

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Ecosystem trophic structure and fishing effort simulations of a major fishing ground in the northeastern Mediterranean Sea (Thermaikos Gulf)

Donna Dimarchopoulou^{a,*,1}, Konstantinos Tsagarakis^b, Georgios Sylaios^c, Athanassios C. Tsikliras^a

^a Laboratory of Ichthyology, School of Biology, Aristotle University of Thessaloniki, Greece

^b Institute of Marine Biological Resources and Inland Waters, Hellenic Centre for Marine Research, Aghios Kosmas, 16777, Athens, Greece

^c Department of Environmental Engineering, Democritus University of Thrace, Xanthi, Greece

ARTICLE INFO

Keywords:

Whole-ecosystem model
Environmental effects
Fishing impacts
Ecosystem indicators
Aegean Sea

ABSTRACT

Ecosystem modelling constitutes a useful tool for the ecosystem approach to fisheries management, which demands a shift to more complex models that include multi-species trophic interactions, environmental and anthropogenic forcing. The Thermaikos Gulf is a shallow gulf in the northwestern Aegean Sea (Greece) and one of the major fishing grounds of the northeastern Mediterranean concentrating high fishing effort of trawlers and purse-seiners and producing more than 20% of the total Greek catches. In the present work, we developed an Ecosim base model and ran Ecosim simulations for 26 years (2000–2025), including the calibration period (2000–2016), aiming to describe the food web structure and function of the Thermaikos Gulf, identify main components and interactions among the 33 functional groups, assess the ecosystem impacts of fishing over time, and compare ecosystem properties with other Mediterranean areas. Overall ecosystem degradation with biomass and catch decline was observed at the end of the calibration period due to the impact of environmental factors and fishing activities. The ecosystem seemed to stabilize in an intermediate state by the end of the projection years, but with an overall biomass and catch decline. Fishing effort reduction after 2016 resulted in higher biomass and catches compared to 2014–2015, that could not however reach the 2000 levels in most cases. The examined fishing effort reduction scenarios clearly showed that the more the fishing effort is reduced, the higher the biomass in the ecosystem and the lower the catches obtained compared to the baseline scenario. In a nutshell, since environmental drivers may be harder to predict or control, lowering the exploitation levels is an important step towards the rebuilding of overfished marine resources and more resilient ecosystems.

1. Introduction

Various anthropogenic activities, including increased fisheries exploitation, have been impacting the Mediterranean Sea large marine ecosystem for millennia resulting in altered, structurally and functionally simplified food webs over time, with top predators being gradually replaced by intermediate consumers and basal species of lower trophic levels (Lotze et al., 2011). Much like terrestrial ecosystems (Pimm, 1991), simplifying the sea has unintended consequences, both ecologically and economically, as ecosystem shifts towards poorer, less complex communities decrease organism resilience to disease, invasion, eutrophication, and climate change (Howarth et al., 2014). These factors may

in turn delay the recovery of disturbed ecosystems, thus prolonging the duration of restructured food webs that are characterized by altered ecological functions (Frank et al., 2011). While the term “disturbance” might be given different meanings by scientists, it is often used to describe highly human-modified habitats (Pimm, 1991). In the sea, direct exploitation through fishing has historically been the first human impact on marine resources that would perturb ecosystems on a multitude of levels (Lotze, 2004).

Indubitably, there are contradictory views on the success of conventional fisheries management practices (Cardinale and Svedäng, 2008; Cowan et al., 2012), with few well-managed regions in which fish and invertebrate stocks are recovering (Ricard et al., 2012; Hilborn

* Corresponding author;

E-mail addresses: ddimarch@bio.auth.gr, ddimarch@uri.edu (D. Dimarchopoulou).

¹ Current affiliation: Department of Fisheries, Animal and Veterinary Sciences, College of the Environment and Life Sciences, University of Rhode Island, Kingston, Rhode Island, United States of America.

<https://doi.org/10.1016/j.ecss.2021.107667>

Received 10 December 2020; Received in revised form 4 October 2021; Accepted 18 November 2021

Available online 20 November 2021

0272-7714/© 2021 Elsevier Ltd. All rights reserved.

et al., 2020) and numerous poorly managed regions where stocks continuously decline or have been stable at levels below the maximum sustainable yield MSY (Froese et al. 2012, 2018a). Nevertheless, the relative failure of single-species fisheries management (Stergiou, 2002; Froese et al., 2018a) and the negative effect of commercial fishing across different levels of biological organization including marine organisms, habitats and ecosystems (Jennings and Kaiser, 1998) resulted in the need for a more holistic consideration of marine ecosystems. This led to an ecosystem based fisheries management (EBFM, Pikitch et al., 2004), which can still be compatible with the concept of MSY (Pauly and Froese, 2020). Although the term EBFM was coined during the 1990s (US National Research Council, 1998), the concept of marine ecosystem modelling, which is an important tool for EBFM, has been increasingly appearing in the scholarly literature since the early 1980s (Morissette, 2007).

Since then, ecosystem models have been and, today, they (in particular Ecopath with Ecosim, EwE) are extensively used (Colléter et al., 2015) to address ecological questions and evaluate the ecosystem effects of fishing exploitation (Coll et al., 2006; Libralato et al., 2010; Piroddi et al., 2010; Bănarău et al., 2013), explore management policy options (Celic et al., 2018), analyze the impact and placement of marine protected areas (Libralato et al., 2006b; Valls et al., 2012; Prato et al., 2016), and model the effect of environmental changes (Díaz López et al., 2008; Barausse et al., 2009; Bayle-Sempere et al., 2013). Ecopath base models represent static, mass-balanced snapshots of the studied ecosystems that describe the food web structure in terms of species/groups' relative abundance and their trophic interactions, while the Ecosim module of the approach offers a time dynamic modelling capability for simulating past and future fishing and environmental impacts to explore management policies (Christensen et al., 2005). More than 40 EwE models have been developed across the Mediterranean Sea (Piroddi et al., 2015), the vast majority of which in the northern coastline (Coll and Libralato, 2012), while the eastern part of the basin has the lowest number of models; in Israel (Corrales et al., 2017b), Cyprus (Michailidis

et al., 2019), Turkey (Saygu et al., 2020) and Greece (Aegean Sea: Tsagarakis et al., 2010; Dimarchopoulou et al., 2019b).

The Thermaikos Gulf is a semi-enclosed embayment in the north-western Aegean Sea (Fig. 1), with its exploited open water part being one of the most important fishing grounds of the northeastern Mediterranean Sea in terms of number of vessels operating and landed biomass (Stergiou et al., 2007; Sylaios et al., 2010; Dimarchopoulou et al., 2018). The gulf is divided into three sub-areas of varying fishing restriction regimes and resulting fishing pressure, ranging from the total ban of large-scale fisheries (trawlers and purse seiners) in its innermost part (low exploitation level since small-scale coastal fishing vessels do operate seasonally), that has led to higher biomass and somatic length of exploited species, to full exploitation in its central part (Dimarchopoulou et al., 2018). Despite its high productivity and partial protection, the catch in the Thermaikos Gulf has been in overall decline since the 1990s, following the overall declining trend in the eastern Mediterranean catches as a result of the ongoing fisheries overexploitation that has led to the biomass-at-sea declines of exploited fish and invertebrate populations (Tsikliras et al., 2015; Froese et al., 2018a).

Indeed, a recent assessment of Mediterranean stocks showed that the ratio of the fishing mortality (F) to the mortality that ensures sustainable yields is very high ($F/F_{msy} = 1.8$; values over 1 indicate overfishing) and effort reductions are required (Froese et al., 2018a). The Common Fisheries Policy of the European Union has called for rebuilding the biomass of all commercially exploited stocks by ending overfishing, i.e. reducing fishing pressure (F) to or below the maximum sustainable level (F_{msy}) by 2015, latest by 2020 (see Froese et al., 2021 and references therein). The recovery of overexploited marine stocks might be swift or delayed depending on how prolonged the intense overexploitation and altered ecosystem states are and how much that has affected stock resilience; in any case, recovery would be a “win-win” result for fisheries and conservation that would ultimately raise catches, revenues and food security (Neubauer et al., 2013).

In the present work, the EwE modelling approach and the theoretical

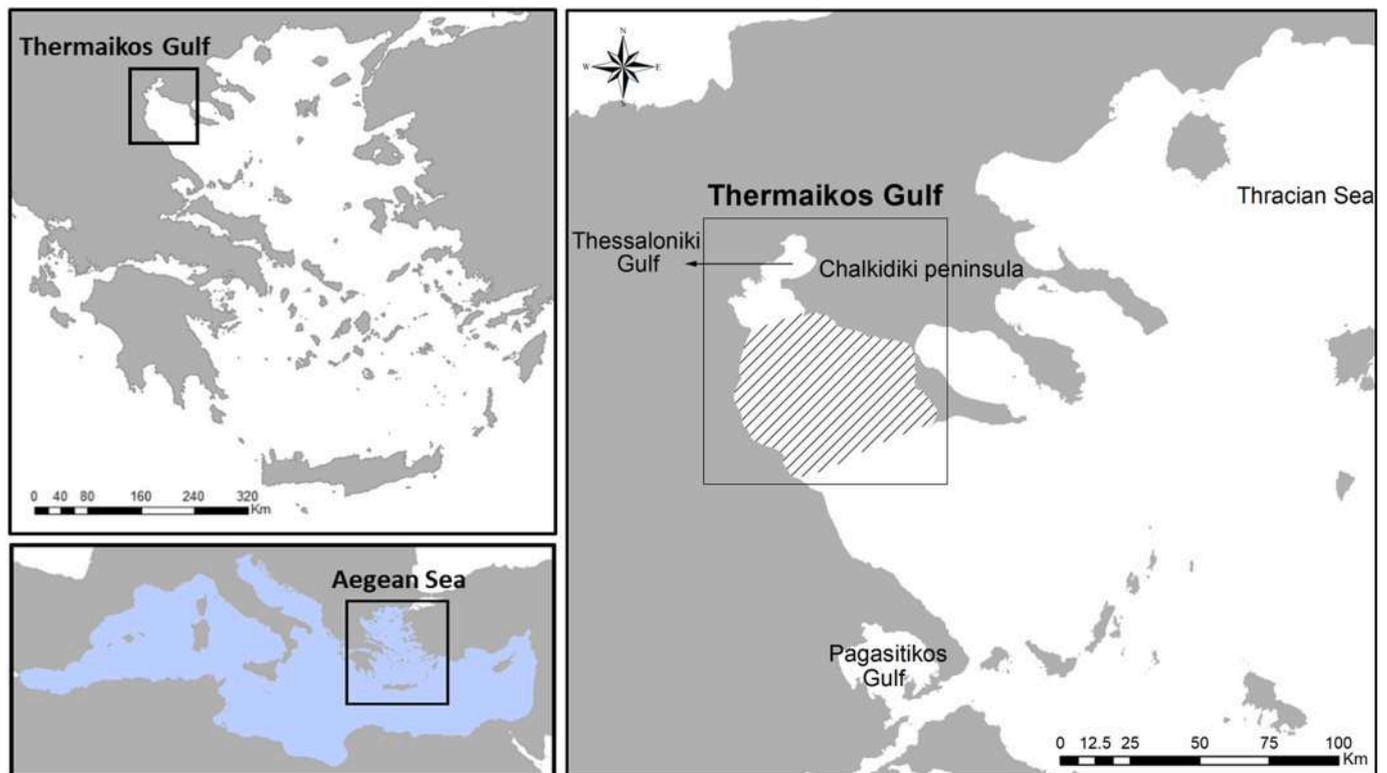


Fig. 1. Map showing the entire area (rectangle) and the modelled part (crosshatch shading) of the Thermaikos Gulf, north Aegean Sea, Greece, eastern Mediterranean.

ecology concepts included therein (Christensen and Walters, 2004) were applied to the marine environment and were used to explore the dynamics of a Greek marine ecosystem and the fisheries exploiting it, within a general management and conservation context. In order for the study to be relevant for conservation and management, the base model was subsequently used to investigate the temporal dynamics of the studied ecosystem, which is affected both by natural as well as anthropogenic factors, and various scenarios of fishing effort reduction were examined aiming to potentially improve stock status (i.e. rebuild biomass-at-sea) and increase future catches. The main objectives were (i) to describe the multi-species structure and functioning of one of the most productive Mediterranean Sea ecosystems, (ii) highlight main species of interest (both to ecosystem functioning and fisheries), (iii) investigate trophic interplay and cascading effects between the levels of the community that are neglected in single-species approaches, (iv) quantitatively assess the direct and indirect effects of perturbations on species and interaction pathways, (v) investigate the dynamics of the ecosystem over time, (vi) test the effect of future fishing reduction scenarios on the biomass and catch of main functional groups of interest. This study complements a previous work that explored the structure and dynamics of another Greek gulf (Pagasitikos Gulf) which, unlike the highly exploited Thermaikos Gulf, is partially protected, as fishing with towed gears has been prohibited in it for decades (Dimarchopoulou et al., 2019b).

2. Materials and methods

2.1. Description of the study area and its fisheries

The northwestern Aegean Sea includes the gulfs of Thessaloniki and Thermaikos, as well as the gulfs of the Chalkidiki Peninsula (Fig. 1). The Thermaikos Gulf is a shallow water area having a maximum depth of 100 m, with mud, sandy mud and muddy sand sediments (Poulos et al., 2000), and receiving the outflows of large river systems (Gallicos, Axios, Loudias and Aliakmon) that discharge about 207 m³/s into the area, with significant temporal variability (Kallianiotis et al., 2004). The exact area of the Thermaikos Gulf that was modelled here is shown with crosshatch shading in Fig. 1.

The Thermaikos Gulf is considered one of the most productive fishing grounds in the Greek Seas (Stergiou et al., 2007). Hence, following the northeastern part of the Aegean (Thracian Sea), the Thermaikos Gulf has the second highest concentration of trawler fishing effort in the Aegean Sea (Fig. 1). Its coastal part is subject to several fishing restrictions, while its innermost part (Thessaloniki Bay and Gulf, and inner Thermaikos Gulf) is protected from large-scale fishing activities, as bottom trawl and purse-seine fishing have been totally banned since 1978 (Dimarchopoulou et al., 2018). In total, 48% of trawling in the Aegean takes place in the fished part of the Thermaikos Gulf and the Thracian Sea, while 20% of purse-seining in the Aegean Sea takes place in the Thermaikos Gulf. According to the Fleet Register (CFR, 2018), in 2014, 1460 vessels were registered in seven ports of the Thermaikos Gulf, 58 of which were trawlers (using bottom trawls, OTB), 29 were purse seiners (using purse-seines, PS), 10 were beach seiners (SB) and 1373 were small-scale coastal vessels using a variety of fishing gears.

Three demersal fishes (red mullet *Mullus barbatus* and surmullet *Mullus surmuletus* and European hake *Merluccius merluccius*), two crustaceans (caramote prawn *Melicertus kerathurus* and deep-water rose shrimp *Parapenaeus longirostris* and two cephalopods (cuttlefish *Sepia* spp. and octopus *Octopus* spp.) are the main target species of the trawl fishery in the Thermaikos Gulf (Stergiou et al., 2007; HELSTAT, 2018). Three small and medium sized pelagic fishes (European anchovy *Engraulis encrasicolus*, European pilchard *Sardina pilchardus* and Atlantic chub mackerel *Scomber colias*) are the main target species of purse seiners in the area. Finally, the small-scale coastal fisheries fleet of the Thermaikos Gulf targets a wide variety of species some of which are also targeted by the trawling fleet (e.g. red mullet and surmullet, and

caramote prawn) and by the purse seiners (e.g. European pilchard).

2.2. Ecopath modelling approach

For the description of the Thermaikos Gulf ecosystem we used the widely applied EwE approach (Version 6.5; www.ecopath.org; Christensen and Walters, 2004) to build a mass balanced model of the trophic interactions among most components of the studied ecosystem covering the trophic spectrum, from low trophic levels to top predators, including the fishing fleets operating in the area. Organisms are categorized in functional groups (FGs), i.e. species or groups of (ecologically or taxonomically) related species that share similar population dynamics and ecological function. FGs are linked via feeding interactions and the balance of the energy input and output of all living groups is expressed through two master equations that have repeatedly been presented in the literature (e.g. Hattab et al., 2013; Piroddi et al., 2016; Dimarchopoulou et al., 2019b): one for the production of each FG (Supplementary Eq. A1) that equals predation plus natural mortality plus biomass accumulation, plus net migration (emigration – immigration) plus other mortality, and another one for the food consumption of each FG (Supplementary Eq. A2) that equals production, respiration and unassimilated food (Christensen et al., 2005).

The input parameters for each of the FGs were the diet composition (DC; proportion of the prey in the diet of the predator), the proportion of food that is not assimilated (U/Q; dimensionless, entered as a proportion of consumption), the catches (Y; t/km²/year), biomass (B; wet weight t/km²), production/biomass ratio (P/B; year⁻¹) which is equal to the total mortality rate (Pauly et al., 2000), and consumption/biomass ratio (Q/B; year⁻¹). Ecotrophic efficiency (EE; dimensionless, between 0 and 1) is the fraction of the production that is used in the system through predation, fishing or migration and it was left to be estimated by the software.

2.2.1. Input parameters and functional groups

The food web of the Thermaikos Gulf was organized in 33 FGs that encompassed 2 planktonic, 7 invertebrate, 19 fish, and 2 detritus groups, as well as sea turtles, seabirds and dolphins, covering most of the trophic spectrum of the ecosystem while focusing on commercial fishes and invertebrates. More than a hundred taxa were included in the 33 FGs as listed in the landings (HELSTAT, 2018) and survey (Kallianiotis et al., 2004) data of the studied area and the literature (Table A1 supplement). At first, the listed taxa were categorized in 29 FGs according to their importance to fisheries and management (e.g. European hake, pilchard and anchovy are highly commercial species in Greece and as a result they form separate single-species FGs in the model: see also Tsagarakis et al., 2010; Dimarchopoulou et al., 2019b), their phylogenetic or ecological relation and available data. However, 53 fish taxa of lower fishing relevance and abundance in the ecosystem remained uncategorized. For 40 of those taxa, quantitative diet information, in the form of stomach content data, were available and were used to perform a cluster analysis (using Ward's method and Euclidean distances in Statgraphics Centurion XVI) that resulted in forming 4 more FGs (Demersal fishes 1–4) (Fig. 2). Finally, the remaining 13 fish taxa were assigned to one of those 4 FGs based on general knowledge of their feeding preferences, behaviour and ecology (Table A1 supplement).

The model was constructed for the years 1998–2000 when reliable data (mainly catches and biomass) were available, i.e. average values over those three years were used. In order to have an EwE model that would be relevant for ecosystem based management, we followed the common practice in which the baseline Ecopath model is based on the earliest time when reliable data are available so that sufficiently long times series can then be used for the fitting process (Heymans et al., 2016). Biomass data were obtained from local scientific trawl surveys (Kallianiotis et al., 2004; Mediterranean International Trawling Survey Program: MEDITS) for demersal fish and invertebrate species, acoustic surveys for small pelagic fish (Tsagarakis et al., 2015) as well as

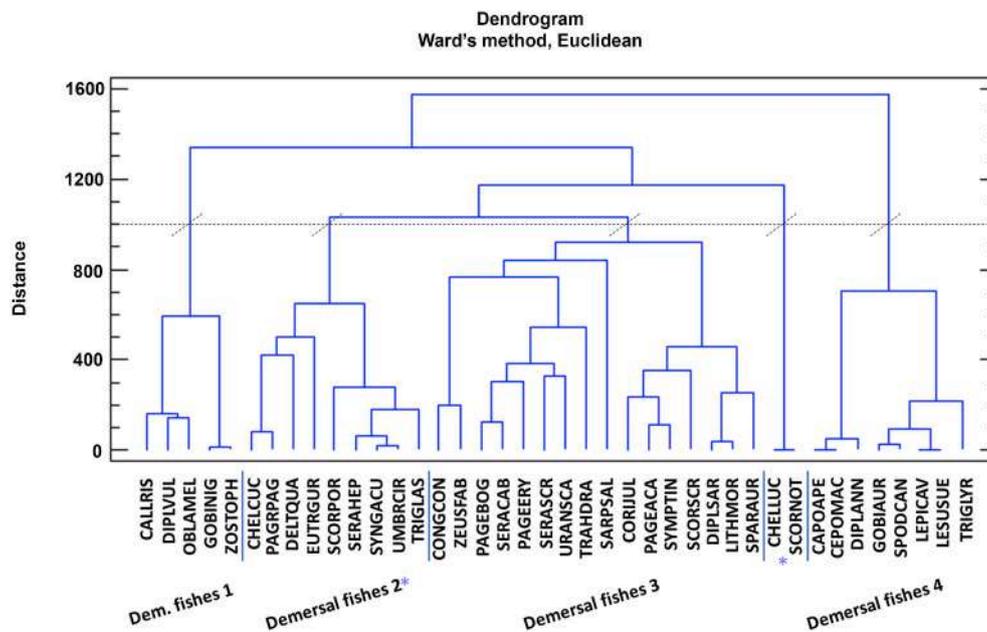


Fig. 2. Cluster analysis of the diet composition of 40 fish species for their categorization in functional groups. Species codes are given in Table A2 of the supplement.

information available in the literature and other models. Since the MEDITS catchability coefficient cannot be equal to 1 for any species (Mulazzani et al., 2015), to obtain absolute biomass estimates, we used species-specific catchability based on the demersal, benthic, or pelagic behaviour of each species; e.g. the survey estimates about 10–15% of the total biomass of species exhibiting demersal or benthic behavior, respectively (Smith et al., 2003; Sánchez and Olaso, 2004; Fiorentino et al., 2013; Agnetta et al., 2019). P/B and Q/B values for fishes were estimated using empirical equations (Pauly, 1980) and relevant life history tools in FishBase (Froese and Pauly, 2019), while for the rest of the FGs they were obtained from the literature and other models (Table A1 supplement).

