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Managing fisheries and ecosystems: current good practices and the EcoScope project experience

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Ecosystem Based Management (EBM) is a comprehensive way of managing fisheries and marine resources. As such, it needs a large and complex suite of concepts and tools to address a variety of problems ranging from climate change, through various forms of water pollution, to trophic interactions and social-economic sustainability. Industry, scientists, managers, and policy makers involved in the fisheries sector are the main actors in EBM. EBM objectives based on policy needs, legal requirements, and ecosystem considerations may target specific fish stocks, or encompass several ecosystem components aiming for balanced fisheries, but they need to address the trade-offs between maximizing economic gains versus sustainable fisheries and healthy ecosystems. Fishing at Maximum Sustainable Yield (MSY), setting ecosystem reference points, discards ban, avoiding bycatch of protected species, habitat protection, accounting for the effects of climate change, achieving good environmental status, setting effective marine protected areas, and considering ecosystem effects from marine spatial planning, are all examples of EBM objectives. The EcoScope project aimed to address ecosystem degradation, anthropogenic impacts, and unsustainable fisheries by developing an efficient, holistic, ecosystem-based approach to sustainable fisheries management that can easily be used by policy makers and advisory bodies. The EcoScope consortium reflects an interdisciplinary advisory team of biologists, modelers, economists, and social scientists. It performed comprehensive reviews of data, data gaps, and various tools (models, indicators, management evaluation procedures). An online platform, toolbox, academy, and a mobile application are end products delivered and maintained by EcoScope to facilitate knowledge sharing, communication, and education. The EcoScope project has built modules ready

to be used in the implementation of EBM, but a more direct approach by the responsible organizations, such as ICES, FAO, GFCM and the EC, is needed to set explicit and formal research and managerial frameworks for implementing and coordinating the EBM activities.

KEYWORDS

ecosystem management, fisheries, ecosystem models, overfishing, fisheries socio-economics, management measures

1 Introduction

The ecosystem approach to fisheries (EAF) was introduced in 2001 with the Reykjavik Declaration on Responsible Fisheries in the Marine Ecosystem (Garcia et al., 2003). While the term was not used in the Reykjavik Declaration, organizations such as the International Council for Exploration of the Sea (ICES) and the Food and Agriculture Organization (FAO) of the United Nations adopted EAF for incorporating ecosystem considerations into fishery management. In 2002, the World Summit on Sustainable Development determined that the EAF should be implemented by 2010 (FAO, 2003, 2008, 2009). The term ecosystem-based management (EBM) was defined in the Ecosystem Principles Advisory Panel Report to the US Congress in 1998 (US EPAP, 1998). Steps toward actual implementation of the ecosystem approach followed much later (e.g. Fulton et al., 2019; Townsend et al., 2019; Bastardie et al., 2021; Ramírez-Monsalve et al., 2021; EU, 2022a). Over the years, the management of ecosystems and fisheries has been included in the context of slightly different formulations of Ecosystem Approach to Fisheries (EAF, Garcia et al., 2003), Ecosystem Approach to Fisheries Management (EAFM, EU, 2022a), Ecosystem Based Fisheries Management (EBFM, Craig and Link, 2023), Ecosystem Based Management (EBM, Link and Browman, 2014; Craig and Link, 2023). These formulations have some pronounced differences (Garcia et al., 2003), or describe different application levels of ecosystem management (Patrick and Link, 2015; Dolan et al., 2016); however, the multitude of similar terms creates linguistic uncertainty (Dolan et al., 2016) that might lead to confusion among stakeholders and the general public. The different types of fisheries management approaches (including Single Species fisheries management, SSFM) were addressed in EcoScope (Table 1). As EBM encompasses all other levels, further in this paper we refer to it.

Mapping of the legal base and the main policy players was one of the first tasks in EcoScope (Rodriguez-Perez et al., 2023). Several international acts are relevant to managing fisheries and ecosystems (Table 2). The identification of the EBM starts with the definition of relevant policy problems to be solved (FAO, 2003; Townsend et al., 2019, Table 3). A thorough knowledge of the existing legal and policy basis is a necessary prerequisite in this process (Tables 2, 3).

In the EU, the Common Fisheries Policy (CFP; EU, 1970) reformed in 2013 (CFP; EU, 2013; Tables 2, 3) provides directions that are relevant for the implementation of the ecosystem approach, in particular: the Technical Measures Regulation (EU, 2019a), the Data Collection Framework Regulation, (DCF; EU, 2017a), the Deep Sea Stocks in the Northeast Atlantic Regulation (EU, 2016), and the European Maritime and Fisheries Fund Regulation (EMFF; EU, 2014a; Rodriguez-Perez et al., 2023). Unlike the CFP which aims to regulate the fisheries, the Marine Strategy Framework Directive (MSFD; EU, 2008; Table 2) aims to achieve Good Environmental Status (GES) through an ecosystem approach to the management of human activities, and therefore accentuates on keeping safe and healthy ecosystems and their services. Other EU regulations such as the Habitats Directive (HD, EU, 1992), the Water Framework Directive (WFD, EU, 2000), the Birds Directive (BD, EU, 2010), and the Maritime Spatial Planning Directive (MSPD, EU, 2014b), also emphasize nature protection and ecosystem management (Tables 2, 3). The EU Biodiversity Strategy 2030 (EU BS 2030; EU, 2020) is a core part of the European Green Deal (EU, 2019b; Table 3). A core commitment under the BS is the expansion of protected areas to cover 30% of the sea. For fisheries, it sets the targets to maintain or reduce fishing mortality to or under Maximum Sustainable Yield (MSY) levels; to eliminate or reduce bycatch, particularly for sea mammals, turtles, and birds; and to tackle practices that damage the seabed. The Nature Restoration Regulation (NRR, coming into force in mid-2026; EU, 2024), as a key element of the BS, aims to restore ecosystems, habitats, and species, to enable the long-term sustained recovery of biodiverse and resilient nature, and to achieve the EU's climate mitigation and adaptation objectives. The General Fisheries Commission for the Mediterranean (GFCM) 2030 strategy (FAO, 2021) is binding for the Mediterranean and Black Sea member countries of the GFCM, and includes targets on achieving sustainable fisheries and aquaculture and constraining by-catch of Protected, Endangered, and Threatened Species (PETS).

In this paper, we aim to review the main issues with the state-of-the-art implementation of the EBM, and to share the EcoScope project experience on that matter. The main objective of EcoScope is to pilot the EBM implementation in European seas: the Baltic Sea, the North Sea, the Bay of Biscay, the Balearic Sea, the Adriatic Sea, the Black Sea, the Aegean Sea, and the Levantine Sea. In doing so,

TABLE 1 Levels of fisheries management (sensu Link and Browman, 2014) addressed in EcoScope.

