Ecotrophic perspective in fisheries management: a review of Ecopath with Ecosim models in European marine ecosystems

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The aim of this work is to present the food web models developed using the Ecopath with Ecosim (EwE) software tool to describe structure and functioning of various European marine ecosystems (eastern, central and western Mediterranean Sea; Black Sea; Bay of Biscay, Celtic Sea and Iberian coast; Baltic Sea; North Sea; English Channel, Irish Sea and west Scottish Sea; and Norwegian and Barents Seas). A total of 195 Ecopath models based on 168 scientific publications, which report original, updated and modified versions, were reviewed. Seventy models included Ecosim temporal simulations while 28 implemented Ecospace spatiotemporal dynamics. Most of the models and publications referred to the western Mediterranean Sea followed by the English Channel, Irish Sea and west Scottish Sea sub-regions. In the Mediterranean Sea, the western region had the largest number of models and publications, followed by the central and eastern regions; similar trends were observed in previous literature reviews. Most models addressed ecosystem functioning and fisheries-related hypotheses while several investigated the impact of climate change, the presence of alien species, aquaculture, chemical pollution, infrastructure, and energy production. Model complexity (i.e., number of functional groups) increased over time. Main forcing factors considered to run spatial and temporal simulations were trophic interactions, fishery, and primary production. Average scores of ecosystem indicators derived from the Ecopath summary statistics were compared. Uncertainty was also investigated based on the use of the Ecosampler plug-in and the Monte Carlo routine; only one third of the reviewed publications incorporated uncertainty analysis. Only a limited

number of the models included the use of the ECOIND plug-in which provides the user with quantitative output of ecological indicators. We assert that the EwE modelling approach is a successful tool which provides a quantitative framework to analyse the structure and dynamics of ecosystems, and to evaluate the potential impacts of different management scenarios.

1 Introduction

Due to the complex nature of interactions within marine ecosystems, it is imperative to view and study them as a whole, complementing single-species assessments with ecosystem considerations (Marshall et al., 2019; Howell et al., 2021). The factors that compose marine ecosystems, as biological entities (fauna and flora) and environmental elements (e.g., nutrients), perform important processes either individually or synergistically (Borja et al., 2014; Armoškaitė et al., 2020). Worldwide, marine ecosystems have been facing a multitude of perturbations that threaten their structure and functioning (Elliott et al., 2015), with most important stressors being related to fisheries (Froese et al., 2018), climate change (Bruno et al., 2018) and non-indigenous species (Galil et al., 2018). Recent assessments demonstrate that marine ecosystems are being degraded or altered (Newton et al., 2020; Korpinen et al., 2021). Climate change has brought about rising temperatures that may trigger regime shift dynamics (Möllmann et al., 2021) while ocean acidification may further weaken the ecological resilience of European seas (Galdies et al., 2020). The introduction of alien species can affect entire ecosystems, especially in regional semi-enclosed seas such as the Baltic Sea (Dobrzycka-Krahel and Medina-Villar, 2020), the Black Sea (Shalovenkov, 2019) and the Mediterranean Sea (Zenetos et al., 2017). Much of the pressure also comes from anthropogenic activities; i.e., exploration and extraction of natural resources, transportation, infrastructure and pollution, including the discarding of fishing gears (Korpinen et al., 2021). In addition to natural resources removals, intensive bottom trawling physically damages the seabed by destroying habitats (Woods and Verones, 2019).

The European continent is characterized by great geomorphological complexity and diversity, both on land and at sea (Costello et al., 2006). A multitude of marine ecosystems exists, ranging from lower latitudes, with the closed and relatively warm Mediterranean Sea, to higher latitudes, with the eutrophic Baltic Sea and the Barents Sea, which is frozen during winter (Heiskanen et al., 2016). Marine ecosystems can be divided into two main categories, the deep seas and the shallow seas (Galparsoro et al., 2012). The deep seas (Mediterranean Sea and Black Sea) were created by geotectonic activity while the shallow seas (Adriatic Sea, Baltic

Sea and North Sea) were created by the melting of glaciers covering large areas of land (Galparsoro et al., 2012). Moreover, there are the ecosystems related to the Atlantic Ocean (Bay of Biscay and Celtic Sea) on the western European coasts, which are directly affected by its geophysical and environmental conditions (Holt et al., 2014). European marine ecosystems are also distinguished by the many estuarine wetlands (Newton et al., 2014), which are important to local communities and exploited for aquaculture (Gamito and Erzini, 2005; Díaz López et al., 2008; Izquierdo-Gomez et al., 2016) and wind power plants (Halouani et al., 2020).

Software programs simulating ecosystem dynamics have facilitated the holistic study of marine ecosystems. Ecosystem modelling has provided a means for incorporating management perspectives (Fath et al., 2019); i.e., by implementing scenarios related to fisheries management, climatic and other environmental conditions (e.g., Scotti et al., 2022a), as well as the establishment of marine protected areas (MPAs; Dahood et al., 2020). Ecopath with Ecosim (EwE: Polovina, 1984; Christensen and Walters, 2004a) is the most widely used software tool for modelling marine food webs. It is suitable for examining the impacts of human and environmental stressors on the food web, as it is easy to use and offers a wide range of freely available modules and plug-ins (Pauly et al., 2000). It is based on the static depiction of a food web in a mass-balanced state over a specific time period (Ecopath) and uses differential equations for time simulations (Ecosim: Walters et al., 1997). Further extensions integrate temporal simulations with spatial dynamics and visualization (Ecospace: Walters et al., 1999), and support trophic conversion, configuring the food web as biomass movements from lower to higher trophic levels (EcoTroph: Gascuel and Pauly, 2009).

Ecological Network Analysis (ENA) is a toolkit of matrix manipulation techniques for the modelling of mass-balanced networks (Ulanowicz, 2004). Some ENA algorithms are available in EwE and enable calculating indicators summarizing ecosystem structure and functioning; the ENAtool routine also allows incorporating uncertainty levels in input data (Guesnet et al., 2015). Ecological indicators from ENA can be used to identify the state and health of the ecosystem (Heymans et al., 2016). This routine has been further expanded with a plug-in calculating standardised ecological indicators (ECOIND: Coll and Steenbeek, 2017). Additional plug-ins were established and incorporated into

the main software program over the years (1) to assess parameters' uncertainty (Ecosampler: Steenbeek et al., 2018), and (2) to estimate concentrations and densities of contaminants and radioisotopes in aquatic environments (Ecotracer: Walters and Christensen, 2018). Other modules available in the base EwE version include (1) policy optimization of fisheries management (Christensen and Walters, 2004b), (2) spatial optimization of marine protected areas (Christensen et al., 2009), and (3) value chain modelling evaluating the socioeconomic benefits of fisheries (Christensen et al., 2011).

Reviews of EwE applications have previously been completed for the Mediterranean Sea (Coll and Libralato, 2012) and at global scale (Pikitch et al., 2014; Colléter et al., 2015; Coll et al., 2015; Vasslides et al., 2017; Craig and Link, 2023; Stock et al., 2023), highlighting that EwE has the lion's share in food web modelling with an increasing number of models through the years; i.e., over 430 models stored in an open-access database of EwE models called EcoBase (Colléter et al., 2015) and over 500 publications (Coll et al., 2015). The EcoBase initiative (http://ecobase.ecopath.org) is a collaborative project that aims at gathering published EwE models in a digital open-access repository where the models and their metadata are discoverable and easily accessible, with the goal of facilitating further meta-analyses and reviews (Colléter et al., 2015). However, since EcoBase is based on the principle of optional self-uploading by model developers, it does not cover all EwE models exhaustively, especially when it comes to modified versions of original models that examine new research items.

Our review aims to fill the gaps from the EcoBase repository by including all published models to date, original and updated versions, focusing on European seas' ecosystems, which are regulated by common mechanisms and rules for achieving the sustainable management of European fishing fleets and conservation of fish stocks. The EU Marine Strategy Framework Directive (MSFD; EU, 2008) and the revised EU Common Fisheries Policy (CFP; EU, 2013) represent relevant regulations for the management of the European seas. They recognise the need of an integrated understanding of food web characteristics, ecosystem functioning and fisheries management, an intent that can be facilitated by the EwE modelling approach. The main objective of this work was to review all published EwE models across European seas (Ecopath, Ecosim, Ecospace, and EcoTroph), aiming to (1) gather and present all EwE models to provide an overview of their main research topics, (2) discuss the hypotheses and objectives of each model by compiling their metadata, (3) identify the modelled areas, (4) highlight gaps in research, and (5) perform a comparative synthesis by assessing ecosystem health and resilience with ecosystem indicators derived from the models. To facilitate these objectives, we divided the EwE models according to nine major areas: (1) eastern Mediterranean Sea, (2) central Mediterranean Sea, (3) western Mediterranean Sea, (4) Black Sea, (5) Bay of Biscay, Celtic Sea and Iberian coast, (6) Baltic Sea, (7) North Sea, (8) English Channel, Irish Sea and west Scottish Sea, and (9) Norwegian and Barents Seas. The ECOIND plug-in (Coll and Steenbeek, 2017), which is integrated in the EwE software tool to calculate ecological indicators, was also included in the analysis.

