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Spatiotemporal fishing effort simulations and restriction scenarios in Thermaikos Gulf, Greece (northeastern Mediterranean Sea)

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ABSTRACT

Spatiotemporal simulation modeling is used in the context of ecosystem-based fisheries management to investigate different management options, including the size and allocation of marine protected and fisheries restricted areas. Here, we used ECOSPACE to assess the effectiveness of existing and potential future spatiotemporal fishing restrictions in the heavily exploited Thermaikos Gulf, Greece for the years 2000–2025 (calibration period 2000–2016; projection period 2017–2025). ECOSPACE combines temporal biomass and commercial catch data with spatial habitat and other environmental data, as well as species ecological preferences, feeding, and dispersal rates to depict changes in trophic interactions, biomasses, and commercial catches in time and space. ECOSPACE simulations supported the empirical data demonstrating that fisheries restricted areas are effective tools for rebuilding the biomass of exploited stocks, with their size and location playing a significant role in the way that different organisms respond to protection. Nevertheless, our results suggested that in order to achieve the highest benefits of protection, fisheries restricted areas would need to be accompanied by a parallel reduction in total fishing effort, rather than a redistribution of fishing activities. Such redistribution would just move the pressure on the boundaries of protected areas, causing a local increase of commercial catches owing to the beneficial spillover effects of protection. One of the tested spatiotemporal restriction scenarios (MPA 5) suggests certain additional management measures on top of the existing restrictions for all four fishing fleets operating in the area. This scenario predicted a considerable increase in the biomass of key commercial and vulnerable species groups, including hake, flatfishes, anglerfish, sharks, and rays and skates, by the end of the simulation period in 2025.

1. Introduction

The Mediterranean Sea has been experiencing overexploitation (Colloca et al., 2013; Tsikliras et al., 2015) that has altered the structure and function of its ecosystems (Dimarchopoulou et al., 2021) and has caused stock status deterioration across the vast majority of commercial fish and invertebrate stocks (Froese et al., 2018; Hilborn et al., 2020). Beyond fishing, Mediterranean marine ecosystems are also pressured by several other human activities and their impacts such as habitat degradation, pollution, climate change and species invasions (Coll et al., 2010) that may act additively or even synergistically (Mora et al., 2013; Agnetta et al., 2022) and need to be taken into account within an ecosystem-based management context (Corrales et al., 2018). Notably, the invasion of alien species highly impacts the entire Mediterranean Sea and is particularly worrying for the eastern part of the basin due to the high number of Lessepsian migrant species entering through the Suez Canal (Katsanevakis et al., 2016; Karachle et al., 2017).

Technical measures controlling the fishing effort going into the fishery (i.e., input controls), such as spatiotemporal restrictions that regulate fishing activities in specific areas or seasons of the year, are key

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tools used in the Mediterranean Sea and Greek waters for the management of fish stocks (Bellido et al., 2020). A complete picture of spatial fisheries management initiatives in the Mediterranean Sea is provided by Pipitone et al. (2014). In the context of more holistic and inclusive ecosystem approaches to fisheries management, marine protected areas (MPAs) have been endorsed as an effective tool both for the conservation of habitats and biodiversity as well as for the protection and recovery of overexploited stocks (Maestro et al., 2019; Sala et al., 2021). MPAs were initially created to preserve aquatic ecosystems and biodiversity by minimizing anthropogenic pressures in spatially defined areas (Allison et al., 1998). They are usually divided into zones of varying protection levels that range from strict protection within no-take reserves to zones of sustainable resource exploitation (Baelde 2005). In no-take marine reserves, any kind of extractive activities, including fishing, are not allowed, thus providing a safe space where depleted populations can rebuild their biomass and degraded habitats can be restored (Gell and Roberts 2003). From a fisheries management perspective, the focus of protected areas is on the recovery of commercially important but overexploited fish populations and the rebuilding of depleted stocks (Kelleher 1999). It has been shown that MPAs can improve fisheries yields while protecting biodiversity as well, meaning that MPAs and responsible fisheries management are complementary rather than mutually exclusive (Sala et al., 2021). In the face of current and future threats, ocean warming and unsustainable extractive practices (Hidalgo et al., 2022), pollution, and invasive species challenge the conservation efforts implemented to protect biodiversity (Galil 2017). However, despite these challenges, MPAs still serve as ocean-based climate solutions for climate change mitigation by contributing to the resilience of marine social-ecological systems to climate change, carbon sequestration, coastal protection, biodiversity, the reproductive capacity of marine organisms, and the catch and income of fishers (Jacquemont et al., 2022).

Fisheries restricted areas (FRAs) are primarily designed to improve the status of particular exploited stocks of interest and enrich the respective fisheries but do also complement MPAs in biodiversity and habitat conservation (Rodríguez-Rodríguez et al., 2016). The FRAs of the Aegean Sea in Greece have recently been reviewed, identified and mapped based on national and international fisheries, environmental, archaeological and maritime legislation that defines spatiotemporal restrictions of all fishing gears, revealing that 38% of the area is ruled by permanent fishing restrictions, while 28% is covered by seasonal FRAs (Petza et al., 2017). The existing FRAs (Supplementary Figure S1) in the second most productive Greek fishing ground, Thermaikos Gulf, northwestern Aegean Sea, that ban medium-scale fishing activities (trawling and purse seining) all year round in the innermost part of the gulf and also in areas close to the shore, have been shown to improve the biomass and size structure of targeted populations within their boundaries (Dimarchopoulou et al., 2018). The aforementioned spatial fisheries restrictions were also shown to benefit non-commercial stocks that form part of the by-catch or discarded catch but are likewise affected by fishing activities, especially bottom trawling (Dimarchopoulou et al., 2018). Similar results were also reported from the Gulf of Castellammare, in Sicily, central Mediterranean Sea (Pipitone et al., 2023).

Despite the general consensus on the need for establishing MPAs and FRAs (Petza et al., 2019), it is clear that if they are to meet their goals, the right choice of location, spatial extent (horizontal over space and vertical in depth) and number, as well as sufficient staffing and budgeting are quite critical. Indeed, boundaries that are drawn by purely political processes might largely overlook the different aspects of the life histories of marine species (e.g., spawning and nursery locations) that play an important role in MPA and FRA design (Browman and Stergiou 2004; Claudet et al., 2008; Gill et al., 2017). Systematic conservation planning and marine spatial planning are valuable tools to identify priority areas for protection, while minimizing potential conflicts between socioeconomic and ecological targets (Markantonatou et al., 2021). Ecosystem models that take into account multiple compartments of ecosystems, from primary producers to top predators, such as ECOSPACE, the spatial and time dynamic module of ECOPATH WITH ECOSIM (EWE), are useful tools for fisheries scientists and managers to analyze the impact and placement of MPAs and FRAs (Christensen and Walters 2004) in the context of the ecosystem-based fisheries management (Heymans et al., 2020). The entire Mediterranean Sea has been modeled with ECOSPACE at high spatial resolution to inform ecosystem-based management in the region (Piroddi et al., 2022). Some of the more local applications of ECOSPACE in the Mediterranean Sea have been in the Adriatic Sea where scenarios of MPA establishment and overall reduction of fishing effort were examined (Fouzai et al., 2012); in the Gulf of Gabes where the size and location of hypothetical MPAs, as well as alternative spatial management scenarios were investigated (Abdou et al., 2016; Halouani et al., 2016); in the southern Catalan Sea where cumulative spatial and temporal effects of environmental drivers and fishing were modeled (Coll et al., 2016).

The food web of the Thermaikos Gulf major fishing ground has been described with an ECOPATH model whose temporal dimensions were further extended with ECOSIM, unveiling historical trends of ecosystem degradation due to ocean warming and high fishing pressure. This model predicted that fishing effort reduction can lead to the rebuilding of stocks (Dimarchopoulou et al., 2022). Here, the previously constructed model of Thermaikos Gulf was complemented with spatial environmental data (e.g., sea surface temperature, depth, habitat type), as well as species' functional responses, to dynamically allocate fish and invertebrate biomass in space. Spatiotemporal simulations were also run aiming to reveal the impacts of environmental drivers and fishing on the biomass and commercial catches of marine populations and their distribution within the studied area over time. A baseline scenario incorporating the existing spatial fishing restrictions was examined along with six alternative spatiotemporal MPA scenarios, as has been previously performed (Fouzai et al., 2012). The main objective of comparing the effectiveness of different MPA scenarios was to investigate the impact of MPA allocation and characteristics, regarding the level of protection enforced on the biomass and commercial catches of the different components of the studied ecosystem. Results may inform decisions regarding the implementation of the Common Fisheries Policy and Maritime Spatial Planning Directive, or complement management plans for reaching conservation targets framed by the Marine Strategy Framework Directive and the Biodiversity Strategy 2030 by providing implications of alternative MPA placement scenarios and a deeper understanding of their impacts on the fisheries sector.