Management type	Description	References	EcoScope applications
Single species fisheries management (SSFM)	Single-species stock assessments based around the surplus production and optimal exploitation concepts.	Beverton and Holt, 1957; Gulland, 1971	Assessed over 300 stocks (and functional groups) across European Seas and provided estimates for stock specific reference points.
Ecosystem approach to fisheries management (EAFM)	Ecosystem factors are included in the stock assessment, while the social and political dimensions are not necessarily addressed explicitly.	Ward et al., 2002; Garcia et al., 2003; Pitcher et al., 2009	1) Development of the EcoScope Toolbox: fisheries scoring index (FISH) that combines fisheries and population indicators; 2) Assessment of ecosystem components: functional groups, megafauna, habitats, benthic status, marine communities.
Ecosystem based fisheries management (EBFM)	It recognizes the combined physical, biological, economic, and social trade-offs that affect fisheries, and the need to address these trade-offs when optimizing fisheries yields from an ecosystem context	Pikitch et al., 2004; Link, 2010; Link and Browman, 2014	1) Development and application of marine ecosystem models (MEMs) combining the effect of management, policy and climate scenarios on ecosystem components; 2) Analysis of social and economic indicators, value-chain, and policy optimization models.
Ecocentric fisheries management (ECFM)	It acknowledges the intrinsic value of marine ecosystems, regardless of human use, aiming to maintain its health, structure, and function.	Leopold, 1949; Tsikliras et al., 2023	Development of the EcoScope Toolbox: marine ecosystem scoring index (MESSI) that incorporates several ecosystem components, including socioeconomic indicators.
Ecosystem based management (EBM)	It characterizes the movement towards a more cooperative and holistic approach to marine resource management and includes all anthropogenic pressures to the ecosystem	Leslie and McLeod, 2007; Link and Browman, 2014; Craig and Link, 2023	1) Construction of the EcoScope Platform composed of homogenized and georeferenced datasets; 2) Application of the MSP Challenge Simulation Platform for the eastern Mediterranean and the western Baltic Sea including all human activities such as wind energy production, aquaculture, oil extraction, shipping, and fisheries.

EcoScope provides building blocks to be used in assembling the necessary science, managerial, communication, and educational frameworks in Europe.

2 EBM data

EBM needs copious data, and the issue of its scarcity has been raised on a number of occasions (Murawski, 2007; Patrick and Link, 2015; Heymans et al., 2020; Rodriguez-Perez et al., 2023). Data gaps were also found to be a significant barrier reducing the statistical and explanatory power, as well as the predictive ability of models needed in EBM (Heymans et al., 2020). Given the call for more and better data, EcoScope aimed to identify and fill gaps in biological, fisheries, ecological, and socio-economic knowledge across marine ecosystem components and models (Supplementary Material (SM), Abucay et al., 2023; Kesner-Reyes et al., 2025). A short description of the fisheries, ecological, and socio-economic data required for EBM and their deficiencies are presented in the SM.

3 EBM tools

3.1 Fisheries models and indicators

Single stock assessment models (SSMs) are in use with EBM, together with single stock management practices of MSY and total allowable catch (TAC), as well as management strategy evaluations (MSEs) based on operational SSMs. In addition, SSMs are used to

produce input data for multi-species and marine ecosystem models (MEMs), bio-economic models, and ecosystem MSE. EcoScope applied tools suitable for assessing data poor stocks such as most of the stocks in the Mediterranean and Black Sea. Commercial and non-commercial fish and invertebrate stocks were assessed in the context of MSY based on a series of new tools: catch maximum sustainable yields (CMSY++; Froese et al., 2023) for commercial species with catch and survey data, and Abundance Maximum Sustainable Yields (AMSY; Froese et al., 2020) for non-commercial stocks for which catch data are lacking but time-series of survey data are available. In data rich situations, when size and/or age structure of catches and abundance surveys are available, statistical catch-at-age models are commonly used, such as stock synthesis (SS3; Methot and Wetzel, 2013), assessment for all (a4a; Jardim et al., 2015), and yield-per-recruit analyses (e.g. STECF, 2023).

A series of community indicators were examined to assess ecosystem health and anthropogenic effects (climate and fisheries) on marine communities to complement the analysis of species distributions. These indicators include recently developed metrics such as the N90 diversity indicator, which is sensitive to both fishing and environmental impacts on diversity (Farriols et al., 2015), the BEnthos Sensitivity Index to Trawling Operations (BESITO; González-Irusta et al., 2018), and widely used indicators such as the mean weighted trophic level of the catch (mTLc), the Fishing-in-Balance index (FiB), and the Fishing Sustainability Index (FSI), which have been used to assess the effect of fisheries on marine ecosystems (Cury et al., 2005). The mean temperature of the catch has been used to evaluate the effect of climate change and variability in marine communities. The populations of sharks and rays were

TABLE 2 Main legislative and policy acts creating the institutional basis for the EBM.

Legislative act	Relevance to the EBM	Reference			
EU legislation					
Common Fisheries Policy (CFP)	Lays out the rules for sustainably managing European fishing fleets and conserving fish stocks.	EU, 1970, 1983a, b, 2013			
Habitat Directive (HD)	Aims to achieve Favourable Conservation Status (FCS) of listed habitats and species (including 9 marine habitats, cetaceans and sea turtles). Member States must designate Sites of Community Importance (SCI)/Special Areas of Conservation (SAC), which are part of the Natura 2000 network.	EU, 1992			
Water Framework Directive (WFD)	Aims to achieve Good Ecological Status for all EU surface and groundwaters including marine waters.	EU, 2000			
Marine Strategy Framework Directive (MSFD)	The EU's most holistic directive on protecting the marine environment aiming to achieve Good Environmental Status GES in European marine waters by 2020 through an ecosystem approach to the management of human activities in the sea.	EU, 2008			
Birds Directive (BD)	Aim to achieve Favourable Conservation Status (FCS) of listed bird species (including seabirds). Member States must designate Special Protection Areas (SPA) which are part of the Natura 2000 network.	EU, 2010			
Maritime Spatial Planning Directive (MSPD)	Common framework for maritime spatial planning in the EU; requires implementation of an ecosystem-based approach and keeping the collective pressure of all human activities within levels compatible with GES.	EU, 2014b			
European Green Deal	Reach zero net emissions of greenhouse gases in the EU by 2050; protect, conserve, and enhance EU environment. Supplemented by the EU Biodiversity Strategy 2030.	EU, 2019b, 2020			
EU Action plan for fisheries	Aims to contribute to getting and keeping fish stocks to sustainable levels; reduce the impact of fishing on the seabed; minimize fisheries impacts on sensitive species.	EU, 2023			
Other international agreements					
Bonn Convention on Migratory Species (CMS)	UN treaty for the conservation and sustainable use of migratory animals and their habitats.	UN, 1979			
United Nations Fish Stocks Agreement on highly migratory and straddling fish stocks (UNFSA)	Establishes rights and obligations for States to conserve and manage fish stocks and associated species, and to protect marine biodiversity.	UN, 1995			
United Nations Convention on the Law of the Sea (UNCLOS)	International framework for activities in the ocean, including conservation and sustainable use of marine resources.	UN, 1982			
Convention on Biological Diversity (CBD)	International treaty for the conservation and sustainable use of biological diversity, and for fair and equitable sharing of the benefits from the use of genetic resources.	UN, 1992			
GFCM 2030 strategy	Common vision and guidance on achieving sustainable fisheries and aquaculture in the Mediterranean and Black Sea region.	FAO, 2021			