2 European areas and overview of published EwE models

This review was based on an overview of all EwE models that have been developed for European marine ecosystems to date. At first, an inventory of the models stored in the EcoBase repository was made and metadata were cross-referenced with the corresponding publications (Tables S1, S2). An exhaustive and thorough search was then conducted using literature search engines (Scopus, Google Scholar and Web of Science) to find all available publications with EwE applications in peer-reviewed journals. This systematic search was executed following the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) methodology, which is based on article selection, screening and the extraction of information (Moher et al., 2010), and has been successfully applied in other review exercises (Corrales et al., 2020a). The starting year of eligibility was not defined but a cut-off date of available publications was set as to the first quarter of 2023. For a more efficient realisation of this task, keywords (e.g., "Ecopath", "Ecosim", "Ecospace", and "EcoTroph") were used in correspondence with the nine European areas and their sub-regions. The goal was to identify all subsequent publications that might be based on one original base model modifying or updating it, and that have not yet been included in EcoBase. Values of the indicators derived from the Ecopath summary statistics were compiled to infer ecosystem health and state, and for comparative analysis (Table 1). Finally, analyses of the publications and models were performed in relation to research topic (i.e., ecosystem functioning and ecological roles, fisheries, aquaculture, alien species, environment and climate) and software modules used; cumulative trends of EwE publications over time were highlighted. It is, however, noteworthy that several publications explored more than one topic. Moreover, forcing factors used to drive the spatio-temporal simulations with Ecosim and Ecospace were examined (Vasslides et al., 2017; Stock et al., 2023). Emphasis was also given to publications that used additional analyses based on the ECOIND plug-in to further demonstrate the utility of ecological indicators. These indicators are widely applied by scientists to characterize environmental and fishing impacts related to management (Coll and Steenbeek, 2017). A panel map of the nine European regions and the areas modelled was created to visualize EwE models and modules used. European areas and an overview of the models are described in the following sections.

2.1 Eastern Mediterranean Sea

The Levantine Sea is part of the eastern Mediterranean basin, which is strongly affected by increasing sea temperature and faces the greatest invasion of marine species in the world (Edelist et al., 2013). The warm, saline and ultra-oligotrophic ecosystem of the Levantine Sea results in very low primary production (Varkitzi et al., 2020). This heavily impacted ecosystem is exposed to climate change and multiple pressures and might benefit of using ecological and trophic models to understand its responses to concurrent stress

TABLE 1 Ecological indicators derived from the Ecopath module of the EwE software tool.

Indicator	Description	Behavior	Reference
Total System Throughput (TST)	Sum of all flows (consumption, exports, respiratory flows, flows to detritus)	Higher in systems with more compartments; it increases along the development of an ecosystem towards mature stages	Ulanowicz, 1986; Scotti et al., 2022b
Total primary production (PP)	Sum of primary productivity from all compartments	Higher in eutrophic or upwelling systems	Christensen and Walters, 2004a
Total PP/Total respiration	Ratio indicating maturity	Higher in immature systems (>1), affected with organic pollution	Odum, 1971
Total PP/biomass	Ratio indicating maturity	Declines over time in immature systems	Odum, 1971
Biomass/TST	Ratio indicating maturity	Higher in systems close to maturity	Odum, 1971
Net system production	Difference between total PP and total respiration	Higher in immature systems, closer to zero in mature systems	Christensen and Walters, 2004a
Respiration/biomass	Thermodynamic order function	Increases with biomass	Odum, 1971
Gross efficiency	Sum of fisheries catches to total PP	Higher in upwelling systems (catches of lower trophic level species), lower in systems with underexploited stocks	Marten and Polovina, 1982
Mean Trophic Level of the catch (MTLc)	Fisheries position in the food web	Higher in systems with fisheries targeting apex predators and high trophic-level consumers	Pauly et al., 1998
Connectance	Ratio of actual to possible food web links	Higher in systems with higher number of functional groups	Nee, 1990
System Omnivory index	Distribution of trophic interactions in the food web	Larger than zero in systems where functional groups feed on multiple trophic levels	Pauly et al., 1993
Niche overlap	Index describing response to the distribution of resources	Prey and predator interactions used to identify possible aggregations of functional groups	Pianka, 1973
Particle size distribution	Index of growth (ratio of biomass to weight)	Higher in systems with higher biomass estimates of larger species	Sheldon et al., 1972
Ascendency	Index describing resilience	Decreases in systems with low internal constraints (i.e. with a high resilience) and increases with energy transfer efficiency	Ulanowicz, 1986; Scotti et al., 2022b
Finn Cycling index	Index describing maturity	Higher in systems displaying the capacity to reuse energy/matter	Finn, 1976
Trophic aggregation	Assembly of the Lindeman spine	It enables quantifying the trophic transfer efficiency between discrete trophic levels	Lindeman, 1942; Ulanowicz and Kemp, 1979
Primary production required to sustain fisheries (PPR)	Ratio describing fisheries sustainability	It exhibits higher values in upwelling and shelf ecosystems	Pauly and Christensen, 1995
Mixed trophic impact	Impact of interactions between functional groups	Pairwise summary of net impacts between functional groups in response to biomass changes (it also includes fisheries impact)	Ulanowicz and Puccia, 1990
Keystoneness	Key groups of the system	It helps identifying functional groups with structuring role and considerable ecosystem impact despite their relatively low biomass	Libralato et al., 2006; Valls et al., 2015

Description, behavior and reference are provided for each indicator and those that are part of the included ENA toolkit routine are in bold.

factors and anthropogenic activities (Albouy et al., 2013; Corrales et al., 2018; Shabtay et al., 2018; Grossowicz et al., 2020). A large part of the Levantine Sea, the Israeli Mediterranean coast, was modelled with Ecopath (Corrales et al., 2017a), Ecosim (Corrales et al., 2017b; Corrales et al., 2018) and Ecospace (Ofir et al., submitted)[1] to determine the impacts that alien species, sea warming and fisheries have on the ecosystem. The consequences of alien species and fisheries have also been studied in other parts of the Levantine

basin such as the insular shelf ecosystem of Cyprus (Michailidis et al., 2019; Michailidis et al., 2023) and the Gulf of Mersin in Turkey (Saygu et al., 2020). Moreover, EwE was applied to model the effects of aquaculture (Livne et al., 2020), to inform marine spatial planning (Shabtay et al., 2018), and to assess energy- (Grossowicz et al., 2020) and economy-related (Peled et al., 2020; Michael-Bitton et al., 2022) questions.

The Aegean Sea is a relatively closed area in the western part of the eastern Mediterranean Sea, located between Greece and Turkey, with numerous islands and islets (Keramidas et al., 2022). It is one of the most productive areas of the eastern Mediterranean basin, especially its northern part (Tsiaras et al., 2012). It is, however, facing the threats of increasing temperature and alien species

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1   Ofir, E., Corrales, X., Coll, M., Heymans, J. J., Goren, M., Steenbeek, J., et al. (under review). Evaluation of fisheries management policies in the alien species-rich Eastern Mediterranean under climate change. *Front. Mar. Sci.*

invasion, although at a lesser extent than the Levantine Sea (Katsanevakis et al., 2020). In the north, the inflow of nutrient-rich and lower salinity waters originating from the Black Sea and large rivers (Lykousis et al., 2002) supports large biomasses of commercially important small and medium pelagic fishes. This complex interplay between stress factors and biodiversity stimulated the implementation of trophic models to assess the state of the food web and the impact of fisheries (Tsagarakis et al., 2010; Papapanagiotou et al., 2020; Tsagarakis et al., 2021; Tsagarakis et al., 2022). Ecopath and Ecosim models were also developed at a regional scale to assess trophic interactions and fisheries impacts in Thermaikos Gulf (Dimarchopoulou et al., 2022), Pagasitikos Gulf (Dimarchopoulou et al., 2019), and Saronikos Gulf (Papantoniou et al., 2021). Moreover, an Ecopath model was built to examine the effects that fish overexploitation, due to commercial fisheries in Greece and Turkey, has on the whole Aegean ecosystem (Keramidas et al., 2022).

2.2 Central Mediterranean Sea

The Adriatic Sea is a body of water in the northernmost part of the Mediterranean Sea, which separates the Italian Peninsula from the Balkans (Kourafalou, 1999). It is divided into two basins, the northern being the shallowest and the southern being the deepest (Russo and Artegiani, 1996). The Adriatic's salinity is lower than in other Mediterranean basins because the Adriatic collects a third of the freshwater flowing into the Mediterranean Sea thus acting as a dilution basin (Russo and Artegiani, 1996). The northern and central parts of the Adriatic Sea were studied extensively over past years with Ecopath and Ecosim because of their ecosystem characteristics and commercial fisheries concentration (Coll et al., 2007; Barausse et al., 2009; Coll et al., 2009a; Pranovi and Link, 2009; Coll et al., 2010; Libralato et al., 2010; Libralato et al., 2015; Celić et al., 2018); spatial-explicit versions were constructed using Ecospace (Fouzai et al., 2012; Steenbeek et al., 2013). Two Ecopath models, on the microbenthic loop (Vassallo et al., 2006) and the benthopelagic fauna (Vassallo et al., 2017) were developed in southern Adriatic coasts, while an Ecopath model was built for the Strait of Sicily to evaluate the extent of bentho-pelagic coupling in the food web (Agnetta et al., 2019).