Diet composition data were extracted from other models and published reviews regarding the Mediterranean fish species (Stergiou and Karpouzi, 2002; Karachle and Stergiou, 2017); priority was given to information from the study area or adjacent areas, but in case such data were not available, information from other areas of the Mediterranean or similar species were used (Table A1 supplement). It should be noted that seabirds were set to mainly feed on discards, that by default have a trophic level of 1, and imported material of uncertain origin; as a result, the present model seemed to underestimate the trophic level of seabirds, as it has been pointed out for other functional groups of organisms in previous models (Lassalle et al., 2014). Also, it made seabirds more sensitive to changes in fishing effort. Landings data were based on reconstructed landings per fishing fleet and gear used and per subarea of Greece (Moutopoulos and Stergiou, 2012), while discards were estimated as a proportion of the landings for each fleet (Tsagarakis et al., 2014). Four fishing fleets that exploit the studied ecosystem were included in the model, namely trawlers, purse seiners, beach seiners and small-scale coastal vessels. All the input parameters for multi-species FGs were estimated using weighted averages based on the biomass contribution of each species to the respective FG.

Ensuring mass balance was the next important step after editing and entering the required data into EwE. Initial model runs were not mass balanced, with EE values of some FGs being greater than 1 which indicated that mortality was too high (Hattab et al., 2013). An ecological step-by-step balancing process was then followed that entailed manually modifying input parameters such as biomass, mortality rates, diets etc. (often researchers start by adjusting the diet matrix, since diet composition is the parameter with the highest uncertainty) looking for data

inconsistencies, to gradually achieve mass balance (Christensen and Walters, 2004). A selected subset of pre-balance (PREBAL) diagnostics proposed by Link (2010), and suggested as a best practice by Heymans et al. (2016), were implemented to evaluate the initial conditions of the model, i.e. model structure and data quality examined in conjunction with general ecological and fishery principles. The diagnostics showed that the model structure and data quality fulfilled several of the biomass (rule of thumb: compared across taxa, predators biomass should be less than that of their prey), vital rates and production/removals (rule of thumb: total, scaled values should follow a decomposition with increasing trophic level) criteria (Supplementary Fig. A1).

EwE allowed us to estimate various indicators related to ecosystem structure and food web dynamics to describe the studied ecosystem as a whole (Christensen et al., 2005) and compare it to other models of exploited Mediterranean ecosystems that have generally been built according to similar criteria (Tsagarakis et al., 2010; Dimarchopoulou et al., 2019b; Michailidis et al., 2019). In particular, a set of statistics, ecological indicators and network analyses were performed to (i) quantify the total flows taking place in the studied ecosystem and indicate its size in comparison to other systems (total system throughput), (ii) assess the system's maturity status which can be related to its exploitation level based on Odum (1971) theory (total primary production over total respiration, net system production, total primary production over total biomass, total biomass over total throughput), (iii) highlight the varying impact of different organisms in the food web (mixed trophic impact, keystone) and indicate if it is more linear or complex and web-like (system omnivory index) to identify potential cascading effects, and (iv) assess the overall quality of the model (pedigree index). These indicators are presented and described in more detail in Table 1.

2.3. Ecosim temporal dynamic modelling

The Ecosim module of the EwE approach was then applied to the Ecopath base model and was used to analyze the main dynamics of the food web over time. Ecosim takes the initial parameters from the underlying base model and provides temporal dynamic simulations (Walters et al., 1997) using a system of differential equations that depend on time to express the biomass growth rate of a FG as follows (Christensen and Walters, 2004):

Table 1
Detailed description of the ecological indicators and analyses examined for the ecosystem of the Thermaikos Gulf.

Ecological indicator/analysis	Description/references
Total system throughput	Represents the sums of all flows in the system, i.e. the total consumption, exports, respiratory flows and flows to detritus and serves as an important indicator of the size of the ecosystem in terms of flows (Ulanowicz, 1986; Christensen et al., 2005).
Total primary production/total respiration	The ratio can be used to describe the state of maturity of an ecosystem (Odum, 1971) where immature systems, in their early developmental stages, have production that is expected to exceed respiration and thus the ratio is greater than 1 (Christensen et al., 2005).
Net system production	The difference between primary production and respiration gives the net system production which is expected to be higher in immature systems and approximate zero in mature ones (Christensen et al., 2005).
Total primary production/total biomass	The ratio declines over time in immature systems where production exceeds respiration for most FGs and biomass accumulation is observed (Christensen et al., 2005).
Total biomass/total throughput	The ratio may take any positive value and it reaches a maximum when the system is at its most mature state (Christensen et al., 2005).
System Omnivory Index	Indicates how the trophic interrelations are distributed among trophic levels and is therefore used to characterize the more or less extended web-like features of the studied system Pauly et al., 1993. A larger than zero value of the omnivory index suggests feeding on many trophic levels rather than specialization by feeding on just a single trophic level (Christensen et al., 2005; Suppl. Eq. A3).
Ecopath pedigree index	Categorizes the origin of a given input (the type of data on which it is based), and specifies the likely uncertainty associated with the input, i.e. the reliability of the data and overall quality of the model (Morissette, 2007).
Mixed Trophic Impact (MTI)	The MTI plot depicts the relative direct and indirect impact of a very small increase in the biomass of a group on the biomass of another group (Suppl. Eq. A4), thus revealing straight forward predator-prey effects but also indirect cascade effects on a prey's prey or competitor (Christensen et al., 2005).
Keystoneness	The keystone index is used to identify groups that have considerable impact and play an important role in the studied ecosystem either despite their low biomass (keystone groups) or as a result of their high biomass (dominant groups) (Libralato et al., 2006a; Suppl. Eq. A5).

$$\frac{dB_i}{dt} = g_i \sum_{j=1}^n Q_{ji} - \sum_{j=1}^n Q_{ij} + I_i - (M_i + F_i + e_i) * B_i$$

where dB_i/dt : the biomass change rate of FG i during the time interval dt ; g_i : the growth efficiency; Q_{ij} : the consumption rate of FG i by FG j ; I_i : the immigration rate; e_i : the emigration rate; M_i : the other non-predation natural mortality rate; F_i : the fishing mortality rate; B_i : the biomass of the FG i . The first term of the equation represents FG biomass growth, the second term represents FG biomass consumption while the third term represents the balance between fish movements in and out of the gulf and mortality (natural and fishing).

Calculations of consumption rates are based on the “foraging arena” theory (Walters et al., 1997; Ahrens et al., 2012), which assumes that aquatic organisms are divided into fractions vulnerable and invulnerable to predation risk, with predator-prey interactions being confined to spatially restricted foraging arenas. The level of vulnerability is indicative of how the biomass of different groups in the ecosystem is controlled. It expresses the effect that a large increase in predator abundance would have on the predation mortality of a given prey and it

is a significant model parameter that can be modified during calibration so that predictions fit better to observed historical data. Low vulnerability values (close to 1) indicate that no considerable increase in predation mortality on a prey will be caused by an increase in predator biomass (prey control or bottom-up effects), while high vulnerability values mean that a potential doubling of predator biomass would result in about double the predation mortality it causes on a particular prey (predator control or top-down effects) (Christensen et al., 2005).

2.3.1. Calibrating the EwE model and simulating reference and management scenarios

Analyses performed with Ecosim can benefit from including time series reference data of biomass and catches over a historical period of time, along with estimates of fishing effort changes over the same period. Time series data contribute to the reasonable tuning of the model to real world data highlighting the potential of the model to replicate the known history of the system, thus facilitating its use as an ecosystem-based fisheries management tool (Christensen et al., 2005). The Ecosim model of the Thermaikos Gulf was fitted to available historical biomass data for the period 2001–2014 [available relative catch per unit effort (CPUE) values for 8 out of 14 years] as obtained from the MEDITS bottom trawl scientific surveys (Kallianiotis et al., 2004) and landings data for the period 2000–2016 as obtained from the Hellenic Statistical Authority (HELSTAT, 2018) and reconstructed with the methodology used in Moutopoulos and Stergiou (2012). For 2016, the official data were corrected to account for the presentist bias induced by including the catches of an extra fleet in official reports for 2016 onwards without any hindcasting for the entire time series (Tsikliras et al., 2020). A correlation matrix (Spearman) between the catch time series of the FGs, showing only the significant relationships and respective correlation coefficients, was created in R (“ggcorrplot” package). Catch correlations were added as an additional diagnostic test to highlight any pattern of collinearities that might affect the tuning and behavior of the model and justify the better or poorer capturing of the observed patterns. Fishing capacity by gear type for the four fleets (the number of trawlers, purse seiners, beach-seiners and small-scale coastal vessels; years 2000–2016) were extracted from the European Community Fishing Fleet Register (CFR, 2018) and were considered as a proxy for relative fishing effort to force the model during the fitting procedure.

In order to fit the model to the time series of observed data (2000–2016) we followed the steps proposed by Mackinson et al. (2009) and adopted by others (e.g., Heymans et al., 2016; Corrales et al., 2017a). This stepwise fitting procedure uses alternative hypotheses to test the combination of different factors that affect the ecosystem, namely fishing, trophic interactions among FGs (the 20 most sensitive to vulnerability changes prey-predator pairs were used to improve the fit of the model: Coll et al., 2009; Halouani et al., 2016) and the environment. The environment was represented with three parameters: i) primary production anomalies (i.e. a forcing function applied to the primary producer that represents historical changes in productivity affecting organism biomasses in the ecosystem; 8 spline points were used for smoothing) were estimated through the software's routines and were added every year to the initial phytoplankton values representing an environmental parameter that might influence the trophic interactions among the compartments of the food web (Supplementary Fig. A2; Christensen et al., 2005; Coll et al., 2009); ii) sea surface temperature -SST-time series (mean-monthly values, spatially-averaged over the Thermaikos Gulf, derived from CMEMS MEDSEA_REANALYSIS_PHYS_006_004) were used to force the consumer functional groups of sardine, anchovy, and horse mackerels (Supplementary Fig. A3; Szalaj et al., 2021); iii) chlorophyll-a -chl-a- time series (derived from the biogeochemical validated model of the Copernicus Marine Environmental Service CMEMS: MEDSEA_REANALYSIS_BIO_006_008) were used to force the primary producer, i.e. phytoplankton (Supplementary Fig. A4). Fluctuations in the abundance of sardine, anchovy, and horse mackerels have been shown to be affected by SST in the Mediterranean

Sea (Tsikliras et al., 2019 and references therein). The goodness of fit was assessed with the reduction of the sum of squared deviations (SS) of observed values from predicted ones (Christensen et al., 2005) and the best model was chosen based on the lowest Akaike's information criterion (AIC: Mackinson et al., 2009; Heymans et al., 2016; Corrales et al., 2017a; corrected for a small number of observations, AICc).

Three biomass-based ecological indicators that depend on the abundance of each FG in the studied food web were used to assess ecological changes in the Thermaikos Gulf ecosystem through time: i) the ratio of invertebrate to fish biomass, ii) the ratio of demersal to pelagic fish biomass and iii) the biomass of predatory organisms (Coll and Steenbeek, 2017; Corrales et al., 2017a). Indicators reflect changes in the structure of marine food webs that can be related to fishing as the increasing fishing impact in marine ecosystems results in seas with fewer predators and piscivorous demersal fish and more low trophic level invertebrates and planktivorous pelagic fish (Pauly et al., 1998).

Simulations were extended from 2017 to 2025 to represent future scenarios of reduced fishing effort and examine the response of the Thermaikos Gulf ecosystem to alternative management plans, as previously performed for a nearby area (Pagasitikos Gulf: Dimarchopoulou et al., 2019b). The baseline scenario 0 (business-as-usual) assumed constant fishing effort as in the last year of the calibration period, while the three alternative scenarios corresponded to reduction in fishing effort by 10% (Scenario 1), 30% (Scenario 2) and 50% (Scenario 3) compared to the baseline Ecosim scenario. The first three tested scenarios (1–3) correspond to the exploitation scenarios examined by Froese et al. (2018a), who used the current status and exploitation pattern of numerous European (including Mediterranean) stocks to predict future biomass and catch trajectories, and propose fishing effort reduction suggestions based on the time required for rebuilding. The reduction in fishing effort was applied to all four fleets equally and referred to the reduced number of vessels operating in the area. Two more scenarios were also examined to enable comparisons with Pagasitikos Gulf where fishing with towed gears has been prohibited for decades (Dimarchopoulou et al., 2019b): a fourth scenario (Scenario 4), in which beach-seiners were prohibited (more realistic to actually be implemented), and a fifth scenario (Scenario 5), in which all towed gears (bottom trawls and beach-seines) were totally banned after 2016.

In an effort to address the uncertainty in the input data, the sensitivity of Ecosim's outputs to Ecopath input parameters was tested using the Monte Carlo approach. Twenty Monte Carlo trials based on a

coefficient of variation (CV) around the input parameters for biomass, P/B, Q/B (Supplementary Table A6) gave 20 different biomass outcomes for each FG (Supplementary Figure A5). As performed by Dimarchopoulou et al. (2019b), the most certain, according to the pedigree, input values for biomass, P/B and Q/B were not perturbed (CV = 0), while for the less certain ones, as well as those of FGs with high relative impact and keystone in the ecosystem (zooplankton, squids, and other gadiforms), the CV was obtained from the quality of the data as defined in the pedigree routine (Supplementary Table A4). The CVs ranged from 0.05 (i.e. a 10% change around the mean initial value of the parameter) to 0.4 (i.e. an 80% change around the mean initial value of the parameter; Supplementary Table A6).

3. Results

3.1. Ecopath base model

The Thermaikos Gulf food web was described by 33 FGs of lower to higher trophic level compartments of the ecosystem and it was represented graphically with a flow diagram (Fig. 3) that provides information on the trophic level, biomass and habitat of each compartment, as well as the estimated trophic flows among the organisms. Model results revealed an ecosystem organized in four trophic levels. The highest trophic levels (TL > 4) were observed for dolphins (TL = 4.5), large and medium pelagic fishes, anglerfish (TL = 4.2) and hake (TL = 4.1), while the FGs of benthic invertebrates, polychaetes, benthic small crustaceans, zooplankton, seabirds, red mullets and crabs presented lower TL values ranging from 2 to 3 (Table 2; Fig. 3). The input data and resulting output parameters of the balanced model are shown in Table 2 and Tables A1 and A3 of the supplement.

The model was not balanced when first run, so there was a need to modify input data of the FGs that presented EE values greater than 1 (10 in total). The original biomass values for shrimps, octopuses and cuttlefish and demersal fishes 1 were increased as they were unrealistically low when compared to the biomass of predators in the system. In these cases, the landings data were considered more trustworthy, and so were the predator biomasses obtained through the trawling surveys which were more focused on recording fish (Dimarchopoulou et al., 2019b). For shrimps we lowered the catchability factor of trawlers to account for the small individuals that are not caught by the gear. Regarding octopuses and cuttlefish, we increased their biomass based also on the

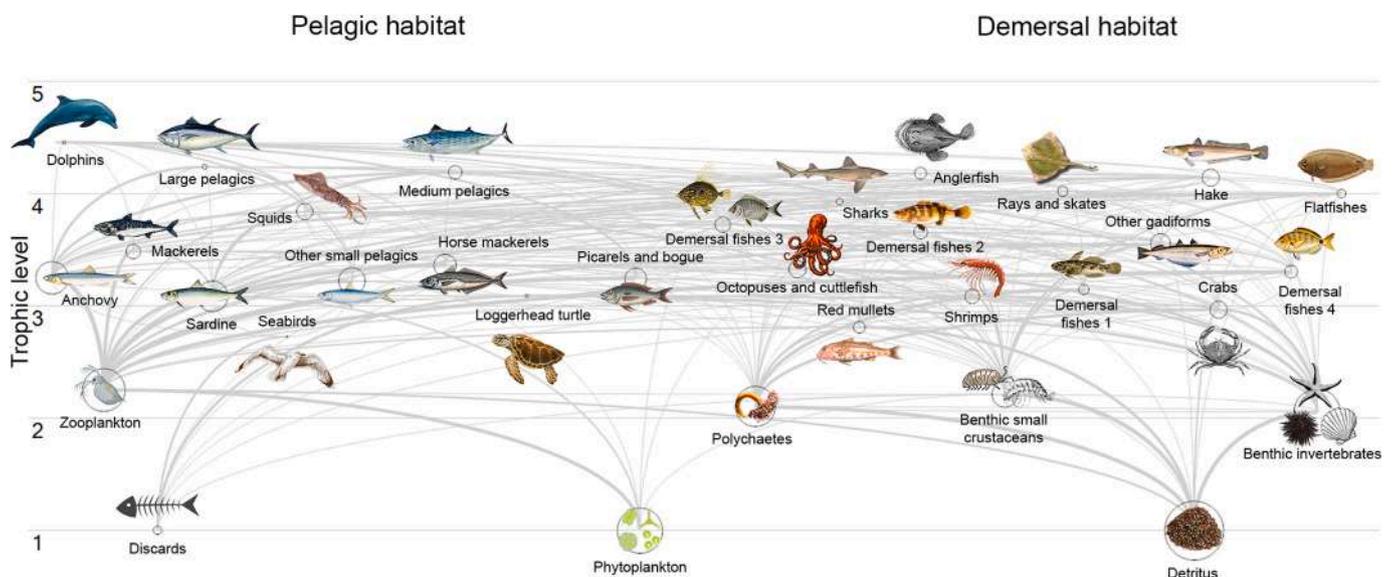


Fig. 3. Flow diagram of the Thermaikos Gulf ecosystem (years 1998–2000) organised by 33 functional groups' trophic levels and by pelagic or demersal habitat (organisms not in scale).

Table 2

Input and output (bold) parameters of the Thermaikos Gulf Ecopath model. FG functional group; TL trophic level; B biomass (t/km²); P/B production/biomass (yr⁻¹); Q/B consumption/biomass (yr⁻¹); EE ecotrophic efficiency; P/Q production/consumption.

	FG	TL	B	P/B	Q/B	EE	P/Q
1	Phytoplankton	1.00	7.866	117.300		0.744	
2	Zooplankton	2.25	6.100	62.470	186.380	0.764	0.335
3	Benthic small crustaceans	2.21	1.110	7.686	57.120	0.993	0.135
4	Polychaetes	2.10	4.808	1.712	13.083	0.988	0.131
5	Shrimps	3.09	0.306	3.339	7.896	0.999	0.423
6	Crabs	2.97	0.412	2.541	5.187	0.997	0.490
7	Benthic invertebrates	2.05	8.710	1.215	3.434	0.995	0.354
8	Octopuses and cuttlefish	3.33	0.392	2.900	5.807	1.000	0.499
9	Squids	3.84	0.363	2.600	26.470	0.997	0.098
10	Red mullets	2.81	0.196	1.908	7.192	0.994	0.265
11	Anglerfish	4.18	0.203	1.100	3.777	0.211	0.291
12	Flatfishes	4.00	0.107	1.820	8.741	0.995	0.208
13	Other gadiforms	3.55	0.580	1.450	6.493	1.000	0.223
14	Hake	4.14	0.400	0.587	3.700	0.998	0.159
15	Demersal fishes 1	3.14	0.150	2.400	9.306	0.995	0.258
16	Demersal fishes 2	3.66	0.246	1.600	7.739	0.996	0.207
17	Demersal fishes 3	3.72	0.322	1.400	4.592	0.991	0.305
18	Demersal fishes 4	3.30	0.237	1.900	11.105	0.995	0.171
19	Picarels and bogue	3.25	0.663	1.500	8.339	0.992	0.180
20	Sharks	3.93	0.071	0.698	4.080	0.988	0.171
21	Rays and skates	4.02	0.141	1.000	3.394	0.717	0.295
22	Anchovy	3.25	2.250	1.753	6.693	0.995	0.262
23	Sardine	3.09	1.950	1.778	11.668	0.997	0.152
24	Horse mackerels	3.36	0.732	1.000	7.315	0.994	0.137
25	Mackerels	3.49	0.294	1.022	6.448	0.994	0.158
26	Other small pelagics	3.22	1.170	1.400	6.365	0.997	0.220
27	Medium pelagics	4.19	0.250	0.425	3.706	0.257	0.115
28	Large pelagics	4.24	0.049	0.400	2.529	0.864	0.158
29	Loggerhead turtle	3.09	0.020	0.160	2.680	0.781	0.060
30	Seabirds	2.73	0.001	4.780	111.610	0.000	0.043
31	Dolphins	4.46	0.020	0.080	13.810	0.213	0.006
32	Discards	1.00				0.987	
33	Detritus	1.00	31.440			0.412	

landings data to account for the individuals mostly caught by gears other than the bottom trawl used in the survey. Similarly, we increased the biomass of demersal fishes 1 as they are mostly encountered in shallower depths than the ones covered by the bottom trawl survey (Froese and Pauly, 2019). Finally, for crabs, flatfishes, demersal fishes 2 and 4, sharks, anchovy and sardine we tweaked the diet matrix as diet composition is the most uncertain parameter in the model (Piroddi et al.,

2016). The contributions of the abovementioned FGs to the diet of their predators were adjusted so that consumption was redirected to other relevant FGs such as benthic invertebrates, anglerfish, demersal fishes 3, rays and skates, other small pelagic fishes.