assessed using JARA (Just Another Red-List Assessment), which is a Bayesian state-space model that allows both process error and uncertainty to be incorporated into International Union for Conservation of Nature (IUCN) Red List assessments (Sherley et al., 2020). Finally, three ecosystem indicators and the accompanying thresholds were used to detect and delineate ecosystem fisheries exploitation or ecosystem overfishing: the Ryther index, the Fogarty ratio index, and the Friedland ratio index (Link and Watson, 2019). These indices rely on catch and satellite data, linking fisheries catch/landings to primary production through established constraints of trophic transfer efficiency. They have been previously applied on a global (Link and Watson, 2019) and regional scale (Link et al., 2020; Link, 2021) to determine the degree to which ecosystem overfishing may be occurring, if at all.

Implementing EBM is complex due to the many aspects that have to be considered, such as multi-species interactions, environmental/climate forcing, habitat status, human activities, and stakeholder acceptance. Marine ecosystem models (MEMs) are capable of predicting the effects of management decisions on some of these interrelated variables and can therefore make an

important contribution to an effective EBM implementation. The term MEM refers to temporally and/or spatially dynamic models that simulate the marine food-web or the entire ecosystem by incorporating physical, chemical, and biological (i.e. food web) processes under the influence of natural and anthropogenic stressors (Steenbeek et al., 2021). Because models can differ in their structures and functioning, not all ecosystem models can address all EBM policy needs equally. For example, not all MEMs can address spatial issues such as MPAs, and species interactions in the models can be based on functional groups, trophic levels, or size classes, making MSY hard to address. Comprehensive overviews of how MEMs can be used to help EBM are presented by Townsend et al. (2019); Chust et al. (2022), and Craig and Link (2023).

In EcoScope, the common ecosystem modeling platform Ecopath with Ecosim (EwE; Christensen et al., 2024; De Mutsert et al., 2024) was used to create MEMs in different European Sea basins. EwE models use information on fish biomass dynamics, as well as information on other non-fish trophic groups and fisheries, to build mass balanced models (Ecopath), which are then validated as time dynamic models (Ecosim) using time series data

TABLE 3 International legislation addressing EBM needs, objectives, tools, and management measures to achieve them (modified from Rodriguez-Perez et al., 2023).

Legal base	EBM needs	EBM objectives	EBM tools	Management measures (MMs)
	TAC; Maintain fishing pressure at MSY or less; Apply MSY to mixed fisheries	Maintain all stocks at MSY	Combination of SSMs and MEMs	TAC; Catch limits, Effort control
	Discarding	Minimize discards	MEMs	Landing obligation
CFP	MPAs; FRAs	Protect ecosystems through spatial regulations/MPAs	Spatial ecosystem models	MPAs and FRAs
	Long-term predictions of management scenarios; Strategic EBM	Recovery and sustainable fishing of all stocks in a changing environment	Long-term strategic simulations; ERPs	Adaptive management
	Regionalization; EBM through ACs and MSRGs	Manage regional ecosystems and fisheries	SSA, EM	Regional MMs
BD	Incidental bycatch of PETS	Protect PETS	MEM	Technical devices on fishing gear; Set time and area closures
HD	Reduce seabed impacts; Select the most suitable areas to implement the MSFD threshold values	Protect habitat	Spatial ecosystem models	MPAs Self-controlled fishing (related to eco-labeling)
MSFD	Protect PETS; Define maximum allowable mortality, and find areas to protect species/ life-stages	Protect PETS	Spatial ecosystem models	MPAs
	Ensure natural ecosystem processes are not disturbed	Ensure GES	EM	Adaptive management
	Biodiversity indicators	Protect/enhance biodiversity	EM, Kempton's Q, TL, Network-based indices	Adaptive management
MSPD	Marine Spatial Planning	Manage fishing and ecosystems in space	EM	Adaptive management
Green deal	Climate change; Integrate effects in management scenarios	Mitigate climate effects	LTL models; End-to-end models	Adaptive management
NRR	Restoring 15% of degraded habitats by 2030	Define and identify different habitat areas to restore	Spatial ecosystem models	MPAs
EU BS 2030	Find suitable areas for the 30/10% targets	Protect ecosystems through spatial regulations/restrictions on fishing	Spatial ecosystem models	MPAs, FRAs, OECMs
	FRAs	Protect PETS and habitat through spatial regulations	Spatial ecosystem models	FRAs
GFCM 2030 strategy	Maintain fishing pressure at MSY or less; Apply MSY to mixed fisheries	Maintain all stocks at MSY	SSMs, MEMs	Multiannual plans for stocks

Abbreviations used: CFP is Common Fisheries Policy, BD is Bird Directive, HD is Habitat Directive, MSFD is Marine Strategy Framework Directive, MSPD is Maritime Spatial Planning Directive, NRR is Nature Restoration Regulation, EU BS 2030 is EU Biodiversity Strategy 2030, TAC is Total Allowable Catch; MSY is Maximum Sustainable Yield; SSMs are Single-species Models; MEMs are Marine Ecosystem Models; PETS is Protected, Endangered, and Threatened Species; MPAs are Marine Protected Areas; FRAs are Fisheries Restricted Areas; GES is Good Environmental Status; LTL is Low Trophic Level; TL is Trophic Level; ERPs are Ecosystem Reference Points; AC is Advisory Council; MSRG is Member State Regional Group; OECMs are Other Effective area-based Conservation Measures.

(Christensen et al., 2024). These can be further expanded spatially with 3-dimensional spatial-temporal dynamic models (Ecospace, Steenbeek et al., 2013). EwE models can be coupled with low trophic level (LTL) models (Libralato and Solidoro, 2009; Akoglu et al.,

2015) to ensure the bottom-up processes are well represented and feed into the higher trophic level interactions represented by EwE. EwE models were compiled and applied to all EcoScope case studies. Environmental and management scenarios were

developed and tested in accordance with policy needs (e.g. CFP, MSFD, national policies), and to explore climate change impacts. Policy scenarios under deep uncertainty were tested in relation to future climate conditions and the impact of fisheries and non-indigenous species (NIS). The input and output data for all these models and indicators are freely available online within the EcoScope platform (https://data.ecoscopium.eu).