In the eastern Ionian Sea, EwE models were built to investigate ecosystem functioning (Piroddi et al., 2016), fisheries (Piroddi et al., 2010; Piroddi et al., 2011a; Moutopoulos et al., 2013; Moutopoulos et al., 2018) and aquaculture (Piroddi et al., 2011b). Four Ecopath models were constructed for the areas of Salento (northeastern sector) and Calabria (southwestern sector) to characterize ecosystem functioning (Ricci et al., 2019; Ricci et al., 2021), while one model of the Gulf of Taranto was assembled to assess interactions between cetaceans and commercial fisheries (Carlucci et al., 2021). Outside of the European waters, an Ecopath model was developed for the Gulf of Gabes, Tunisia (Hattab et al., 2013). It was extended to implement spatio-temporal simulations (Abdou et al., 2016; Halouani et al., 2016; Abdou et al., 2020) and trophic analysis (Halouani et al., 2015). These models, even though were developed for the northern African coasts, were included in the review because they are located in the central Mediterranean Sea and adjacent to European waters.

2.3 Western Mediterranean Sea

The Balearic Sea is part of the wider north-west Mediterranean Sea and is considered to be the most productive area of the otherwise oligotrophic Mediterranean Sea (D'Ortenzio and Ribera d'Alcalà, 2009). It is a breeding ground for small pelagic fishes such as the European anchovy (Engraulis encrasicolus). Moreover, it represents a major fishing ground for commercial fisheries and a highly exploited ecosystem (Papaconstantinou and Farrugio, 2000). The south Catalan Sea is in the northern part of the Balearic archipelago and is the most modelled area of the Mediterranean Sea (Coll and Libralato, 2012). It has been extensively modelled using EwE, either considering a static framework (Ecopath: Coll et al., 2006a; Coll et al., 2006b; Coll et al., 2009b; Navarro et al., 2011) or implementing temporal (Ecosim: Coll et al., 2008a; Coll et al., 2008b; Coll et al., 2012; Forrestal et al., 2012; Coll et al., 2013; Tecchio et al., 2013) and spatiotemporal (Ecospace: Coll et al., 2016a; Pennino et al., 2020) simulations. An Ecopath model that describes food web traits and resilience to fisheries exploitation was developed for the wider area of the northwestern Mediterranean Sea (Corrales et al., 2015). Smaller-scale models were constructed for other regions of the western Mediterranean Sea: the Gulf of Lions (Bănaru et al., 2013; Vilas et al., 2021; Seyer et al., 2023), the Gulf of Alicante (García-Rodríguez et al., 2021), the Santa Pola Bay (Bayle-Sempere et al., 2013; Izquierdo-Gomez et al., 2016), the Cerbère-Banyuls (France), Cap de Creus (Spain) and Medes Islands (Spain) MPAs (Corrales et al., 2020b), and the Port Cros; case studies integrating the EcoTroph plug-in are also available (Valls et al., 2012; Prato et al., 2014). Further east, in the wider areas of the Tyrrhenian and Ligurian seas, EwE models were built focusing on fisheries (Pinnegar and Polunin, 2004; Albouy et al., 2010; Vanalderweireldt et al., 2022), aquaculture (Díaz López et al., 2008), MPAs (Prato et al., 2016) and the microbenthic loop (Fabiano et al., 2004; Vassallo et al., 2012; Vassallo et al., 2013; Vassallo et al., 2022).

2.4 Black Sea

The Black Sea is a marginal sea located at the northeast of the Mediterranean Sea, which is connected with the Aegean Sea through the Sea of Marmara. It is the world's largest body of water with a meromictic basin as the deep waters do not mix with the upper layers that receive oxygen from the atmosphere (Sabatino et al., 2020). As a result, over 90% of the deeper Black Sea volume is anoxic and water circulation is primarily controlled by basin topography and fluvial inputs, which result in a strongly stratified vertical structure (Reeburgh et al., 1991). In the previous decades, significant trophic transformations occurred in the basin, with the most remarkable being the introduction and extreme expansion of the warty comb jelly (Mnemiopsis leidyi), an invasive ctenophore from the western Atlantic. In particular, the outburst of M. leidyi in the late 1980s was facilitated by the simultaneous action of overfishing, climate and nutrient enrichment (Bodini et al., 2018). The abrupt increase in the size of M. leidyi population led to a dramatic drop in commercially important small pelagics like the European anchovy due to competition for the same food sources (mostly copepods) and intraguild predation on its eggs (Kideys, 2002).

Two EwE models were created for the Black Sea, focusing on fishing effects on the food web along a timeline of 30 years, starting from the 1960s (Daskalov, 2002), and assessing the relationships that later linked overfishing to the successful establishment of the warty comb jelly (Gucu, 2002). Moreover, for better understanding food web dynamics, four Ecopath models of the Black Sea were constructed. These models focus on reference periods that match significant structural changes in the food web: (1) the pre-eutrophication period of 1960s, (2) the intense eutrophication phase of 1980s, (3) the regime shift of early-1990s with warty comb jelly displacing the European anchovy, and (4) the post-eutrophication period of the late-1990s with increasing top-down control of another invader, i.e., the brown comb jelly (*Beroe ovata*) over *M. leidyi* (Akoglu et al., 2014). Finally, three Ecopath models were recently developed in the Sea of Marmara, the connecting water body between the Black Sea and the Aegean Sea, investigating fisheries impacts in the food web during the period of three decades (Saygu et al., 2023).

2.5 Bay of Biscay, Celtic Sea and Iberian coast

The Bay of Biscay is a relatively large and deep gulf of the northeast Atlantic Ocean, located south of the Celtic Sea. It is considered a very productive area due to the upwelling characteristics and the drainage waters of large rivers (Borja et al., 2008). It displays a high biodiversity with many habitats and marine species, including endangered and protected species like cetaceans and seabirds (Matear et al., 2019). It faces intense human pressure, including industrialised commercial fisheries from France and Spain, and significant marine transportation (Lorance et al., 2009). EwE models were developed for the Bay of Biscay/Celtic Sea ecosystem (Bentorcha et al., 2017), the Bay of Biscay as a whole (Moullec et al., 2017; Corrales et al., 2022), including a specific focus on its continental shelf only (Lassalle et al., 2011; Lassalle et al., 2012; Lassalle et al., 2014; Le Marchand et al., 2022), and the Celtic Sea (Hernvann et al., 2020). The southern part of the Bay of Biscay, the Cantabrian Sea, is comparatively less studied, with an Ecopath model developed for 1994 to assess fisheries impacts on the food web of the continental shelf (Sánchez and Olaso, 2004). A single Ecopath model was developed describing the trophic network of the Gironde Estuary for the late-1990s/early-2000s (Lobry et al., 2008). The Gironde Estuary is one of the largest and least-polluted estuaries in northern Europe (Sautour and Castel, 1995) and its basin is connected with the Bay of Biscay.

South of the Bay of Biscay and Celtic Sea lies the west coast of the Iberian Peninsula. An Ecopath model was developed for the Gulf of Cadiz, located at the southern part of the west coast, investigating the trophic relationships and fishing impacts in an exploited ecosystem (Torres et al., 2013). Further north, EwE models were constructed for the Portuguese and Galician coasts, focusing on food web structure and ecological roles (Veiga-Malta et al., 2019; Giralt Paradell et al., 2020; Giralt Paradell et al., 2021), small pelagic fisheries (Szalaj et al., 2021) and climate (Szalaj et al., 2022). Smaller parts of the west coast of the Iberian Peninsula and lagoon ecosystems were modelled separately;

namely, the Ria Formosa (Gamito and Erzini, 2005), the Mondego Estuary (Patrício and Marques, 2006; Baeta et al., 2011), the Ria de Aveiro (Bueno-Pardo et al., 2018) and the Ria de Arousa (Outeiro et al., 2018). In the southernmost part of the NE Atlantic is the Azores archipelago, composed of nine islands under Portuguese jurisdiction, where an Ecopath model was developed to describe the food web and vulnerabilities of an open-ocean ecosystem (Morato et al., 2016). Finally, a theoretical seamount ecosystem of the NE Atlantic was used as the basis for a trophic model to examine the potential effects of an increase in primary productivity (Morato et al., 2009).

2.6 Baltic Sea

The Baltic Sea is a marginal sea of the northeastern Atlantic Ocean, with limited water exchange between the two water bodies (Barale, 2008). It is considered one of the largest brackish water bodies in the world and its salinity is significantly lower than that of ocean waters (Vuorinen et al., 2015), defining its inherent low biodiversity (Ojaveer et al., 2010). As saltwater is denser than freshwater, the bottom of the Baltic Sea is saltier than the surface (Sohlenius et al., 2001). This condition creates vertical stratification of the water column, i.e., a halocline, which represents a barrier to the exchange of oxygen and nutrients and fosters completely separate marine environments (Väli et al., 2013). The Baltic Sea has been exposed to the simultaneous action of multiple interacting pressures, a feature that qualifies this ecosystem as an ideal site to predict the impact and formulate mitigation of future coastal perturbations (Reusch et al., 2018). As the Baltic proper is subject to most of the human pressures, such as fishing, nutrient pollution and climate change, scientific research and development of ecosystem models in the Baltic Sea have been concentrated mostly there (Korpinen et al., 2022; Reckermann et al., 2022). Several EwE models have been developed in this area, including Ecopath (Sandberg et al., 2000; Harvey et al., 2003; Tomczak et al., 2012; Tomczak et al., 2013), Ecosim (Österblom et al., 2007; Niiranen et al., 2013; Costalago et al., 2019) and Ecospace (Bauer et al., 2018; Bauer et al., 2019) applications, focusing mostly on primary production fluctuations and climate change impacts on the food webs. Recently, an EwE model of the western Baltic Sea was constructed to assess the impact that alternative fisheries management strategies have on the status of commercial stocks, diversity of top predators and fishing yield (Scotti et al., 2022a). At a smaller scale, an Ecopath model was developed for an open coastal area in the southwestern part of the Bothnian Sea to evaluate radioactive fluxes in the food web using the Ecotracer tool (Sandberg et al., 2007). Finally, separate Ecopath models were created for five southeastern Baltic Sea ecosystems to compare the structure of their carbon flow networks: the Puck Bay, the Curonian Lagoon, the Lithuanian coast, the coastal area of the Gulf of Riga and the Pärnu Bay (Tomczak et al., 2009).

