagrangian tool for modelling ichthyoplankton dynamics. Environmental Modelling & Software, 23(9), 1210-1214. https://doi.org/10.1016/j.envsoft.2008.02.005, 2008.

Libralato, S., Caccin, A. and Pranovi, F.: Modeling species invasions using thermal and trophic niche dynamics under climate change. Frontiers in Marine Science, 2, 29. https://doi.org/10.3389/fmars.2015.00029, 2015.

Libralato, S. and Solidoro, C.: A bioenergetic growth model for comparing Sparus aurata's feeding experiments. Ecological Modelling, 214(2-4), pp.325-337. https://doi.org/10.1016/j.ecolmodel.2008.02.024, 2008.

~~Link, J.S., Fulton, E.A. and Gamble, R.J.: The northeast US application of ATLANTIS: a full system model exploring marine ecosystem dynamics in a living marine resource management context. Progress in Oceanography, 87(1-4), 214-234. https://doi.org/10.1016/j.pocean.2010.09.020, 2010.~~

Maravelias, C. D., Haralabous, J., & Papaconstantinou, C.: Predicting demersal fish species distributions in the Mediterranean Sea using artificial neural networks. Marine Ecology Progress Series, 255, 249-258. https://doi.org/10.3354/meps255249, 2003.

Maunder, M.N. and Punt, A.E.: A review of integrated analysis in fisheries stock assessment. Fisheries Research, 142, 61-74. https://doi.org/10.1016/j.fishres.2012.07.025, 2013.

ha formattato: Inglese (Stati Uniti)

ha formattato: Inglese (Stati Uniti)

ha formattato: Inglese (Stati Uniti)

ha formattato: Inglese (Stati Uniti)

Maury, O.: An overview of APECOSM, a spatialized mass balanced "Apex Predators ECOSystem Model" to study physiologically structured tuna population dynamics in their ecosystem. Progress in Oceanography, 84(1-2), 113-117. https://doi.org/10.1016/j.pocean.2009.09.013, 2010.

Melaku Canu, D., Laurent, C., Morello, E.B., Querin, S., Scarcella, G., Vrgoc, N., Froglia, C., Angelini, S. and Solidoro, C.: Nephrops norvegicus in the Adriatic Sea: Connectivity modeling, essential fish habitats, and management area network. Fisheries Oceanography, 30(4), 349-365. https://doi.org/10.1111/fog.12522, 2021.

Melo-Merino, S. M., Reyes-Bonilla, H., & Lira-Noriega, A.: Ecological niche models and species distribution models in marine environments: A literature review and spatial analysis of evidence. Ecological Modelling, 415, 108837. https://doi.org/10.1016/j.ecolmodel.2019.108837, 2020.

Methot, R.D., Wetzel, C.R.: Stock Synthesis: a biological and statistical framework for fish stock assessment and fishery management. Fisheries Research, 142, 86-99. https://doi.org/10.1016/j.fishres.2012.10.012, 2013.

Morello, E.B., Plagányi, É.E., Babcock, R.C., Sweatman, H., Hillary, R. and Punt, A.E.: Model to manage and reduce crown-of-thorns starfish outbreaks. Marine Ecology Progress Series, 512, 167-183. DOI: 10.3354/meps10858, https://doi.org/10.3354/meps10858, 2014.

Nielsen, J.R., Thunberg, E., Holland, D.S., Schmidt, J.O., Fulton, E.A., Bastardie, F., Punt, A.E., Allen, I., Bartelings, H., Bertignac, M. and Bethke, E.,: Integrated ecological–economic fisheries models—Evaluation, review and challenges for implementation. *Fish and fisheries*, *19*(1), pp.1-29. https://doi.org/10.1111/faf.12232, 2018.

Nisbet, R.M., Jusup, M., Klanjscek, T. and Pecquerie, L.: Integrating dynamic energy budget (DEB) theory with traditional bioenergetic models. Journal of Experimental Biology, 215(6), pp.892-902. https://doi.org/10.1242/jeb.059675, 2012.

North, E. W., Z. Schlag, R. R. Hood, M. Li, L. Zhong, T. Gross, and V. S. Kennedy. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. Marine Ecology Progress Series 359: 99-116, https://doi.org/10.3354/meps07317, 2008.