EcoScope also created Ecological Niche Models (ENM), which predict the actual or potential distribution of a species across a geographic area and time based on environmental and geophysical data (Coro et al., 2016). EcoScope used multiple Artificial Intelligence (AI)-based ENMs to determine the native areas of 1,508 rare and commercial fish and invertebrate species, marine mammals, and reptiles that were indexed by AquaMaps (www.aquamaps.org) as residing in the European Seas based on empirical observations (Coro et al., 2024). The ENMs included Maximum Entropy, AquaMaps, Artificial Neural Networks, and Support Vector Machines. These models were combined into species-specific ensemble models to make the best use of their complementary features and to increase ecological niche prediction accuracy. Distribution maps were produced according to IPCC Representative Concentration Pathways (RCPs) 4.5 and 8.5, representing future environmental projections under mediumand high-greenhouse gas emission scenarios, respectively. The resulting species distribution maps are available through the EcoScope Platform (https://data.ecoscopium.eu), and are used in assessing ecosystem models and simulations. Additionally, a biodiversity-richness map was produced from the ensemble models and published on the platform.

3.2 Fisheries socio-economic modeling

Modeling tools used for EBM (from SSMs to complex end-toend modeling approaches) can be strengthened by: 1) re-expressing their outputs in socio-economic terms, and 2) by constraining relationships among model components using socio-economic factors (Thébaud et al., 2023). However, the use of food web models to assess the socio-economic consequences of change, albeit driven by the environment or management actions, on the fisheries systems has been very limited (Chakravorty et al., 2024). Food web models were found to be effective at characterizing the socio-economic importance of fisheries systems, and at simulating the socio-economic consequences of environmental or policy driven changes in the system. We developed an approach for assessing the socio-economic consequences in fisheries systems built upon existing capabilities of EwE: the value chain plugin (Christensen et al., 2011) and the policy search routine (Christensen and Walters, 2004). The framework aims to produce socioeconomic indicators to explicitly address trade-offs among economic, social, and ecological objectives. Within EcoScope, the framework is being used to: (a) assess the consequences of alternative fishing effort restrictions on fleet profitability, fishers' salaries, and employment contributions of Greek fleets operating in the Aegean Sea; (b) characterize the consequences of species

invasions on the Israeli EEZ seafood value chain; (c) identify the consequences of fishing effort reductions across the Balearic Islands seafood value chain over time; and (d) highlight the trade-offs between existing management arrangements and fisheries policies that are optimized to maximize fisheries revenue, employment, biodiversity, or ecosystem maturity in the Aegean Sea, Balearic Islands, Baltic Sea, Israeli EEZ, and North Sea.

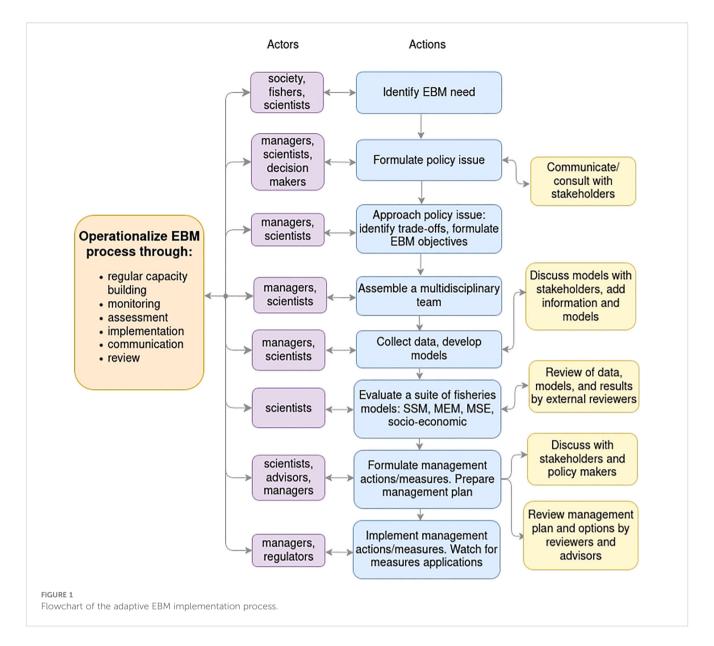
4 EBM implementation

4.1 Policy goals, actors and communication with stakeholders

The correct, clear, and transparent formulation of policy questions for EBM is important to kick off the implementation process (Townsend et al., 2019). Understanding policy and regulatory framework issues were mentioned as a problem in the stakeholder survey (Rodriguez-Perez et al., 2023), including weak policy frameworks for EBM, insufficient inclusion of ecosystem aspects by decision makers in requests to scientists, poor enforcement of regulations, and the complexity of different regulatory mechanisms in different countries. Identifying the policy question is often difficult and needs to be an interactive process within the existing management framework. It should be supported by the existing legislation relative to EBM (Tables 2, 3). Link et al. (2019) pointed out the different strengths of EBM-related regulations, differentiating between rather strict mandates of some protective or forbidding rules (e.g. protecting PETS), and more "relaxed" instructions (soft law, such as international law or conventions). Many EBM-related regulations seem to be holistic, and require several further steps for formulating operational measures regulating the fisheries and protecting/ restoring ecosystems.

Fisheries industry, scientists, managers, and policy makers are the main actors involved in the EBM implementation (Figure 1). Their involvement is ensured through their participation in organizations (usually international and cooperative) providing advice to the EU on EBM (Figure 1; Ramírez-Monsalve et al., 2021; Rodriguez-Perez et al., 2023). Collaboration and communication between various actors are essential because they clarify objectives, promote information exchange, and facilitate the identification of trade-offs (Townsend et al., 2019). The roles and functions of the various actors are detailed in the SM. It is important to have regular open communication between various stakeholders to build trust and provide transparency of the process. This also helps the review process and mitigates the risk of model and advice rejection (Townsend et al., 2019). In the EU, the advisory councils (ACs) are a focal point of stakeholder communication because they provide experience-based information and a platform to discuss social, economic, and ecological outcomes (EU, 2017b; Ramírez-Monsalve et al., 2021).