2.7 North Sea

The North Sea is a shelf sea on the European continental shelf, connected to the Atlantic Ocean through the English Channel in the

south and the Norwegian Sea in the north (Lüdmann et al., 2021). It is a relatively shallow sea, with a mean depth of 90 meters (Lee, 1980). Due to the large human population and high level of industrialization along its shores, the wildlife of the North Sea has suffered from pollution, overhunting, and overfishing, with most of the commercial fisheries stocks considered to be either fully exploited or overexploited (Akbari et al., 2022). The North Sea is Europe's main fishing ground, accounting for over 5% of international commercial fish caught, concentrated mostly in the southern part of the coastal waters (Mackinson et al., 2018). An Ecopath model representing the total area of the North Sea was created for 1981, known as the '*Year of the Stomach*', when more than 55,000 fish were sampled and analysed for their stomach contents through an ICES-coordinated project (Christensen, 1995a). Other EwE models were developed for different periods (Beattie et al., 2002; Mackinson and Daskalov, 2007; Heymans et al., 2011a; Romagnoni et al., 2015) while an Ecosim model of the same area, using multiple environmental drivers, served as the basis for multi-annual plans regarding fisheries and management in the North Sea (Mackinson, 2014). An EwE model was constructed for the southern part of the North Sea to focus on fisheries management (Stäbler et al., 2016; Stäbler et al., 2018); the model was then used as a backbone to develop an Ecospace application integrating habitat preferences (Püts et al., 2020; Püts et al., 2023). In the western part of the North Sea, Ecopath models were developed for the northeastern coast of Scotland (Otogo et al., 2015) and the Eden Estuary (Watson et al., 2020).

2.8 English Channel, Irish Sea and west Scottish Sea

The English Channel is a strait of the Atlantic Ocean that separates southern England from northern France, and is linked to the southern part of the North Sea by the Strait of Dover (Smith, 1989). It is the busiest shipping area in the world (Glegg et al., 2015) and has been exposed to environmental problems caused by accidents involving ships with toxic cargos and oil spills (Vieites et al., 2004). Despite the intense marine traffic, it remains an important ecosystem for marine species that inhabit its numerous bays and estuaries, especially in the western part, including marine mammals such as the grey seal (*Halichoerus grypus*) and the harbour seal (*Phoca vitulina*; Vincent et al., 2017). Separate EwE models were developed for the western part (Araújo et al., 2005; Araújo et al., 2006; Araújo et al., 2008) and the eastern part (Villanueva et al., 2009; Daskalov et al., 2011; Metcalfe et al., 2015). An area of the eastern English Channel, the Bay of Seine, has been extensively modelled with EwE because of its ecological characteristics and multiple anthropogenic disturbances. Several models have been constructed giving insights on food web structure (Rybarczyk and Elkaïüm, 2003; Tecchio et al., 2015), energy facilities disturbance (Pezy et al., 2017; Raoux et al., 2017; Raoux et al., 2019; Halouani et al., 2020; Noguès et al., 2022) and climate change (Bourdaud et al., 2021). At a smaller scale, food web models were created for the Bay of Somme (Rybarczyk et al.,

2003), the Bay of Mont Saint Michel (Arbach Leloup et al., 2008), the Tamar Estuary (Watson et al., 2020) and the Canche Estuary (Selleslagh et al., 2012)

Further north, the continental shelf of the west coast of Scotland, including the waters around the islands in the Sea of the Hebrides, has been extensively modelled with Ecopath (Alexander et al., 2015), Ecosim (Heymans et al., 2011b; Serpetti et al., 2017; Baudron et al., 2019) and Ecospace (Sayer et al., 2005; Alexander et al., 2016; Serpetti et al., 2021). The Irish Sea is an extensive body of water that separates the islands of Ireland and Great Britain and is linked to the sea of the west coast of Scotland in the north by the North Channel, engulfing numerous estuaries with great biodiversity. However, it is considered to be one of most radioactively contaminated seas in the world with high amounts of nuclear waste, like ^{137}Cs, Pu, and ^{241}Am, discharged daily into it from the Sellafield nuclear site (Ray et al., 2020). This discharge contaminates seawater, sediments and marine life, and several EwE models were developed to address these issues (Tierney et al., 2018; Bentley et al., 2019a; Bentley et al., 2019b; Bentley et al., 2019c; Bentley et al., 2020). Finally, an Ecopath model was built for the Faroe Islands marine ecosystem in 1997 and extended with spatio-temporal simulations to 2007 for modelling spatial fishing restrictions (Zeller and Reinert, 2004).

2.9 Norwegian and Barents Seas

The Norwegian Sea is a marginal sea of the Atlantic Ocean, located northwest of Norway and north of the North Sea. Unlike the majority of the world seas, most of the bottom of the Norwegian Sea is not part of a continental shelf and therefore it is characterised by deep waters (Sætre, 1999). It is in fact a transition zone between Boreal and Arctic conditions, and is thus inhabited by biodiversity of both climatic regions, including many seabirds and marine cetaceans (Jørgensen et al., 2022). In the northeast, its waters are linked to the Barents Sea, which is located in the southern part of the Arctic Ocean (Johannesen et al., 2012). Contrarily to the Norwegian Sea, the Barents Sea is a relatively shallow shelf sea (Gudlaugsson, 1993). The Barents Sea contains the world's largest remaining population of Atlantic cod (*Gadus morhua*) while the Norwegian Sea is one of the most important spawning grounds of the Atlantic herring (*Clupea harengus*), defining them as very important commercial fishing grounds (Ottersen et al., 2014; Pampoulie et al., 2015). EwE models were developed to describe these systems, focussing on the Norwegian Sea and Barents Sea ecosystem as a whole (Dommasnes et al., 2001; Bentley et al., 2017), on the Barents Sea ecosystem (Blanchard et al., 2002; Megrey and Aydin, 2009; Pedersen et al., 2021; Pedersen, 2022) and the Pechora Sea (Larsen et al., 2016). The coastal areas of the Norwegian Sea, known as fjords, are unique and important and have been modelled using EwE to study the Arctic ecosystem functioning (Pedersen et al., 2008; Pedersen et al., 2016), the red king crab (*Paralithodes camtschaticus*) invasion (Pedersen et al., 2018), and ocean warming impacts on kelp forests (Vilas et al., 2020a; Vilas et al., 2020b).

3 Results

Overall, 195 Ecopath models, 70 Ecosim models, 28 Ecospace models and 8 EcoTroph models from the European seas were extracted from 168 peer-reviewed journal publications (Figure 1). Altogether, a total of 301 EwE models were reviewed and analysed, including original models (n=212, 70%), their updated versions with the inclusion of Supplementary Data and information (n=32, 11%), and variant versions with modifications of the original or updated models according to the research subject and needs (n=57, 19%). While the models covered nine different regions, most publications referred to the western Mediterranean Sea (n=31, 18%) while the Black Sea had the fewest (n=4, 2%). More than half of all publications dealt with the investigation of food web structure, functioning and ecological roles (35%), and fisheries (28%; Figure 2). The majority of the models were mass-balanced Ecopath base models, most of which were in the western Mediterranean Sea (n=37, 19%), followed by the Bay of Biscay, Celtic Sea and Iberian coast region (n=35, 18%). In the Mediterranean Sea, the western region was described by most models (n=57, 46%) and publications (n=31, 40%), and is followed by central (n=39, 31% and n=27, 35%) and eastern regions (n=29, 23% and n=19, 25%). The cumulative number of EwE models increased with time, with the highest rate of increase observed for Ecopath models (Figure 3). Almost half of the models were published in the 2010s (49%), with a high number of publications appearing after 2020 (28%). The number of functional groups (FGs) included in the models exhibited similar patterns, with an increasing trend (i.e., higher resolution in food web construction) over time; their number ranged from 8 up to 108,