Panzeri D., Bitetto I., Carlucci R., Cipriano G., Cossarini G., D'Andrea L., Masnadi F., Querin S., Reale M., Russo T., Scarcella G., Spedicato M.T., Teruzzi A., Vrgoč N., Zupa W. and Libralato S.: Developing spatial distribution models for demersal species by the integration of trawl surveys data and relevant ocean variables. In: Copernicus Marine Service Ocean State Report, Issue 5, Journal of Operational Oceanography, 14:sup1, s114–s123; DOI: 10.1080/1755876X.2021.1946240, 2021.

Panzeri, D., Russo, T., Arneri, E., Carlucci, R., Cossarini, G., Isajlović, I., Krstulović Šifner, S., Manfredi, C., Masnadi, F., Reale, M., Scarcella, G.,Solidoro C., Spedicato M.T., Vrgoč N., W. Zupa, Libralato S.: Identifying priority areas for spatial management of mixed fisheries using ensemb le of multi-species distribution models. *Fish and Fisheries*, *25*(2), pp.187-204. https://doi.org/10.1111/faf.12802 , 2024

Paris, C.B., Helgers, J., Van Sebille, E. and Srinivasan, A.: Connectivity Modeling System: A probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. Environmental Modelling & Software, 42, 47-54. https://doi.org/10.1016/j.envsoft.2012.12.006, 2013.

ha formattato: Inglese (Regno Unito)

ha formattato: Inglese (Regno Unito)

Codice campo modificato

Pastres, R., Pranovi, F., Libralato, S., Malavasi, S. and Torricelli, P.:'Birthday effect'on the adoption of alternative mating tactics in *Zosterisessor ophiocephalus*: evidence from a growth model. Journal of the Marine Biological Association of the United Kingdom, *82*(2), pp.333-337. https://doi.org/10.1017/S0025315402005520, 2002.

Pedersen, M.W. and Berg, C.W.: A stochastic surplus production model in continuous time. Fish and Fisheries, 18(2), 226-243. https://doi.org/10.1111/faf.12174, 2017.

Petrik, C.M., Stock, C.A., Andersen, K.H., van Denderen, P.D. and Watson, J.R.: Bottom-up drivers of global patterns of demersal, forage, and pelagic fishes. Progress in Oceanography, 176, 102124. https://doi.org/10.1016/j.pocean.2019.102124, 2019.

Piroddi, C., Akoglu, E., Andonegi, E., Bentley, J.W., Celić, I., Coll, M., Dimarchopoulou, D., Friedland, R., de Mutsert, K., Girardin, R., Garcia-Gorriz, E., Grizzetti, B., Hernvann, P.-Y., Heymans, J.J., Müller-Karulis, B., Libralato, S., Lynam, C.P., Macias, D., Miladinova, S., Moullec, F., Palialexis, A., Parn, O., Serpetti, N., Solidoro, C., Steenbeek, J., Stips, A., Tomczak, M.T., Travers-Trolet, M., and Tsikliras, A.C.: Effects of nutrient management scenarios on marine food webs: a Pan-European Assessment in support of the Marine Strategy Framework Directive. Frontiers in Marine Science, 8, 596797. https://doi.org/10.3389/fmars.2021.596797, 2021.

Pirotta, E., Booth, C.G., Calambokidis, J., Costa, D.P., Fahlbusch, J.A., Friedlaender, A.S., Goldbogen, J.A., Harwood, J., Hazen, E.L., New, L. and Santora, J.A.: From individual responses to population effects: Integrating a decade of multidisciplinary research on blue whales and sonar. Animal Conservation, 25(6), pp.796-810. https://doi.org/10.1111/acv.12785, 2022.

Pittman, S.J. and Brown, K.A.: Multi-scale approach for predicting fish species distributions across coral reef seascapes. PloS one, 6(5), e20583. https://doi.org/10.1371/journal.pone.0020583, 2011.

Plaganyi E.: Models for an ecosystem approach to fisheries. FAO Fisheries Technical Paper, 477, 1-108. Available at https://www.fao.org/4/a1149e/a1149e.pdf, 2007 (last access: 28/07/2024).