The EcoScope consortium involving biologists, modelers, economists, and social scientists reflects the interdisciplinary science team needed to advise the implementation of EBM. To



provide successful EBM advice, the team of scientists should include researchers, arbiters, advisers, and participatory experts (facilitators, mediators; Linke et al., 2023). However, as a team of interdisciplinary scholars, the EcoScope consortium lacks the means of collaboration with the main actors necessary for implementing project results into practice as well as directly communicate needs and tools. As it was carried out, the communication with stakeholders in EcoScope relied mostly on surveys (including workshops) rather than direct interaction. In order to provide efficient advice, the research team should participate in the decision process, ensuring that the tools produced, are tailored to purpose and contribute to EBM-related decision making. This can be achieved by associating future projects with dedicated EBM activities carried out by the ICES, GFCM, and ACs. Future projects could formally seek support for involvement in dedicated EBM efforts by the EC, ICES or other relevant organizations.

4.2 Objectives, trade-off between fisheries profits, ecosystem consideration, and societal needs

EBM objectives need to be formulated based on actual policy requirements, legal requirements, and ecosystem considerations. In some cases, they touch only on specific components of the ecosystem (e.g. the recovery of certain stocks), while in others they may encompass several components, aiming for balanced fisheries within the ecosystem, or addressing the trade-offs between sustainable fisheries and healthy ecosystems (Tables 3, 4; Rice and Duplisea, 2014). Setting double (e.g. optimize fishing, protect ecosystems) or multiple objectives (e.g. when recovering PETS, mitigating climate change, and enhancing human wellbeing are added to the first two, Table 4) unsurprisingly creates trade-offs, which need to be dealt with (Table 4).

A typical trade-off discussed for a long time for multispecies fisheries (Mace, 2001; Rice and Duplisea, 2014; Trenkel, 2018) is

TABLE 4 Examples of EBM objectives, trade-offs, and management measures (MMs).

MM	Objectives	Trade-offs	Reference
MSY	Fishing all stocks at MSY	Maximize catch vs. overfishing less productive stocks	Mace, 2001; Rice and Duplisea, 2014; Craig and Link, 2023
ERPs	Fishing all stocks at ERPs allowing to maintain desirable ecosystem state	Optimize catch and profits vs. sustain a healthy ecosystem, conserve/recover PETS	Chagaris et al., 2020; Scotti et al., 2022; Morrison et al., 2024
Landing obligation	Sustainable fishing without discarding	Discards to support human uses (e.g. fish meal) vs. support for marine scavengers (birds, cetaceans). Cost of processing discards vs. revenues from fish meal	Celić et al., 2018; Moutopoulos et al., 2018; Onofri and Maynou, 2020
MSY	Assess the resilience of EU fisheries to climate impacts	Maximize catch vs. reduce fishing mortality to mitigate climate effects and overfishing of stocks in poor state	EU, 2022b; Bastardie et al., 2022
Regulate fishing daily	Minimize bycatch of PETS while conducting sustainable fishing	Sustain profitable fishing vs. protecting PETS	Townsend et al., 2019; Link et al., 2019; Tommasi et al., 2021
MSY	Fishing at MSY vs. achieve and sustain GES	Fishing at MSY vs. achieve and sustain GES	Lynam and Mackinson, 2015; Stäbler et al., 2016; Baudron et al., 2019; Uusitalo et al., 2022
MPA	Protect nature, enhance ecosystem resilience to climate change	Economic activities (incl. fishing, aquaculture, gas exploration) vs. nature conservation in Israelli EEZ, in the southeastern Mediterranean	Shabtay et al., 2025
MSP	Produce green energy	Green energy vs. fishers' access and species (mammals, birds) conservation. Fishers access vs. "reserve" and "reef" effects on ecosystem production and biodiversity	Alexander et al., 2016; Raoux et al., 2017; Lester et al., 2018; Halouani et al., 2020; Nascimento et al., 2025

how to fish all stocks at optimal levels simultaneously (e.g. at MSY, Table 4). It is generally accepted that fishing of all stocks at MSY (from SSM estimates) is impossible because less productive stocks tend to be overfished (Table 4, Mace, 2001; Stäbler et al., 2016; Baudron et al., 2019; Craig and Link, 2023). Significantly reduced fishing rates (by 20 - 50%) are required in order to achieve sustainable yield of all species (Stäbler et al., 2019).

An alternative of trying to optimize MSY of all species is to estimate ecosystem reference points (ERPs, Table 4, Morrison et al., 2024) for all exploited stocks that will allow optimal fishing and will simultaneously sustain desirable ecosystem state. The desirable ecosystem state may reflect various objectives defined by the managers. ERPs can be holistic (i.e. an ERP for the whole ecosystem) or individual stocks could each have an ERP to ensure that low productivity stocks are not overfished and other ecosystem components (e.g. PETS) stay healthy (Scotti et al., 2022; Morrison et al., 2024).

Discarding is a practice recognized by the stakeholders to be possibly affected by the EBM (landing obligation, LO, Table 4). Several studies demonstrate that the LO would have negative or modest effects on harvested stocks and that limiting discards may have negative effects on scavenger populations of PETS. However, discarding catch may also have other negative effects on PETS - e.g. increased incidental catch (Darby et al., 2023). A task of the EBM is therefore to accommodate a better balance between avoiding discarding practices and sustaining vulnerable ecosystem components.

The trade-off between contradicting objectives of profitable fishing and PETS protection (mammals, sharks, sea turtles, Table 4) in the California current ecosystem has for instance been accommodated by using spatial model daily forecasts (tuned by weather forecasts) allowing for the fisheries to avoid bycatch of protected PETS.

The current fisheries management frameworks can be challenged by unfavorable climate impacts, and the implementation of EBM is a way to accommodate future changes in the fisheries. There are several studies of impacts of climate on fish stocks and fisheries using MEMs (e.g. Bentley et al., 2017; Serpetti et al., 2017; Papantoniou et al., 2023), and such studies were also performed in EcoScope (e.g. Ofir et al., 2023; Keramidas et al., 2023, 2024). However, none of these describe actual management measures (MM) to mitigate climate impacts.

An EU study that evaluated the resilience of the fisheries managed under the CFP to climate change (Table 4, EU, 2022b; Bastardie et al., 2022) found that healthy and well-assessed stocks are more resilient than stocks in a poor state, and that short-lived species are more impacted, but recover quicker after climate shocks such as heat waves. Bioeconomic models (Bastardie et al., 2014; EU, 2022b) showed that fishing fleets with low profitability will not be resilient to climate-induced shocks. Climate change may lead to situations where management rules are not followed, resource resilience can be jeopardized, or fleets' constraints are too high, affecting their economic resilience. Low fishing mortality and adaptive management may improve resilience and buffer against climate shocks, but at the cost of reducing short-term profits (Table 4).