2. Materials and methods

2.1. Thermaikos Gulf Ecopath and Ecosim background

The ECOPATH base model was developed to describe the food web of Thermaikos Gulf [33 Functional Groups (FGs)] representing the average state of the ecosystem for the period 1998–2000. The model was further expanded in time with ECOSIM using available time series of biomass (i.e., a survey-based biomass index in t/km^2 derived from local experimental trawl surveys; Mediterranean International Trawling Survey Program MEDITS: Spedicato et al., 2019), commercial catches (landings plus discards), and fishing effort. The ECOSIM model was fitted to observed data for the period between 2000 and 2016 (Dimarchopoulou et al., 2022), and projections up to 2025 were performed assuming stable effort. The chosen ECOSIM model with the best fit to the observed historical data of biomass and commercial catches took into account the trophic interactions (the fitting routine estimated vulnerabilities for 20 prey-predator pairs), fishing activities, and environmental drivers (primary production anomaly and sea surface temperature), while the sensitivity of ECOSIM outputs to ECOPATH input parameters with various degrees of uncertainty was tested using Monte Carlo simulations (Dimarchopoulou et al., 2022). While the ECOSIM model fitting to observed biomass values was weak, it was able to more effectively capture long-term catch trends of benthic and demersal FGs, such as flatfishes, demersal fishes 2, 3, 4, whose commercial catches are highly correlated since they are caught in similar habitats and with similar gear, but did a poorer job with catches of large pelagics, horse mackerels, and hake, among others (Dimarchopoulou et al., 2022).

To consider the complexity inherent to species distributions, the spatially explicit time dynamic ECOSPACE module of EwE was used to add a spatial component to the ECOPATH with ECOSIM model of Thermaikos Gulf by dynamically allocating biomass across a two-dimensional grid.

2.2. *Ecospace: covered area, habitats, environmental data*

The first step when building an ECOSPACE model is to define the spatial grid cells as a baseline map of the studied area. The cells can be located either at sea or land, while the former ones are assigned to a particular marine habitat type, depth and relative primary production (Fig. 1; Christensen et al., 2005). Functional groups (FGs) can move from one cell to its four adjacent cells according to their ability to move or be transported by physical processes from one cell to another (dispersal rate), their habitat preference, foraging behavior (when organisms search for their prey) and predation risk they face in each cell (Walters et al., 1999). In the more recently updated foraging capacity model of ECOSPACE (Christensen et al., 2014), the proportion of a cell that can be used by a FG is a continuous value from 0 to 1 (continuous habitat suitability factor) and is determined by functional responses to multiple environmental factors. This means that foraging capacity is driven by various physical, oceanographic, and environmental factors like depth, bottom type, temperature etc., which have cumulative impacts on the ability of FGs to forage within a cell (Christensen et al., 2014).

The spatial domain of the ECOSPACE model covered the outer Thermaikos Gulf (approximately 2,800 km^2) as defined in Dimarchopoulou et al. (2018). The baseline map consisted of overall 4,757 square cells of approximately 1.4 km^2 each, out of which 1,995 cells formed the study area, 1,856 were land and 906 cells were assigned to water but were excluded because they were outside of the designated study area (Fig. 1). Values of depth, photosynthetically active radiation (PAR), sea surface temperature (SST), and relative primary productivity (PP) for the studied area were extracted from the Bio-ORACLE database (Fig. 1; Tyberghein et al., 2012; Assis et al., 2018) and were used to drive the foraging capacity and hence distribution of FGs. The environmental envelopes or environmental preference functions needed to parameterize the functional responses linking the aforementioned environmental drivers with the FGs were obtained from the literature (Supplementary Figures S2-S4; Supplementary Table S1).

Also, each study area cell was assigned to a total of three substrate types (referred to in ECOSPACE and this paper as “habitats”: Christensen et al., 2004) as derived from the EUNIS (2019)/full-detail habitat classification in EMODnet (https://emodnet.eu/seabed-habitat-map-europe): i) mud (including fine mud and sandy mud bottoms), ii) sand (including sand and muddy sand bottoms) and iii) *Posidonia oceanica* seagrass meadows (the seagrass meadows layer was also enriched by data provided in Sini et al., 2017; Topouzelis et al., 2018).

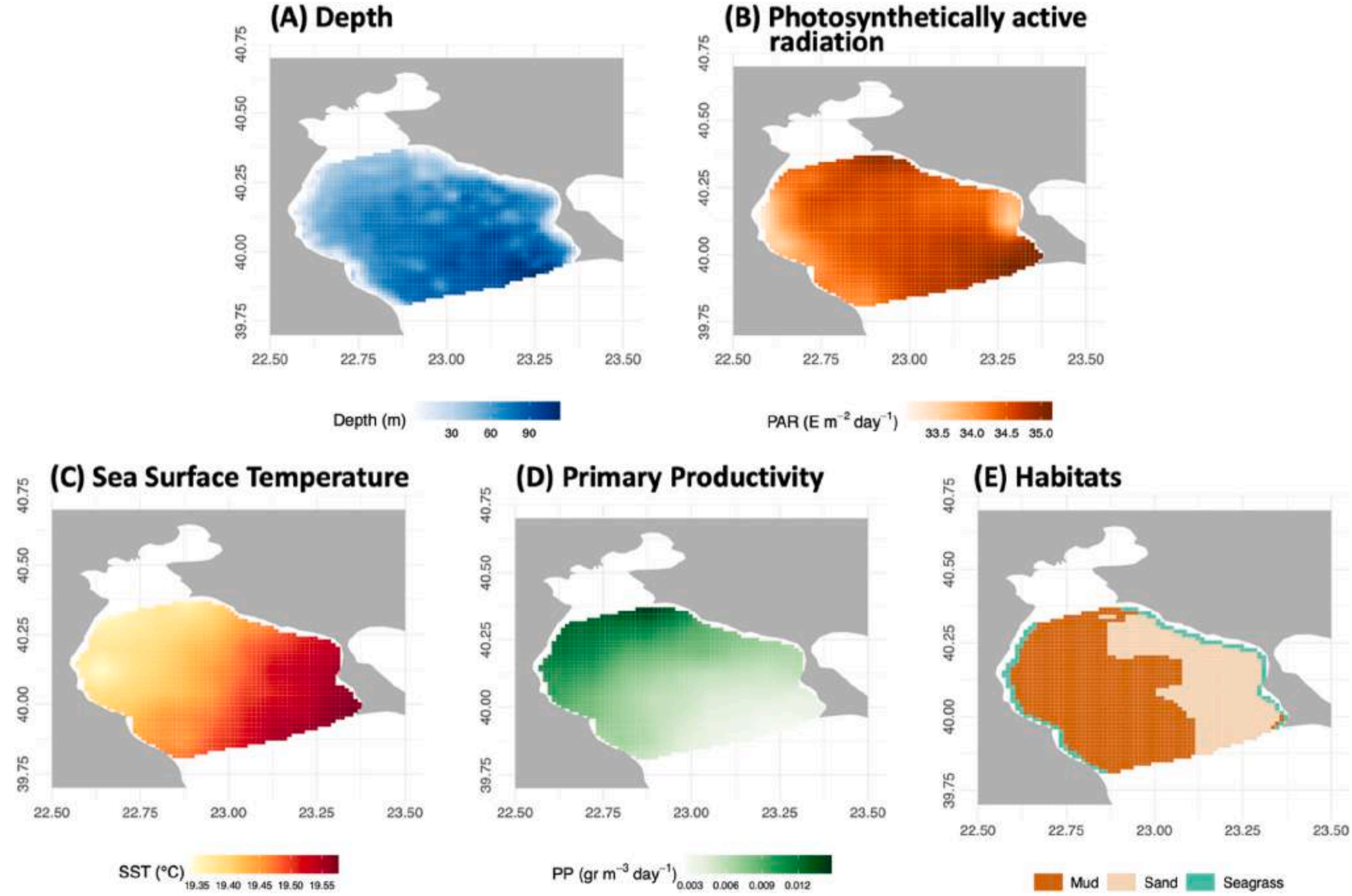


Fig. 1. The baseline map of Thermaikos Gulf that was used in the ECOSPACE model and the spatial distribution of the different parameters driving the model. The grey areas represent land cells, while the white areas (at the top, bottom and middle right of the maps) represent the cells that were assigned to water but were excluded from the study area. Panel (A): depth (m). Panel (B): photosynthetically active radiation (PAR measured in E*m-2*day^{-1}). Panel (C): sea surface temperature (SST measured in ^{o}C). Panel (D): relative primary productivity (PP measured in gr*m^{-3}*day^{-1}). Panel (E): the substrate (referred to as “habitat” in ECOSPACE) type assigned to each cell in the study area (green: seagrass meadows; dark brown: mud; light brown: sand).

The FGs were matched to preferred habitats (Supplementary Table S2) according to the ecology and biology of the modeled species (Froese and Pauly 2022; Palomares and Pauly 2022; for details on the FGs, please refer to Supplementary Table S2 and the supplementary material of Dimarchopoulou et al., 2022). Also, to facilitate the presentation of results, FGs were grouped based on their preferred environment (Froese and Pauly 2022; Palomares and Pauly 2022) as benthic, demersal, and pelagic (Table 1).