Plagányi, É.E., Punt, A.E., Hillary, R., Morello, E.B., Thébaud, O., Hutton, T., Pillans, R.D., Thorson, J.T., Fulton, E.A., Smith, A.D. and Smith, F.: Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish and Fisheries, 15(1), 1-22. https://doi.org/10.1111/j.1467-2979.2012.00488.x, 2014.

Pollock, L.J., Tingley, R., Morris, W.K., Golding, N., O'Hara, R.B., Parris, K.M., Vesk, P.A. and McCarthy, M.A.: Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods in Ecology and Evolution, 5(5), 397-406. https://doi.org/10.1111/2041-210X.12180, 2014.

Privitera-Johnson, K.M., Methot, R.D. and Punt, A.E.: Towards best practice for specifying selectivity in age-structured integrated stock assessments. Fisheries Research, 249, 106247. https://doi.org/10.1016/j.fishres.2022.106247, 2022.

Punt, A.E.: Spatial stock assessment methods: a viewpoint on current issues and assumptions. Fisheries Research, 213, 132-143. https://doi.org/10.1016/j.fishres.2019.01.014, 2019.

~~Punt, A.E. and Butterworth, D.S.: The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals Arctocephalus pusillus pusillus and the Cape hakes~~

~~Merluccius capensis and M. paradoxus. South African Journal of Marine Science, 16(1), 255-285. https://doi.org/10.2989/025776195784156494, 1995.~~

Reiss, H., Cunze, S., König, K., Neumann, H. and Kröncke, I.: Species distribution modelling of marine benthos: a North Sea case study. Marine Ecology Progress Series, 442, 71-86. DOI: 10.3354/meps09391, 2011.

Rose, K.A., Fiechter, J., Curchitser, E.N., Hedstrom, K., Bernal, M., Creekmore, S., Haynie, A., Ito, S.I., Lluch-Cota, S., Megrey, B.A. and Edwards, C.A.: Demonstration of a fully-coupled end-to-end model for small pelagic fish using sardine and anchovy in the California Current. *Progress in Oceanography*, *138*, pp.348-380. https://doi.org/10.1016/j.pocean.2015.01.012 2015.

Rose, K.A., Holsman, K., Nye, J.A., Markowitz, E.H., Banha, T.N., Bueno-Pardo, J., Deslauriers, D., Fulton, E.A., Huebert, K.B., Huret, M. and Ito, S.I.: Advancing bioenergetics-based modeling to improve climate change projections of marine ecosystems. *Marine Ecology Progress Series*, *732*, pp.193-221. https://doi.org/10.3354/meps14535~~,~~, 2024.

Senina, I., Lehodey, P., Sibert, J. and Hampton, J.: Integrating tagging and fisheries data into a spatial population dynamics model to improve its predictive skills. Canadian Journal of Fisheries and Aquatic Sciences, 77(3), 576-593. https://doi.org/10.1139/cjfas-2018-0470, 2020.

Serpetti, N., Baudron, A.R., Burrows, M.T., Payne, B.L., Helaouet, P., Fernandes, P.G. and Heymans, J.J.: Impact of ocean warming on sustainable fisheries management informs the Ecosystem Approach to Fisheries. Scientific Reports, 7(1), 1-15. https://doi.org/10.1038/s41598-017-13220-7, 2017.

Sibly, R.M., Grimm, V., Martin, B.T., Johnston, A.S.A., Kulakowska, K., Topping, C.J., Calow, P., Nabe-Nielsen, J., Thorbek, P., Deangelis, D.L.: Representing the acquisition and use of energy by individuals in agent-based models of animal populations. Methods Ecol Evol 4: 151–161. https://doi.org/10.1111/2041-210x.12002, 2013.

~~Shin, Y.J. and Cury, P.: Exploring fish community dynamics through size-dependent trophic interactions using a spatialized individual-based model. Aquatic Living Resources, 14(2), 65-80. https://doi.org/10.1016/S0990-7440(01)01106-8, 2001.~~

Shin, Y.J. and Cury, P.: Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. Canadian Journal of Fisheries and Aquatic Sciences, 61(3), 414-431. https://doi.org/10.1139/f03-154,~~,~~ 2004.