Statistics for the Thermaikos Gulf (northwestern Aegean Sea) are presented in comparison to other models in the eastern Mediterranean Sea, namely the Pagasitikos Gulf (western part of the central Aegean Sea:

Table 3

Statistics, flows and ecological indicators for the Thermaikos Gulf in comparison to models from other eastern Mediterranean areas (Thracian Sea: Tsagarakis et al., 2010; Cyprus: Michailidis et al., 2019; Pagasitikos Gulf: Dimarchopoulou et al., 2019b; Gulf of Mersin: Saygu et al., 2020). Basic descriptive characteristics of the models are also provided.

	Thermaikos	Pagasitikos	Thracian	Mersin	Cyprus	Units
Basic description						
No. of functional groups	33	31	40	48	40	
Time period	1998–2000	2008	2003–6	2009–13	2015–17	
State of exploitation	high	semi-protected	high	high	moderate	
Nature of the system	semi-closed	semi-enclosed	semi-closed	shelf	insular shelf	
Model area	3339	639	8374	4352	1608	km ²
Index						
Sum of all consumption	1386	1456	867	489		t/km ² /year
Sum of all exports	514	249	275	114		t/km ² /year
Sum of all respiratory flows	417	486	270	255		t/km ² /year
Sum of all flows into detritus	868	761	563	292		t/km ² /year
Total system throughput	3185	2951	1976	1150	1034	t/km ² /year
Sum of all production	1350	1114	791	505		t/km ² /year
Calculated total net primary production	923	712	536	369		t/km ² /year
Total primary production/total respiration	2.21	1.47	1.99	1.45	2.04	
Net system production	506	227	266	114		t/km ² /year
Total primary production/total biomass	23	9.1	16.21	15.69	13.06	
Total biomass/total throughput	0.01	0.03	0.02	0.02		/year
Total biomass (excluding detritus)	40	78	33	23	19	t/km ²
System Omnivory Index	0.2	0.25	0.18	0.16	0.23	
Ecopath pedigree index	0.53	0.53	0.61	0.63	0.62	

Dimarchopoulou et al., 2019b), the adjacent Thracian Sea and Strymonikos Gulf (henceforth referred to as Thracian Sea: Tsagarakis et al., 2010), Gulf of Mersin (northern Levantine Sea: Saygu et al., 2020) and Cyprus (northern Levantine Sea: Michailidis et al., 2019) ecosystems. The Thermaikos Gulf was the largest system in terms of flows (total system throughput 3185 t/km²/year) with more complex web-like trophic interactions among FGs than the Thracian Sea and Gulf of Mersin, as indicated by the system omnivory index of 0.2 (Table 3). According to the indicators of total primary production/total respiration, net system production and total biomass/total throughput, the Thermaikos Gulf seemed to be an immature system in early developmental stages more like the Thracian Sea than the rest of the compared systems. The model was built with input data of reasonable quality and was therefore typical in its uncertainty (Supplementary Table A4: uncertainty of every input value for each parameter was estimated based on the quality of input data; when species-specific local data were used, then the uncertainty was the lowest) like Pagasitikos Gulf (Ecopath pedigree index 0.53; Table 3).

Although zooplankton presented the highest value of the keystone index and impact (Fig. 4), it could not be characterized as a keystone group in the studied ecosystem due to its high relative biomass. On the other hand, squids and other gadiforms were shown to be an integral component of the Thermaikos Gulf ecosystem having a quite high overall impact (i.e. total impact on the ecosystem as estimated through the mixed trophic impact analysis right below) and keystone-ness despite their relatively low biomass. The loggerhead turtle and seabirds were the groups of the lowest importance in the system.

Based on the Mixed Trophic Impact (MTI) analysis (Fig. 5), polychaetes were shown to have the highest positive direct impact on demersal fishes 1 as a result of their prey-predator relationship, whereas zooplankton had the highest negative impact on itself, as did many other groups, due to cannibalism and increased within-group competition for resources. Apart from the direct negative impact of predatory groups (such as large pelagic fishes, medium pelagic fishes, anglerfish and hake) on their prey (medium pelagic fishes, squids, rays and skates, and demersal fishes 1 respectively), indirect positive impact on their prey's

food (squids, benthic small crustaceans, anchovy, and polychaetes respectively) or competitor (mackerels, rays and skates, demersal fishes 3, and red mullets respectively) was also observed. As far as the impact of the fishing fleets on the various compartments of the ecosystem is concerned, small scale fisheries had the highest overall negative impact, particularly affecting dolphins, the loggerhead turtle, large pelagic fishes and flatfishes due to fishing and bycatch, while benefiting demersal fishes 1 and other gadiforms by removing some of the predation mortality exerted on them by flatfishes (Fig. 5).

3.2. Fitting to time series data

The Ecosim model with the best fit to the observed historical data of biomass and catches was the one with the lowest AICc value (-257.1; min SS = 267.1) that took into account the fishing activities and environmental parameters (primary production anomaly and SST) and improved the model fit by 74.7% compared to the baseline model (step 17 in Table 4). Nevertheless, as this model could not reproduce the trends of target functional groups satisfactorily, we adopted the practice of Corrales et al. (2017a) and chose the second best model that still demonstrated a credible statistical behavior (AICc = -248.5, min SS = 248.3, improved the model fit by 68.8% compared to the baseline model; step 20 in Table 4) and also was able to reproduce the trends of main functional groups well. The chosen model accounted for trophic interactions between certain predators and their prey, fishing activities, and environmental drivers (primary production anomaly and SST). The fitting routine also estimated vulnerabilities for 20 prey-predator pairs. Eleven out of the twenty (55%) vulnerabilities were low (value close to 1; Supplementary table A5) indicating that in the studied ecosystem it is not so much predator biomass that determines prey mortality rates, but it is more the physiological or behavioural factors of the prey (bottom-up control: Christensen and Walters, 2004). The lowest vulnerabilities (closest to 1.00) were estimated for the predator-prey interactions of horse mackerels-zooplankton, squids-sharks, squids-other small pelagics, and polychaetes-benthic invertebrates.

There was an overall satisfactory match of the catches estimated by

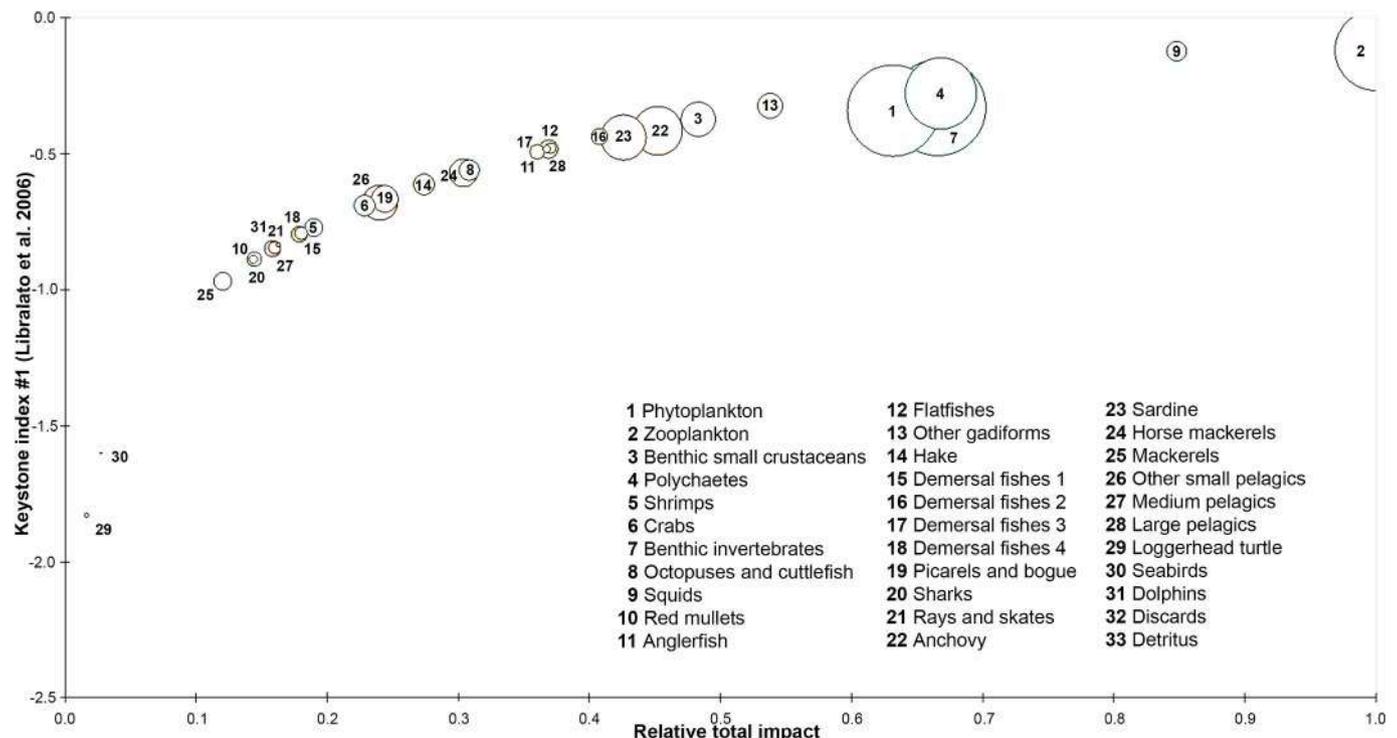


Fig. 4. Keystone index and relative total impact of each functional group of the Thermaikos Gulf Ecopath model. Circle size indicates the % relative biomass of each group.

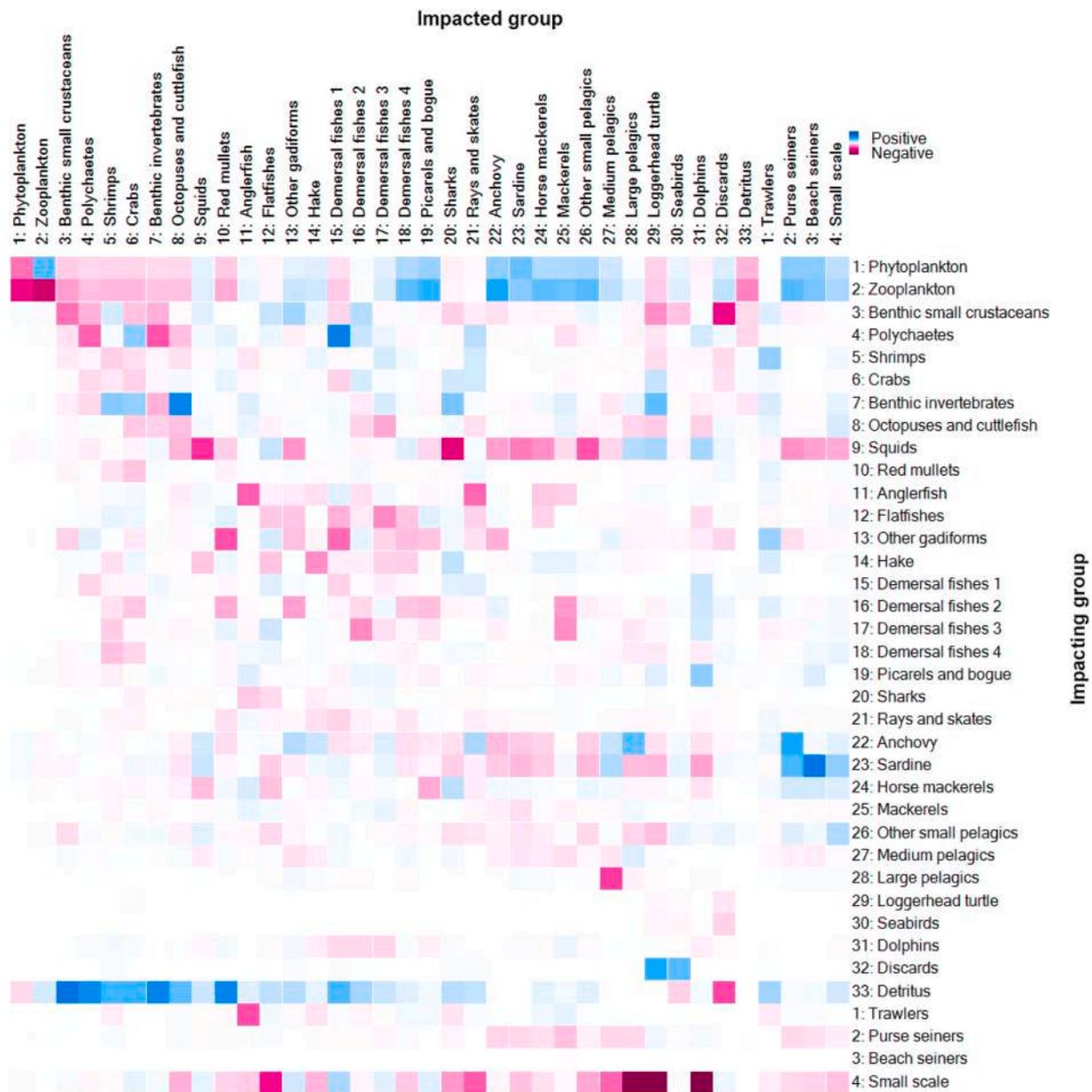


Fig. 5. Mixed trophic impact analysis of the Thermaikos Gulf Ecopath model. Impact on and by the four fishing fleets is also shown (1–4).

Ecosim and the observed data, as can be seen in the cases of flatfishes, demersal fishes 2, 3, 4, rays and skates, mackerels, other small pelagic fishes (Fig. 6). However, for some FGs, such as crabs, large pelagic fishes, red mullets, hake, the model could not follow the data well, while for sardine and horse mackerels the model seemed to overestimate catches (Fig. 6). The correlation matrix between the catch time series of the FGs (Fig. 7) revealed 100 significant correlations out of the 276 possible combinations (36%), 62% of which were strong (correlation coefficient ≥ 0.7), 33% were moderate ($0.4 \leq$ correlation coefficient < 0.7) and 5% were weak (correlation coefficient < 0.4). The FGs whose catches were shown to be overall highly correlated were generally demersal fish species, i.e. other gadiforms, sharks, flatfishes, demersal fishes 1–4, rays and skates, horse mackerels, and also other small pelagics. The matching of the biomass estimated by Ecosim and the observed data seemed more problematic with cases of scaling discrepancies (Fig. 8). The match was satisfactory for crabs, octopuses and cuttlefish and hake, while flatfishes seemed to be underestimated by the model and anchovy seemed to be overestimated.

3.3. Ecosim simulations and future scenarios

The basic Ecosim simulation (scenario 0: business-as-usual) for biomasses and catches for 33 FGs of the Thermaikos Gulf ecosystem revealed overall persistent declining trends for important ecological and commercial groups from 2000 to 2016, when observed data were available. In the projection years, i.e. after 2016, a subsequent increase and a following stabilization at an intermediate level compared to the previous years was forecasted; that was mainly driven by the primary production anomaly (Figs. 6, 8 and 9, and Table 5). The total biomass and total catches were predicted to decrease by the end of the simulation period in 2025, by 11 and 19%, respectively, while the biomass of 7 FGs (21%) showed a marginal increase that varied from $< 1\%$ (sardine) to 8% (mackerels) and the biomass of 6 mostly predatory FGs (18%) showed a more pronounced increase varying from 10% (anglerfish) to 204% (large pelagic fishes). However, the biomass increase did not result in a subsequent increase of the catches as might be expected, except for anglerfish and large pelagic fishes (Table 5). Commercially important FGs such as the horse mackerels, anchovy, and red mullets were

Table 4

Model fits according to the steps applied by Mackinson et al. (2009) including trophic interactions, fishery and environmental drivers (primary production anomaly and chlorophyll *a* -chl_a- on the primary producer and sea surface temperature -SST-on sardine, anchovy, and horse mackerels). The chosen model is shown in bold italics; it has the second biggest improvement (%) compared to the baseline model and the second lowest AICc (Heymans et al., 2016; Scott et al., 2016).

Steps	Vs	ASP	K	min SS	AICc	Improved (%)
1. Baseline (B)	0	0	0	348.4	-147.2	
2. B & trophic interactions	20	0	20	348.4	-105.4	-28.4
3. B & environment (pp anomaly)	0	8	8	285	-226.3	53.7
4. B, trophic inter., & env. (pp anomaly)	20	8	28	281.2	-189.4	28.7
5. B, trophic inter., & env. (pp anomaly + chl _a)	20	8	28	276.4	-197.6	34.2
6. B and environment (SST)	0	0	0	343.2	-154.4	4.9
7. B, trophic inter., & env. (SST)	20	0	20	340.7	-116.0	-21.2
8. B & env. (pp anomaly + SST)	0	8	8	277.7	-238.7	62.2
9. B, trophic inter., & environment (pp anom + SST)	20	8	28	271.4	-206.2	40.1
10. B, trophic inter., & env. (pp anom + SST + chl _a)	20	8	28	267.8	-212.6	44.4
11. B & fishery	0	0	0	332.7	-169.1	14.9
12. B, fishery, & environment (pp anom)	0	8	8	273.5	-245.9	67.1
13. B, trophic interactions, & fishery	20	0	20	323.2	-141.0	-4.2
14. B, trophic inter., fishery, & env. (pp anom)	20	8	28	265.3	-217.0	47.4
15. B, trophic inter., fishery, & env. (pp anom + chl _a)	20	8	28	265.9	-216.0	46.7
16. B, fishery, & env. (SST)	0	0	0	328.8	-174.7	18.7
17. B, fishery, & env. (pp anom + SST)	0	6	8	267.1	-257.1	74.7
18. B, trophic inter., fishery, & env. (SST)	20	0	20	318.3	-148.3	0.8
19. B, trophic inter., fishery, & env. (pp anom + chl _a + SST)	20	8	28	258.1	-230.1	56.3
20. B, trophic inter., fishery, & env. (pp anom + SST)	20	8	28	248.3	-248.5	68.8

*Vs: vulnerabilities; ASP: anomaly spline points; K: number of parameters estimated; SS: sum of squares; AICc: Akaike Information Criterion.

predicted to marginally decrease in biomass (2–8%) with the respective catches suffering even greater losses (21–24%). The uncertainty around the biomass trajectories of the studied functional groups based on 20 Monte Carlo simulations are given in Supplementary Fig. A5 in the form of 5% and 95% percentiles.

Regarding the reduced fishing effort scenarios compared to the baseline scenario, the first three assumptions were predicted to lead to slightly higher biomass in the ecosystem (0.2–0.8%, scenario 1–3), proportionally to the reduction in fishing pressure, with catches decreasing accordingly (Table 6 and Fig. 8). Catches increased over time right after the implementation of the effort reduction scenarios in 2017 and by the end of the projection period in 2025 they reached a level that was generally lower than the baseline scenario. Only the 2025 catches of large pelagic fishes were predicted to increase in scenarios 1–3 (8–25%

increase) compared to the baseline scenario. The most profound biomass increase was observed in the predatory FGs of large and medium pelagic fishes (20.4–150.7% and 5.8–35.9% respectively, scenario 1–3) and also in other small pelagic fishes (7.3–39.9%, scenario 1–3). All predatory FGs were predicted to increase in biomass by 1.5 (dolphins) to 5.1% (hake) in scenario 1 and by 8.4–23.3% in scenario 3 (Table 6). The higher predicted biomass of predatory FGs resulted in the subsequent biomass decrease of their preys, such as picarels and bogue (0.6–2.7% biomass decrease in scenario 1–3), crabs (0.8–4.2% biomass decrease in scenario 1–3), demersal fishes 1 (6.3–32% biomass decrease in scenario 1–3). Scenario 4 (no beach-seiners after 2016) did not practically differ from the baseline scenario (Table 6; Fig. 9). It only resulted in a marginal biomass increase of large pelagics (0.3%), sardine, demersal fishes 3, and squids (0.1%). Marginal catch decreases were predicted for loggerhead turtles (3%), sardine, picarels and bogue, and squids (1%). Scenario 5 (no bottom-trawlers and beach-seiners after 2016) resulted in a marginal total biomass decrease of 0.1% and a total catch decrease of 9% (Table 6; Fig. 9). The most profound biomass increase under scenario 5 was predicted for anglerfish (15.9%) and hake (10.6%), quite similar to scenario 2. The biomass ratio of demersal over pelagics, as well as the biomass of predators, presented considerable decrease by the end of the calibration period in 2016 by about 15 and 38% respectively and increased in 2025, marginally exceeding the initial level (Fig. 10). The invertebrate to fish biomass ratio showed the opposite pattern as it increased by 93% in 2016 and then fell lower than the initial value in 2000 (Fig. 10). According to the fishing effort reduction scenarios, the biomass of predators was predicted to increase proportionally to the reduction in effort, while the invertebrate/fish and demersal/pelagic ratios were predicted to decrease proportionally to the reduction in effort (Fig. 10). Scenario 4 (no beach seiners after 2016) resulted in almost identical biomass ratios as the baseline scenario, while scenario 5 (no beach seiners and bottom trawlers after 2016) resulted in higher demersal to pelagic biomass ratios compared to all other scenarios (Fig. 10).