2.3. *Ecospace: functional group dispersal and vulnerability*

Distribution of species across the baseline map was defined by functional responses of the FGs to environmental factors such as depth and temperature, as well as by the base dispersal rate of each FG expressed as distance travelled per year in kilometers (km), and the relative dispersal and feeding rate in non-preferred habitats. The values for the above parameters were set as default in ECOSPACE (Christensen et al., 2005) or were modified as shown in Table 1: the base dispersal rates were set to 3 km/year for non-dispersing species with low mobility, 30 km/year for demersal species with medium mobility and 300 km/year for pelagic species with high mobility. For the relative dispersal rate in unsuitable habitats values ranged from 1 to 5 according to the mobility of the species, representing the number of times an FG would multiply its base dispersal rate in order to return to its preferred habitat (Fouzai et al., 2012; Abdou et al., 2016).

The vulnerability of an FG to predation in unsuitable habitats was assumed to be twice as high compared to preferred ones, as set by default in the software. Finally, the relative feeding rate in non-preferred habitats, which represents the fact that species are less likely to find and consume appropriate food when outside of their preferred habitat, was based on the trophic level of the FGs and was set as 0.95 for primary producers, as photosynthesis is not really influenced by habitat type; 0.01 for species of intermediate trophic levels (TL = 2.00–3.49), 0.3 for medium-high trophic levels (TL = 3.50–3.99) and 0.6 for species of higher trophic levels (TL > 4.00) (Fouzai et al., 2012; Abdou et al., 2016).

2.4. *Ecospace: fisheries and management scenarios*

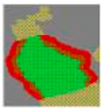
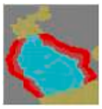
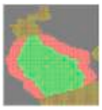
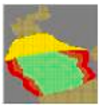
The four fishing fleets of trawlers, purse seiners, boat/beach seiners and small-scale coastal vessels of the ECOPATH base model were included in ECOSPACE and fishing zones were defined according to the habitat type. All fishing activities were assumed to be legal and abiding by the enforced spatial and temporal restrictions, which is not always the case (Dimarchopoulou et al., 2018). FRAs where trawling is forbidden based on seasonal and permanent regulations (Dimarchopoulou et al., 2018), were added. The permanent measure included in the model bans trawling within 3 nautical miles from the coast (20% of the study area), while the seasonal one bans trawling within 6 nautical miles from the coast (an additional 18% of the study area) during June, July, August and September. The permanent purse seining restriction that bans this fishing activity within 300 m off the coast was not taken into account in the model, since the surface area of the prohibition occupied in each cell was less than 75% of the modeled cell's area. The aforementioned trawling restrictions were used as the reference scenario (Business as Usual - BaU) of the current situation. Six spatiotemporal management scenarios with the addition of hypothetical MPAs, i.e., cells that are permanently or temporally protected from different forms of fishing, were examined for Thermaikos Gulf and are described in detail in Table 2. The ECOSPACE model mimics reality by using a relatively simple

Table 1

Input parameters used in the Thermaikos Ecospace model for each functional group (FG). TL: trophic level.

	FG	TL	Environment	Base dispersal rate (km/year)	Relative dispersal in bad habitat (proportion)	Rel. vulnerability to predation in bad habitat	Rel. feed rate in bad habitat (proportion)
1	**Phytoplankton**	1.0	–	3	1	2	0.95
2	**Zooplankton**	2.3	pelagic	3	1	2	0.01
3	**Benthic small crustaceans**	2.2	benthic	3	1	2	0.01
4	**Polychaetes**	2.1	benthic	3	1	2	0.01
5	**Shrimps**	3.1	benthic	30	2	2	0.01
6	**Crabs**	3.0	benthic	3	2	2	0.01
7	**Benthic invertebrates**	2.1	benthic	3	1	2	0.01
8	**Octopuses and cuttlefish**	3.3	benthic	30	2	2	0.01
9	**Squids**	3.8	demersal	30	2	2	0.3
10	**Red mullets**	2.8	demersal	30	2	2	0.01
11	**Anglerfish**	4.2	benthic	30	3	2	0.6
12	**Flatfishes**	4.0	benthic	30	2	2	0.6
13	**Other gadiforms**	3.6	demersal	30	3	2	0.3
14	**Hake**	4.1	demersal	30	3	2	0.6
15	**Demersal fishes 1**	3.1	demersal	30	3	2	0.01
16	**Demersal fishes 2**	3.7	demersal	30	3	2	0.3
17	**Demersal fishes 3**	3.7	demersal	30	3	2	0.3
18	**Demersal fishes 4**	3.3	demersal	30	3	2	0.01
19	**Picarels and bogue**	3.2	dem-pel	300	3	2	0.01
20	**Sharks**	3.9	demersal	30	3	2	0.3
21	**Rays and skates**	4.0	benthic	30	4	2	0.6
22	**Anchovy**	3.3	pelagic	300	4	2	0.01
23	**Sardine**	3.1	pelagic	300	4	2	0.01
24	**Horse mackerels**	3.4	pelagic	300	4	2	0.01
25	**Mackerels**	3.5	pelagic	300	5	2	0.01
26	**Other small pelagics**	3.2	pelagic	300	4	2	0.01
27	**Medium pelagics**	4.2	pelagic	300	5	2	0.6
28	**Large pelagics**	4.2	pelagic	300	5	2	0.6
29	**Loggerhead turtle**	3.1	dem-pel	300	5	2	0.01
30	**Seabirds**	2.3	–	300	5	2	0.01
31	**Dolphins**	4.5	dem-pel	300	5	2	0.6
32	**Discards**	1.0	–	10	5	2	1
33	**Detritus**	1.0	–	10	5	2	1

Table 2
Detailed description of the business-as-usual (BaU) spatiotemporal fishing restrictions in Thermaikos Gulf, as well as the six marine protected area (MPA) scenarios with hypothetical combinations of fishing restrictions tested in the Ecospace model.

Scenario		Description	Restricted gears	Restriction type	Area protected	Map
BaU	Business as usual (Greek legislation for Thermaikos Gulf; Dimarchopoulou et al., 2022)	permanent trawling ban within 3 nm from the coast; seasonal (June–September) trawling ban within 6 nm from the coast	OTB	Spatiotemporal	20% permanent trawling ban 🟥 18% seasonal trawling ban ▨	
MPA 1	Medium-scale vessel restrictions	permanent ban of medium-scale fisheries (trawlers and purse seiners) within 6 nm from the coast	OTB PS	Spatial	38% permanent medium-scale fishing ban 🟥	
MPA 2	Fishing restrictions	the northern part of the study area is not fished by any of the four fleets; the central and southern coastal parts continue BaU	OTB PS BS SSC (nets, traps, lines)	Spatiotemporal	26% total fishing ban 🟨 12% permanent trawling ban 🟥 12% seasonal trawling ban ▨	
MPA 3	Boat seining restrictions	no boat seining allowed, business as usual trawling ban	OTB BS	Spatiotemporal	100% permanent boat seining ban 🟩 20% permanent trawling ban 🟥 18% seasonal trawling ban ▨	
MPA 4	Small-scale coastal vessel restrictions	small-scale coastal vessels are not allowed to fish in April and May, BaU trawling ban	OTB SSC (nets, traps, lines)	Spatiotemporal	100% seasonal small-scale fishing ban 🟦 20% permanent trawling ban 🟥 18% seasonal trawling ban ▨	
MPA 5	Combination of 1-3-4	permanent ban of medium-scale fisheries (trawlers and purse seiners) within 6 nm from the coast; no boat seining allowed; small scale coastal vessels are not allowed to fish in April and May	OTB PS BS SSC (nets, traps, lines)	Spatiotemporal	38% permanent large-scale fishing ban 🟥 100% permanent boat seining ban 100% seasonal small-scale fishing ban 🟩	
MPA 6	Combination of 2-3-4	the northern part of the study area is not fished by any of the four fleets; the central and southern coastal parts continue BaU; no boat seining allowed; small-scale coastal vessels are not allowed to fish in April and May	OTB PS BS SSC (nets, traps, lines)	Spatiotemporal	26% total fishing ban 🟨 12% permanent trawling ban 🟥 12% seasonal trawling ban ▨ 100% permanent boat seining ban 100% seasonal small-scale fishing ban 🟩	

*OTB: otter bottom trawl; PS: purse seine; BS: boat seine; SSC: small-scale coastal vessels.

"gravity model" to redistribute fishing effort across the modeled area based on profitability (Walters et al., 1999). The distribution of fishing effort in the BaU scenario and the redistribution of fishing effort in the tested scenarios (MPA1-6) for each fleet included in the model is given in Supplementary Figures S5-S8.