Sibert, J.R., Hampton, J., Fournier, D.A. and Bills, P.J.: An advection–diffusion–reaction model for the estimation of fish movement parameters from tagging data, with application to skipjack tuna (Katsuwonus pelamis). Canadian Journal of Fisheries and Aquatic Sciences, 56(6), 925-938. https://doi.org/10.1139/f99-017, 1999.

Steenbeek, J., Buszowski, J., Christensen, V., Akoglu, E., Aydin, K., Ellis, N., Felinto, D., Guitton, J., Lucey, S., Kearney, K. and Mackinson, S.: Ecopath with Ecosim as a model-building toolbox: source code capabilities, extensions, and variations. Ecological Modelling, 319, 178-189. https://doi.org/10.1016/j.ecolmodel.2015.06.031, 2016.

Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., Buszowski, J. and Christensen, V.: Bridging the gap between ecosystem modeling tools and geographic information systems: Driving a food web model with external spatial–temporal data. Ecological Modelling, 263, pp.139-151. https://doi.org/10.1016/j.ecolmodel.2013.04.027, 2013.

ha formattato: Collegamento ipertestuale, Inglese (Stati Uniti)

Codice campo modificato

Stock, C.A., Alexander, M.A., Bond, N.A., Brander, K.M., Cheung, W.W., Curchitser, E.N., Delworth, T.L., Dunne, J.P., Griffies, S.M., Haltuch, M.A. and Hare, J.A.: On the use of IPCC-class models to assess the impact of climate on living marine resources. Progress in Oceanography, 88(1-4), 1-27. https://doi.org/10.1016/j.pocean.2010.09.001, 2011.

Thorson, J. T., Shelton, A. O., Ward, E. J., & Skaug, H. J.: Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. ICES Journal of Marine Science, 72, 1297-1310. https://doi.org/10.1093/icesjms/fsu243, 2015.

Thorson, J.T., Ianelli, J.N., Larsen, E.A., Ries, L., Scheuerell, M.D., Szuwalski, C. and Zipkin, E.F.: Joint dynamic species distribution models: a tool for community ordination and spatio-temporal monitoring. *Global Ecology and Biogeography*, *25*(9), pp.1144-1158. https://doi.org/10.1111/geb.12464 , 2016

Tittensor, D.P., Novaglio, C., Harrison, C.S., Heneghan, R.F., Barrier, N., Bianchi, D., Bopp, L., Bryndum-Buchholz, A., Britten, G.L., Büchner, M. and Cheung, W.W.: Next-generation ensemble projections reveal higher climate risks for marine ecosystems. Nature Climate Change, 11(11), 973-981. https://doi.org/10.1038/s41558-021-01173-9, 2021.

Travers, M., Watermeyer, K., Shannon, L.J. and Shin, Y.J.: Changes in food web structure under scenarios of overfishing in the southern Benguela: comparison of the Ecosim and OSMOSE modelling approaches. Journal of Marine Systems, 79(1-2), 101-111. https://doi.org/10.1016/j.jmarsys.2009.07.005, 2010.

Ursin, E.: A mathematical model of some aspects of fish growth, respiration, and mortality. *Journal of the Fisheries Board of Canada*, *24*(11), pp.2355-2453, 1967.

Walters, C., Pauly, D. and Christensen, V.: Ecospace: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with emphasis on the impacts of marine protected areas. Ecosystems, 2, 539-554. https://doi.org/10.1007/s100219900101, 1999.

Walters, C., Pauly, D., Christensen, V. and Kitchell, J.F.: Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems, 3, 70-83. https://doi.org/10.1007/s100210000011–, 2000

Competing interests

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

Data and/or code availability

Not applicable.

Authors contribution

Not Applicable

Acknowledgements

A draft version of this paper benefited from comments and suggestions received by Vinko Bandelj (OGS), Elisa Donati (UNITS and OGS), Celia Laurent (OGS), Ivano Vascotto (OGS), Damiano Baldan (OGS), Fabrizio Gianni (OGS) and Davide Agnetta (OGS).