The MSFD and the CFP are not harmonized to achieve similar ecosystem goals. Conforming to both EU policies will require the inclusion of the ecosystem effects of fishing (Baudron et al., 2019; Stäbler et al., 2016), as well as the development of specific ecological indicators and reference points that reflect the GES descriptors (Bourdaud et al., 2016; Fu et al., 2019; Ito et al., 2023). While reductions in fishing effort may lead to improvements in both the state of stocks and some GES indicators (e.g. D1-biodiversity, D4-food web; Lynam and Mackinson, 2015), trade-offs between fishery

and ecosystem objectives may still occur even when fishing is sustainable (Stäbler et al., 2016; Baudron et al., 2019; Uusitalo et al., 2022). Although MEM (e.g., EwE) simulations can help reconcile conflicting policy objectives of the CFP and the MSFD, there is considerable uncertainty about how to include MSFD conservation objectives into new or existing management frameworks (van Hoof, 2015).

Establishing MPAs has a broader objective to protect marine nature, and therefore on most occasions, it is beyond the specific scope of EBM, spanning into the field of maritime spatial planning and ecosystem management. However, the restrictions on the fisheries and the conflicts between fishing and nature conservation, in general, make the MPAs subject to fisheries management and therefore to EBM (Table 4). Recently, Shabtay et al. (2025) described the efforts to propose a network of MPAs for implementation in the Israeli EEZ. The project revealed and tried to streamline substantial challenges in the MPA implementation process, such as establishing and filling information gaps, solving user conflicts (including fisheries restrictions), generating public interest and encouraging the public to endorse the project, and implementation issues such as convincing the government to accept and apply the master plan (Shabtay et al., 2025).

An example of EBM application in Maritime Spatial Planning (MSP) is the assessment of mutual effects between offshore wind farms (OWFs) and fishing (Punt et al., 2009, Table 4). The negative effects such as increased mortality of migrating marine birds (Furness et al., 2013), and increased noise and vibrations that might change long-distance spatial movement of marine mammals (Teilmann and Carstensen, 2012), are more pronounced during the early development phases. A framework combining EwE modeling, the MSP Challenge tool, and an Environmental Impact Assessment metric has been developed to capture these effects, providing a suitable means to assess ecosystem-level impacts across the construction, operation, and decommissioning phases of OWFs (Nascimento et al., 2025). Positive impacts include a "reserve effect" that increases fish biomass via the spill-over into fishing areas (Halouani et al., 2020), and a "reef effect" colonization of the installations by benthic food organisms contributing to upper trophic levels' biomass (Raoux et al., 2017). As a result, the construction and operation of OWFs induces trade-offs between fisheries, ocean use sectors, and PETS (Lester et al., 2018).

The demand for research on the socio-economic aspects of EBM to support decision and policy making has increased, with the EU pushing towards transformative change which harnesses the power of citizens, businesses, and communities. In EcoScope, a socio-economic survey was carried out in Bulgaria, Malta, and the UK, in order to get a better understanding of the perceptions, preferences, and expectations of the public for EBM and its economic value (Briguglio et al., 2025a). Overall, the results indicated an insufficient knowledge of specific EBM terminology, yet a positive perception of the values associated with EBM, and a strong support for policy interventions.

The socio-economic analyses conducted in EcoScope demonstrated how including the human dimensions of fisheries systems in EBM can facilitate comparisons and trade-off analyses that can help assess the outcomes of policy objectives (e.g., increasing seafood contribution to national food security, improving fleet profitability, reducing unsafe subsidies, increasing female representation in seafood sector employment, among others), as well as identify which sectors, fleet segments, and countries are most vulnerable to supply side or environmental shocks, and can also help identify data gaps and inform future data collection and monitoring efforts. At present, coupling ecology and economics is a must in the provision of scientific advice for the EBM. Further integration of the biophysical and human dimensions of fisheries systems is on the agenda, needing to bring together new algorithms, mandatory socio-economic data collection, adaptive management, and cross-sector and interdisciplinary collaboration.

5 Toward operational EBM

Effective implementation of EBM requires it to be conceived and structured as an adaptive, iterative process that involves formulating policies and legislation, acquiring knowledge, developing and testing models, applying MMs, and conducting ongoing surveillance (Figure 1). The "pull-push" mechanism of demanding/providing EBM advice that currently exists in the EU cannot satisfy the needs for effective operational EBM (Ramírez-Monsalve et al., 2021). Successful operational EBM requires: 1) welldefined management objectives (Tables 3, 4); 2) a clear management process receptive to the evaluation of trade-offs; 3) a suite of well-documented state-of-the-art models; 4) early and iterative engagement among scientists, stakeholders, and managers; 5) a model development process and fusion of suitable models in a collaborative, interactive, and iterative interdisciplinary team; and 6) a rigorous and iterative review process involving independent reviewers, institutions, and stakeholders (Townsend et al., 2019; Craig and Link, 2023).

Monitoring the outcomes of implementation is critical for the effectiveness of the EBM process (Tallis et al., 2010). It involves designing and establishing monitoring programs that identify how the chosen management actions affect the management targets (Levin et al., 2009). Much of the data collected during the monitoring can be used in future EBM, allowing scientists and managers to move from data poor to data rich situations, improving the rigor and sophistication of their decisions with each iteration. When governance is stable and multiple agencies cooperate, an integrated, coordinated, and efficient monitoring program can be established across agencies. Under less ideal governance situations, where funding for monitoring is questionable or the maintenance of monitoring programs is unlikely, the monitoring program can be designed to target critical time frames or areas, or to take advantage of remote sensing. The interdisciplinary team, together with managers and stakeholders, would establish an adaptive management framework that includes existing monitoring plans. Monitoring and adaptive management plans would be integrated, and their efficiencies would be evaluated (Tallis et al., 2010).

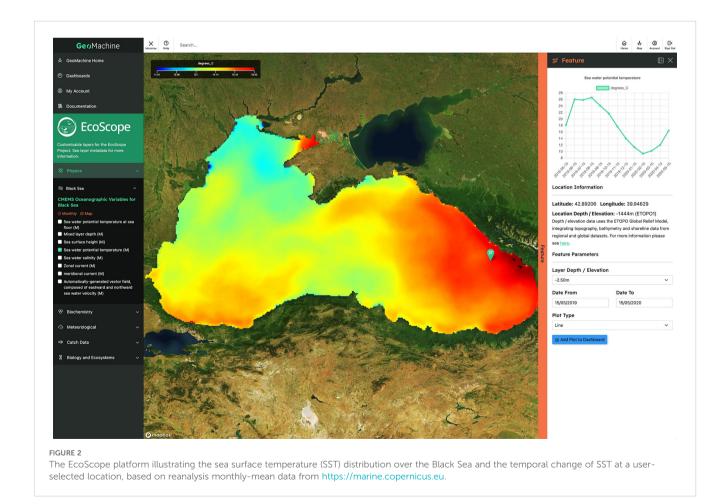
Once the EBM process is operational, its components and subprocesses need constant iterative adaptive updating. Data

collection, knowledge base, and models need to be improved and tailored through periodic workshops by interdisciplinary teams of scientists and managers. Models, recommendations, and advice need to be re-evaluated through a series of reviews at different levels (experts and stakeholders). Communication between modelers, managers, and stakeholders is essential, and would enable model and procedure refinement, and ensure their usefulness. Communication with stakeholders would enable scientists to respond to urgent and critical events by providing strategic and tactical advice for holistic planning and operational applications (Townsend et al., 2019).