3. Results

For validation of the developed ECOSPACE model, beyond discussions with local experts on the validity of the modeled distributions, the observed survey-based biomass index values from local experimental trawl surveys in Thermaikos Gulf (Kallianiotis et al., 2004; Spedicato et al., 2019) for hake, shrimps, anglerfish, and picarels and bogue were superimposed over the modeled biomass results for the year 2014, i.e., the last year for which both biomass and catch observed values were available (Fig. 2). The model seems to capture the distribution of picarels and bogue quite accurately, while predictions for shrimps do not match the observed values. The modeled and observed distribution for

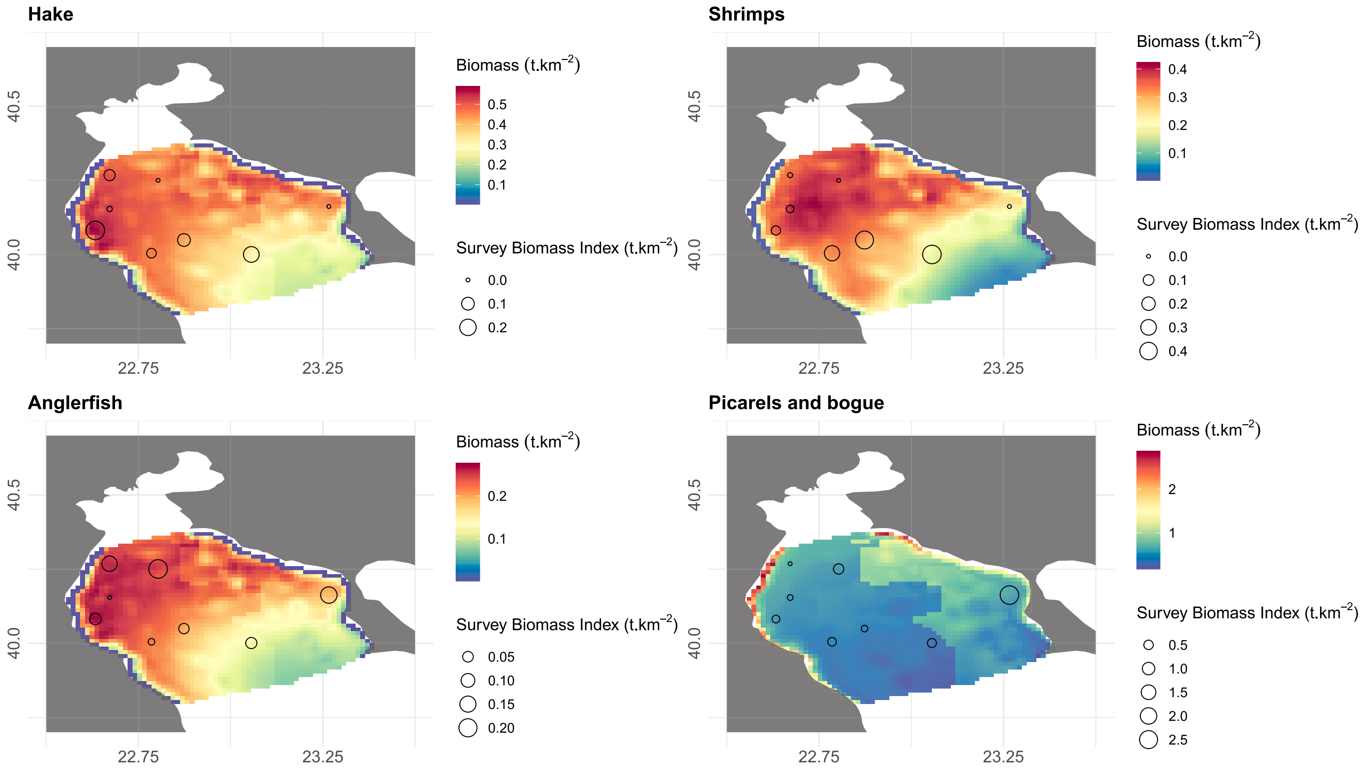


Fig. 2. Observed survey-based biomass index values (circles; t/km^2) from local experimental trawl surveys in Thermaikos Gulf for 2014, superimposed over the ECOSPACE modeled biomass results (interpolated color gradient; t/km^2) for the same year, i.e., the last year for which both biomass and commercial catch observed values were available.

anglerfish and hake are in partial agreement: the model captures well the high biomass of hake on the western part of the gulf and of anglerfish on the northwestern part, while it disagrees with observed values in the rest of the area. For commercial catches, we performed Spearman correlations between modeled catch (from the ECOSPACE spatial simulations, averaged by year and across the study area) and observed catch (time series of averaged values by year and across the study area that was an input to ECOSIM) by functional group (Supplementary Table S3). Overall, all FGs with associated observed commercial catch values ($n = 22$) showed a significant strong positive correlation (rho = 0.71; $p < 0.01$) between modeled and observed catches. When individually examined, 41% ($n = 9$) of the FGs exhibited significant correlations between modeled and observed catches, with all but one being strong or very strong (Supplementary Table S3). The spatial distribution of the biomass and commercial catches of FGs of the model is given in the form of maps for the same year, 2014 (Figs. 3 and 4).

The ECOSPACE simulation of the business-as-usual scenario (BaU) for Thermaikos Gulf predicted a small increase in total higher trophic level group (HTL; excluding FGs 1–4, 7, 32, 33) biomass (1.7%) but a higher decrease in commercial catch (11%) from 2000 to 2025, i.e., by the end of the simulation period, but with 14 out of the 26 HTL FGs (54%) showing higher biomass and one FG (large pelagics) also resulting in higher commercial catches (17%; Table 3). Large pelagics were projected to have the highest biomass increase (56.1%), while seabirds exhibited the lowest biomass increase (0.4%) in 2025 (BaU scenario: Table 3). Regarding the FGs of high relative impact in the studied ecosystem (see Fig. 4 regarding the keystone index and relative total impact in Dimarchopoulou et al., 2022), the biomass of squids was predicted to increase by 4.2%, whereas the biomass of other gadiforms seemed to be decreasing by 10.4% in 2025.

As far as the examined spatial scenarios are concerned, several target species seemed to benefit from the establishment of the MPAs (Supplementary Tables S4-S9). In particular, anglerfish, demersal fishes 2, sharks, sardines, horse mackerels, mackerels, medium pelagics, large pelagics, loggerhead turtles, seabirds consistently benefited from all six tested MPA scenarios in terms of biomass (Table 4). The highest biomass increase was predicted for large pelagics under Scenarios MPA 2 (153%) and MPA 6 (293.4%). Overall, Scenario MPA 5 (Table 4) resulted in the highest increase (3.3%) of total higher trophic level group biomass compared to the reference scenario with a predicted increase in 85% of the FGs, including several ecologically and commercially important species, by < 0.1% (demersal fishes 4) to 97% (large pelagics). Beyond large pelagics, other FGs with a high relative biomass increase were loggerhead turtles (36.8%), medium pelagics (19.4%), seabirds (12%) and flatfishes (8.8%). All of the tested scenarios resulted in a smaller overall HTL group biomass increase compared to the BaU scenario, with MPA 1 predicted to have the second highest biomass increase (1.7%). In all scenarios at least 55% of the FGs were predicted to have higher total biomass compared to the BaU scenario. The spatial distribution of the biomass of benthic, demersal, and pelagic FGs for each tested scenario (MPA1-6) compared to the BaU scenario is given in the form of maps for the year 2025, i.e., the end of the simulation period (Fig. 5). Overall, it can be seen from the graphs that biomass is projected to increase (blue shaded areas) within the boundaries of areas where fishing restrictions are enforced.

Total commercial catches were lower in all tested scenarios compared to the BaU scenario, except for MPA 3 that resulted in the same catches overall (Table 5; Supplementary Tables S4-S9). Scenario MPA 6 was predicted to have the highest commercial catch decline (27%) owing to several FGs such as anchovy (36% catch decline), red mullets (33%), sardine (29%), followed by MPA 2 (20%) and MPA 5 (16%). However, despite the projected total commercial catch declines, large pelagics and loggerhead turtles were shown to have consistently higher catches in all scenarios, from a slight increase of 1% in MPA 3 to a considerable increase of 180% in MPA 6 (Table 5). The spatial distribution of the commercial catches of benthic, demersal, and pelagic FGs