4. Discussion

The Thermaikos Gulf is a highly productive area (Sylaios et al., 2010) that is highly impacted by various human activities, and it requires consistent monitoring to ensure its sustainable exploitation and successful management in the context of EBFM (Poulos et al., 2000; Dimarchopoulou et al., 2018; Petala et al., 2018). The ecological model of the Thermaikos Gulf presented in this study, constitutes the first representation of the structure and functioning of this coastal ecosystem and quantification of the long-term effects of fishing by integrating the best available local biological, fisheries, and environmental data for organisms across all trophic levels. Indeed, we acknowledge that the lack of a complete biomass time series for more functional groups, as well as the lack of multi-stanza consideration, add to the uncertainty of the model results, which was actually put forward through Monte Carlo simulations (Supplementary Fig. A5). In fact, all models have an inherent level of uncertainty that stems from the quantity and quality of input data (Steenbeek et al., 2018). Nevertheless, despite these limitations, we maintain that the present ecosystem model of the Thermaikos Gulf provides a useful tool in the data-poor eastern Mediterranean (Dimarchopoulou et al., 2017) and adds to the EwE models of other exploited areas that have been developed in the Aegean Sea (Tsagarakis et al., 2010; Dimarchopoulou et al., 2019b).

The unique “quality footprint” of the Thermaikos Gulf base model, expressed through a pedigree index (Table 1) of 0.53, classifies it as a medium-high quality model (0.4–0.599: Morissette, 2007) right in agreement with the Ecopath model of Pagasitikos Gulf (Table 3; Dimarchopoulou et al., 2019b), but lower than the ones in the Thracian Sea (Tsagarakis et al., 2010), Cyprus (Michailidis et al., 2019) and Gulf of Mersin (Saygu et al., 2020), probably owing to the input production and consumption values having been calculated from empirical

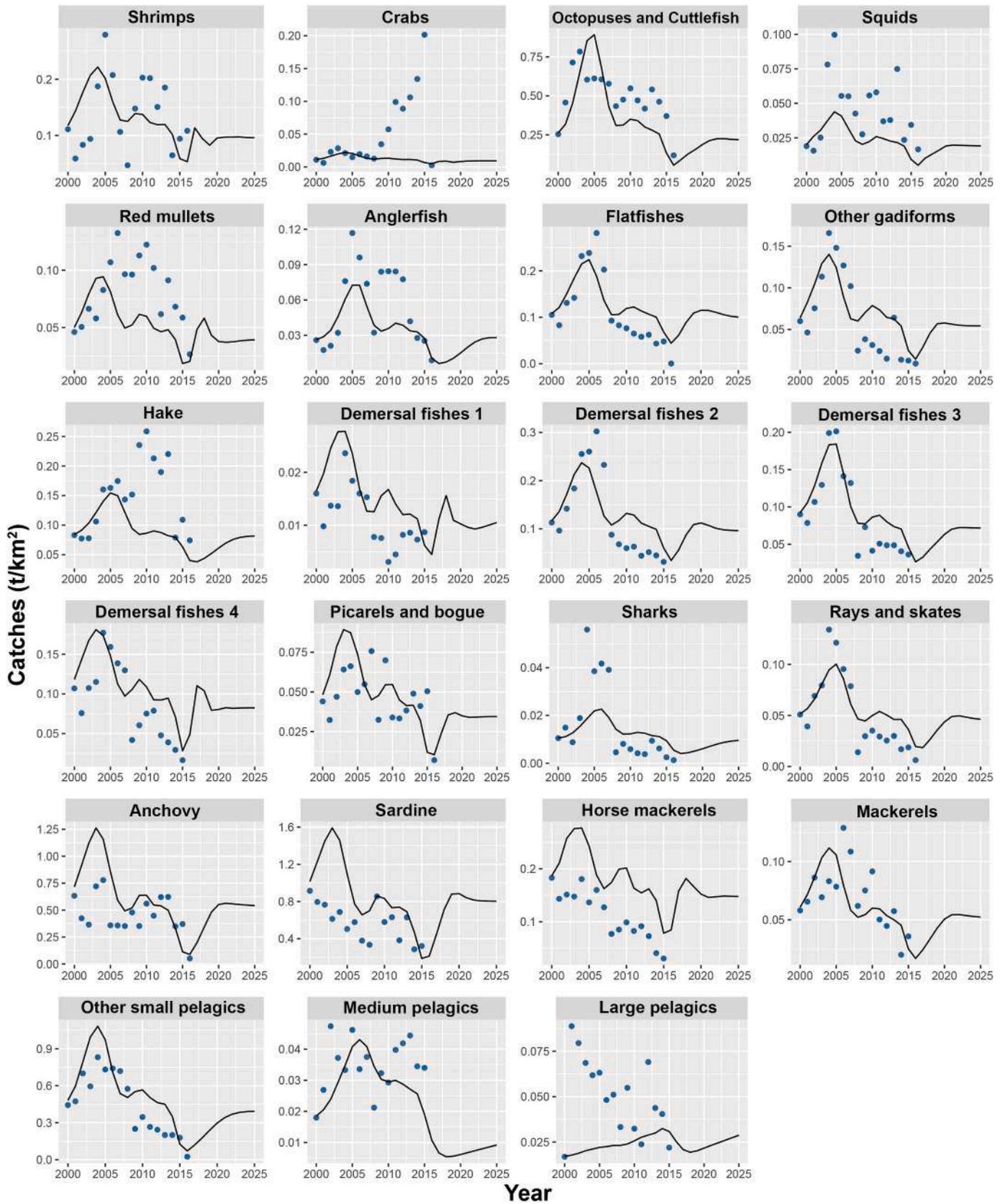


Fig. 6. Catches predicted by the Ecosim model (lines) for each functional group of the Thermaikos Gulf from 2000 to 2025, in comparison to reconstructed official catches (points) (based on Moutopoulos and Stergiou, 2012).

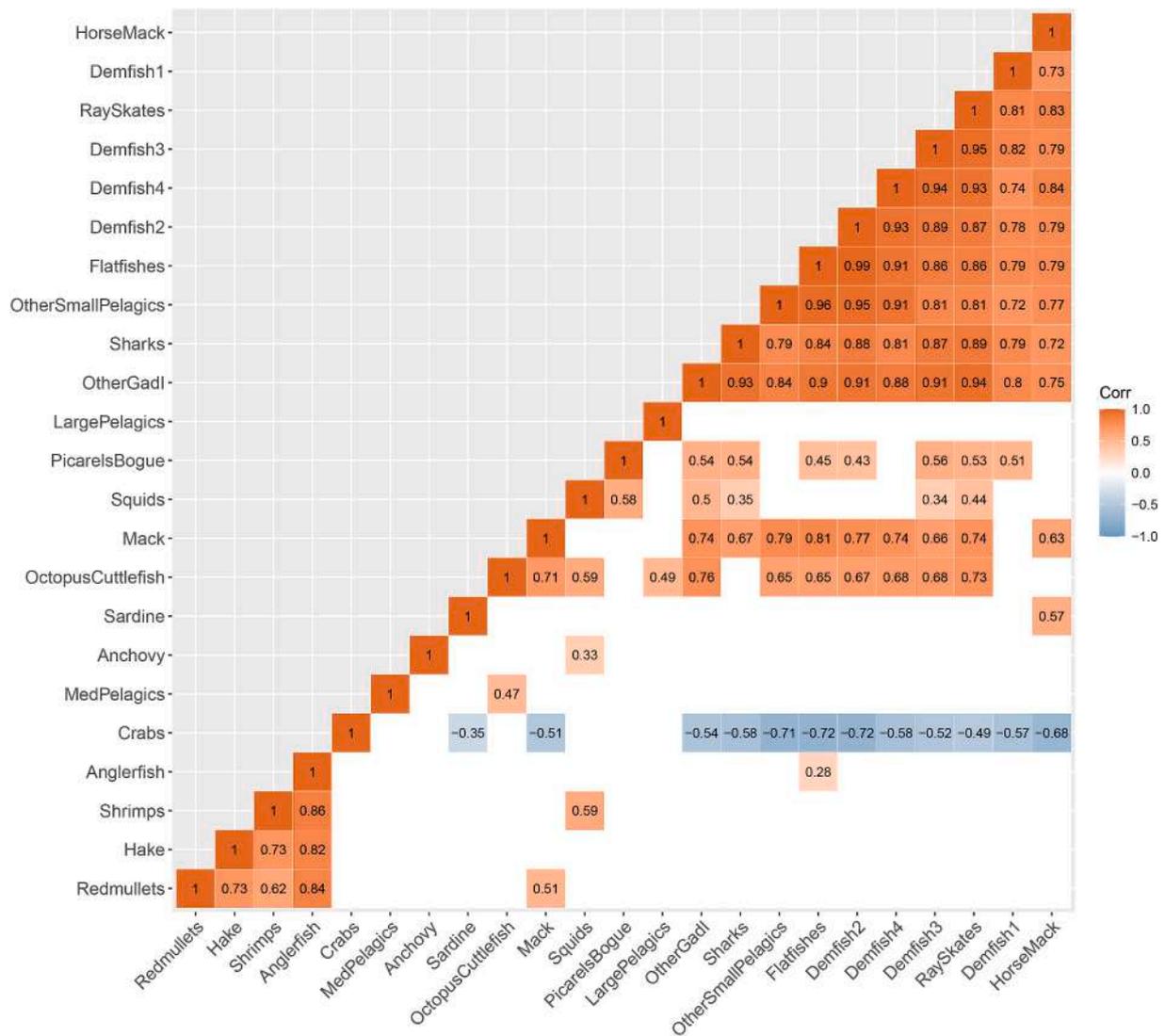


Fig. 7. Correlation matrix between the catch time series of 23 functional groups of the Thermaikos Gulf EwE model depicting only the significant relationships and the respective correlation coefficients (−1 negative, +1 positive correlation).

equations or derived from other models. Despite the varying exploitation level and difference in the nature of the systems, these specific models of nearby regions share similarities regarding the number of FGs, the aggregation across trophic levels, the top predator specifications and the lack of bacterial FGs and can, therefore, be compared through indicators that are robust to model construction (Heymans et al., 2016). The summary statistics indicate that the Thermaikos Gulf is an immature system, with a high system production, much above zero, that exceeds respiration (Table 1), probably owing to its intense exploitation by numerous fishing vessels, including bottom trawlers. It has been shown that fishing exploitation may lead the ecosystem to a less mature state, whereas banning fishing with towed gears may drive change in bottom complexity, as well as benthos and fish species composition from disturbed to mature ecosystems (Watling and Norse, 1998). These results were quite similar to the highly exploited northern Adriatic (Coll et al., 2007) and Thracian Seas (Tsagarakis et al., 2010), but different from Pagasitikos Gulf that is under a semi-protected regime with towed gears being prohibited for half a century (Dimarchopoulou et al., 2019b).

Keystone FGs are the ones that have a keystone index (Table 1) value close to or above zero (Libralato et al., 2006a). In the Thermaikos Gulf model, squids were shown to have a great influence in the trophic web of the Thermaikos Gulf presenting a high keystone index, a finding that is

in accordance with several other models from the Mediterranean (Barousse et al., 2009; Tsagarakis et al., 2010; Dimarchopoulou et al., 2019b). Since squid species are believed to have a major structuring role in marine ecosystems, as important consumers that link different trophic levels and habitats, ecosystem models can highly contribute to investigating the poorly understood impact and ecological role of cephalopods within the studied systems, by quantifying the wide range of their trophic relationships and allowing simulations to the future that can be useful for management (de la Chesnais et al., 2019). In the present model, squids along with other gadiforms had the highest negative impact on their preys resulting from high consumption rate of mainly zooplankton, anchovy and sardine. This can have both ecosystem and fisheries implications. Firstly, through such a cascading trophic effect, squids and other gadiforms may indirectly benefit primary producers (one phytoplankton group in the present model) by reducing the abundance of the herbivores feeding on them (Schmitz et al., 1997). Furthermore, since anchovy and sardine are the dominant pelagic species in the landings composition of the Thermaikos Gulf, similarly to the Thracian Sea and Pagasitikos Gulf (Tsikliras and Stergiou, 2007), the highly impacting FGs of squids and other gadiforms seem to be competing with local fishers (Hjermann et al., 2004) for these important exploited resources of the area (Tsagarakis et al., 2010; Dimarchopoulou et al., 2019b).

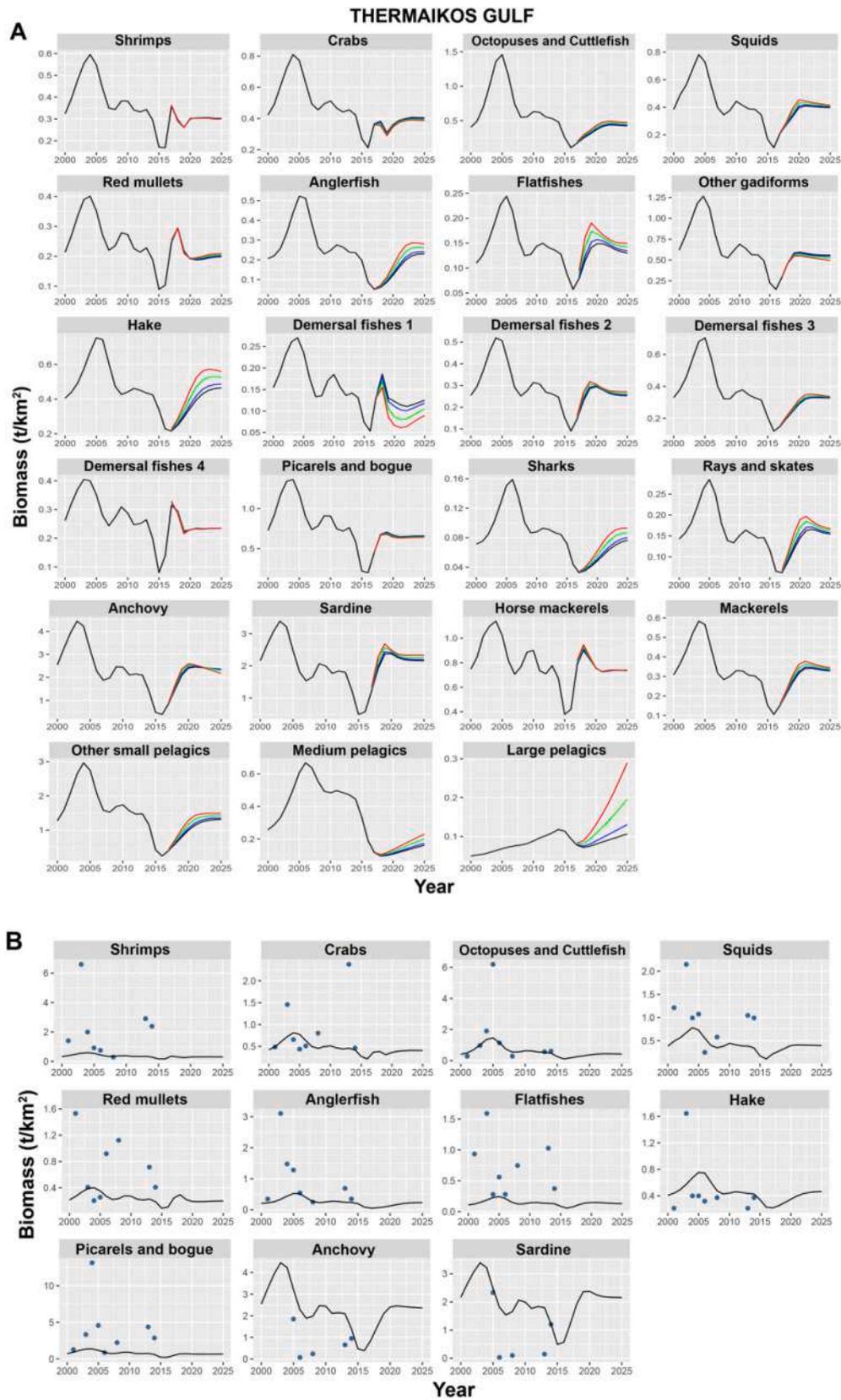


Fig. 8. Biomass predicted by the Ecosim model for each functional group of the Thermaikos Gulf from 2000 to 2025, according to the business-as-usual scenario (black line) and three scenarios of reduced fishing effort by 10% (blue), 30% (green) and 50% (red) after 2016 [A], in comparison to available observed biomass values (points) [B]. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

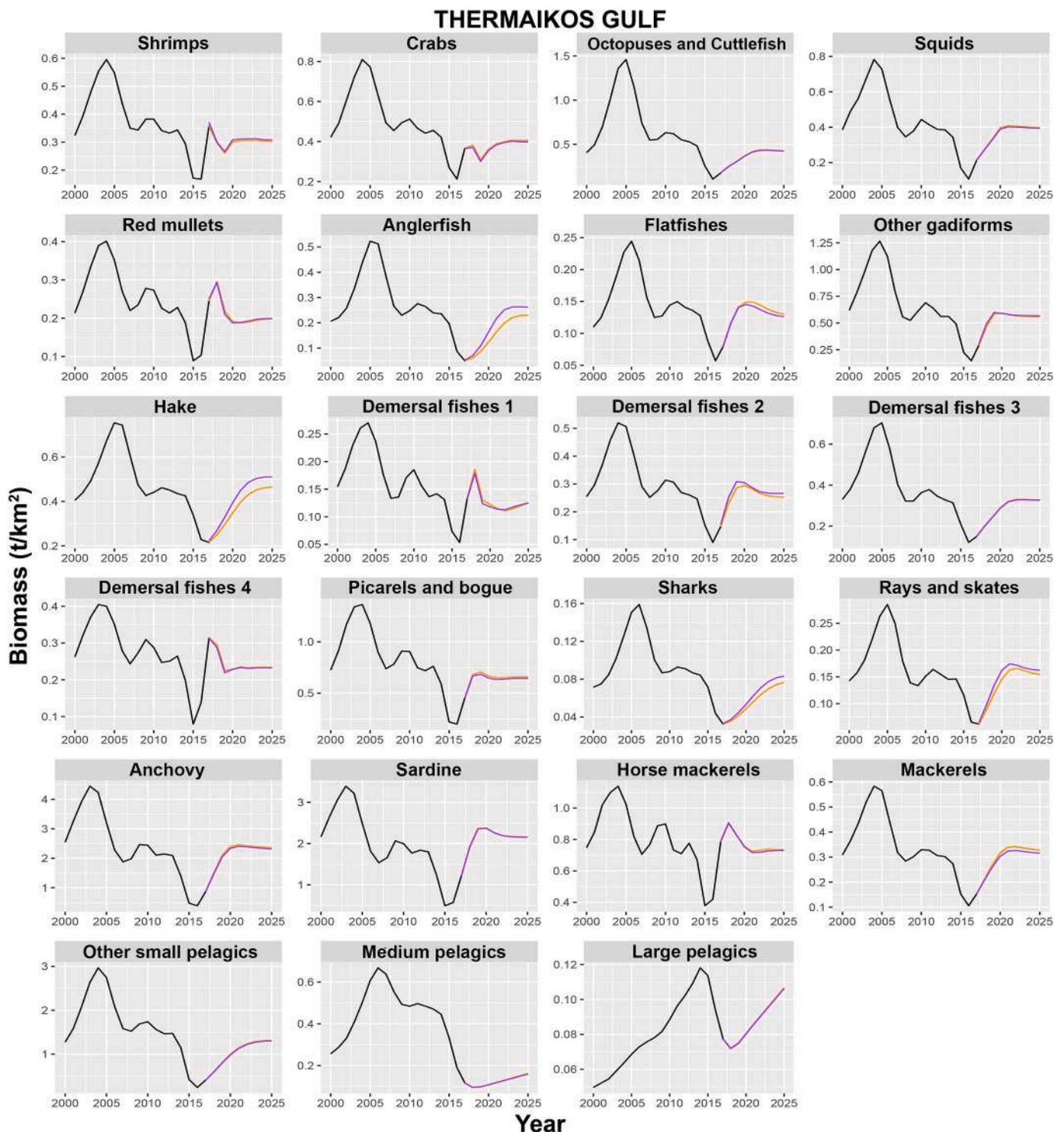


Fig. 9. Biomass predicted by the Ecosim model for each functional group of the Thermaikos Gulf from 2000 to 2025, according to the business-as-usual scenario (black line) and two scenarios of reduced fishing effort in which beach seiners (orange) and both bottom trawlers and beach seiners (purple) are banned after 2016. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The Thermaikos Gulf EwE model benefitted from tuning it with times series of observed catch and biomass values that increase confidence in the model's predictions (Coll et al., 2008). The model was able to capture more realistically long-term trends in some FGs (e.g. flatfishes, demersal fishes 2, 3, 4) that are the main targets of coastal and bottom-trawl fisheries throughout the year. Nine FGs including more than 70 species that live on or near the sea bottom (demersal) and are targeted by trawlers and small scale coastal vessels (Stergiou et al.,

2007) had highly correlated catch time series. That can be related to habitat and fleet characteristics, as well as the multi-gear and multi-species nature of the northern Aegean (Tsagarakis et al., 2010) and Mediterranean Sea fisheries (Stergiou et al., 2016). As a result, and also due to the fact that there were less biomass time series available for the fitting process, the model was mostly tuned to these correlated catch time series of some demersal FGs. Nevertheless, as it also happens in other similar studies, the model failed to follow the trend in highly

Table 5

Ecosim simulation results for the Thermaikos Gulf for the scenario 0: business-as-usual. FG: functional group. Biomass (Bi) and catch (Ca) values (t/km^2) and ratios at the starting year (2000: data were averaged over three years, i.e. 1998-2000) and the end of the simulation period (2025: to account for estimate uncertainty an average of 2023–2025 was used). Blue represents an increase of biomass and catch in 2025 compared to 2000.