6 Building of the EBM knowledge base and stakeholder involvement: EcoScope platform, toolbox, academy, app and knowledge exchange forum

To facilitate data preservation, sharing, and usage by interested stakeholders, the EcoScope consortium developed, and will maintain in the future, the EcoScope platform (https://data.ecoscopium.eu, Figure 2), which is a key output of the

project. The EcoScope platform is a geographical information system that hosts meteorological, oceanographic, biogeochemical, environmental, biological, fishery, and socio-economic datasets, and homogenizes them into common standard types and formats following international protocols. The environmental data are both historical and forecasts, cover all study areas, and are assembled, compiled, and integrated from multiple external databases and platforms such as CMEMS, EMODnet, NOAA, ECMWF, SMHI, Sentinel 2 and 3, CORDEX, IPCC. These data are combined with data from biological (e.g., FishBase, SeaLifeBase) and fisheries databases providing data on biomass, catches, and discards (e.g. GFCM, ICES, FAO, Sea Around Us project), marine mammal distribution (ACCOBAMS), biodiversity (Marine IBA e-atlas), fish and invertebrate species distributions and observations (AquaMaps, OBIS, GBIF), and fishing effort (Global Fishing Watch). All data are homogenized, georeferenced and quality checked, and form the back-end of the Ecoscope Platform (https://ecoscopium.eu/ecoscope-platform). The EcoScope platform is a modular tool linking data with environmental and human drivers, indicators, and models that couples predictions of changes in marine biogeochemistry with ecosystem productivity within a framework of climate change and increased anthropogenic forcing. The platform is based on state-of-the-art methodologies and adopts an Agile approach to ingest the diverse datasets. A series



of user stories was considered for designing and providing shared services required by the external stakeholders. This platform is expected to help European decision makers in the long-term management of fishery activities, addressing pressing challenges like climate change and fisheries economy constraints.

The EcoScope Toolbox features a comprehensive set of standardized fisheries, community, ecosystem, and climate indicators, integrated into two unified scoring indices (one for assessing the health of fisheries and another one for assessing ecosystem health (https://ecoscopium.eu/ecoscope-toolbox, Table 1). To align with EBM principles, the toolbox also incorporates some socio-economic indicators, available as time series and specific to ecosystems rather than countries. Where feasible, the individual indicators are connected to outputs from ecosystem models (EwE), stock assessments, and various datasets on oceanography, climate, environment, and fisheries available within the EcoScope platform. The scoring indices have been codesigned and evaluated by scientists and stakeholders to assist decision-making and EBM implementation. The toolbox can be applied anywhere in the world at various scales depending on the data and boundaries, and has a set of metrics that can be used independently to support international and local policies with the EBM.

In addition, the fisheries and ecosystem information and expertise are used to assess ecosystem status and change through the maritime spatial planning (MSP) challenge simulation platform (https://www.mspchallenge.info/msp-challenge-simulation-platform.html). The MSP Challenge simulation platform is an extension of the pre-existing software platform https://www.mspchallenge.info/applying MEMs (EwE) and incorporating dynamic ecosystem and climate conditions under deep uncertainty. It aims to engage advisers, managers and other stakeholders to carry out robust decisions and to promote adaptive management in accordance with the EU and national policies and legislation (Nascimento et al., 2025).

The EcoScope academy is the educational pillar of the project and includes a collection of online self-paced chapters contained in a course entitled "Ecocentric fisheries management" (https://ecoscope.getlearnworlds.com). The academy is addressed to postgraduate and undergraduate students, young scientists, and policymakers, building up the required knowledge for understanding the complexity and the necessity of EBM. It is used to disseminate the methodological approach of EcoScope and to transfer knowledge to all relevant stakeholders, as well as to support the proper usage of the developed platform and decision-making toolbox, and to facilitate the development and implementation of EBM policies.

The EcoScope app (https://ecoscopium.eu/ecoscope-app) is designed to empower citizens to contribute to the preservation of marine ecosystems by reporting marine hazards such as fishing in protected areas, sightings of invasive species, or marine pollution incidents.). These reports are transmitted in real time to the relevant authorities, ensuring that each issue is promptly addressed and managed. This mechanism facilitates a continuous flow of valuable data from the field, enabling stakeholders to monitor and respond

to critical challenges in marine conservation. By collecting and centralizing information from users across regions, the app helps create a more comprehensive picture of activities impacting the marine environment, such as the spread of invasive species and fishing practices in ecologically sensitive areas. These data are not only instrumental in shaping immediate actions, but also serve as a valuable resource for scientists, policymakers, and governments.

The EcoScope stakeholder knowledge exchange forum (KEF) aims to achieve maximum participation, advice, and support from key ecosystem-based fisheries stakeholders to ensure the tools are useful for them and meet their needs. It comprises all stakeholders that were identified as key EBM players in the initial stakeholder mapping, as well as the stakeholders that have actively signed up via https://ecoscopium.eu/stakeholders. The results from the first stakeholder workshop have been instrumental in understanding stakeholder needs, guiding the design of the tools, and ensuring they are fit for purpose. The last workshop will showcase the final tools to all stakeholders in the KEF, and we will collect further feedback and advice on future challenges for EBM, additional needs, and how to best develop the tools further.

7 Discussion

The main objective of the EcoScope project is to help develop an efficient ecosystem-centered approach to fisheries management by providing the necessary data, tools, and communication media directly to users. With respect to this, the building of the EcoScope applications such as MEMs developed for the different sea basins and their availability for testing and use by stakeholders in the EcoScope platform, toolbox, and app were the project's most essential outputs. This said, we can ask ourselves whether the achievements of the project are sufficient to help the implementation of EBM in Europe, and what problems and limitations we have encountered, that should be avoided in similar future efforts (Table 5).

The EcoScope project showed clear limitations (Table 4), some of which are inherent to the EBM process itself. One of them is the difficult communication of the EBM concept (Briguglio et al. 2025b). During the EcoScope survey (Rodriguez-Perez et al., 2023), stakeholders identified several barriers in implementing EBM: a lack of clarity of the EBM concept, including no common understanding of what the concept means; no guidelines on how EBM could work and be implemented; and no agreed definition, and therefore different interpretations, perceptions, and expectations among the various stakeholders. Policy and regulatory framework issues were also identified as a problem, including poor policy frameworks for EBM, insufficient inclusion of ecosystem aspects by decision makers, insufficient enforcement of regulations, and the complexity of different regulatory mechanisms in different countries. In addition, stakeholder communication issues were seen as a barrier in implementing EBM, including insufficient coordination, different mindsets, and a lack of common vision. Some of these problems can be traced back to the uncertainty in the formulation of the concepts (see Ch. 1), but

TABLE 5 Achievements and limitations of EcoScope, and possible future solutions.