although most of the models (32%) were composed of 31 to 40 FGs (Figure 4). Regarding forcing factors driving spatio-temporal dynamics and used for hindcasting, most of them were related to trophic interactions with the estimation of vulnerabilities (74%), fisheries (74%) and primary production (61%) (Figure 5). The bulk of Ecopath models describes trophic networks in the 1990s (n=58, 30%) and 2000s (n=67, 34%) while no model has a starting year before 1950. Ecosim models had a simulation timeframe reaching up to 150 years, monitoring biomass, fisheries and climate changes over a two-century period while Ecospace displayed a shorter simulation timeframe; i.e., less than 100 years, because of its spatial nature and resulting data and computational requirements, demanding longer simulation runs (Walters et al., 1999).
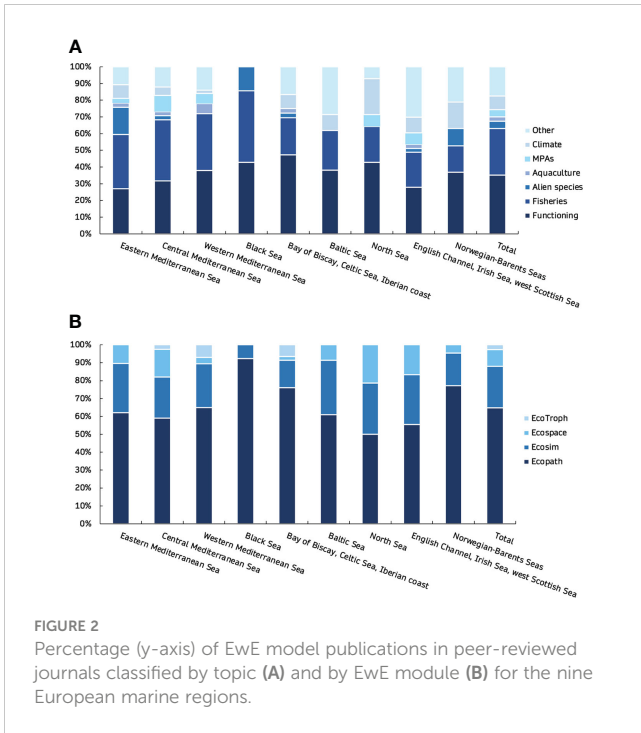
3.1 Ecosystem indicators and summary statistics

Ecological indicators obtained from Ecopath summary statistics for the models in the nine European marine regions are given as weighted averages for each area, including the minimum and maximum range limits (Table 2). These indicators were scaled and visualised as radar charts for comparisons (Figure 6). The largest average Ecopath modelling area was found for the Norwegian-Barents Sea region (almost 1 million km^2) while the smallest was that of the western Mediterranean Sea region (below 5,000 km^2), indicating the presence of many smaller models. A pattern of increasing modelling area with decreasing latitude was observed. The Norwegian-Barents Sea and the North Sea regions had the highest number of FGs (47 each), followed by the western
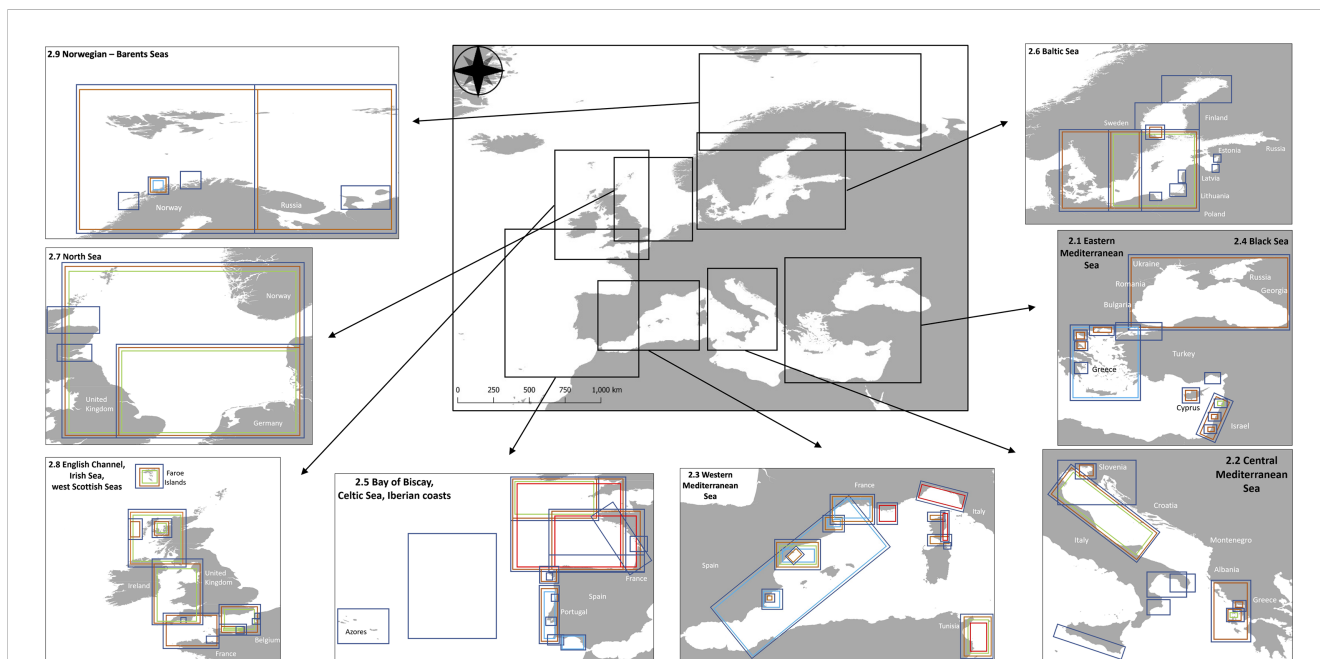

FIGURE 1
Map showing the nine European marine regions considered in this review. Colored rectangles encompass the approximate area modelled with EwE in all nine regions, including Ecopath models (blue rectangles), Ecosim models (orange rectangles), Ecospace models (green rectangles), EcoTroph models (red rectangles), and ECOIND plug-in expansions (light blue rectangles).

FIGURE 2
Percentage (y-axis) of EwE model publications in peer-reviewed journals classified by topic **(A)** and by EwE module **(B)** for the nine European marine regions.

FIGURE 4
Number of functional groups (y-axis) in relation with time of Ecopath models **(A)** and divided by size classes **(B)** in all nine reviewed European marine regions. The dotted line illustrates the trend identified with a linear model, indicating a correlation with highly statistical significance (p value < 0.001).
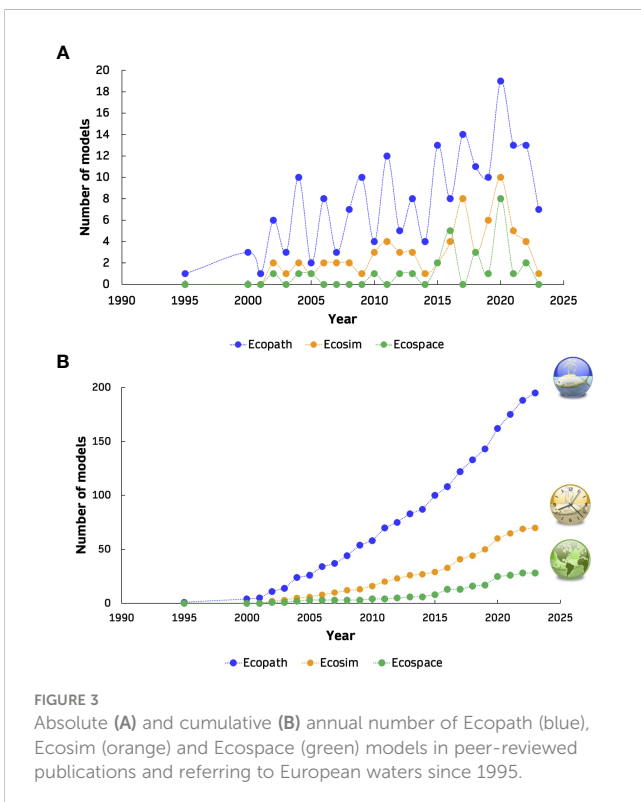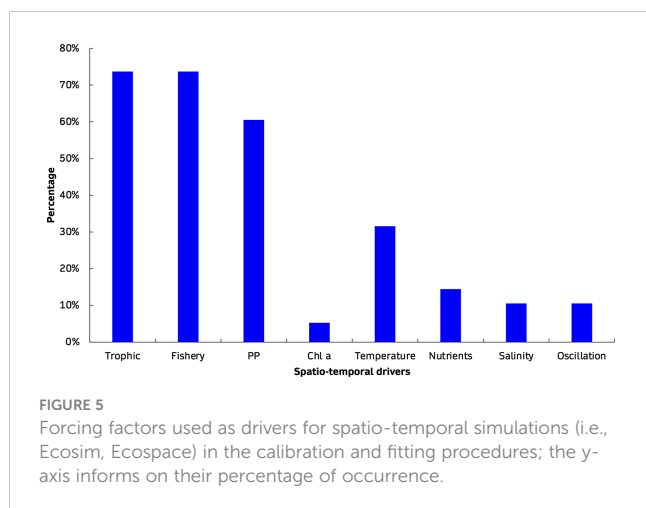
Mediterranean Sea (41); the Black Sea had the fewest (13) and total average number of FGs was 34.