FG	Bi			Ca		
	Bi2000	Bi2025	2025/2000	Ca2000	Ca2025	2025/2000
1	Phytoplankton	8.81	7.94	0.90		
2	Zooplankton	7.13	6.06	0.85		
3	Benthic small crustaceans	1.38	1.10	0.79		
4	Polychaetes	5.33	4.84	0.91		
5	Shrimps	0.32	0.30	0.94	0.12	0.10
6	Crabs	0.42	0.41	0.96	0.01	0.01
7	Benthic invertebrates	9.42	8.68	0.92	0.01	0.01
8	Octopuses and cuttlefish	0.41	0.43	1.06	0.26	0.22
9	Squids	0.39	0.40	1.04	0.02	0.02
10	Red mullets	0.21	0.20	0.92	0.05	0.04
11	Anglerfish	0.21	0.23	1.10	0.03	0.03
12	Flatfishes	0.11	0.13	1.21	0.11	0.10
13	Other gadiforms	0.62	0.56	0.90	0.06	0.05
14	Hake	0.41	0.46	1.13	0.08	0.08
15	Demersal fishes 1	0.15	0.12	0.78	0.02	0.01
16	Demersal fishes 2	0.25	0.25	1.00	0.12	0.10
17	Demersal fishes 3	0.33	0.33	0.99	0.09	0.07
18	Demersal fishes 4	0.26	0.23	0.89	0.12	0.08
19	Picarels and bogue	0.73	0.66	0.91	0.05	0.03
20	Sharks	0.07	0.07	1.03	0.01	0.01
21	Rays and skates	0.14	0.16	1.11	0.05	0.05
22	Anchovy	2.54	2.38	0.94	0.72	0.55
23	Sardine	2.16	2.16	1.00	1.01	0.80
24	Horse mackerels	0.75	0.74	0.98	0.19	0.15
25	Mackerels	0.31	0.33	1.08	0.06	0.05
26	Other small pelagics	1.27	1.30	1.02	0.48	0.39
27	Medium pelagics	0.26	0.15	0.59	0.02	0.01
28	Large pelagics	0.05	0.10	2.04	0.02	0.03
29	Loggerhead turtle	0.02	0.02	1.21	0.00	0.97
30	Seabirds	0.00	0.00	0.86		
31	Dolphins	0.02	0.02	0.96	0.00	0.75
32	Discards	0.36	0.32	0.90		
33	Detritus	37.18	31.62	0.85		
	TOTAL	82.03	72.71	0.89	3.70	2.98
					0.81	

migratory species that only seasonally occur in the area and are poorly represented in EwE, such as the large pelagic fishes (Coll et al., 2008; Corrales et al., 2017a; Piroddi et al., 2017)..

The overall declining trend in the biomass of most FGs over the historical period 2000–2016 supports previous findings which highlight the bad stock status and declining biomass-at-sea in the Greek Seas as estimated by stock assessment models (Froese et al., 2018a), as well as intense fisheries exploitation and declining catches compared to historical values (Tsikliras et al., 2013). Such decreasing biomass pattern of targeted demersal and pelagic species has also been observed in other similar models in the western, central and eastern Mediterranean and was attributed to a combination of driving factors including fishing, trophic interactions and environmental changes (Coll et al. 2008, 2009; Corrales et al., 2017a). Notably, in Israel, alien species were shown to thrive over time in the area, most probably at the expense of native species (Corrales et al., 2017a). Alien species invasions have been recorded to cause a decline in local populations and are suspected to therefore induce a reduction of genetic diversity, loss of functions,

processes, and habitat structure (Galil, 2007). Since many marine alien species have already been recorded in the Thermaikos Gulf, but not in alarming numbers yet (Katsanevakis et al., 2013), the observed declining biomass trends of local commercial species can be concerning; thus, putting alien species in the picture would be worth investigating in the future, provided their presence in the area is established and relevant data are available.

The general increase and stabilization of biomass and catches in the projection years at overall lower levels compared to the starting year, are mainly driven by the primary production anomaly predicted by the model. Apart from environmental drivers in the form of primary production anomaly, SST also contributed to the fitting of the model to observed biomass and catches, indicating that SST is closely linked to system productivity. Marine hotspots of high productivity are usually linked to low SST that may result from oceanographic processes such as upwellings and river outflows and are important areas for fish aggregation and fisheries production (Valavanis et al., 2004). Accordingly, increasing SST, that can potentially be caused by ocean warming, is

Table 6

Ecosim simulation results for the Thermaikos Gulf for three scenarios of fishing effort reduction by 10, 30 and 50% compared to the business-as-usual scenario. FG: functional group. Biomass (Bi) and catch (Ca) ratios at the end of the simulation period (2025: to account for estimate uncertainty an average of 2023–2025 was used). Blue represents higher (ratio >1) biomass or catch.

FG	10%		30%		50%		No BS		No OTB & BS		
	Bi	Ca	Bi	Ca	Bi	Ca	Bi	Ca	Bi	Ca	
1	Phytoplankton	1.002		1.004		1.005		1.000		0.999	
2	Zooplankton	0.999		0.997		0.996		1.000		1.001	
3	Benthic small crustaceans	0.997		0.992		0.987		1.000		0.993	
4	Polychaetes	1.001		1.004		1.006		1.000		1.000	
5	Shrimps	0.998	0.90	0.993	0.69	0.989	0.49	1.000	1.00	1.019	0.53
6	Crabs	0.992	0.89	0.974	0.68	0.958	0.48	1.000	1.00	0.985	0.57
7	Benthic invertebrates	0.997	0.90	0.992	0.69	0.985	0.49	1.000	1.00	1.003	0.36
8	Octopuses and cuttlefish	1.023	0.92	1.068	0.75	1.114	0.56	1.000	1.00	0.996	0.91
9	Squids	1.013	0.91	1.036	0.73	1.053	0.53	1.001	0.99	0.989	0.18
10	Red mullets	1.012	0.91	1.033	0.72	1.055	0.53	1.000	1.00	1.008	0.69
11	Anglerfish	1.052	0.95	1.154	0.81	1.252	0.63	1.001	1.00	1.159	0.22
12	Flatfishes	1.031	0.93	1.085	0.76	1.129	0.56	1.000	1.00	0.964	0.94
13	Other gadiforms	0.981	0.88	0.943	0.66	0.901	0.45	1.000	1.00	1.017	0.25
14	Hake	1.051	0.95	1.148	0.80	1.233	0.62	1.001	1.00	1.106	0.72
15	Demersal fishes 1	0.937	0.84	0.811	0.57	0.680	0.34	1.000	1.00	1.014	1.01
16	Demersal fishes 2	1.013	0.91	1.039	0.73	1.068	0.53	1.000	1.00	1.046	0.79
17	Demersal fishes 3	1.007	0.91	1.024	0.72	1.041	0.52	1.001	1.00	0.997	0.95
18	Demersal fishes 4	0.999	0.90	0.998	0.70	0.999	0.50	1.000	1.00	0.993	0.98
19	Picarels and bogue	0.994	0.89	0.983	0.69	0.973	0.49	1.000	0.99	0.979	0.96
20	Sharks	1.052	0.95	1.153	0.81	1.249	0.62	1.000	1.00	1.097	0.78
21	Rays and skates	1.022	0.92	1.060	0.74	1.087	0.54	1.000	1.00	1.042	0.77
22	Anchovy	1.000	0.90	0.987	0.69	0.952	0.48	1.000	1.00	0.982	0.98
23	Sardine	1.017	0.92	1.049	0.73	1.080	0.54	1.001	0.99	0.998	0.99
24	Horse mackerels	1.001	0.90	1.003	0.70	1.006	0.50	1.000	1.00	0.990	0.92
25	Mackerels	1.014	0.91	1.037	0.73	1.055	0.53	1.001	1.00	0.960	0.95
26	Other small pelagics	1.033	0.93	1.092	0.76	1.144	0.57	1.000	1.00	0.990	0.99
27	Medium pelagics	1.073	0.97	1.229	0.86	1.399	0.70	1.002	1.00	0.984	0.98
28	Large pelagics	1.204	1.08	1.743	1.22	2.507	1.25	1.003	1.00	0.998	0.99
29	Loggerhead turtle	1.040	0.91	1.103	0.75	1.165	0.57	1.000	0.97	0.948	0.92
30	Seabirds	0.974		0.912		0.838		1.000		0.882	
31	Dolphins	1.015	0.91	1.048	0.73	1.084	0.54	1.000	1.00	1.004	1.00
32	Discards	0.921		0.749		0.563		0.999		0.760	
33	Detritus	1.001		1.003		1.004		1.000		1.000	
	TOTAL	1.002	0.91	1.005	0.73	1.008	0.54	1.000	1.00	0.999	0.91

likely to lead to more intense stratification, reduced nutrient input in the euphotic zone and ultimately lower productivity (Dunstan et al., 2018). In the north Aegean Sea, biological traits were used to detect the effects of different fisheries management scenarios on the ecosystem, which predicted decrease of thermophilic traits of marine organisms, such as high optimal temperature and summer spawning, something that could mitigate the anticipated climate change effects (Papapanagiotou et al., 2020).

As in other areas of the Mediterranean Sea (Adriatic Sea: Coll et al., 2009; Levantine Sea: Corrales et al., 2017a), temporal trends in ecological indicators pointed out ecological changes in the food web structure of the Thermaikos Gulf as a whole showing a historical trend of ecosystem degradation (Dimitriou et al., 2018). Ecosystems respond differently to the various pressures and ecological indicators can be negatively affected by fishing or the environment, while at the same time they can be positively influenced by some other driver (Large et al., 2015). The biomass of predators in the Thermaikos Gulf (anglerfish, flatfishes, hake, rays and skates, medium pelagic fishes; except for large pelagic fishes and dolphins that were stable or slightly increasing) presented an overall decline during the calibration period with a more profound decrease from 2005 to 2016, hence indicating ecosystem changes due to intense fishing. The respective decrease in the demersal to pelagic biomass ratio and the slight increase of the invertebrate to fish biomass ratio also corroborated these findings. It should be noted that

the observed trend of the demersal to pelagic ratio could potentially be biased due to the inherent model-fitting issues reported. Nevertheless, the decreasing demersal to pelagic ratio has also been previously reported in the landings of the northern Aegean Sea (Thermaikos Gulf included, along with the Thracian Sea and Pagasitikos Gulf) for the period 1990–2003 (Tsikliras and Stergiou, 2007), a finding that also denotes depletion of demersal stocks and possible decline of large pelagic stocks that then compels local fisheries to rely on the lower part of the food web with smaller, short-lived species. Fishing is known to selectively remove large individuals and large species that are long-lived and grow more slowly; thus, exploited ecosystems end up hosting more small-sized species and individuals at the cost of larger ones (Stergiou and Tsikliras, 2011). This is reflected on the catches derived from these systems that are characterized by reduced mean trophic level as they consist of more short-lived, low TL invertebrates and planktivorous pelagic fish rather than high TL, piscivorous demersal fish, i.e. the *fishing down marine food webs* phenomenon (Pauly et al., 1998). The shrinking of the Mediterranean marine food webs has been confirmed using catch, biomass, survey data and somatic size indicators (Stergiou and Tsikliras, 2011; Tsikliras et al., 2015; Dimarchopoulou et al., 2018).

As also shown in another semi-enclosed ecosystem in Greece (Pagasitikos Gulf; Dimarchopoulou et al., 2019b), all the future scenarios of reduced fishing effort resulted in higher biomass in the ecosystem but fewer catches, with the reduction in fishing pressure

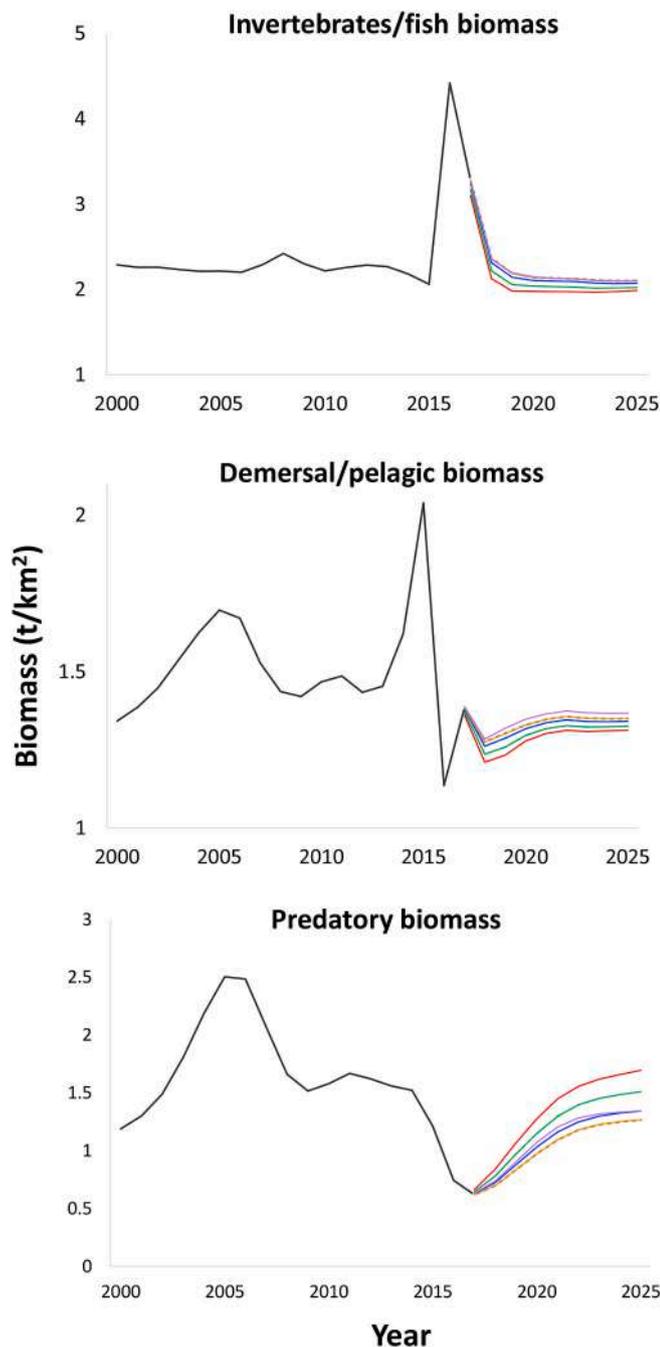


Fig. 10. Ecological indicators of the Thermaikos Gulf ecosystem estimated for the calibration period 2000–2016 (solid line) and the projection period 2017–2025 under the baseline scenario (dashed line) and the three fishing effort reduction scenarios (10%: blue; 30%: green; 50%: red). Note: the y-axis was modified for presentation purposes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

being proportional to the biomass increase and catch decrease among the tested scenarios. Within each scenario, catches increased considerably right after 2016 (as it would be expected to happen in an over-exploited system based on the yield curve for a given species), but in most cases they could not reach or exceed the levels of 2000. As demonstrated by Froese et al. (2018a) stocks can be rebuilt, but it may take a few years for catches to reach or exceed their initial level right before the implementation of reduced fishing effort. However, this doesn't mean that the ecosystem will be able to produce catch levels of

25 years ago after less than 10 years (2017–2025) of reduced effort, as seen here. Even though environmental parameters were a significant driver of changes in the Thermaikos Gulf ecosystem, fishing did remain a highly impacting anthropogenic activity as shown by the results of the scenarios and as also presented in previous works in the Mediterranean (Coll et al., 2008; Corrales et al., 2017a; Dimarchopoulou et al., 2019b). Notably, the inner part of the Thermaikos Gulf that is protected from large-scale fishing activities hosts fish and invertebrate populations of higher biomass and healthier size structure (indicated by the presence of more and larger fish: Jennings and Blanchard, 2004; Froese et al., 2018b) compared to the exploited part (Dimarchopoulou et al., 2018). The biomass increase in the three future scenarios was shown to be generally higher in top predators, which are known to be more intensely targeted by fishing activities (Myers and Worm, 2003) because of their higher price (Tsikliras and Polymeros, 2014), and lower for prey FGs that are consumed in higher rates following the proliferation of their predators as predicted by the model.

Although the Pagasitikos Gulf has been trawler-free for decades (Dimarchopoulou et al., 2019b), it would not be realistic for trawlers to be totally banned from the fished part of the Thermaikos Gulf since this gear provides a considerable proportion of the catches of the northern Aegean Sea. Rather, some reduction in the fishing days (on a weekly or monthly basis) would be more feasible in the medium term. On the other hand, the beach seiners that operate in the Thermaikos Gulf are only a few and banning those would result in marginally higher biomass for important commercial groups (squids, anglerfish, hake, demersal fishes 3, sardine, mackerels, medium and large pelagics), while it would slightly decrease discards. Beach seining has indeed been shown to be a less sustainable gear that causes fish abundance reductions (Vieira et al., 2020). In fact, in 2013, Greece issued a ban on beach seining but the gear was later re-instated through an experimental fishing license issued for the entire fleet (around 200 vessels throughout Greece) and there is still a small amount of beach seining catch being reported in the official landings (Moutopoulos, 2020). Previous independent research in Greek waters has shown that, when operating above *Posidonia oceanica* meadows, beach seining is non-selective regarding species composition (88 species are reported in Kalogirou et al., 2010) and collects the highest percentage of undersized individuals (juveniles) compared to all other gears operating in Greek waters (Tables 4 and 5 in Stergiou et al., 2009). The number of species collected is significantly reduced when the gear operates over sandy habitats (Kalogirou et al., 2012).

Ecosystem models like EwE can make use of time series data to perform and validate projections in the future (that are plausible given the initial model configuration), which can then be helpful in assessing ecosystem status and adjusting management practices to successfully meet future conservation and sustainability targets (Brasier et al., 2019). Obviously though, since models are mathematical abstractions of real complicated systems and therefore hold an inherent level of uncertainty that has to do with the quality and reliability of the input data, they should be treated and analyzed with attention (Steenbeek et al., 2018).

This study confirms at an ecosystem level what should already have been known from single-species stock assessments but failed to be reflected in fisheries management: that the less we fish, the more the available biomass to exploit in the future. What single-species stock assessments cannot predict is the effect any management decision might have on the remaining components of the ecosystems, including other exploited or unexploited populations, in combination with environmental forcing that may determine the energy available across the food web. The biggest natural experiment of the century on the effects of fishing on marine populations (the recent lockdown due to the COVID-19 outbreak) has also proven that stock and ecosystem rebuilding can only be possible with less fishing and temporal/spatial closures (Piroddi et al., 2020; Kemp et al., 2020). The obvious solution of slowing the rate at which resources are becoming depleted doesn't only apply to the aquatic environment, but also to other exhaustible overexploited natural resources such as arable land, fossil fuels, and forest vegetation

(Subramanian, 2018).

In conclusion, the model simulations highlighted the important role of environmental factors, in particular ocean warming, as well as fishing activities on shaping ecosystem changes in species, communities and the food web. And while environmental changes can be quite stochastic and hard to control (Jameson et al., 2002), fishing effort is a parameter that can be regulated to ensure more resilient ecosystems in the face of global change (Rainer Froese interviewed by Erik Stokstad in March 2019). In the historically overexploited Mediterranean Sea where the impacts of overfishing are obvious in the bad status of the stocks (Colloca et al., 2013; Tsikliras et al., 2015), reducing exploitation levels is expected to result in the rebuilding of stocks that may then lead to higher catches in the medium term with considerably higher income for the fishers (Froese et al., 2018a). Future work focuses on the spatial component of EwE in the Thermaikos Gulf, as it is the combination of spatial fishing restrictions and protected areas with overall effort reductions that will ensure stock rebuilding to previous biomass levels (Dimarchopoulou et al., 2019a).

Author statement

DD: conceptualization, methodology, formal analysis, writing – original draft, writing – review & editing, visualization. KT: methodology, formal analysis, writing – review & editing. GS: formal analysis, writing – review & editing. ACT: conceptualization, methodology, formal analysis, writing – review & editing, supervision, funding acquisition.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgements

This work was part of the European DG-MARE funded project “PROTOMEDEA” (Contract no: SI2.721917). ACT and GS were supported by the H2020 project “ODYSSEA” (Contract No. 727277). The authors would like to sincerely thank Ioannis Keramidas for his valuable contribution to building the Ecosim model, as well as Xavier Corrales for his useful advice.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2021.107667>.