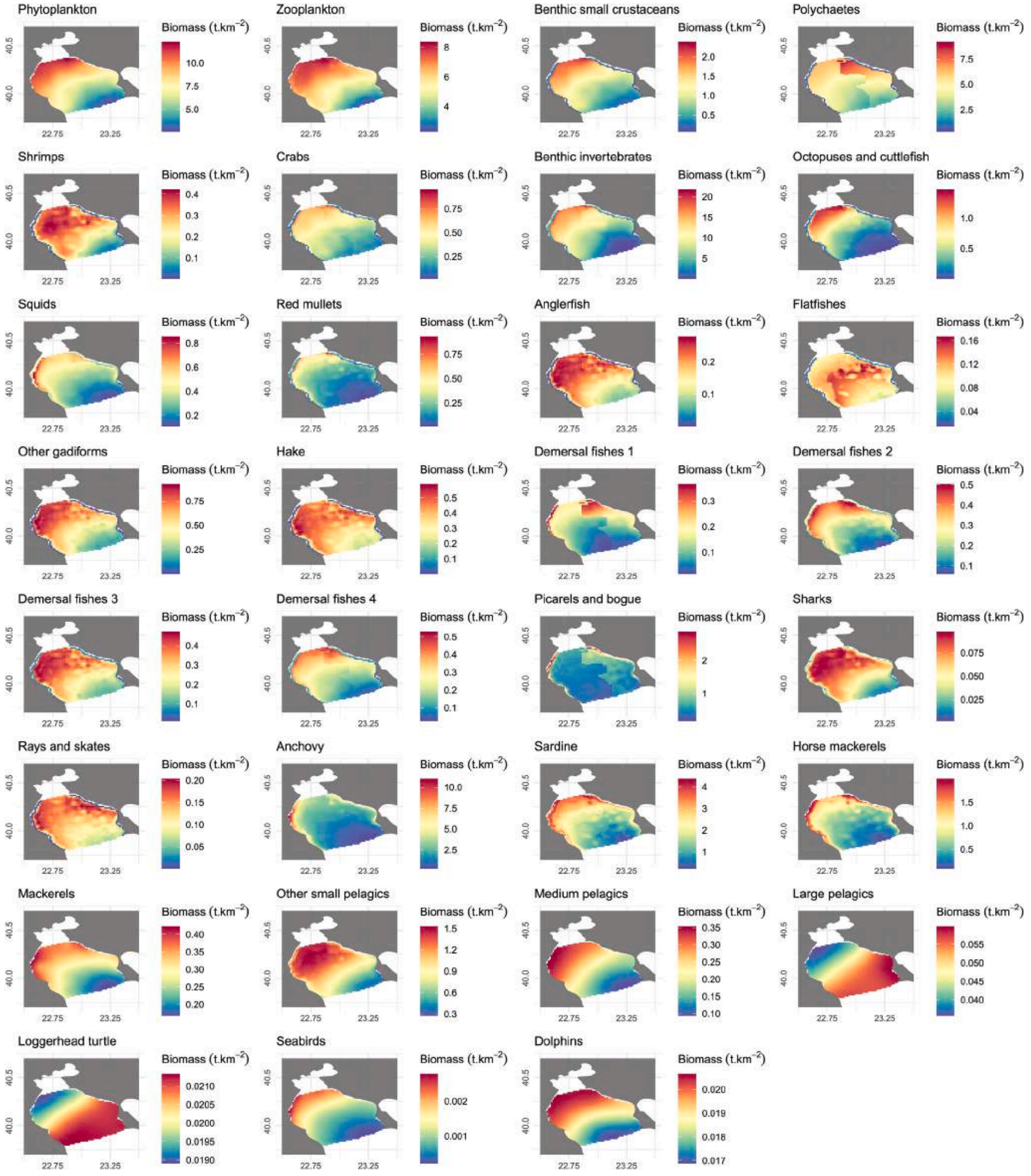


Fig. 3. ECOSPACE model predictions of the spatial distribution of biomass (color gradient represents relative values; t/km^2) for each functional group in the Thermaikos Gulf model (business-as-usual scenario) in 2014, the last year for which both biomass and commercial catch observed values were available.

for each tested scenario (MPA1-6) compared to the BaU scenario is given in the form of maps for the year 2025, i.e., the end of the simulation period (Fig. 6). It seems in the related scenarios MPA 2 and 6, where the northern part of the gulf is closed to all fishing activities, that elevated commercial catches (blue shaded areas) are predicted to occur at the boundaries of the closed areas, but also in the open areas overall. The same pattern can be seen for related scenarios MPA 1 and 5 where a permanent ban of medium-scale fisheries (trawlers and purse seiners) within 6 nm from the coast is being tested.

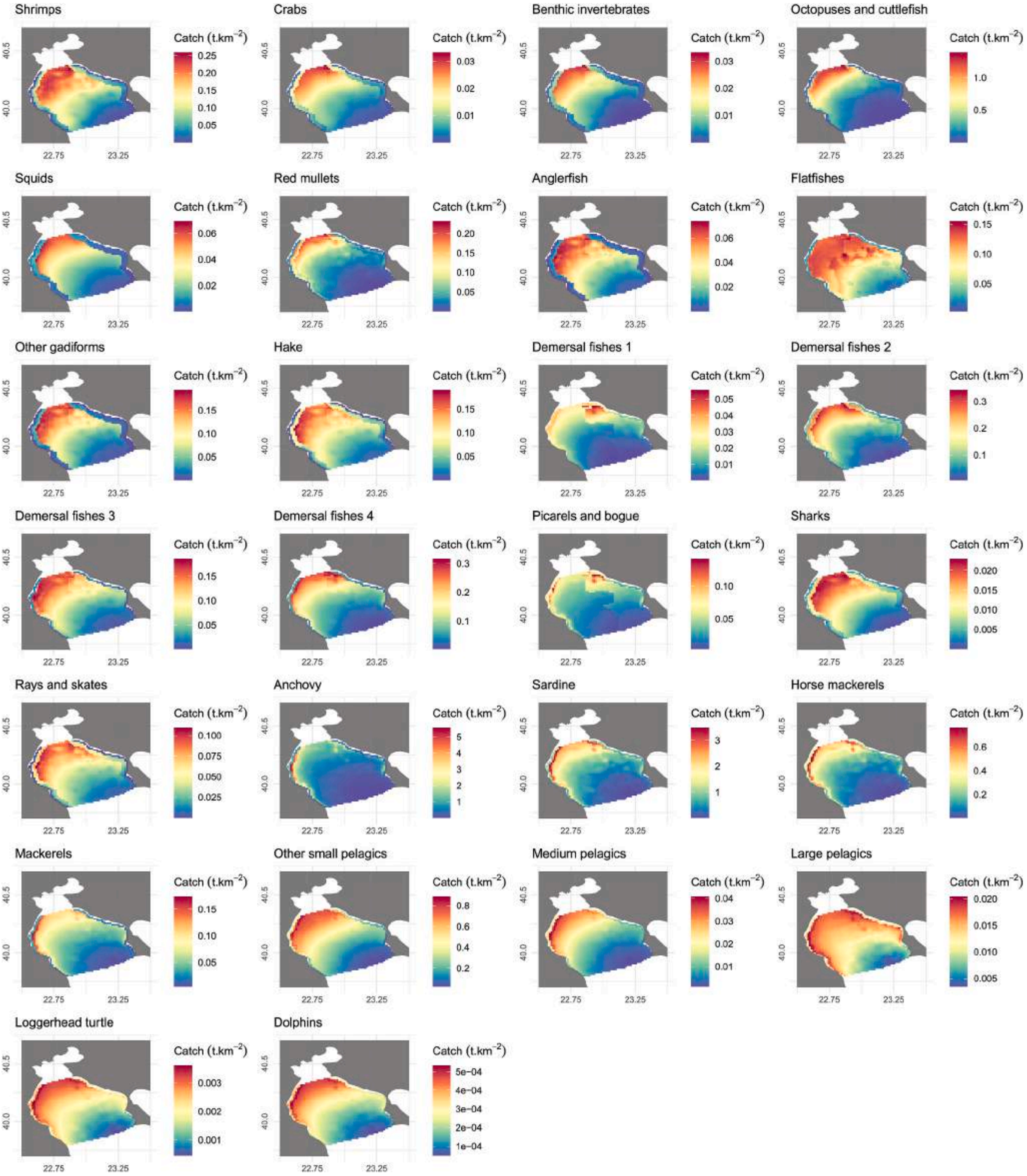


Fig. 4. ECOSPACE model predictions of the spatial distribution of commercial catches (color gradient represents relative values; t/km^2) for each fished functional group in the Thermaikos Gulf model (business-as-usual scenario) in 2014, the last year for which both biomass and commercial catch observed values were available.

4. Discussion

Spatiotemporal models may be used to examine alternative hypothetical management scenarios, including MPA placement, and provide an initial screening capability with predictions of how biomass and commercial catches will change under various tested scenarios aiming to serve as a starting point for deliberation, informing conservation policies and designing adaptive management approaches (Salomon et al., 2002; Shabtay et al., 2018; Piroddi et al., 2021). Simulated MPA scenarios can be either realistic and potentially readily implementable products for managers (Fouzai et al., 2012), or more theoretical with the main intention being to contribute to a deeper knowledge and understanding

Table 3

Ecospace simulation results for Thermaikos Gulf for the business-as-usual scenario (BaU). FG: functional group. Biomass (Bi) and commercial catch (Ca) values (t/km^2) and ratios at the starting year (2000) and the end of the simulation period (2025). Bold italic numbers represent an increase of biomass and commercial catch in 2025 compared to 2000. Total HTL refers to total biomass or catch of higher trophic level FGs and excludes FGs 1–4, 7, 32, 33.