EBM needs and actions	Achievements	Limitations	Possible solutions		
EBM data	EBM data				
Fisheries data	It assembled previously unused data and identified data gaps.	Some regional data were not taken into account in data-gap analyses.	To involve more regional expertise.		
Ecosystem data	It assembled and used previously unused data and collected new data on <i>ad hoc</i> data needs.	Still a lot of ecosystem and socio-economic data are needed to better define and fit EBM models and indicators	To organize efficient data collection and monitoring and process previously collected raw data.		
EBM tools	EBM tools				
SSMs	It applied state-of-the art methods in data-limited situations to assess several commercial and non-commercial marine populations.	Data-limited SSMs are less accurate and have limited applications for fisheries management. More advanced models such as MSE can be used.	To bring in better data and apply size/age structured SSMs. To develop better fit-for-purpose indicators and models.		
MEMs	It applied advanced MEMs in eight case studies, and made them available to users on interactive internet platforms. Run future climate scenarios and explored deep uncertainty in MEMs.	Several useful applications of MEMs were not or only partially developed: ETPs and MPAs simulations among others.	To make a better use of the developed MEMs for EBM applications.		
Social-economic and well-being assessments	It performed surveys and coupled socio-economic models and indicators with MEMs.	Insufficient socio-economic data are hampering the ability of otherwise advanced models and algorithms to bring significant results.	Mandatory socio-economic data collection needs to be implemented in the EU MSs.		
EBM implementation					
Communication with stakeholders	It carried out surveys of EBM needs and perceptions. It developed interactive EcoScope Platform, Toolbox, app, MSP Challenge, KEF.	The project consortium was not directly involved in the decision-making process and interaction with the main EBM actors.	The project partners need to be directly involved with the dedicated assessment and advice working groups.		
Upgrade and monitoring	It will support products and services after the life span of the project through business models for the EcoScope Platform, Toolbox, app and MSP challenge.	Supporting and interactively developing EBM knowledge base and monitoring need dedicated activities that surpass the of support of interactive platforms and apps.	The project results and experience need to be effectively transferred to operational assessment and advice working groups.		

others result from the mismatch between the environmental and fisheries regulations and advisory bodies with regard to EBM in the EU and elsewhere (Dolan et al., 2016; Ramírez-Monsalve et al., 2021). For example, the CFP deals mainly with fishing, and aims to sustain maximum yields, while the HD, MSFD, MSPD, and BD target environmental and biodiversity protection, and wider ecosystem management (e.g. achieving GES, setting protected zones and renewable energy projects). By trying to accommodate these diverging goals (creating perhaps impossible trade-offs), the EcoScope project (and possibly other similar efforts) is leaving the field of EBM and entering a wider field where it possibly lacks focus and sufficient expertise. The separation between environmental and fisheries regulations and advisory bodies was acknowledged by the EC, which proposed to address the harmonization of ocean policies in the new European Ocean Pact (EU, 2025).

It is clear that the EcoScope consortium's communication with stakeholders is only indirect and therefore lacks the potential to acquire knowledge and contribute to management decisions interactively with the main actors. In future, project participants should be directly involved with the dedicated assessment and advice groups. Such involvement, however, needs to be authorized by the advisory administration in the EU, and future consortia must earn their place at the decision-making scene and gain the trust of the main actors responsible for the EBM implementation.

It is a considerable challenge to support the EcoScope products beyond the project's life span. As mentioned in Ch. 5, operational EBM needs constant interactive updating of its policy plans, data collection and knowledge base. EcoScope aims to solve these problems by putting in place viable business models to ensure sustainable operation and update of its products and services in the future. The business models are aiming at future investments from private and public funds to ensure that the EcoScope platform, toolbox, app, and MSP challenge platform fulfill their tasks with the EBM implementation, stakeholder communication, and education.

The geographical scope of EcoScope includes eight sea basins, which have very different ecosystem, fisheries, and management properties. Although the project consortium tried to cover all areas equally, it was not possible to apply all analyses everywhere. SSM assessments and some of the MEM applications (EwE) were carried out in all areas, but others such as socio-economic value chain models were applied only to the Israeli and Balearic Islands cases, and the MSP Challenge simulations – only to the eastern Mediterranean and western Baltic Sea (Nascimento et al., 2025).

The complex nature and bulk quantity of data and tools needed make the development of EBM challenging and expensive. Data collection, identification, and filling of data gaps are essential for EBM development. Nevertheless, a shortage of certain data cannot be the reason to side step the ecosystem approach. When data are

missing, modeling, scenario development, and plausible assumptions could be used to fill the gaps and to take on board ecosystem considerations.

The EcoScope project developed modules ready to be used in the EBM implementation in Europe. We feel, however, that a more direct approach should be taken by the responsible organizations, such as the European Commission and the agencies that advise the EC (ICES, GFCM), to explicitly define and set formal research and managerial frameworks for implementing and coordinating EBM activities. To do so, they need to actively communicate with key stakeholders such as the fishing industry, environmentalists, scientists, and advisors, and further develop the legal and institutional background (e.g. by adding to and/or revising the CFP and MSFD, and others) of EBM.

EBM needs a large and complex suite of concepts and tools to deal with a variety of problems ranging from climate change, through various forms of water pollution, to biological trophic interactions and social-economic sustainability. Despite certain criticisms that have been raised due to slow and sometimes badly coordinated approaches, lack of conceptual clarity, insufficient data, complex methodology, and lack of efficient communication, EBM has been developing and evolving toward operational implementation. To paraphrase W.S. Churchill's famous quote (https://winstonchurchill.org/resources/quotes/the-worst-form-of-government) about democracy: EBM is probably not the most efficient form of management for fisheries or the ecosystem; however, we have no alternative but to maintain our ecosystems healthy and productive in order to be able to use them sustainably.

Author contributions

GD: Conceptualization, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. Sd: Formal analysis, Visualization, Writing – original draft, Writing – review & editing. MS: Formal analysis, Visualization, Writing – original draft, Writing – review & editing. SK: Visualization, Writing – review & editing. MB: Formal analysis, Writing – review & editing. GG: Writing – review & editing. JH: Writing – review & editing. AR: Formal analysis, Writing – review & editing. JS: Writing – review & editing. GS: Formal analysis, Visualization, Writing – review & editing. AT: Funding acquisition, Writing – review & editing.

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Supplementary material

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