References

- Agnetta, D., Badalamenti, F., Colloca, F., D'Anna, G., Di Lorenzo, M., Fiorentino, F., Garofalo, G., Gristina, M., Labanchi, L., Patti, B., Pipitone, C., Solidoro, C., Libralato, S., 2019. Benthic-pelagic coupling mediates interactions in Mediterranean mixed fisheries: an ecosystem modeling approach. *PLoS One* 14, e0210659.
- Ahrens, R.N.M., Walters, C.J., Christensen, V., 2012. Foraging arena theory. *Fish Fish.* 13, 41–59.
- Bănar, D., Mellon-Duval, C., Roos, D., Bigot, J.-L., Souplet, A., Jadaud, A., Beaubrun, P., Fromentin, J.-M., 2013. Trophic structure in the Gulf of Lions marine ecosystem (north-western Mediterranean Sea) and fishing impacts. *J. Mar. Syst.* 111–112, 45–68.
- Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y., Palmeri, L., 2009. Trophic network model of the Northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. *Estuar. Coast Shelf Sci.* 83, 577–590.
- Bayle-Sempere, J.T., Arreguín-Sánchez, F., Sanchez-Jerez, P., Salcido-Guevara, L., Fernandez-Jover, D., Zetina-Rejón, M.J., 2013. Trophic structure and energy fluxes around a Mediterranean fish farm. *Ecol. Model.* 248, 135–147.
- Brasier, M.J., Constable, A., Melbourne-Thomas, J., Trebilco, R., Griffiths, H., Van de Putte, A., Sumner, M., 2019. Observations and models to support the first marine ecosystem Assessment for the southern ocean (MEASO). *J. Mar. Syst.* 197, 103182.
- Cardinale, M., Svedäng, H., 2008. Mismanagement of fisheries: policy or science? *Fish. Res.* 93, 244–247.
- Celic, I., Libralato, S., Scarcella, G., Raicevich, S., Marceta, B., Solidoro, C., 2018. Ecological and economic effects of the landing obligation evaluated using a quantitative ecosystem approach: a Mediterranean case study. *ICES (Int. Council. Explor. Sea) J. Mar. Sci.* 75, 1992–2003.
- CFR (2018) European Commission 2018. Brussels: Common Fisheries Registry.
- de la Chesnais, T., Fulton, E.A., Tracey, S.R., Pecl, G.T., 2019. The ecological role of cephalopods and their representation in ecosystem models. *Rev. Fish Biol. Fish.* 29, 313–334.
- Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecol. Model.* 172, 109–139.
- Christensen, V., Walters, C.I., Pauly, D., 2005. November 2005. In: *Ecopath with Ecosim: a User's Guide*, edition. Fisheries Centre, University of British Columbia, Vancouver, p. 154 (available online at www.ecopath.org).
- Coll, M., Libralato, S., 2012. Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. *Fish Fish.* 13, 60–88.
- Coll, M., Steenbeek, J., 2017. Standardized ecological indicators to assess aquatic food webs: the ECOIND software plug-in for Ecopath with Ecosim models. *Environ. Model. Software* 89, 120–130.
- Coll, M., Palomera, I., Tudela, S., Sardà, F., 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. *J. Mar. Syst.* 59, 63–96.
- Coll, M., Santojanni, A., Palomera, I., Tudela, S., Arneri, E., 2007. An ecological model of the Northern and Central Adriatic Sea: analysis of ecosystem structure and fishing impacts. *J. Mar. Syst.* 67, 119–154.
- Coll, M., Palomera, I., Tudela, S., Dowd, M., 2008. Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978–2003. *Ecol. Model.* 217, 95–116.
- Coll, M., Santojanni, A., Palomera, I., Arneri, E., 2009. Food-web changes in the Adriatic Sea over the last three decades. *Mar. Ecol. Prog. Ser.* 381, 17–37.
- Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., Christensen, V., 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecol. Model.* 302, 42–53.
- Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., Bellido, J.M., Fiorentino, F., 2013. Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. *Fish Fish.* 14, 89–109.
- Corrales, X., Coll, M., Ofir, E., Piroddi, C., Goren, M., Edelist, D., Heymans, J.J., Steenbeek, J., Christensen, V., Gal, G., 2017a. Hindcasting the dynamics of an Eastern Mediterranean marine ecosystem under the impacts of multiple stressors. *Mar. Ecol. Prog. Ser.* 580, 17–36.
- Corrales, X., Ofir, E., Coll, M., Goren, M., Edelist, D., Heymans, J.J., Gal, G., 2017b. Modeling the role and impact of alien species and fisheries on the Israeli marine continental shelf ecosystem. *J. Mar. Syst.* 170, 88–102.
- Cowan Jr., J.H., Rice, J.C., Walters, C.J., Hilborn, R., Essington, T.E., Day Jr., J.W., Boswell, K.M., 2012. Challenges for implementing an ecosystem Approach to fisheries management. *Marine and Coastal Fisheries* 4, 496–510.
- Díaz López, B., Bunke, M., Bernal Shirai, J.A., 2008. Marine aquaculture off Sardinia Island (Italy): ecosystem effects evaluated through a trophic mass-balance model. *Ecol. Model.* 212, 292–303.
- Dimarchopoulou, D., Stergiou, K.I., Tsikliras, A.C., 2017. Gap analysis on the biology of Mediterranean marine fishes. *PLoS One* 12, e0175949.
- Dimarchopoulou, D., Dogrammatzi, A., Karachle, P.K., Tsikliras, A.C., 2018. Spatial fishing restrictions benefit demersal stocks in the northeastern Mediterranean Sea. *Sci. Rep.* 8, 5967.
- Dimarchopoulou, D., Keramidas, I., Markantonatou, V., Tsagarakis, K., Tsikliras, A.C., 2019a. Spatial fishing restriction scenarios in Thermaikos Gulf. *Proceedings of the Hellenic Conference of Ichthyologists* 17, 82–85.
- Dimarchopoulou, D., Keramidas, I., Tsagarakis, K., Tsikliras, A.C., 2019b. Ecosystem models and effort simulations of an untrawled gulf in the central Aegean Sea. *Frontiers in Marine Science* 6, 648.
- Dimitriou, E., Panagiotopoulos, I., Mentzafou, A., Anagnostou, C., 2018. Assessing the anthropogenic impacts on the fluvial water and sediment fluxes into the Thermaikos Gulf, northern Greece. *Environmental Engineering and Management Journal* 17, 1053–1068.
- Dunstan, P.K., Foster, S.D., King, E., Risbey, J., O'Kane, T.J., Monselesan, D., Hobday, A. J., Hartog, J.R., Thompson, P.A., 2018. Global patterns of change and variation in sea surface temperature and chlorophyll a. *Sci. Rep.* 8, 14624.
- Fiorentino, F., Patti, B., Colloca, F., Bonanno, A., Basilone, G., Gancitano, V., Garofalo, G., Goncharov, S., Gristina, M., Sinacori, G., Mazzola, S., 2013. A comparison between acoustic and bottom trawl estimates to reconstruct the biomass trends of sardine and anchovy in the Strait of Sicily (Central Mediterranean). *Fish. Res.* 147, 290–295.
- Frank, K.T., Petrie, B., Fisher, J.A.D., Leggett, W.C., 2011. Transient dynamics of an altered large marine ecosystem. *Nature* 477, 86–89.
- FishBase. World wide web electronic publication. In: Froese, R., Pauly, D. (Eds.), 2019. Available at: www.fishbase.org. (Accessed February 2019).
- Froese, R., Zeller, D., Kleisner, K., Pauly, D., 2012. What catch data can tell us about the status of global fisheries. *Mar. Biol.* 159, 1283–1292.
- Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A.C., Dimarchopoulou, D., Scarcella, G., Quaas, M., Matz-Lück, N., 2018a. Status and rebuilding of European fisheries. *Mar. Pol.* 93, 159–170.
- Froese, R., Winker, H., Coro, G., Demirel, N., Tsikliras, A.C., Dimarchopoulou, D., Scarcella, G., Probst, W.N., Dureau, M., Pauly, D., 2018b. A new approach for estimating stock status from length frequency data. *ICES (Int. Council. Explor. Sea) J. Mar. Sci.* 75 (6), 2004–2015.
- Froese, R., Tsikliras, A.C., Scarcella, G., Gascuel, D., 2021. Progress towards ending overfishing in the northeast Atlantic. *Mar. Pol.* 125, 104282.

- Galil, B.S., 2007. Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. *Mar. Pollut. Bull.* 55, 314–322.
- Halouani, G., Abdou, K., Hattab, T., Romdhane, M.S., Lasram, F.B.R., Le Loc'h, F., 2016. A spatio-temporal ecosystem model to simulate fishing management plans: a case of study in the Gulf of Gabes (Tunisia). *Mar. Pol.* 69, 62–72.
- Hattab, T., Ben Rais Lasram, F., Albouy, C., Romdhane, M.S., Jarboui, O., Halouani, G., Cury, P., Le Loc'h, F., 2013. An ecosystem model of an exploited southern Mediterranean shelf region (Gulf of Gabes, Tunisia) and a comparison with other Mediterranean ecosystem model properties. *J. Mar. Syst.* 128, 159–174.
- HELSTAT, 2018. Hellenic statistical Authority. Statistics on Sea fisheries per year and per area. Available at: <http://www.statistics.gr/en/statistics/-/publication/SPA03/>. (Accessed February 2018).
- Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, W., 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. *Ecol. Model.* 331, 173–184.
- Hilborn, R., Amaroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., de Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., Kurota, H., Little, L.R., Mace, P., McClanahan, T., Melnychuk, M.C., Minto, C., Osio, G.C., Parma, A.M., Pons, M., Segurado, S., Szuwalski, C.S., Wilson, J.R., Ye, Y., 2020. Effective fisheries management instrumental in improving fish stock status. *Proceedings of the National Academy of Sciences of the United States of America PNAS* 117 (4), 2218–2224.
- Hjermann, D.O., Ottersen, G., Stenseth, N.C., 2004. Competition among fishermen and fish causes the collapse of Barents Sea capelin. *Proc. Natl. Acad. Sci. Unit. States Am.* 101 (32), 11679–11684.
- Howarth, L.M., Roberts, C.M., Thurstan, R.H., Stewart, B.D., 2014. The unintended consequences of simplifying the sea: making the case for complexity. *Fish Fish.* 15, 690–711.
- Jameson, S.C., Tupper, M.H., Ridley, J.M., 2002. The three screen doors: can marine “protected” areas be effective? *Mar. Pollut. Bull.* 44, 1177–1183.
- Jennings, S., Blanchard, J.L., 2004. Fish abundance with no fishing: predictions based on macroecological theory. *J. Anim. Ecol.* 73, 632–642.
- Jennings, S., Kaiser, M.J., 1998. In: Blaxter, J.H.S., Southward, A.J., Tyler, P.A. (Eds.), *The Effects of Fishing on Marine Ecosystems*, vol. 34. *Advances in Marine Biology*, pp. 201–352.
- Kallianiotis, A.A., Vidoris, P., Sylaios, G.K., 2004. Fish species assemblages and geographical sub-areas in the North Aegean Sea, Greece. *Fish. Res.* 68, 171–187.
- Kalogirou, S., Corsini-Foka, M., Sioulas, A., Wennhage, H., Pihl, L., 2010. Diversity, structure and function of fish assemblages associated with *Posidonia oceanica* beds in an area of the eastern Mediterranean Sea and the role of non-indigenous species. *J. Fish. Biol.* 77, 2338–2357.
- Kalogirou, S., Wennhage, H., Pihl, L., 2012. Non-indigenous species in Mediterranean fish assemblages: contrasting feeding guilds of *Posidonia oceanica* meadows and sandy habitats. *Estuar. Coast Shelf Sci.* 96, 209–218.
- Karachle, P.K., Stergiou, K.I., 2017. An update on the feeding habits of fish in the Mediterranean Sea (2002–2015). *Mediterr. Mar. Sci.* 18, 43–52.
- Katsanevakis, S., Zenetos, A., Poursanidis, D., Nunes, A.L., Deriu, I., Bogucarskis, K., Cardoso, C., 2013. ELNAIS meets EASIN: distribution of marine alien species in Greece using EASIN mapping services and ELNAIS spatial data. *Mediterr. Mar. Sci.* 14, 95–98.
- Kemp, P., Froese, R., Pauly, D., 2020. COVID-19 provides an opportunity to advance a sustainable UK Fisheries Policy in a post-Brexit brave new world. *Mar. Pol.* 120, 104114.
- Large, S.I., Fay, G., Friedland, K.D., Link, J.S., 2015. Critical points in ecosystem responses to fishing and environmental pressures. *Mar. Ecol. Prog. Ser.* 521, 1–17.
- Lassalle, G., Chouvelon, T., Bustamante, P., Niquil, N., 2014. An assessment of the trophic structure of the Bay of Biscay continental shelf food web: comparing estimates derived from an ecosystem model and isotopic data. *Prog. Oceanogr.* 120, 205–215.
- Libralato, S., Christensen, V., Pauly, D., 2006a. A method for identifying keystone species in food web models. *Ecol. Model.* 195, 153–171.
- Libralato, S., Tempesta, M., Solidoro, C., Spoto, M., 2006b. An ecosystem model applied to Miramare Natural Marine Reserve: limits, advantages and perspectives. *Biol. Mar. Mediterr.* 13, 386–395.
- Libralato, S., Coll, M., Tempesta, M., Santojanni, A., Spoto, M., Palomera, I., Arneri, E., Solidoro, C., 2010. Food-web traits of protected and exploited areas of the Adriatic Sea. *Biol. Conserv.* 143, 2182–2194.
- Link, J.S., 2010. Adding rigor to ecological network models by evaluating a set of pre-balance diagnostics: a plea for PREBAL. *Ecol. Model.* 221 (12), 1580–1591.
- Lotze, H.K., 2004. Repetitive history of resource depletion and mismanagement: the need for a shift in perspective. In: Browman, H.I., Stergiou, K.I. (Eds.), *Perspectives on Ecosystem Based Approaches to the Management of Marine Resources*, vol. 274. *Marine Ecology Progress Series*, pp. 282–285.
- Lotze, H.K., Coll, M., Dunne, J.A., 2011. Historical changes in marine resources, food-web structure and ecosystem functioning in the Adriatic Sea, Mediterranean. *Ecosystems* 14, 198–222.
- Mackinson, S., Daskalov, G., Heymans, J.J., Neira, S., Arancibia, H., Zetina-Rejón, M., Jiang, H., Cheng, H., Coll, M., Arreguin-Sanchez, F., 2009. Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. *Ecol. Model.* 220, 2972–2987.
- Michailidis, N., Corrales, X., Karachle, P.K., Chartosia, N., Katsanevakis, S., Sfenthourakis, S., 2019. Modelling the role of alien species and fisheries in an Eastern Mediterranean insular shelf ecosystem. *Ocean Coast Manag.* 175, 152–171.
- Morissette, L., 2007. Complexity, Cost and Quality of Ecosystem Models and Their Impact on Resilience: a Comparative Analysis, with Emphasis on Marine Mammals and the Gulf of St. Lawrence. Unpublished Ph.D. thesis, University of British Columbia, Vancouver, p. 260. Available from: <https://www2.fisheries.com/archives/grad/abstracts/lmphdthesis.pdf>.
- Moutopoulos, D.K., 2020. Greece (including Crete): updated catch reconstruction to 2018. In: Derrick, B., Khalfallah, M., Relano, V., Zeller, D., Pauly, D. (Eds.), *Updating to 2018 the 1950–2010 Marine Catch Reconstructions of the Sea Around Us: Part I—Africa, Antarctica, Europe and the North Atlantic*, vol. 28. *Fisheries Centre Research Report*, pp. 179–187, 5.
- Moutopoulos, D., Stergiou, K., 2012. Spatial disentangling of Greek commercial fisheries landings by gear between 1928–2007. *Journal of Biological Research-Thessaloniki* 18, 265–279.
- Mulazzani, L., Manrique, R., Trevisan, G., Piccinetti, C., Malorgio, G., 2015. The relationship among catch, fishing effort, and measures of fish stock abundance: implications in the Adriatic Sea. *Can. J. Fish. Aquat. Sci.* 72, 410–421.
- Myers, R.A., Worm, B., 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423, 280–283.
- Neubauer, P., Jensen, O.P., Hutchings, J.A., Baum, J.K., 2013. Resilience and recovery of overexploited marine populations. *Science* 340, 347–349.
- Odum, E.P., 1971. *Fundamentals of Ecology*. W.B. Saunders Co, Philadelphia, p. 574.
- Papapanagiotou, G., Tsagarakis, K., Koutsidi, M., Tzanos, E., 2020. Using traits to build and explain an ecosystem model: Ecopath with Ecosim modelling of the north Aegean Sea (eastern Mediterranean). *Estuarine, Coastal and Shelf Science* 236, 106614.
- Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *ICES (Int. Council. Explor. Sea) J. Mar. Sci.* 39, 175–192.
- Pauly, D., Froese, R., 2020. MSY needs no epitaph—but it was abused. *ICES (Int. Council. Explor. Sea) J. Mar. Sci.* 78 (6), 2204–2210.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.Jr, 1998. Fishing down marine food webs. *Science* 279, 860–863.
- Pauly, D., Christensen, V., Walters, C., 2000. Ecopath, Ecosim, and Ecospace as tools for evaluating ecosystem impact of fisheries. *ICES J. Mar. Sci.* 57, 697–706.
- Pauly, D., Soriano-Bartz, M., Palomares, M.L., 1993. In: Christensen, V., Pauly, D. (Eds.), *Improved construction, parametrization and interpretation of steady-state ecosystem models* 26.
- Petala, M., Tsiroidis, V., Androulidakis, I., Makris, Ch, Baltikas, V., Stefanidou, A., Genitsaris, S., Antoniadou, C., Rammou, D., Moustaka-Gouni, M., Chintiroglou, C.C., Darakas, E., 2018. In: *Monitoring the Marine Environment of Thermaikos Gulf. Proceedings of the XIV Protection and Restoration of the Environment (PRE) Conference*, pp. 762–774.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, K.J., 2004. Ecosystem-based fishery management. *Science* 305, 346–347.
- Pimm, S.L., 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. The University of Chicago Press, Ltd., London.
- Piroddi, C., Giovanni, B., Christensen, V., 2010. Effects of local fisheries and ocean productivity on the northeastern Ionian Sea ecosystem. *Ecol. Model.* 221, 1526–1544.
- Piroddi, C., Coll, M., Liqueste, C., Macias, D., Greer, K., Buszowski, J., Steenbeek, J., Danovaro, R., Christensen, V., 2017. Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. *Sci. Rep.* 7, 44491.
- Piroddi, C., Coll, M., Steenbeek, J., Macias Moy, D., Christensen, V., 2015. Modelling the Mediterranean marine ecosystem as a whole: addressing the challenge of complexity. *Mar. Ecol. Prog. Ser.* 533, 47–65.
- Piroddi, C., Moutopoulos, D.K., Gonzalvo, J., Libralato, S., 2016. Ecosystem health of a Mediterranean semi-enclosed embayment (Amvrakikos Gulf, Greece): assessing changes using a modeling approach. *Contin. Shelf Res.* 121, 61–73.
- Piroddi, C., Colloca, F., Tsikliras, A.C., 2020. The living marine resources in the Mediterranean Sea large marine ecosystem. *Environmental Development* 100555.
- Poulos, S.E., Chronis, G.T., Collins, M.B., Lykousis, V., 2000. Thermaikos Gulf coastal system, NW Aegean Sea: an overview of water/sediment fluxes in relation to air-land-ocean interactions and human activities. *J. Mar. Syst.* 25, 47–76.
- Prato, G., Barrier, C., Francour, P., Cappanera, V., Markantonatou, V., Guidetti, P., Mangialajo, L., Cattaneo-Vietti, R., Gascuel, D., 2016. Assessing interacting impacts of artisanal and recreational fisheries in a small marine protected area (portofino, NW Mediterranean Sea). *Ecosphere* 7 (12). Article e01601.
- Ricard, D., Minto, C., Jensen, O.P., Baum, J.K., 2012. Examining the knowledge base and status of commercially exploited marine species with the RAM Legacy Stock Assessment Database. *Fish Fish.* 13, 380–398.
- Sánchez, F., Olaso, I., 2004. Effects of fisheries on the Cantabrian Sea shelf ecosystem. *Ecol. Model.* 172, 151–174.
- Saygu, I., Heymans, J.J., Fox, C.J., Özbilgin, H., Eryaşar, A.R., Gökçe, G., 2020. The importance of alien species to the food web and bottom trawl fisheries of the Northeastern Mediterranean, a modelling approach. *J. Mar. Syst.* 202, 103253.
- Schmitz, O.J., Beckerman, A.P., O'Brien, K.M., 1997. Behaviorally mediated trophic cascades: effects of predation risk on food web interactions. *Ecology* 78 (5), 1388–1399.
- Scott, E., Serpenti, N., Steenbeek, J., Heymans, J.J., 2016. A stepwise fitting procedure for automated fitting of Ecopath with Ecosim models. *Software* 5, 25–30.
- Smith, C.J., Marrs, S.J., Atkinson, R.J.A., Papadopoulou, K.N., Hills, J.M., 2003. Underwater television for fisheries-independent stock assessment of Nephrops norvegicus from the Aegean (eastern Mediterranean) Sea. *Mar. Ecol. Prog. Ser.* 256, 161–170.