	FG	Bi2000	Bi2025	Bi 2025/2000	Ca2000	Ca2025	Ca 2025/2000
1	**Phytoplankton**	7.708	7.747	***1.005***			
2	**Zooplankton**	5.837	5.779	0.990			
3	**Benthic small crustaceans**	1.068	1.038	0.972			
4	**Polychaetes**	4.679	4.500	0.962			
5	**Shrimps**	0.307	0.271	0.882	0.112	0.090	0.805
6	**Crabs**	0.413	0.381	0.924	0.011	0.009	0.843
7	**Benthic invertebrates**	8.533	8.072	0.946	0.008	0.007	0.915
8	**Octopuses and cuttlefish**	0.392	0.419	***1.069***	0.257	0.253	0.985
9	**Squids**	0.362	0.377	***1.042***	0.018	0.018	0.989
10	**Red mullets**	0.201	0.207	***1.032***	0.047	0.045	0.959
11	**Anglerfish**	0.201	0.188	0.934	0.027	0.024	0.904
12	**Flatfishes**	0.107	0.116	***1.083***	0.102	0.089	0.866
13	**Other gadiforms**	0.564	0.505	0.896	0.061	0.053	0.866
14	**Hake**	0.397	0.403	***1.015***	0.082	0.073	0.886
15	**Demersal fishes 1**	0.152	0.132	0.868	0.016	0.012	0.763
16	**Demersal fishes 2**	0.247	0.251	***1.017***	0.113	0.101	0.899
17	**Demersal fishes 3**	0.320	0.301	0.940	0.087	0.068	0.784
18	**Demersal fishes 4**	0.233	0.225	0.968	0.113	0.084	0.789
19	**Picarels and bogue**	0.652	0.619	0.951	0.043	0.034	0.789
20	**Sharks**	0.071	0.069	0.968	0.010	0.009	0.865
21	**Rays and skates**	0.139	0.132	0.948	0.050	0.040	0.810
22	**Anchovy**	2.270	2.453	***1.081***	0.687	0.660	0.960
23	**Sardine**	1.945	2.062	***1.060***	0.950	0.846	0.891
24	**Horse mackerels**	0.730	0.737	***1.010***	0.189	0.164	0.870
25	**Mackerels**	0.291	0.301	***1.034***	0.055	0.048	0.880
26	**Other small pelagics**	1.147	1.161	***1.012***	0.427	0.360	0.843
27	**Medium pelagics**	0.249	0.243	0.973	0.018	0.015	0.832
28	**Large pelagics**	0.049	0.077	***1.561***	0.017	0.020	***1.170***
29	**Loggerhead turtle**	0.020	0.021	***1.038***	0.002	0.002	0.808
30	**Seabirds**	0.001	0.001	***1.004***			
31	**Dolphins**	0.020	0.019	0.969	0.000	0.000	0.766
32	**Discards**	0.358	0.344	0.961			
33	**Detritus**	30.382	30.265	0.996			
	TOTAL	70.043	69.416	0.991	3.495	3.125	0.894
	Total HTL			***1.017***			0.894

of ecosystem function (Abdou et al., 2016). In this work, an Ecospace model was developed for a highly exploited and productive area in Greece, Thermaikos Gulf, in which realistic and potentially implementable scenarios of alternative MPA placement were examined. Although previous work in the Aegean Sea (Markantonatou et al., 2021) proposed alternative scenarios for establishing an MPA network to effectively protect marine biodiversity and concluded that parts of Thermaikos Gulf were consistently suggested as no take zones, it has not considered the aspect of redistributing fishing effort to balance fisheries economic loss.

Unlike the work of Fouzai et al. (2012), but similarly to that of Abdou et al. (2016), the present Ecospace model scenarios did not include reduction in total fishing effort but assumed *status quo* fishing effort that was redistributed beyond the fishing prohibitions' boundaries in the remaining exploited part of the Gulf (see Supplementary Figures S5-S8). This redistribution resulted in a pronounced concentration of fishing activities right at the boundaries and in the areas adjacent to the MPA with a commercial catch increase resembling the "fishing-the-line" phenomenon, which has a notable effect on catch-per-unit-effort and fish density within and outside the MPA (Kellner et al., 2007; Nalmpanti et al., 2021) and is linked to the spillover of individuals towards adjacent unprotected waters (Di Lorenzo et al., 2020) ultimately increasing the profitability of fishing fleets in Ecospace. Empirically, "fishing-the-line" was implied to occur illegally in Thermaikos Gulf based on satellite effort data (Dimarchopoulou et al., 2018). From the Ecospace model, this was particularly noticeable in the commercial catches of pelagic and benthic species in many of the tested scenarios where the increased area of the MPAs resulted in an increase of the boundary and, consequently, a regional increase in commercial catches.

According to the reference scenario, the overall biomass of organisms in the Thermaikos Gulf ecosystem was predicted to slightly increase from 2000 to 2025, while fisheries catches showed a decline by 2025. Generally, the tested MPA scenarios also showed a similar pattern of overall biomass increase (highest for MPA 5) and commercial catch decrease when compared with the reference scenario for 2025 which was the last year of the simulation. Although spatial modifications in the size and allocation of MPAs may benefit certain groups of organisms, such measures are not sufficient (and in many cases seem to have overall adverse results for commercial catches and only neutral for biomass) if not combined with an overall reduction in fishing effort (Abdou et al., 2016). As supported by the simulation results in this work, small MPAs near highly exploited areas may only result in an invariable concentration of fishing operations and commercial catches near the MPA perimeter; therefore, it would be the implementation of large MPAs, with shorter perimeters relative to their total surface, or MPAs in bays and gulfs, with limited neighboring to fished areas, that could help solve this problem (Pauly et al., 2000). If the establishment of a MPA leads to a less impacted healthier community within the MPA, but the redistribution of fishing effort ends up putting more pressure on the rest of the ecosystem, then one question arises (Le Quesne et al., 2007): is this particular MPA considered as an effective tool for the conservation of biodiversity and protection of ecosystem structure? In areas like the Mediterranean where most stocks are not managed by quotas, it is the overall reduction in total fishing effort that, in combination with any protective spatial restriction measures, can effectively address the negative effects of overfishing on marine populations and ecosystems and lead to rebuilding of stocks, something that in the future could be reflected upon elevated commercial catches and revenues for the fishers (Figs.7 and 8 in Froese et al., 2018). Indeed, while stocks can be rebuilt soon after reducing fishing effort (Pipitone et al., 2000), it takes more

Table 4

Ecospace biomass simulation results for Thermaikos Gulf for six MPA (1–6) scenarios compared to the business-as-usual scenario (BaU). FG: functional group. Biomass ratios at the end of the simulation period (2025). Bold italic numbers represent higher (ratio >1) biomass (values of 1.000 in bold mean that biomass was >1 beyond the three decimals). Total HTL refers to total biomass of higher trophic level FGs and excludes FGs 1–4, 7, 32, 33. For details on the scenarios see Table 2.

	Biomass						
	FG	MPA 1	MPA 2	MPA 3	MPA 4	MPA 5	MPA 6
1	**Phytoplankton**	***1.003***	0.999	1.000	***1.001***	***1.003***	0.996
2	**Zooplankton**	0.998	***1.000***	1.000	0.999	0.997	***1.002***
3	**Benthic small crustaceans**	***1.001***	0.993	***1.000***	0.996	0.997	0.996
4	**Polychaetes**	***1.001***	0.993	1.000	***1.001***	***1.002***	0.997
5	**Shrimps**	***1.007***	0.998	***1.007***	***1.003***	***1.004***	***1.002***
6	**Crabs**	***1.004***	0.995	***1.004***	0.987	0.988	0.983
7	**Benthic invertebrates**	***1.001***	0.980	1.000	0.991	0.993	0.977
8	**Octopuses and cuttlefish**	***1.002***	***1.027***	1.000	***1.043***	***1.047***	***1.074***
9	**Squids**	***1.031***	***1.012***	***1.000***	***1.005***	***1.036***	0.992
10	**Red mullets**	0.997	0.996	1.000	***1.011***	***1.009***	***1.017***
11	**Anglerfish**	***1.017***	***1.043***	***1.002***	***1.039***	***1.055***	***1.067***
12	**Flatfishes**	***1.011***	0.979	***1.001***	***1.076***	***1.088***	***1.061***
13	**Other gadiforms**	***1.020***	0.992	***1.005***	0.965	0.979	0.923
14	**Hake**	***1.015***	0.981	***1.000***	***1.027***	***1.042***	0.988
15	**Demersal fishes 1**	0.994	0.950	0.998	0.937	0.933	0.910
16	**Demersal fishes 2**	***1.003***	***1.020***	***1.001***	***1.012***	***1.015***	***1.036***
17	**Demersal fishes 3**	***1.015***	***1.016***	***1.001***	0.995	***1.010***	0.987
18	**Demersal fishes 4**	0.998	***1.003***	***1.000***	***1.002***	***1.000***	***1.009***
19	**Picarels and bogue**	0.996	***1.002***	1.000	0.996	0.993	***1.007***
20	**Sharks**	***1.014***	***1.010***	***1.007***	***1.046***	***1.054***	***1.042***
21	**Rays and skates**	***1.022***	0.964	***1.006***	***1.009***	***1.024***	0.951
22	**Anchovy**	***1.044***	0.939	0.998	0.965	***1.010***	0.846
23	**Sardine**	***1.012***	***1.026***	***1.001***	***1.027***	***1.039***	***1.050***
24	**Horse mackerels**	***1.002***	***1.006***	***1.000***	***1.006***	***1.009***	***1.013***
25	**Mackerels**	***1.040***	***1.017***	***1.001***	***1.001***	***1.042***	***1.008***
26	**Other small pelagics**	0.994	***1.032***	1.000	***1.065***	***1.060***	***1.085***
27	**Medium pelagics**	***1.051***	***1.174***	***1.006***	***1.133***	***1.194***	***1.290***
28	**Large pelagics**	***1.018***	***2.530***	***1.009***	***1.910***	***1.970***	***3.934***
29	**Loggerhead turtle**	***1.077***	***1.140***	***1.079***	***1.355***	***1.368***	***1.457***
30	**Seabirds**	***1.117***	***1.108***	***1.129***	***1.131***	***1.120***	***1.105***
31	**Dolphins**	0.996	***1.004***	***1.001***	***1.030***	***1.027***	***1.029***
32	**Discards**	0.000	0.000	0.000	0.000	0.000	0.000
33	**Detritus**	***1.001***	0.995	***1.000***	***1.001***	***1.003***	0.999
	TOTAL	0.999	0.992	0.995	0.997	***1.001***	0.994
	Total HTL	***1.017***	***1.010***	***1.001***	***1.016***	***1.033***	***1.012***