The Total System Throughput (TST) expresses the sum of all system's flows (total consumption + total export + total respiration + total flows to detritus), representing the size of the system (Ulanowicz, 1986). The North Sea region had the highest average TST (10,285.1 tkm^{-2}year^{-1}) while the eastern Mediterranean
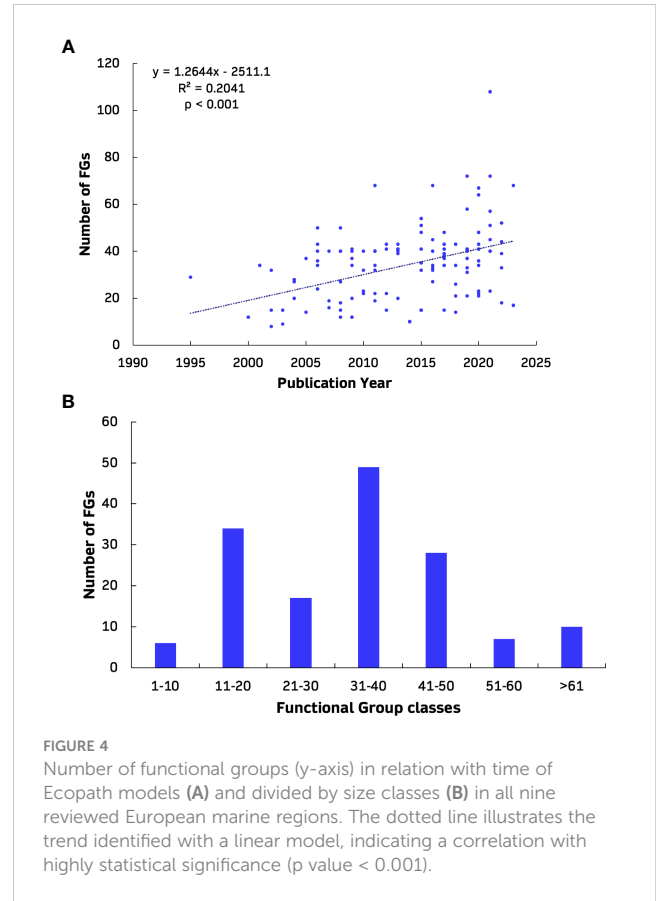
Sea had the lowest (1,767.8 tkm^{-2}year^{-1}), a pattern that is in line with expectation as TST depends on the number of flows in a network (Scharler et al., 2015). The Bay of Biscay, the Celtic Sea and Iberian coast had the highest total primary production, followed by other upwelling or eutrophic areas like the North Sea and the west Scottish Sea. Ecosystem maturity can be expressed as the ratio of total primary production over total respiration (Odum, 1971); the less mature ecosystems were in the Baltic Sea region (8.48) while those closest to maturity were in the Norwegian-Barents Sea region (1.01). In less mature systems the production exceeds the respiration for most groups, leading to ratios greater than 1 (Odum, 1971). Average estimates of total biomass (excluding detritus) were higher in the Bay of Biscay, Celtic Sea and Iberian coast models (851.1 tkm^{-2}) while those in the Black Sea had the lowest values (22.7 tkm^{-2}). Regarding commercial fisheries, the ecosystems with most catches (landings plus discards) were observed in the Bay of Biscay, Celtic Sea and Iberian coast region (14.1 tkm^{-2}year^{-1}) following biomass trends, while lowest levels of fish extraction were found in the Norwegian-Barents Sea region (0.08 tkm^{-2}year^{-1}). Mean trophic level of the catch (MTLc) provides clues about the effect of fisheries on the ecosystem; it is calculated as the weighted average trophic level of the species removed, with their relative biomass contribution to the catch used as a scaling factor (Shannon et al., 2014). A decreasing trend of this indicator in time relates to the progressive overexploitation of fish stocks along the trophic chain, from top predators to lower trophic-level consumers (Pauly et al., 1998). The Bay of Biscay, Celtic Sea and Iberian coast

FIGURE 3
Absolute **(A)** and cumulative **(B)** annual number of Ecopath (blue), Ecosim (orange) and Ecospace (green) models in peer-reviewed publications and referring to European waters since 1995.

FIGURE 5
Forcing factors used as drivers for spatio-temporal simulations (i.e., Ecosim, Ecospace) in the calibration and fitting procedures; the y-axis informs on their percentage of occurrence.

ecosystems had the highest average MTLc scores (3.59), indicating the presence of large predatory species in the catch while central Mediterranean, English Channel, Irish Sea and west Scottish Sea regions had the lowest average scores (<3), which represents highly exploited fish stocks. The System Omnivory index (SOi) is a measure of the distribution of feeding interactions among trophic levels, developed for complexity and connectivity evaluations in the food web (Pauly et al., 1993). The North Sea region had the highest SOi (0.24), indicating that various trophic groups obtain energy from trophic chains of different lengths. However, all models were characterised by low values compared to temperate ecosystems close to the tropics (Christensen, 1995b).

3.2 Ecological indicators of the ECOIND plug-in

A series of algorithms enabling the calculation of various ecological indicators was added to EwE with the ECOIND plug-in (Coll and Steenbeek, 2017). This plug-in returns standardised indicators incorporating a series of biological traits and features, and provides useful tools for further analysis of the ecosystem, in both static and spatio-temporal dynamics. Due to the relatively recent integration of ECOIND into EwE, it was not widely used in the EwE models reviewed here (Table S3). ECOIND results can be extracted adopting a static (Coll and Steenbeek, 2017; Vilas et al., 2020a; García-Rodríguez et al., 2021; Keramidas et al., 2022) or a spatio-temporal dynamic (Bentley et al., 2019a; Corrales et al., 2020b; Hernvann et al., 2020; Vilas et al., 2020b; Vilas et al., 2021; Le Marchand et al., 2022; Piroddi et al., 2022; Szalaj et al., 2022) perspective.

The ECOIND plug-in can facilitate the comparison between ecosystems with respect to food web structure and functioning (Coll and Steenbeek, 2017). In the latest ECOIND edition, indicators are classified into five categories: (1) biomass, (2) catch, (3) trophic, (4) species, and (5) size-based. Various assessments related to the MSFD have already been successfully implemented with ecological indicators derived from models of various types (e.g.,

biogeochemical, hydrodynamic, multi-species, end-to-end) in a number of software programs, including EwE (Lynam and Mackinson, 2015; Susini and Todd, 2021), with encouraging results (Piroddi et al., 2015a). There is a multitude of ecological indicators, which can also inform ecosystem-based fisheries management (EBFM), that have been used to successfully address fisheries (Fay et al., 2013; Lassen et al., 2013; Halouani et al., 2019; Link and Watson, 2019) and climate (Shin et al., 2018) issues. As the stressors affecting marine ecosystems increase, so is the need for testing and validating ecological indicators (Rombouts et al., 2013; Ito et al., 2023). A key issue facing the scientific community is the identification of indicators that are the most suitable to effectively describe the status of ecosystems, helping decision-making bodies (Safi et al., 2019). EwE is based on an interactive approach within the scientific community and ECOIND represents a quick and user-friendly tool for assessments based on ecological indicators (Coll et al., 2016b).

4 Discussion

This review of all published Ecopath with Ecosim (EwE) models of European seas aims to serve as an easily accessible and quick guide for researchers working on ecosystem modelling. This centralised aggregation of European EwE models and their metadata highlights the evolution of models and research topics over time and across space. European seas and the NE Atlantic have been extensively modelled, compared to other regions like the Indian and Antarctic Oceans. Also, the Mediterranean Sea has been modelled as a whole ecosystem with two Ecopath models representing the 1950s and the 2000s, sub-divided into four separate sections: western, Adriatic, Ionian and eastern region (Piroddi et al., 2015b). These sub-models were simulated temporally (Piroddi et al., 2017) with Ecosim to demonstrate the effects of climate change and fisheries, and spatiotemporally with Ecospace (Piroddi et al., 2022) to inform ecosystem-based management (EBM). Scientific projects with adequate funding schemes and data availability can support this trend in European regions (Colléter et al., 2015). However, there are still some European marine ecosystems with no existing models; this is the case of several Mediterranean countries (e.g., Malta, Albania and Montenegro) and the southern part of the Norwegian Sea. As many models assessed by this review are not in EcoBase, we strongly encourage the scientific community to use this repository to store metadata of EwE models and take advantage of this large network of users (Colléter et al., 2015). However, the existence of a quality control evaluating the models stored in the EcoBase, similar with the Ecopath pedigree routine, including also Ecosim and Ecospace models (e.g., a quality measure with a traffic light system), would be beneficial for scientists implementing various meta-analyses. Ecopath models are the most numerous because they are a prerequisite for further developing temporal (Ecosim) and spatial (Ecospace) simulations (Christensen and Walters, 2004a). As several Ecopath models have been already developed in the European seas, a good future suggestion can be their temporal or

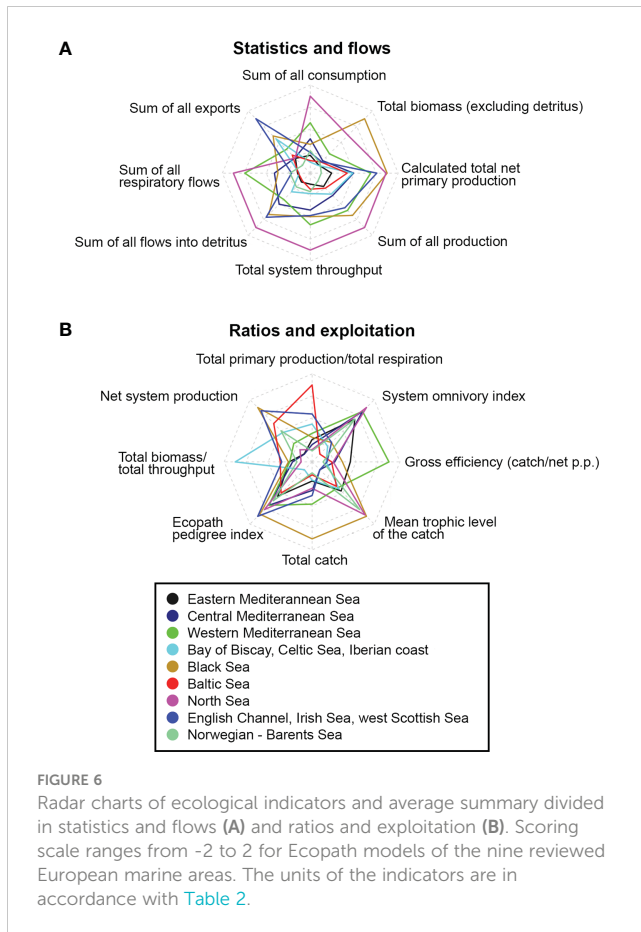TABLE 2 Summary statistics of Ecopath models in European areas of interest.