- Steenbeek, J., Corrales, X., Platts, M., Coll, M., 2018. Ecosampler: a new approach to assessing parameter uncertainty in Ecopath with Ecosim. *Software* 7, 198–204.
- Stergiou, K.I., 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: resharpening Ockham's razor. *Fish. Res.* 55, 1–9.
- Stergiou, K., Karpouzi, V.S., 2002. Feeding habits and trophic levels of Mediterranean fish. *Rev. Fish Biol. Fish.* 11, 217–254.
- Stergiou, K.I., Moutopoulos, D.K., Tsikliras, A.C., 2007. In: Papaconstantinou, C., Zenetos, A., Vassilopoulou, V., Tserpes, G. (Eds.), *Spatial and Temporal Variability in Hellenic Marine Fisheries Landings in State of Hellenic Fisheries*. Hellenic Centre for Marine Research, pp. 141–150.
- Stergiou, K.I., Moutopoulos, D.K., Armenis, G., 2009. Perish legally and ecologically: the ineffectiveness of the minimum landing sizes in the Mediterranean Sea. *Fish. Manag. Ecol.* 16, 368–375.
- Stergiou, K.I., Somarakis, S., Triantafyllou, G., Tsiaras, K.P., Giannoulaki, M., Petihakis, G., Machias, A., Tsikliras, A.C., 2016. Trends in productivity and biomass yields in the Mediterranean Sea large marine ecosystem during climate change. *Environmental Development* 17, 57–74.
- Stergiou, K.I., Tsikliras, A.C., 2011. Fishing down, fishing through and fishing up: fundamental process versus technical details. *Mar. Ecol. Progr. Ser.* 441, 295–301.
- Subramanian, K.R., 2018. The crisis of consumption of natural resources. *International Journal of Recent Innovations in Academic Research* 2 (4), 8–19.
- Sylaios, G.K., Koutroumanidis, T., Tsikliras, A.C., 2010. Ranking and classification of fishing areas using fuzzy models and techniques. *Fish. Manag. Ecol.* 17, 240–253.
- Szalaj, D., Torres, M.A., Veiga-Malta, T., Angelico, M.M., Sobrinho-Goncalves, L., Chaves, C., Alcoforado, B., Garrido, S., Re, P., Cabral, H., Silva, A., 2021. Food-web dynamics in the Portuguese continental shelf ecosystem between 1986 and 2017: unravelling drivers of sardine decline. *Estuar. Coast Shelf Sci.* 251, 107259.
- Tsagarakis, K., Coll, M., Giannoulaki, M., Somarakis, S., Papaconstantinou, C., Machias, A., 2010. Food-web traits of the north Aegean Sea ecosystem (eastern Mediterranean) and comparison with other Mediterranean ecosystems. *Estuar. Coast Shelf Sci.* 88, 233–248.
- Tsagarakis, K., Paliallexis, A., Vassilopoulou, V., 2014. Mediterranean fishery discards: review of the existing knowledge. *ICES J. Mar. Sci.* 71, 1219–1234.
- Tsagarakis, K., Giannoulaki, M., Pyrrounaki, M.M., Machias, A., 2015. Species identification of small pelagic fish schools by means of hydroacoustics in the Eastern Mediterranean Sea. *Mediterr. Mar. Sci.* 16, 151–161.
- Tsikliras, A.C., Polymeros, K., 2014. Fish market prices drive overfishing of the 'big ones'. *Peer J* 2, e638.
- Tsikliras, A.C., Stergiou, K.I., 2007. In: Demersal-pelagic ratio in Greek fish landings (1964–2003). *Rapport du 38 Congres de la Commission Internationale pour l'Exploration Scientifique de la Mer Mediterranee*, p. 622.
- Tsikliras, A.C., Tsiros, V.Z., Stergiou, K.I., 2013. Assessing the state of Greek marine fisheries resources. *Fish. Manag. Ecol.* 20, 34–41.
- Tsikliras, A.C., Dinouli, A., Tsiros, V.Z., Tsalkou, E., 2015. The Mediterranean and Black Sea fisheries at risk from overexploitation. *PLoS One* 10 (3), e0121188.
- Tsikliras, A.C., Licandro, P., Pardalou, A., McQuinn, I.H., Gröger, J.P., Alheit, J., 2019. Synchronization of Mediterranean pelagic fish populations with the North Atlantic climate variability. *Deep-Sea Research II* 159, 143–151.
- Tsikliras, A.C., Dimarchopoulou, D., Pardalou, A., 2020. Artificial upward trends in Greek marine landings: a case of presentist bias in European fisheries. *Marine Policy* in press, 103886.
- Ulanowicz, R.E., 1986. *Growth and Development: Ecosystem Phenomenology*. Springer Verlag, New York, p. 203 (reprinted by iUniverse, 2000).
- US National Research Council, 1998. *Sustaining Marine Fisheries. A Report of the Committee on Ecosystem Management for Sustainable Fisheries*. Ocean Studies Board, Commission on Geosciences, Environment and Resources, National Research Council. National Academy Press, Washington, D.C, p. 167.
- Valavanis, V.D., Kapantagakis, A., Katara, I., Paliallexis, A., 2004. Critical regions: a GIS-based model of marine productivity hotspots. *Aquat. Sci.* 66, 139–148.
- Valls, A., Gascuel, D., Guénette, S., Francour, P., 2012. Modeling trophic interactions to assess the effects of a marine protected area: case study in the NW Mediterranean Sea. *Mar. Ecol. Progr. Ser.* 456, 201–214.
- Vieira, M.L.M., de Lima, C.L.A., de Souza, J.R.B., Feitosa, J.L.L., 2020. Effects of beach seine fishing on the biodiversity of seagrass fish assemblages. *Regional Studies in Marine Science* 40, 101527.
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. *Rev. Fish Biol. Fish.* 7, 139–172.
- Watling, L., Norse, E.A., 1998. Disturbance of the seabed by Mobile fishing gear: a comparison to forest clearcutting. *Conserv. Biol.* 12, 1180–1197.

SUPPLEMENT to “Ecosystem trophic structure and fishing effort simulations of a major fishing ground in the northeastern Mediterranean Sea (Thermaikos Gulf)”

by Dimarchopoulou D, Tsagarakis K, Sylaios G, Tsikliras AC

Table A1 Input data and data sources of the Thermaikos Gulf Ecopath model.

FG / Basic input parameter	Value	Source	Notes
1. Phytoplankton			
Bi	0.46 mg Chla m ⁻³	SeaWiFS Project	Average for years 2002-4 (the oldest of the time series)
P/B	117.3 y ⁻¹	Tsagarakis et al. 2010	
2. Zooplankton			
Bi	6.1 t/km ²	Tsagarakis et al. 2010	modified due to increased phytoplankton biomass and ecosystem temperature
P/B	62.47 y ⁻¹		
Q/B	186.4 y ⁻¹		
Diet			
3. Benthic small crustaceans			Amphipods, isopods, cumaceans etc, including suprabenthos
Bi	1.11 t/km ²	Tsagarakis et al. 2010	modified due to increased ecosystem temperature
P/B	7.686 y ⁻¹		
Q/B	57.12 y ⁻¹		
Diet			
4. Polychaetes			
Bi	4.808 t/km ²	Zarkanellas & Kattoulas 1982	
P/B	1.712 y ⁻¹	Tsagarakis et al. 2010	modified due to increased ecosystem temperature
Q/B	13.08 y ⁻¹		
Diet			
5. Shrimps			<i>Melicertus kerathurus, Parapenaeus longirostris</i>
Bi	0.306 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	3.339 y ⁻¹	Tsagarakis et al. 2010	modified due to increased ecosystem temperature
Q/B	7.896 y ⁻¹		
Diet			
6. Crabs			<i>Carcinus aestuarii, Hommarus gammarus, Liocarcinus depurator, Nephrops norvegicus, Squilla mantis</i>
Bi	0.412 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	2.541 y ⁻¹	Tsagarakis et al. 2010	modified due to increased ecosystem temperature
Q/B	5.187 y ⁻¹		
Diet			

FG / Basic input parameter	Value	Source	Notes
7. Benthic invertebrates			Echinodermata, mollusca, sipuncula etc, excluding decapoda
Bi	8.710 t/km ²	Tsagarakis et al. 2010	modified due to increased ecosystem temperature
P/B	1.208 y ⁻¹		
Q/B	3.334 y ⁻¹		
Diet			
8. Octopuses and cuttlefish			<i>Eledone cirrhosa</i> , <i>Eledone moschata</i> , <i>Octopus vulgaris</i> , <i>Rondeletia minor</i> , <i>Sepia elegans</i> , <i>Sepia officinalis</i> , <i>Sepia orbignyana</i> , <i>Sepietta</i> spp., <i>Sepiola</i> spp.
Bi	0.247 t/km ²	Tsagarakis et al. 2010	Biomass estimates from trawling surveys in Thermaikos Gulf (1998-2000) modified due to increased ecosystem temperature
P/B	2.900 y ⁻¹		
Q/B	5.807 y ⁻¹		
Diet			
9. Squids			<i>Alloteuthis media</i> , <i>Illex coindetii</i> , Loliginidae, <i>Loligo</i> sp., Ommastrephidae
Bi	0.363 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	2.600 y ⁻¹	Tsagarakis et al. 2010	
Q/B	26.47 y ⁻¹		
Diet			
10. Red mullets			<i>Mullus barbatus</i> , <i>M. surmuletus</i>
Bi	0.196 t/km ²	Anonymous 2000	Biomass estimates from trawling surveys in Thermaikos Gulf (1998-2000)
P/B	1.908 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	7.192 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
11. Anglerfish			<i>Lophius budegassa</i> , <i>L. piscatorius</i>
Bi	0.203 t/km ²	Anonymous 2000	Biomass estimates from trawling surveys in Thermaikos Gulf (1998-2000)
P/B	1.100 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	3.777 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
12. Flatfishes			<i>Arnoglossus laterna</i> , <i>Arnoglossus thori</i> , <i>Citharus linguatula</i> , <i>Scophthalmus maximus</i> , <i>Solea solea</i> , <i>Symphurus nigrescens</i>

FG / Basic input parameter	Value	Source	Notes
Bi	0.107 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	1.820 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	8.741 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
13. Other gadiforms			<i>Gaidropsarus mediterraneus, Merlangius merlangus, Micromesistius poutassou, Phycis blennoides, Trisopterus capelanus</i>
Bi	0.580 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	1.450 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	6.493 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
14. Hake			<i>Merluccius merluccius</i>
Bi	0.400 t/km ²	Anonymous 2000	Biomass estimates from trawling surveys in Thermaikos Gulf (1998-2000)
P/B	0.587 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	3.700 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
15. Demersal fishes 1			<i>Callionymus lyra, C. maculatus, C. risso, Callionymus spp., Diplodus vulgaris, Gobius niger, Oblada melanura, Zosterisessor ophiocephalus</i>
Bi	0.150 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	2.400 y ⁻¹	Coll et al. 2009	
Q/B	9.306 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
16. Demersal fishes 2			<i>Chelidonichthys cuculus, C. lastoviza, C. lucerna, Deltentosteus quadrimaculatus, Dicentrarchus labrax, Eutrigla gurnardus, Helicolenus dactylopterus, Pagrus pagrus, Scorpaena notata, S. porcus, Serranus hepatus, Syngnathus acus, Umbrina cirrosa</i>
Bi	0.246 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	1.600 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	

FG / Basic input parameter	Value	Source	Notes
Q/B	7.739 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
17. Demersal fishes 3			<i>Blennius ocellaris, Conger conger, Coris julis, Dentex dentex, D. macrophthalmus, Diplodus sargus sargus, Lithognathus mormyrus, Pagellus acarne, P. bogaraveo, P. erythrinus, Polyprion americanus, Sarpa salpa, Scorpaena scrofa, Serranus cabrilla, S. scribe, Sparus aurata, Symphodus tinctus, Trachinus draco, Uranoscopus scaber, Zeus faber</i>
Bi	0.322 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	1.400 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	4.592 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
18. Demersal fishes 4			<i>Argentina sphyraena, Capros aper, Cepola macrophthalma, Dentex maroccanus, Diplodus annularis, Gobius auratus, Lepidotrigla cavillone, Lesueurigobius friesii, L. suerii, Macroramphosus scolopax, Spondylisoma cantharus, Trigla lyra</i>
Bi	0.237 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	1.900 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	11.100 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
19. Picarels and bogue			<i>Boops boops, Spicara flexuosa, S. maena, S. smarís</i>
Bi	0.663 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	1.500 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	8.339 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
20. Sharks			<i>Mustelus spp., Scyliorhinus canicula, Squalidae</i>
Bi	0.071 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	0.698 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	4.080 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	

FG / Basic input parameter	Value	Source	Notes
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
21. Rays and skates			<i>Leucoraja naevus, Raja clavata, R. radula, Rhinobatidae, Torpedo marmorata</i>
Bi	0.141 t/km ²	Anonymous 2000; Moutopoulos & Stergiou 2012	Biomass estimates from trawling surveys in Thermaikos Gulf and reconstructed fisheries landings (1998-2000)
P/B	1.000 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	3.394 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
22. Anchovy			<i>Engraulis encrasicolus</i>
Bi	2.250 t/km ²	Tsagarakis et al. 2015	Biomass estimates from acoustic surveys in N. Aegean Sea (2005-2008)
P/B	1.753 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	6.693 yr ⁻¹	Tsagarakis et al. 2010	modified due to increased ecosystem temperature
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
23. Sardine			<i>Sardina pilchardus</i>
Bi	1.950 t/km ²	Tsagarakis et al. 2015	Biomass estimates from acoustic surveys in N. Aegean Sea (2005-2008)
P/B	1.778 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	11.670 yr ⁻¹	Tsagarakis et al. 2010	modified due to increased ecosystem temperature
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
24. Horse mackerels			<i>Trachurus mediterraneus, T. trachurus</i>
Bi	0.732 t/km ²	Anonymous 2000	Biomass estimates from trawling surveys in Thermaikos Gulf (1998-2000)
P/B	1.000 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	7.315 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
25. Mackerels			<i>Scomber colias, S. scombrus</i>
Bi	0.294 t/km ²	Anonymous 2000	Biomass estimates from trawling surveys in Thermaikos Gulf (1998-2000)
P/B	1.022 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	6.448 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
26. Other small pelagics			<i>Belone belone, Mugilidae, Sardinella aurita</i>

FG / Basic input parameter	Value	Source	Notes
Bi	1.170 t/km ²	Tsagarakis et al. 2010; Moutopoulos & Stergiou 2012	Adjusted based also on reconstructed fisheries landings (1998-2000)
P/B	1.400 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	6.365 yr ⁻¹	Empirical equation FishBase (Froese & Pauly 2019)	
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
27. Medium pelagics			<i>Auxis thazard, Pomatomus saltatrix, Sarda sarda, Seriola dumerili</i>
Bi	0.250 t/km ²	Tsagarakis et al. 2010	
P/B	0.425 yr ⁻¹	Z=F+M; M=Empirical equation (Pauly, 1980)	
Q/B	3.706 yr ⁻¹	Tsagarakis et al. 2010	Adjusted based on FG species composition
Diet		Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010	
28. Large pelagics			<i>Thunnus spp., Xiphias gladius</i>
Bi	0.049 t/km ²	Tsagarakis et al. 2010	
P/B	0.400 yr ⁻¹		
Q/B	2.529 yr ⁻¹		
Diet			Stergiou & Karpouzi 2002; Karachle & Stergiou 2017 (and references therein); Tsagarakis et al. 2010
29. Loggerhead turtle			<i>Caretta caretta</i>
Bi	0.020 t/km ²	Tsagarakis et al. 2010	
P/B	0.160 yr ⁻¹		
Q/B	2.680 yr ⁻¹		
Diet			
30. Seabirds			<i>Calonectris diomedea, Hydrobates pelagicus, Larus audouinii, L. cachinnans, L. melanocephalus, Phalacrocorax aristotelis, Puffinus yelkouan</i>
Bi	0.001 t/km ²	Tsagarakis et al. 2010	
P/B	4.780 yr ⁻¹		
Q/B	111.61 yr ⁻¹		
Diet			
31. Dolphins			<i>Delphinus delphis, Phocoena phocoena, Stenella coeruleoalba, Tursiops truncatus</i>
Bi	0.015 - 0.03 t/km ²	Tsagarakis et al. 2010	
P/B	0.080 yr ⁻¹		
Q/B	13.81 yr ⁻¹		
Diet		Tsagarakis et al. 2010; Milani et al. 2017	
32. Detritus			
Bi	31.44 t/km ²	Tsagarakis et al. 2010	

References used in Table A1

- Anonymous 2000. National Program for the Collection of Fisheries Data (1998-2000). Technical Report (EC 1543/2000). Fisheries Research Institute and Hellenic Center for Marine Research, Athens, Greece.
- Coll M, Santojanni A, Palomera I, Arneri E (2009) Food-web changes in the Adriatic Sea over the last three decades. *Marine Ecology Progress Series* 381: 17-37.
- Froese R, Pauly D. Editors. (2019) FishBase. World Wide Web electronic publication. www.fishbase.org, version (02/2019).
- Karachle PK, Stergiou KI (2017) An update on the feeding habits of fish in the Mediterranean Sea (2002-2015). *Mediterranean Marine Science* 18(1): 43-52.
- Milani CB, Vella A, Vidoris P, Christidis A, Koutrakis E, Frantzis A, Miliou A, Kallianiotis A (2017) Cetacean stranding and diet analyses in the North Aegean Sea (Greece). *Journal of the Marine Biological Association of the United Kingdom* 98(5): 1011-1028.
- Moutopoulos D, Stergiou K (2012) Spatial disentangling of Greek commercial fisheries landings by gear between 1928-2007. *Journal of Biological Research-Thessaloniki* 18: 265-279.
- Pauly D (1980) On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal du Conseil / Conseil Permanent International pour l'Exploration de la Mer* 39(2): 175-192.
- SeaWiFS Project (2003) SeaWiFS Global Monthly Mapped 9 km Chlorophyll a. Ver. 1. PO. DAAC, CA, USA. Dataset accessed 02/2018.
- Stergiou KI, Karpouzi VS (2002) Feeding habits and trophic levels of Mediterranean fish. *Reviews in Fish Biology and Fisheries* 11: 217-254.
- Tsagarakis K, Coll M, Giannoulaki M, Somarakis S, Papaconstantinou C, Machias A (2010) Food-web traits of the North Aegean Sea ecosystem (Eastern Mediterranean) and comparison with other Mediterranean ecosystems. *Estuarine, Coastal and Shelf Science* 88: 233-248.
- Tsagarakis K, Giannoulaki M, Pyrounaki MM, Machias A (2015) Species identification of small pelagic fish schools by means of hydroacoustics in the Eastern Mediterranean Sea. *Mediterranean Marine Science* 16: 151-161.
- Zarkanellas AJ, Kattoulas ME (1982) The ecology of benthos in the Gulf of Thermaikos, Greece I. Environmental conditions and benthic biotic indices. *Marine Ecology* 3(1): 21-39.

Table A2 Codes and scientific names of species used in the cluster analysis of diet compositions (Fig. 2).

Code	Scientific name	Code	Scientific name
CALLRIS	<i>Callionymus risso</i>	PAGEERY	<i>Pagellus erythrinus</i>
CAPOAPE	<i>Capros aper</i>	PAGRPAG	<i>Pagrus pagrus</i>
CEPOMAC	<i>Cepola macrophthalma</i>	SARPSAL	<i>Sarpa salpa</i>
CHELCUC	<i>Chelidonichthys cuculus</i>	SCORNOT	<i>Scorpaena notata</i>
CHELLUC	<i>Chelidonichthys lucerna</i>	SCORPOR	<i>Scorpaena porcus</i>
CONGCON	<i>Conger conger</i>	SCORSCR	<i>Scorpaena scrofa</i>
CORIJUL	<i>Coris julis</i>	SERACAB	<i>Serranus cabrilla</i>
DELTQUA	<i>Deltentosteus quadrimaculatus</i>	SERAHEP	<i>Serranus hepatus</i>
DIPLANN	<i>Diplodus annularis</i>	SERASCR	<i>Serranus scriba</i>
DIPLSAR	<i>Diplodus sargus</i>	SPARAUR	<i>Sparus aurata</i>
DIPLVUL	<i>Diplodus vulgaris</i>	SPODCAN	<i>Spondyliosoma cantharus</i>
EUTRGUR	<i>Eutrigla gurnardus</i>	SYMPTIN	<i>Symphodus tinca</i>
GOBIAUR	<i>Gobius auratus</i>	SYNGACU	<i>Syngnathus acus</i>
GOBINIG	<i>Gobius niger</i>	TRAHDRA	<i>Trachinus draco</i>
LEPICAV	<i>Lepidotrigla cavillone</i>	TRIGLYR	<i>Trigla lyra</i>
LESUSUE	<i>Lesueurigobius suerii</i>	TRIGLAS	<i>Trigloporus lastoviza</i>
LITHMOR	<i>Lithognathus mormyrus</i>	UMBRCIR	<i>Umbrina cirrosa</i>
OBLAMEL	<i>Oblada melanura</i>	URANSCA	<i>Uranoscopus scaber</i>
PAGEACA	<i>Pagellus acarne</i>	ZEUSFAB	<i>Zeus faber</i>
PAGEBOG	<i>Pagellus bogaraveo</i>	ZOSTOPH	<i>Zosterisessor ophiocephalus</i>

Table A3 Diet composition matrix of the Thermaikos Gulf Ecopath model. Grey cells indicate values <0.01.

	Prey \ predator	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	
1	Phytoplankton	0.6	0.02													0.02							0.131			0.01						
2	Zooplankton	0.2	0.097		0.103			0.09	0.175	0.14	0.018	0.161	0.3	0.137	0.107	0.15	0.152	0.773	0.9	0.142	0.035	1	0.849	0.767	0.6	0.867	0.05	0.05	0.05			
3	Benthic small crustaceans		0.03		0.23	0.06		0.14	0.128	0.184	0.03	0.121	0.305	0.063	0.131	0.2	0.078	0.1	0.05				0.02	0.03	0.04	0.103	0.02					
4	Polychaetes		0.02	0.03	0.2	0.41	0.02	0.06	0.075	0.132	0.06	0.022			0.661	0.12	0.095	0.019	0.045	0.05	0.1			0.047								
5	Shrimps				0.03	0.02		0.01		0.04	0.02	0.012	0.01	0.073	0.018	0.05	0.084	0.045		0.01	0.1				0.01			0.03				
6	Crabs				0.026	0.025		0.05	0.013	0.08		0.012	0.032			0.09	0.038	0.036		0.1	0.1									0.138		
7	Benthic invertebrates		0.03	0.06	0.28	0.31	0.03	0.53	0.02	0.024	0.1	0.04		0.02	0.083	0.02	0.145	0.027		0.2	0.035			0.05	0.084		0.093	0.299				
8	Octopuses and cuttlefish				0.02			0.05	0.035		0.1	0.04		0.04		0.015	0.048			0.08	0.012			0.01				0.01		0.017		
9	Squids								0.045					0.115						0.068				0.035			0.055	0.13	0.01	0.122		
10	Red mullets										0.02		0.031			0.04					0.055											
11	Anglerfish										0.02									0.02												
12	Flatfishes										0.02	0.01		0.012						0.054												
13	Other gadiforms								0.022		0.1	0.12		0.03		0.08	0.022			0.048	0.04						0.066					
14	Hake										0.036			0.04						0.046	0.026					0.01				0.035		
15	Demersal fishes 1											0.08	0.03	0.02		0.015				0.043	0.08									0.107		
16	Demersal fishes 2						0.02				0.05	0.04		0.02			0.05				0.03							0.02		0.135		
17	Demersal fishes 3						0.04					0.12	0.01	0.04							0.03									0.136		
18	Demersal fishes 4										0.036	0.07	0.015	0.04		0.03	0.01			0.028	0.06			0.004								
19	Picarels and bogue						0.01	0.023		0.08			0.032	0.03		0.075	0.055				0.01			0.03			0.03	0.05		0.189		
20	Sharks																															
21	Rays and skates										0.05									0.015												
22	Anchovy								0.156		0.03	0.04	0.184	0.16			0.114			0.018	0.195			0.1		0.294	0.35	0.01	0.04	0.019		
23	Sardine								0.163		0.05		0.01	0.11		0.03	0.05			0.02	0.05			0.13		0.295	0.1	0.05	0.05	0.03		
24	Horse mackerels								0.03		0.13	0.069								0.048	0.01					0.05	0.04	0.05	0.043			
25	Mackerels										0.05	0.02				0.03	0.05									0.02	0.04					
26	Other small pelagics								0.09					0.05		0.03								0.02		0.09	0.062		0.04	0.16		
27	Medium pelagics																															
28	Large pelagics																															
29	Loggerhead turtle																															
30	Seabirds																															
31	Dolphins																															
32	Discards				0.015	0.01							0.013							0.01	0.01								0.32	0.26		
33	Detritus	0.2	0.8	0.81	0.09	0.15	0.9			0.4																0.01						
	Import			0.1			0.05																							0.61		
	Sum	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Table A4 Index values (IV) and confidence intervals (CI \pm %) used to describe the uncertainty range for each input parameter and functional group (FG) of the Thermaikos Gulf Ecopath model.