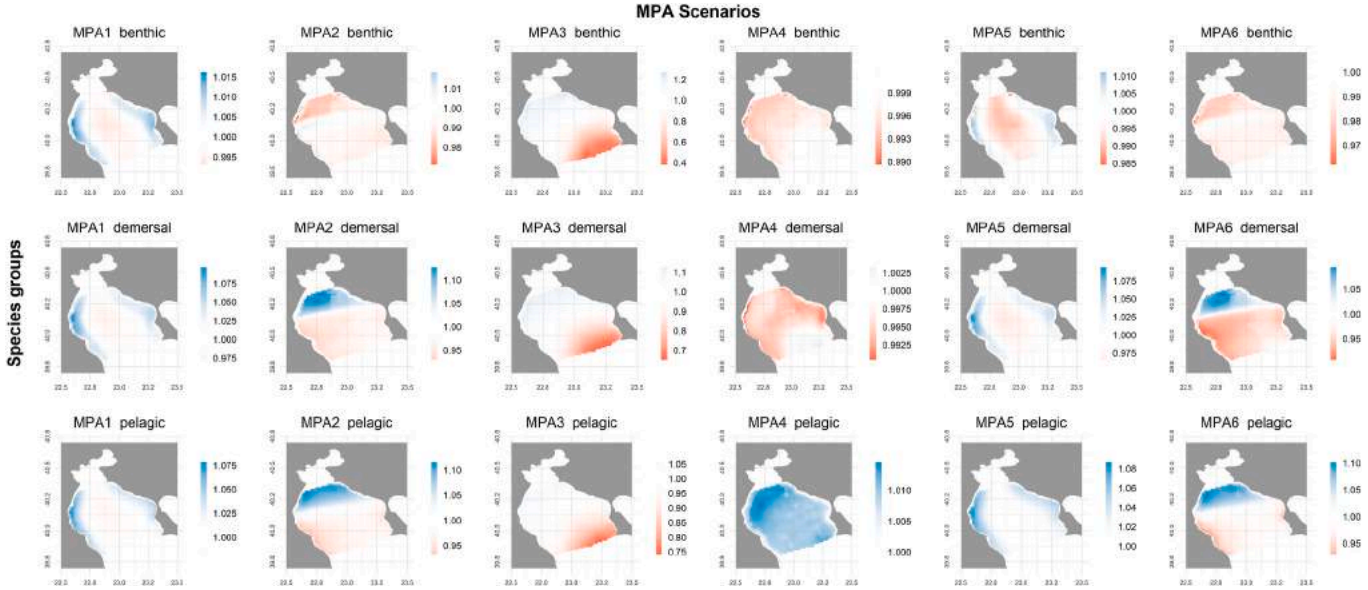


Fig. 5. ECOSPACE model predictions of the biomass spatial distribution of benthic, demersal, and pelagic functional groups in the Thermaikos Gulf model for each tested scenario (MPA1-6) compared to the business-as-usual scenario (BaU) and for the year 2025, i.e., the end of the simulation period (ratios of values measured in t/km^2). A value of 1 indicates the same biomass values between the tested scenarios and BaU, while a value lower or higher than 1 indicates lower or higher biomass in the tested scenario compared to BaU, respectively.

Table 5
Ecospace commercial catch simulation results for Thermaikos Gulf for six MPA (1–6) scenarios compared to the business-as-usual scenario (BaU). FG: functional group. Catch ratios at the end of the simulation period (2025). Bold italic numbers represent higher (ratio >1) catch (values of 1.000 in bold mean that catch was >1 beyond the three decimals). Total HTL refers to total catch of higher trophic level FGs and excludes FGs 1–4, 7, 32, 33. For details on the scenarios see Table 2.

	Commercial catch						
	FG	MPA 1	MPA 2	MPA 3	MPA 4	MPA 5	MPA 6
5	**Shrimps**	***1.003***	0.981	***1.004***	0.916	0.916	0.901
6	**Crabs**	0.998	0.954	***1.002***	0.889	0.885	0.846
7	**Benthic invertebrates**	0.984	0.871	0.999	0.929	0.915	0.813
8	**Octopuses and cuttlefish**	0.996	0.662	0.999	0.888	0.885	0.612
9	**Squids**	0.966	0.810	0.984	0.973	0.921	0.769
10	**Red mullets**	0.984	0.743	0.999	0.889	0.874	0.672
11	**Anglerfish**	0.969	0.807	***1.001***	***1.008***	0.973	0.815
12	**Flatfishes**	***1.009***	0.768	***1.000***	0.921	0.930	0.760
13	**Other gadiforms**	0.989	0.935	***1.003***	0.923	0.909	0.832
14	**Hake**	***1.002***	0.830	1.000	0.920	0.918	0.764
15	**Demersal fishes 1**	0.968	0.885	0.999	0.803	0.773	0.712
16	**Demersal fishes 2**	0.985	0.796	***1.000***	0.891	0.876	0.718
17	**Demersal fishes 3**	***1.018***	0.928	0.997	0.846	0.858	0.763
18	**Demersal fishes 4**	0.994	0.895	0.997	0.844	0.837	0.756
19	**Picarels and bogue**	0.848	0.849	0.985	0.925	0.760	0.778
20	**Sharks**	***1.009***	0.822	***1.005***	0.945	0.949	0.783
21	**Rays and skates**	***1.009***	0.858	***1.003***	0.886	0.888	0.756
22	**Anchovy**	0.784	0.738	0.997	0.917	0.700	0.635
23	**Sardine**	0.932	0.760	0.995	0.931	0.850	0.707
24	**Horse mackerels**	0.917	0.795	0.996	0.904	0.816	0.717
25	**Mackerels**	0.973	0.881	0.995	0.943	0.905	0.820
26	**Other small pelagics**	0.995	0.865	0.998	0.929	0.924	0.802
27	**Medium pelagics**	***1.047***	0.934	***1.006***	0.973	***1.020***	0.884
28	**Large pelagics**	***1.016***	***2.058***	***1.007***	***1.674***	***1.720***	***2.802***
29	**Loggerhead turtle**	***1.061***	***1.074***	***1.066***	***1.130***	***1.138***	***1.165***
31	**Dolphins**	0.995	0.961	***1.001***	0.859	0.855	0.821
	TOTAL	0.928	0.796	0.997	0.921	0.844	0.728
	Total HTL	0.928	0.796	0.997	0.920	0.844	0.728

time (=3–5 years) to detect a positive response in commercial catches and even that cannot guarantee that the ecosystem will be able to produce the highest past catch levels owing to unsustainably high past levels of fishing effort or following a long history of overexploitation (Froese et al., 2018; Dimarchopoulou et al., 2022).

Admittedly, the establishment of MPAs does not always result in straightforward consistent benefits but encompasses more complex interactions and associated trade-offs among the different sectors of the fishery and the various compartments of the ecosystem (Le Quesne et al., 2007). After all, due to the trophic interactions among organisms within the food web, biomass cannot be rebuilt simultaneously for all ecosystem components (Froese et al., 2016), so fisheries managers would have to focus on certain groups benefiting from management measures. Here, out of the six tested MPA management scenarios, MPA 1 and 5 stood out in terms of the number of exploited, commercially relevant (e.g., hake, flatfishes, anglerfish), but also vulnerable (e.g., sharks, rays and skates) benthic and demersal FGs whose biomass responded positively to protection. The magnitude of positive change was more pronounced in scenario MPA 5 in which the overall average biomass increase in commercial FGs reached 10% compared to the BaU scenario. Notable was the predicted increase for pelagic and demersal species that benefit from the permanent spatial fishing bans in purse and boat seining and trawling, as well as the seasonal ban of small-scale coastal vessels. The proposed ban of small-scale coastal fishing in MPA 5 is in line with the 2–4 month spawning period of most Mediterranean fishes that spans from April to August (Tsikliras et al., 2010) and that is expected to shift earlier due to ocean warming and resulting elevated water temperatures (Pauly and Liang 2022). The total boat seining ban suggested in scenario MPA 5 is based on research indicating it is a less sustainable, non-selective gear causing fish abundance reductions over Posidonia beds (Kalogirou et al., 2010; Vieira et al., 2020). In fact, the use of this gear was prohibited in 2013 in Greece, but later on about 200 experimental fishing licenses were reissued for the entire country producing a rather small catch quantity (Moutopoulos 2020) and were withdrawn after 2020.