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

	Bioenergetic models												**Rose et al., 2024**
~~Model~~Acronym	**Model~~Name~~**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for o~~O~~perational 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	~~Potentially~~Good	Yes used as forcings (temperature, light, food, nutrients)	https://www.bio.vu.nl/thb/deb/deblab/add_my_pet/	Koojiman, 2020
	Population and ~~stock assessment~~ fisheries models												**Hilborn and Walters, 2013**
Acronym~~Model~~	**Model~~Name~~**	**Elemental structure~~Elemental structure~~**	**Model Units~~Model Units~~**	**Time units~~Time units~~**	**Spatial structure~~Spatial structure~~**	**Number of species~~Number of species~~**	**Trophic interactions~~Trophic interactions~~**	**Primary model focus, output~~Primary model focus, output~~**	**Maturity**	**Readiness for operational use~~Operational~~**	**Physical/biogeochemical processes~~Physical/biogeochemical processes~~**	**Repository (if open access)**	
SPICT~~Spict~~	S~~s~~tochastic surplus ~~p~~Production model I~~i~~n C~~c~~ontinuous T~~t~~ime	Surplus prodution	Biomass	Year	No	1	No	Biological reference points for fisheries-	High	Poor~~yes~~	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~~Biological reference points~~	Intermediate	~~Yes~~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~~Biological reference points~~	Intermediate	~~Yes~~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~~Biological reference points~~	High	Intermediate~~Yes~~	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~~Biological reference points~~	Poor	Poor~~no~~	No	https://noaa-fisheries-integrated-toolbox.github.io/VPA	Gislason, 1999
	Connectivity models												**Cowen et al., 2009**
Acronym~~Model~~	**Model~~Name~~**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use~~Operational~~**	**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~~No~~	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~~No~~ (computationally complex)	Yes	NA	Rose et al., 2015
	Species Distribution Models												**Elith and Leathwick, 2009**
Acronym~~Model~~	**Model~~Name~~**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use~~Operational~~**	**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~~Potentially~~	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)~~No~~	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~~No~~	Yes included for developing the bioenvelope	NA	Cheung et al., 2013
	Minimal Realistic models												**Plagányi 2007**
Acronym~~Model~~	**Model~~Name~~**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use~~Operational~~**	**Physical/biogeochemical processes**	**Repository (if open access)**	
GADGET	Globally applicable Area Disaggregated General Ecosystem Toolbox ~~(derived from BORMICON)~~	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	~~potentially~~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~~No~~ (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)~~Potentially~~	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~~Yes~~ (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~~No~~	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

Formattato: Allineato a sinistra
Formattato: Allineato a sinistra
Formattato: Allineato a sinistra
ha formattato: Italiano (Italia)
ha formattato: Italiano (Italia)
Formattato: Allineato a sinistra
Formattato: Allineato a sinistra
Formattato: Allineato a sinistra
ha formattato: Tipo di carattere: 11 pt, Grassetto, Colore carattere: Nero
Formattato: Allineato a sinistra
Formattato: Allineato a sinistra
Formattato: Allineato a sinistra
Formattato: Allineato a sinistra
ha formattato: Tipo di carattere: 9 pt, Colore carattere: Nero
Formattato: Allineato a sinistra
Formattato: Giustificato
Formattato: Allineato a sinistra
Formattato: Allineato a sinistra

	Whole Ecosystem Models												Plagányi 2007
Acronym~~Model~~	**Model~~Name~~**	**Elemental structure**	**Model Units**	**Time units**	**Spatial structure**	**Number of species**	**Trophic interactions**	**Primary model focus, output**	**Maturity**	**Readiness for operational use~~Operational~~**	**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~~No~~ (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	Poo~~Nor~~ (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)~~No~~	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~~No~~	Included as off-line coupling	https://github.com/Kenhasteandersen/FEISTY	Blanchard et al., 2009
~~Apecosm~~													

Formattato: Allineato a sinistra

Formattato: Allineato a sinistra

Formattato: Allineato a sinistra

Formattato: Allineato a sinistra

Formattato: Allineato a sinistra

Formattato: Allineato a sinistra

ha formattato: Tipo di carattere: 9 pt, Colore carattere: Nero

Formattato: Allineato al centro