Parameter	Units	2.1 Eastern Mediterranean Sea	2.2 Central Mediterranean Sea	2.3 Western Mediterranean Sea	2.4 Black Sea	2.5 Bay of Biscay, Celtic Sea, Iberian coast	2.6 Baltic Sea	2.7 North Sea	2.8 English Channel, Irish Sea, west Scottish Sea	2.9 Norwegian-Barents Seas
Area modelled	km^2	20253 (1.5-201535)	21382 (405-61000)	4924 (0.6-45547)	103833 (11500-150000)	100148 (8.6-1000000)	103207 (11.5-240000)	411477 (1513.5-570000)	31365 (7.8-190200)	948638 (11.8-3116000)
No of FGs		35 (14-48)	38 (19-72)	41 (12-72)	13 (8-17)	37 (14-52)	15 (12-22)	47 (29-68)	31 (9-51)	47 (27-108)
Sum of all consumption	tkm^{-2}y^{-1}	937.9 (185-1456)	1962.7 (348-4679)	3114 (51.4-21339.9)	485.5 (234.4-832)	1672.2 (277.8-7943.45)	589.4 (68-3435)	4905.7 (2333-6227)	1138.1 (44.2-3905)	1252.1 (207.8-2528.5)
Sum of all exports	tkm^{-2}y^{-1}	307.5 (41.6-686)	379.2 (1.7-960)	660.4 (21-1348.09)	990.6 (48.6-2504)	1096.3 (1.16-4654)	425.3 (8.3-1375)	317 (105-655)	1702 (84.5-6945)	62.4 (-0.67-179.9)
Sum of all respiratory flows	tkm^{-2}y^{-1}	332.3 (96.6-571)	893.7 (174.8-2375.4)	1695.7 (20.2-15151.4)	284.4 (157-449)	852.7 (134.7-2792.8)	310.3 (18-1851)	2039.7 (1501-2658)	488.4 (20.4-1330)	531.5 (106.2-1062.8)
Sum of all flows into detritus	tkm^{-2}y^{-1}	624.3 (283.5-1297)	1708.8 (508.9-4605)	1555 (65.8-5723.2)	1138.5 (191.2-2713)	2335.8 (193.6-17057)	564.2 (53-2246)	3023.1 (1348-3867)	2484.1 (296-12837)	882.5 (82.9-1919.1)
Total System Throughput	tkm^{-2}y^{-1}	1767.8 (583.3-1521)	4944.5 (1033.5-11792)	7025.2 (157.42784)	2998.8 (681.7-6499)	5956.7 (629-24544)	2408.8 (656-8007)	10285.1 (5837-12786)	5832.3 (1161-25017)	2728.6 (399.6-5638.3)
Sum of all production	tkm^{-2}y^{-1}	868.7 (296.4-1521)	1520.9 (599-3303)	2524 (14.83-14006)	1376.9 (286.5-3164)	2816.7 (182-12315)	984.2 (40-3296)	3634.3 (2551-4717.7)	2305.7 (417.1-9371)	486.8 (167.3-1920)
Mean Trophic Level of the Catch		3.21 (2.02-3.47)	2.97 (2.39-3.44)	3.19 (2-3.94)	3.18 (3.03-3.36)	3.59 (3.25-4.08)	3.14 (3.02-3.3)	3.57 (3.42-3.7)	2.89 (2.11-3.61)	3.49 (2.94-4.11)
Gross efficiency		0.004 (0.001-0.01)	0.002 (0.001-0.004)	0.008 (0.0001-0.05)	0.0009 (0.0001-0.002)	0.003 (0.001-0.009)	0.0016 (0.0002-0.0061)	0.0018 (0.0004-0.0027)	0.001 (0.0002-0.003)	0.0005 (0.0004-0.0007)
Calculated total net PP	tkm^{-2}y^{-1}	609.8 (240.2-1243)	1288.4 (495.4-2583)	1859.8 (386.7-7818.1)	1272.9 (256.1-2948)	2335.7 (135.9-11605)	1093.6 (28-3222)	2301.3 (2145-2609)	2015.3 (229.3-8275)	289.4 (110.7-1100.4)
Total PP/Total respiration		2.31 (1.1-4.26)	1.82 (1-2.83)	2.91 (0.8-6.84)	4.05 (1.16-7.9)	2.55 (0.56-8.2)	8.48 (1.05-21.35)	1.16 (0.98-1.4)	5.2 (1.09-22.1)	1.01 (1-1.03)

(Continued)

TABLE 2 Continued

Parameter	Units	2.1 Eastern Mediterranean Sea	2.2 Central Mediterranean Sea	2.3 Western Mediterranean Sea	2.4 Black Sea	2.5 Bay of Biscay, Celtic Sea, Iberian coast	2.6 Baltic Sea	2.7 North Sea	2.8 English Channel, Irish Sea, west Scottish Sea	2.9 Norwegian-Barents Seas
Net system production	tkm^{-2}y^{-1}	277.6 (28.5-672)	340.1 (6.7-746.2)	654.7 (-20.19-1346.4)	988.6 (48.6-2499)	1823.6 (1.16-9492)	1291.7 (8.3-2973.8)	416.9 (189.8-644)	1714.6 (22.9-6945)	
Total PP/Total biomass		18.7 (8-31.9)	14.7 (8.8-23.2)	18.2 (1.5-34)	83.2 (44.8-132)	19.4 (0.9-67.7)	29.2 (5.8-108.2)	4.1 (3.8-4.7)	27.3 (6.9-100.6)	9.2
Total biomass (excluding detritus)	tkm^{-2}	30.6 (8.7-78)	101.3 (21.3-247.7)	218.4 (3.93-1284)	22.7 (1.9-56.2)	851.1 (12.9-13201	79.4 (0.9-361.7)	556.2 (554-558)	86.6 (4.5-245)	59.2 (13.7-118.8)
Total Catch	tkm^{-2}y^{-1}	1.8 (0.4-3.4)	3.5 (0.6-9.5)	6.3 (0.2-36.9)	1.6 (0.03-4.5)	14.1 (3.06-45.1)	0.5 (0.03-1.2)	3.34 (0.8-5.9)	4.9 (1.5-15.9)	0.08 (0.02-0.3)
System Omnivory Index		0.21 (0.16-0.25)	0.23 (0.1-0.36)	0.23 (0.16-0.34)	0.14 (0.07-0.2)	0.15 (0.06-0.27)	0.12 (0.05-0.23)	0.24 (0.22-0.27)	0.15 (0.01-0.33)	0.21 (0.18-0.23
Ecopath Pedigree Index		0.53 (0.11-0.65)	0.58 (0.5-0.66)	0.58 (0.46-0.67)	0.41	0.61 (0.53-0.69)		0.59	0.62 (0.52-0.63)	0.55

Ecosystem indicators are reported as average scores in a weighted scale for each area. For each indicator, minimum and maximum values are in brackets.

Radar charts of ecological indicators and average summary divided
in statistics and flows **(A)** and ratios and exploitation **(B)**. Scoring
scale ranges from -2 to 2 for Ecopath models of the nine reviewed
European marine areas. The units of the indicators are in
accordance with Table 2.

spatio-temporal expansion with Ecosim and Ecospace, which are
comparatively less developed, recognizing nevertheless the
difficulties of obtaining reliable spatial biological and
environmental data for validation and hindcasting (Townsend
et al., 2014; Colléter et al., 2015).

In line with the need for more effective and holistic considerations
in fisheries management, the EBFM approach is key to moving
forward. According to Pikitch et al. (2004), the aim of EBFM is
threefold: (1) to maintain ecosystem health and resilience, and
fisheries sustainability; (2) to take into account all ecosystem
components; and (3) to establish a network of indicators to measure
ecosystem degradation. EwE can inform on ecosystem-based
management (EBM; Piroddi et al., 2022) and more specifically
EBFM, with many representative studies (e.g., Guénette et al., 2006;
Bourdaud et al., 2016) supporting practical implementations (Smith
et al., 2007; Ofir et al., 2022). EBFM takes into consideration the
complex dynamics of ecological, fisheries and human interactions in
management (Long et al., 2015). EwE models embraced this direction,
including aspects of previously ignored ecosystem elements (e.g.,
species interactions, discards and bycatch) to implement a holistic
approach to managing fisheries (Fulton et al., 2014; Trochta et al.,
2018). The EwE modelling framework incorporates fisheries, species
interactions, environmental drivers, human activities, complexity and
uncertainty, all important aspects of EBFM (Collie et al., 2016). In the
future, more emphasis can be placed on plug-ins such as EcoTroph
and/or ECOIND. EcoTroph can provide in fact more insights into the

distribution of biomass and catch among trophic levels, taking into
account the whole trophic spectrum, while ECOIND can further
expand the framework of ecological analyses.