As showed in the biomass and commercial catch distribution maps of the scenarios examined in the present work, potential protection benefits may be negated by high movement rates due to spatial trophic cascade effects that occur within MPAs, where predators (e.g., large pelagics, anglerfish, hake) become abundant owing to local protection, they increasingly consume and lower the density of prey organisms (e.g., anchovy, shrimps, crabs) and then move out of the protected areas for food (Walters et al., 1999). As also observed by Fouzai et al. (2012), although the results of this work demonstrated decline in overall projected commercial catches, there were some cases in which certain fishery sectors showed some benefits (e.g., the fishery of large pelagics showed significantly elevated commercial catches in scenarios MPA 2 and 4–6). That indicates a potential conflict between ecological (biomass rebuilding that usually results from less fishing and thus commercial catches) and socioeconomic (fisheries revenues that result from increased catches with less effort) targets regarding the well-being of the ecosystem versus the economic and social performance of suggested MPAs. No-take MPAs may be considered as a severe management tool by fishers as they deny them access to lucrative fishing grounds forcing them to potentially travel longer to adjacent areas that might, however, benefit from biomass exports from the MPA and provide higher catches (Colléter et al., 2015). Nevertheless, in the Gulf of Gabes in Tunisia, where Ecospace was used as a decision support tool to evaluate alternative fishing management plans, the simulations suggested something that would interest both managers and scientists: despite the varying response of different fishery sectors and groups of organisms to potential management measures, it would be possible for the fishers to maintain the same level of catches even if bottom trawlers operated at 80% of their current capacity, without jeopardizing the ecosystem structure (Halouani et al., 2016).

After discussing all analyses and model outputs, it should be highlighted that the results of this study are dependent on assumptions and limitations of the modeling software. Despite its versatility, Ecospace has several conceptual and operational limitations that should be taken into account when building and parameterizing the models, but most importantly when interpreting results (de Mutsert et al., 2023). Conceptual limitations include the fact that Ecospace is not three-dimensional, and that fishing effort is distributed based only on profitability and fishing cost, while operational limitations relate to decisions made during the initial setup of a model, such as choosing whether to include multi-stanza groups or defining the appropriate cell size that matches data availability and computational demand. Also, Ecospace is strongly dependent on the underlying Ecopath and Ecosim, while parameter uncertainty is currently not fully considered.

In this model, the biomass and commercial catch patterns for large pelagics should be interpreted with caution since the fit of the model to observed data in Ecosim was poor (Fig. 6 in Dimarchopoulou et al., 2022) and the uncertainty around biomass predictions was high (Fig. A5 in the supplement of Dimarchopoulou et al., 2022), and that was carried over to Ecospace. This is evident in other studies as well and has to do with

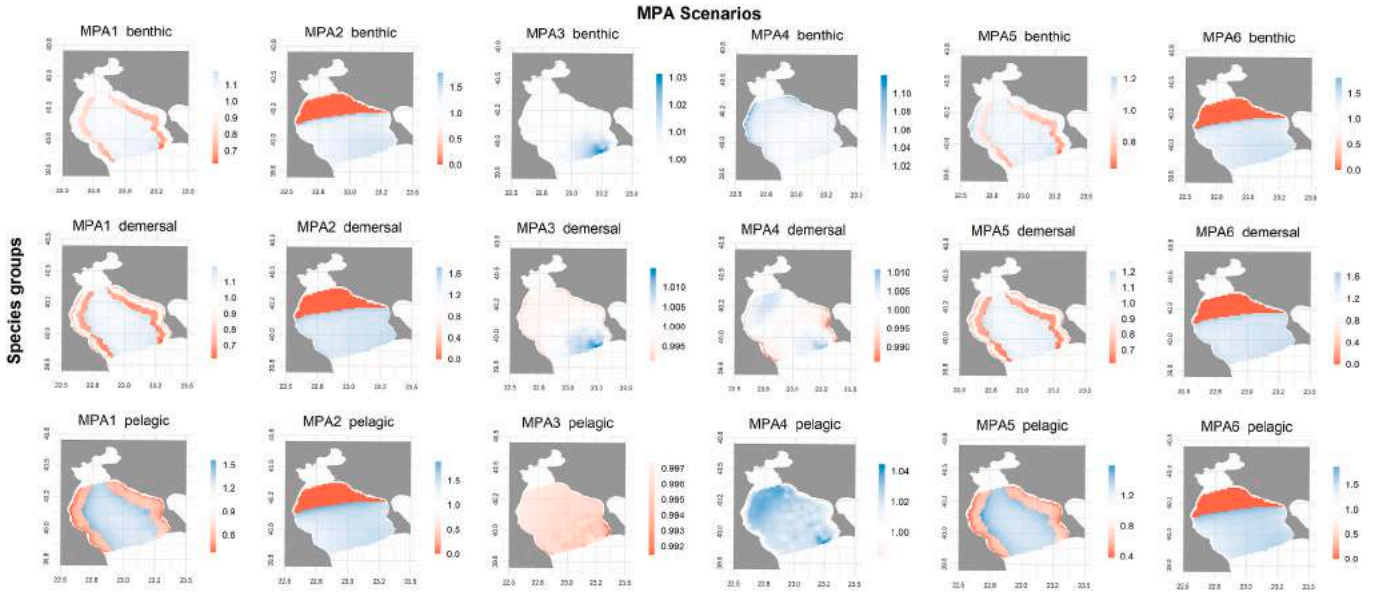


Fig. 6. ECOSPACE model predictions of the commercial catch spatial distribution of benthic, demersal, and pelagic functional groups in the Thermaikos Gulf model for each tested scenario (MPA1-6) compared to the business-as-usual scenario and for the year 2025, i.e., the end of the simulation period (ratios of values measured in t/km^2). A value of 1 indicates the same commercial catch values between the tested scenarios and BaU, while a value lower or higher than 1 indicates lower or higher catch in the tested scenario compared to BaU, respectively.

large pelagics being highly migratory species that occur in the study area seasonally and are therefore not accurately represented with EwE (Coll et al., 2008; Piroddi et al., 2017). Further limitations of the current approach are mainly related to the quality of the available information and the accompanying uncertainty around the data from the study area, such as the spatial resolution of the survey-based biomass index and substrate type, the species' links to environmental parameters, and their quantification of preferences for specific habitat types. Although the aforementioned limitations may challenge the quantitative accuracy of the results, the qualitative patterns provided by ECOSPACE are still useful for researchers and policy makers (Walters et al., 1999). Finally, while computational and financial obstacles play a role in addressing these issues, continuous model advancements on refining and extending the software are underway (de Mutsert et al., 2023).

5. Conclusions

In conclusion, it is informative to consider a combination of food web dynamics, human activities and environmental conditions for a realistic prediction of the complex spatiotemporal dynamics of marine ecosystems that could assist the development of adaptive management plans in a changing ocean (Coll et al., 2016). Despite their inherent uncertainty and limitations, ecosystem models are a useful and effective tool to better understand ecosystem processes, investigate fishing impacts and pose strategic questions within an ecosystem-based context (Christensen and Walters 2004). The ECOSPACE model developed in this work provides the first steps towards understanding the complex spatial and temporal dynamics in a highly exploited and productive Greek fishing ground, Thermaikos Gulf, and developing predictions of regional change. The implementation of the management measures suggested in scenario MPA 1 for medium-scale fisheries (trawling and purse seining) only or for all four fishing fleets operating in the area (boat seining and small-scale fishing on top of the medium-scale fishing; MPA 5) seems to result in the rebuilding of key commercial marine groups. A future step that would complement the present work would be to also test potential MPAs with a concurrent reduction in total fishing effort, as it has been shown by several studies that reducing effort by 20–50% (Froese et al., 2018) would benefit targeted commercial species and would promote their biomass recovery (Adriatic Sea: Fouzai et al., 2012; Pagasitikos Gulf: Dimarchopoulou et al., 2019; Thermaikos Gulf: Dimarchopoulou et al., 2022). At the same time, although performing longer ECOSIM simulations would increase uncertainty, it might allow us to test whether increasing biomass due to reduced effort will eventually lead to higher fisheries catches of targeted groups that are highly suppressed by fishing.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2023.106914.

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