The assessment of ecosystem summary indicators highlighted
some interesting trends. Highest average estimates of total biomass
(excluding detritus) and of trophic flows were observed in
ecosystems at higher latitudes. Positive correlations between
biomass and fishery yields at colder, higher latitude ecosystems
have been observed in the literature (Friedland et al., 2012). Such
systems appear to have high seasonal productivity, being favoured
by advection processes to sustain large shoals of commercially
important fishes (Hunt et al., 2016). However, these systems are
among the first to be affected by ocean warming (Kjesbu et al., 2014;
Lotze et al., 2019). Many publications from the current review (e.g.,
Bentley et al., 2017; Vilas et al., 2020b; Pedersen et al., 2021)
presented models considering the impacts of climate change and
ocean warming (Stock et al., 2023). Consequently, the majority of
the climate-related publications were focused on higher-latitude
ecosystems (63%). In the Mediterranean Sea, chlorophyll a and
primary production gradually decline from the western to the
eastern basin, according to field and satellite data (e.g., Lavigne
et al., 2015; Mattei and Scardi, 2022). As a result, a declining trend
of total biomass and ecosystem size (TST) was observed from west
to east; the Black Sea displayed instead the lowest estimates of total
biomass. As the water moves eastward, it becomes more saline and
oligotrophic, which means there is less organic matter and fewer
nutrients to support abundance (D'Ortenzio and Ribera d'Alcalà,
2009). The highest number of models on alien species was found for
Mediterranean Sea regions, and especially the eastern
Mediterranean Sea, an outcome due to the nature of the basin
that is one of the most invaded seas in the world (Giakoumi et al.,
2019). As expected, upwelling and eutrophic ecosystems (i.e., Bay of
Biscay, Celtic Sea, Iberian coast and North Sea) showed the highest
total primary production. A similar finding was observed in total
catches of these areas, with systems connected to the NE Atlantic
Ocean exhibiting the greatest values. However, the Barents Sea
represents an exception compared to other North Atlantic
ecosystems due to a combination of factors, including lower
species diversity, limited accessibility, shorter fishing season due
to the sea ice, and underestimations, since unreported landings as
well as discards miscalculations are very common (Popov and
Zeller, 2018). The waters of NE Atlantic have upwelling
characteristics, encouraging the reproduction of small pelagic
fishes and the creation of large shoals that drive high fisheries
yields and catch (Bjørndal, 2009; Feijó et al., 2018). The Mean
Trophic Level of the Catch (MTLc) was highest in the Barents Sea
(>4) and generally higher in high latitude regions. These findings
are corroborated by the literature on large boreal ecosystems and
may be explained by the abundance of large marine predators and
elasmobranchs in the catch (Conti and Scardi, 2010). A same
pattern was observed in lower latitude ecosystems; for instance,
the oligotrophic eastern Mediterranean Sea has intermediate total
yields associated with the highest average MTLc in the basin.
However, high biomasses of top predators have not been
observed in the eastern Mediterranean Sea compared to the
central and western parts of the basin, suggesting the MTLc score

in the east can be attributed to lower productivity and density of low trophic level organisms (e.g., small pelagics) in the catch (Tsagarakis et al., 2010).

The complexity of EwE models has increased along time, with a higher number of compartments found in most recent works compared to the oldest. Nevertheless, the number of FGs in most of the models ranged from 30 to 50 (Stock et al., 2023), an aspect that acknowledges the challenges posed by increasing model complexity (Green et al., 2005) and software tools' limitations to achieve mass-balance conditions (Villasante et al., 2016). Ecosim and Ecospace are used to implement simulations in time and space, respectively. Their performance, however, depends on the choice of the forcing factors, which influences calibration and fitting procedures (Mackinson et al., 2009). The majority of the models examined in this review incorporated trophic (vulnerabilities), fishery and primary production drivers, due to the automated fitting procedure available in EwE that includes these factors (Scott et al., 2016). Regarding the environmental drivers, most of the models incorporated temperature (e.g., SST, SBT), as most taxa have a strong connection between temperature and metabolic rates such as growth and consumption (Chabot et al., 2016). Also temperature data are the most easily accessible environmental data (Assis et al., 2018), however they play a crucial role in investigating the effects of climate change, confirming the ecosystem-level relevance of ocean warming, especially at higher latitudes (Grimm et al., 2013).

An issue related to the ecosystem indicators and the development of food web models like EwE is the uncertainty analysis (Evans et al., 2013). Ecosystem models are based on three principles (Levins, 1966): (1) generality (the tolerance limits of modelling applications); (2) realism (the degree of correspondence to reality); and (3) accuracy (the level of uncertainty). The latter is an integral part of complex ecosystem modelling (Milner-Gulland and Shea, 2017) and is considered in Ecopath, through the pedigree routine (Christensen and Walters, 2004a) to assess the integrity of input parameters and the quality of the model. However, the pedigree routine is not used by many models (Colléter et al., 2015). Understanding and addressing model uncertainty is the key to implement management scenarios and supporting robust decision making (Refsgaard et al., 2007). According to Rounsevell et al. (2021), uncertainty is divided in three categories: (1) scenario-based, including linguistic variations, alternative forms of implementation and input parameters interpretation; (2) model-based, encompassing structural limitations, input data reliability and error propagation; and (3) decision making-based, involving data interpretation, communication and translation of results. A newer approach to assess uncertainty in EwE was attained with the development of the Ecosampler plug-in (Steenbeek et al., 2018). Ecosampler is based on a Monte Carlo method (Metropolis and Ulam, 1949), built in EwE for automated input parameter optimization (Kavanagh et al., 2004). The Monte Carlo routine scans potential parameters that can ensure preserving the mass-balanced state of the ecosystem, and Ecosampler stores these plausible sets of models in its repository (Steenbeek et al., 2018). However, only 30% of the reviewed publications used the Monte Carlo routine and its results to perform uncertainty analysis on

input parameters. Despite having its own limitations (e.g., modification of the base model may lead to invalid stored samples), Ecosampler is an add-on option that aims to account for uncertainty. Although uncertainty is often considered a threat, it can improve predictions obtained from ecological models (Larrosa et al., 2016; Rounsevell et al., 2021) and represents an essential condition for using EwE models to inform and support ecosystem-based management (Heymans et al., 2016).

Model validation, also known as skill assessment, is an essential step in evaluating the performance of coupled trophic/physical models, including EwE models (Stow et al., 2009). As a rule of thumb, some steps can be followed to achieve the best possible fit (Heymans et al., 2016). Ecopath input parameters, including data on biomass and catch, can be cross-checked with those from stock assessments and other sources (i.e., acoustic surveys, trawling samplings), enhancing model credibility (Agnetta et al., 2019; Natugonza et al., 2020). The PREBAL routine incorporated on the EwE software tool ensures a diagnostic check in which biomass and trophic flows are calculated for each group in the food web by balancing the input and output (Link, 2010). In the same way, Ecosim calibration is an essential step in Ecosim modelling to verify that the model accurately represents the temporal dynamics of the food web (Haputhantri et al., 2008; Tomczak et al., 2012). The stepwise fitting procedure is an automated routine for vulnerabilities and primary production drivers, which can be used as a skill assessment metric, based on an optimization algorithm (Mackinson et al., 2009; Scott et al., 2016). Ecospace has a multi-frame nature, as it is designed to capture the interactions between multiple species, fisheries, and the environment across a spatially-explicit domain. Model inter-comparison with other species distribution models (SDMs), like generalised linear models (GLMs), generalised additive models (GAMs) or boosted regression trees (BRTs) and cross-validation (Roberts et al., 2017) are skill assessment metrics used to achieve Ecospace modelling validation (Püts et al., 2020; Steenbeek et al., 2021).Simulating complex marine ecosystems and the impact of stressors acting on them is a challenging feat required to enhance EBFM. Despite existing difficulties in modelling ecosystems, this review reported a marked increase of EwE models in recent years, in all European marine areas. The increase in modelling efforts highlights the embracing of the holistic ecosystem management approach, primarily in vulnerable systems where single-species assessments and management alone have proven to be inadequate (Skern-Mauritzen et al., 2016). According to Craig and Link (2023), EwE modelling approach can support EBFM by following certain criteria, including (1) a clear management objective, (2) an accessible and well-constructed model, (3) a communication channel among scientists and decision-making bodies and (4) a versatile modelling approach (i.e., software modules and addressed topics). Other reviews have also assessed ecosystem models and applications globally, regarding the definition of the best suitable modelling approach according to ecosystems' characteristics and issues (Geary et al., 2020; Perryman et al., 2021). EwE is a successful modelling approach allowing to describe the whole food web state. It enables simulating food web changes in time and space, implementing forecast scenarios that can support management

decisions. In the future, other reviews of EwE models, indicators and statistics could be implemented to inform about geographical gaps (e.g., areas with no existing models), possibly assisting global meta-analyses and identification of emerging ecosystem properties.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2023.1182921/full#supplementary-material

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