	FG	Biomass		P/B		Q/B		Diet		Catches	
		IV	CI	IV	CI	IV	CI	IV	CI	IV	CI
1	Phytoplankton	0.4	50	0.2	60	0.2	60				
2	Zooplankton	0	80	0.2	60	0.2	60	0	80		
3	Benthic small crustaceans	0	80	0.2	60	0.2	60	0	80		
4	Polychaetes	1	10	0.2	60	0.2	60	0	80		
5	Shrimps	1	10	0.2	60	0.2	60	0	80	0.5	50
6	Crabs	1	10	0.2	60	0.2	60	0	80	0.5	50
7	Benthic invertebrates	0	80	0.2	60	0.2	60	0	80		
8	Octopuses and cuttlefish	1	10	0.2	60	0.2	60	0	80	0.5	50
9	Squids	1	10	0.2	60	0.2	60	0	80	0.5	50
10	Red mullets	1	10	0.5	50	0.5	50	1	10	0.5	50
11	Anglerfish	1	10	0.5	50	0.5	50	1	10	0.5	50
12	Flatfishes	1	10	0.5	50	0.5	50	1	10	0.5	50
13	Other gadiforms	1	10	0.5	50	0.5	50	1	10	0.5	50
14	Hake	1	10	0.5	50	0.5	50	1	10	0.5	50
15	Demersal fishes 1	0.7	30	0.5	50	0.5	50	0.7	30	0.5	50
16	Demersal fishes 2	0.7	30	0.5	50	0.5	50	1	10	0.5	50
17	Demersal fishes 3	0.7	30	0.5	50	0.5	50	1	10	0.5	50
18	Demersal fishes 4	0.7	30	0.5	50	0.5	50	1	10	0.5	50
19	Picarels and bogue	1	10	0.5	50	0.5	50	1	10	0.5	50
20	Sharks	0.7	30	0.5	50	0.5	50	1	10	0.5	50
21	Rays and skates	1	10	0.5	50	0.5	50	1	10	0.5	50
22	Anchovy	1	10	0.5	50	0.2	60	1	10	0.5	50
23	Sardine	1	10	0.5	50	0.2	60	1	10	0.5	50
24	Horse mackerels	0.7	30	0.5	50	0.5	50	1	10	0.5	50
25	Mackerels	0.7	30	0.5	50	0.5	50	1	10	0.5	50
26	Other small pelagics	0	80	0.5	50	0.5	50	0.7	30	0.5	50
27	Medium pelagics	0	80	0.5	50	0.5	50	0.7	30		
28	Large pelagics	0	80	0.2	60	0.5	50	1	10	0.5	50
29	Loggerhead turtle	0	80	0.2	60	0.2	60	0	80		
30	Seabirds	0	80	0.2	60	0.2	60	0	80		
31	Dolphins	0	80	0.2	60	0.2	60	1	10		
32	Discards	0	80								
33	Detritus	0	80								

Table A5 The 20 trophic interactions that are most sensitive to changes in the vulnerability parameter of the Thermaikos Gulf model. L: low value, Vulnerabilities close to 1. H: High value, Vulnerabilities >> 1. All the remaining interactions have a default vulnerability value of 2.

Prey	Predator												
	Zooplankton	Polychaetes	Shrimps	Octopuses & cuttlefish	Squids	Anglerfish	Flatfishes	Demersal fishes 4	Anchovy	Horse mackerels	Other small pelagics	Medium pelagics	Large pelagics
Phytoplankton	H												
Zooplankton	H							L	L	L	L		
Polychaetes													
Benthic invertebrates		L	L	L									
Octopuses & cuttlefish					L								
Squids					H								
Demersal fishes 1							H						
Sharks					L								
Horse mackerels					H	H							
Other small pelagics					L								
Anchovy												H	H
Sardine												H	
Detritus		L											

Table A6 The variables that were varied with the Monte Carlo approach. Mean values are the initial baseline values as entered in the Ecopath model. The coefficients of variation (CV) define the sample range (mean \pm 2*CV) for each variable that Monte Carlo is able to perturb using normal distributions in order to find alternate mass-balanced models. Empty cells are values not applicable.

	Functional group	Biomass		P/B		Q/B	
		CV	Mean	CV	Mean	CV	Mean
1	Phytoplankton	0.25	7.866	0.3	117.3		
2	Zooplankton	0.4	6.1	0.3	62.47	0.3	186.38
3	Benthic small crustaceans	0.4	1.11	0.3	7.686	0.3	57.12
4	Polychaetes	0	4.808	0.3	1.712	0.3	13.083
5	Shrimps	0	0.306	0.3	3.339	0.3	7.896
6	Crabs	0	0.412	0.3	2.541	0.3	5.187
7	Benthic invertebrates	0.4	8.71	0.3	1.215	0.3	3.434
8	Octopuses and cuttlefish	0	0.392	0.3	2.9	0.3	5.807
9	Squids	0.05	0.363	0.3	2.6	0.3	26.47
10	Red mullets	0	0.196	0	1.908	0	7.192
11	Anglerfish	0	0.203	0	1.1	0	3.777
12	Flatfishes	0	0.107	0	1.82	0	8.741
13	Other gadiforms	0.05	0.58	0.25	1.45	0.25	6.493
14	Hake	0	0.4	0	0.587	0	3.7
15	Demersal fishes 1	0.15	0.15	0	2.4	0	9.306
16	Demersal fishes 2	0.15	0.246	0	1.6	0	7.739
17	Demersal fishes 3	0.15	0.322	0	1.4	0	4.592
18	Demersal fishes 4	0.15	0.237	0	1.9	0	11.105
19	Picarels and bogue	0	0.663	0	1.5	0	8.339
20	Sharks	0.15	0.071	0	0.698	0	4.08
21	Rays and skates	0	0.141	0	1	0	3.394
22	Anchovy	0	2.25	0	1.753	0.3	6.693
23	Sardine	0	1.95	0	1.778	0.3	11.668
24	Horse mackerels	0.15	0.732	0	1	0	7.315
25	Mackerels	0.15	0.294	0	1.022	0	6.448
26	Other small pelagics	0.4	1.17	0	1.4	0	6.365
27	Medium pelagics	0.4	0.25	0	0.425	0	3.706
28	Large pelagics	0.4	0.049	0.3	0.4	0	2.529
29	Loggerhead turtle	0.4	0.02	0.3	0.16	0.3	2.68
30	Seabirds	0.4	0.001	0.3	4.78	0.3	111.61
31	Dolphins	0.4	0.02	0.3	0.08	0.3	13.81

Equations

$$P_i = Y_i + B_i * M2_i + E_i + BA_i + M0_i * B_i \quad (\text{Eq. A1})$$

where P_i is the production of functional group i , Y_i is the total fishery catch rate of i , $M2_i$ is the instantaneous predation rate for group i , E_i the net migration rate (emigration – immigration), BA_i is the biomass accumulation rate for i , while $M0_i$ is the ‘other mortality’ rate for i [$M0_i = P_i * (1 - EE_i) / B_i$] (Christensen & Walters 2004).

$$Q_i = P_i + R_i + UN_i \quad (\text{Eq. A2})$$

where Q_i is the consumption of functional group i , R is respiration of i , and UN is the unassimilated food (Christensen & Walters 2004).

$$OI_i = \sum_{j=1}^n \left(TL_j - (TL_i - 1) \right)^2 * DC_{ij} \quad (\text{Eq. A3})$$

where OI_i is the omnivory index, TL_j is the trophic level of prey j , TL_i is the trophic level of the predator i , and DC_{ij} is the proportion prey j constitutes to the diet of predator i (Christensen et al. 2005).

$$q_{ij} = d_{ji} - f_{ij} \quad (\text{Eq. A4})$$

where q_{ij} is the net impact of functional group i on j , d_{ji} is the fraction of the prey i in the diet of the predator j , and f_{ij} is the fraction of total consumption of i used by predator j . “The mixed trophic impact m_{ij} is then estimated by the product of all the net impacts q_{ij} for all the possible pathways in the trophic web that link the functional groups i and j ” (Libralato et al. 2006a).

$$KS_i = \log [\varepsilon_i (1 - p_i)], \quad \varepsilon_i = \sqrt{\sum_{j \neq i}^n m_{ij}^2}, \quad p_i = \frac{B_i}{\sum_k B_k} \quad (\text{Eq. A5})$$

where KS_i is the keystone index of functional group i , ε_i is the overall effect of each functional group, and p_i is the contribution of the functional group i to the total biomass of the food web (Libralato et al. 2006a).

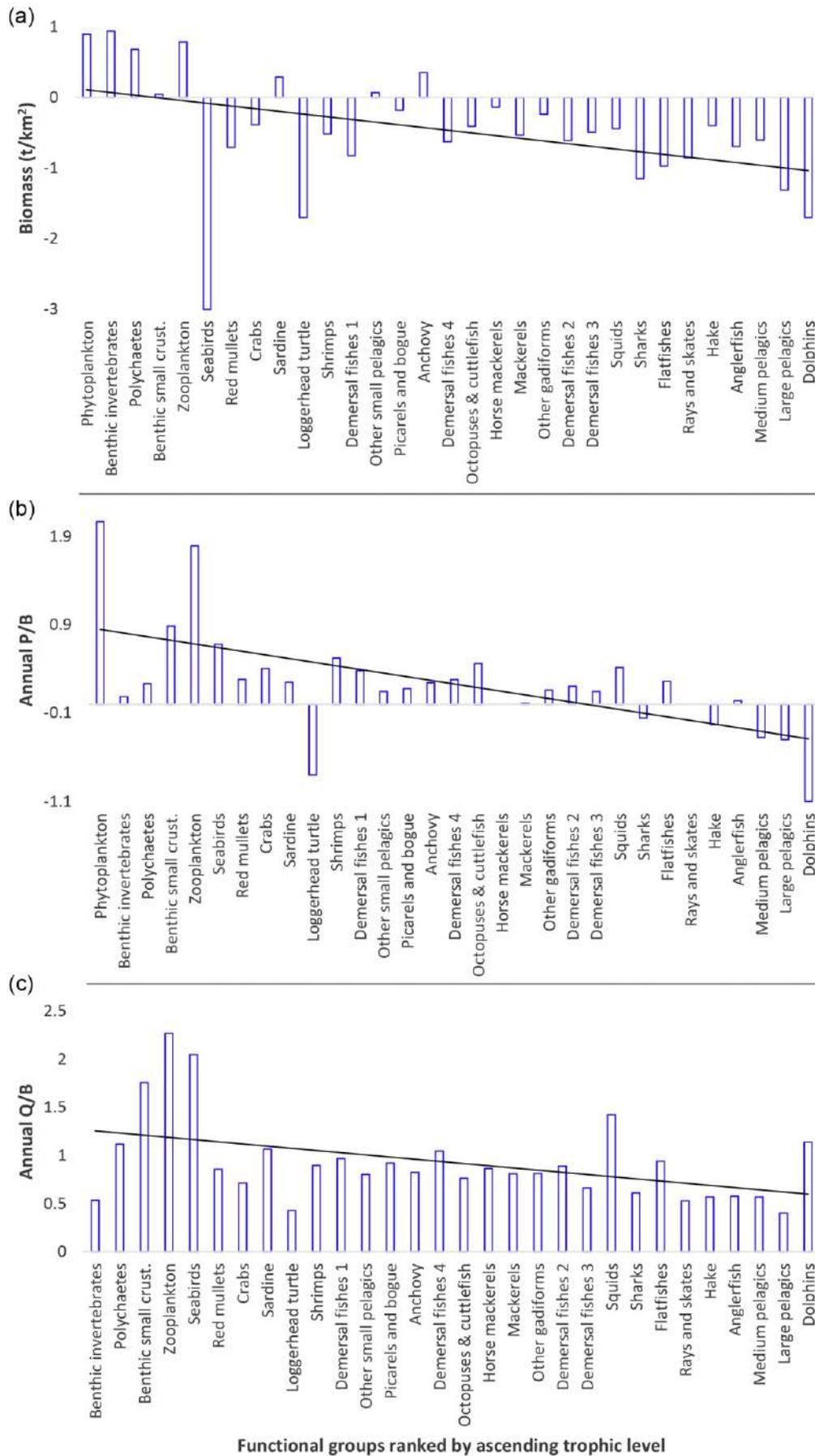


Figure A1 PREBAL of the Thermaikos Gulf model plotting (a) biomass estimates (t/km²), (b) production/biomass ratio (year⁻¹), and (c) consumption/biomass (year⁻¹) on a log scale vs functional groups ranked by trophic level (low to high). Trophic decomposition (trend line) is depicted, demonstrating different declining levels of the studied parameters with increasing trophic level, that can be used in a diagnostic sense (for more see Link 2010 and Heymans et al. 2016).

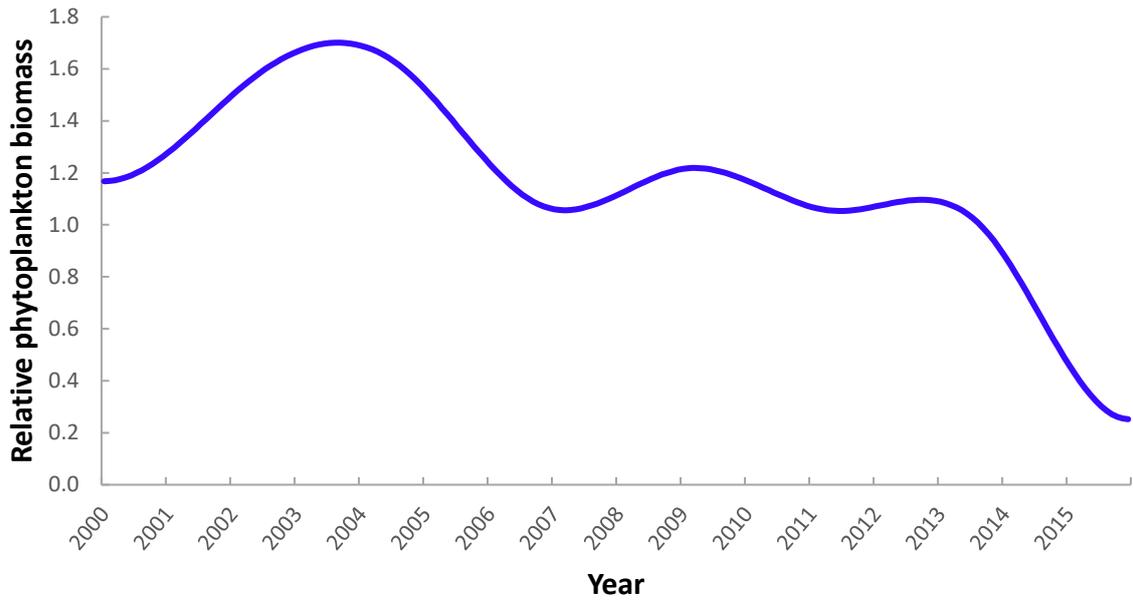


Figure A2 Monthly primary production anomaly resulting from the fitting procedure that expresses the relative phytoplankton biomass estimated for the period 2000-2015 (the year label refers to January).

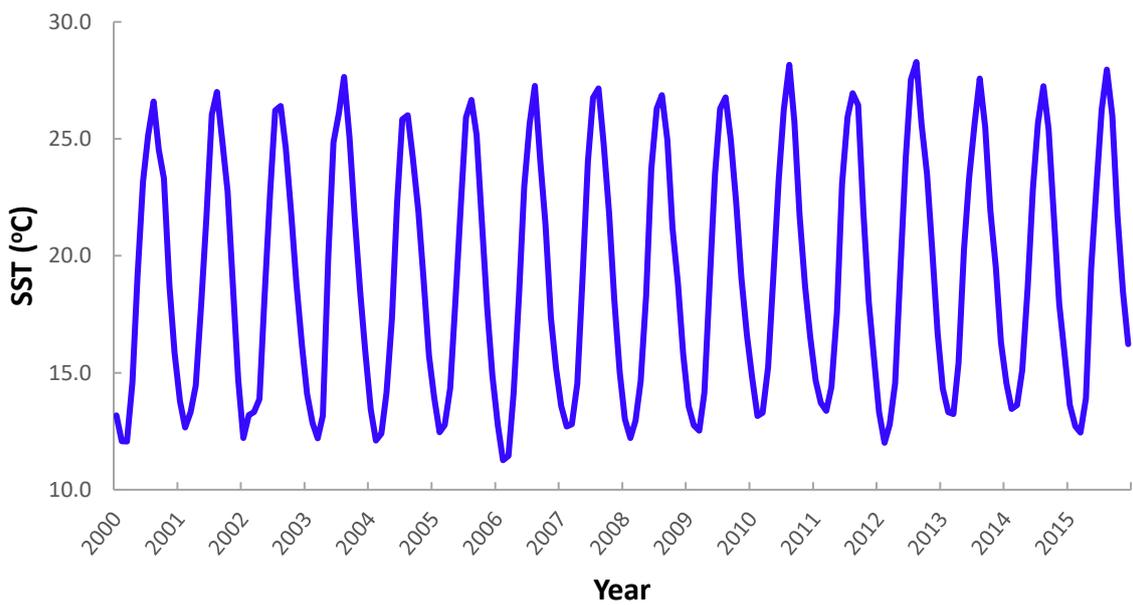


Figure A3 Monthly sea surface temperature (SST) values for the period 2000-2015 (spatially-averaged over the Thermaikos Gulf) that were derived from the Copernicus Marine Environmental Service (CMEMS: MEDSEA_REANALYSIS_PHYS_006_004) and were used to force the biomass of anchovy, sardine, and horse mackerels during the fitting procedure (the year label refers to January).

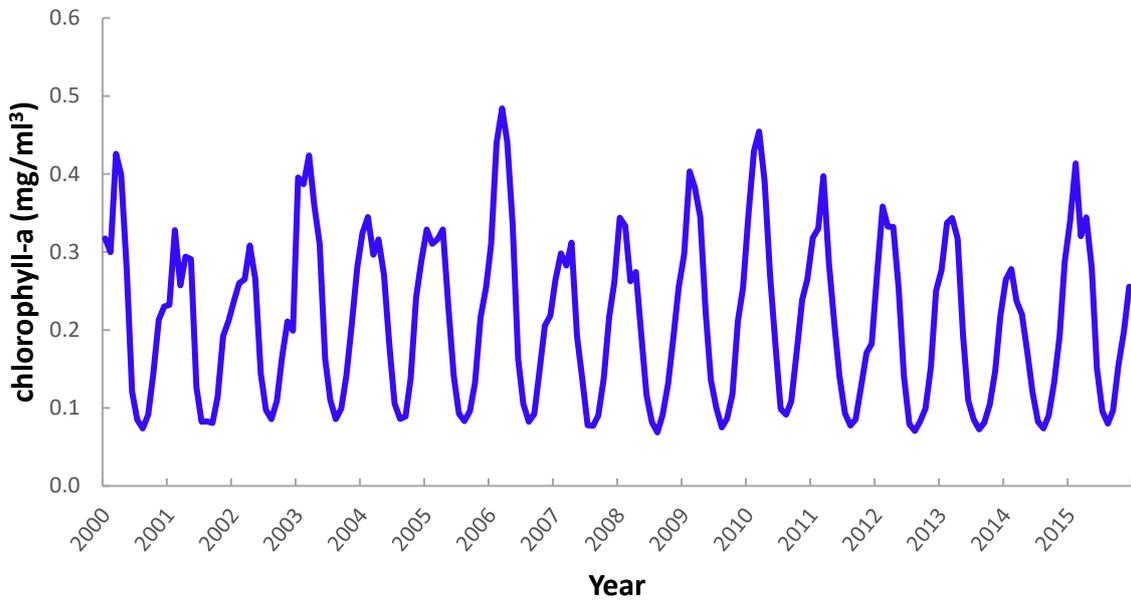
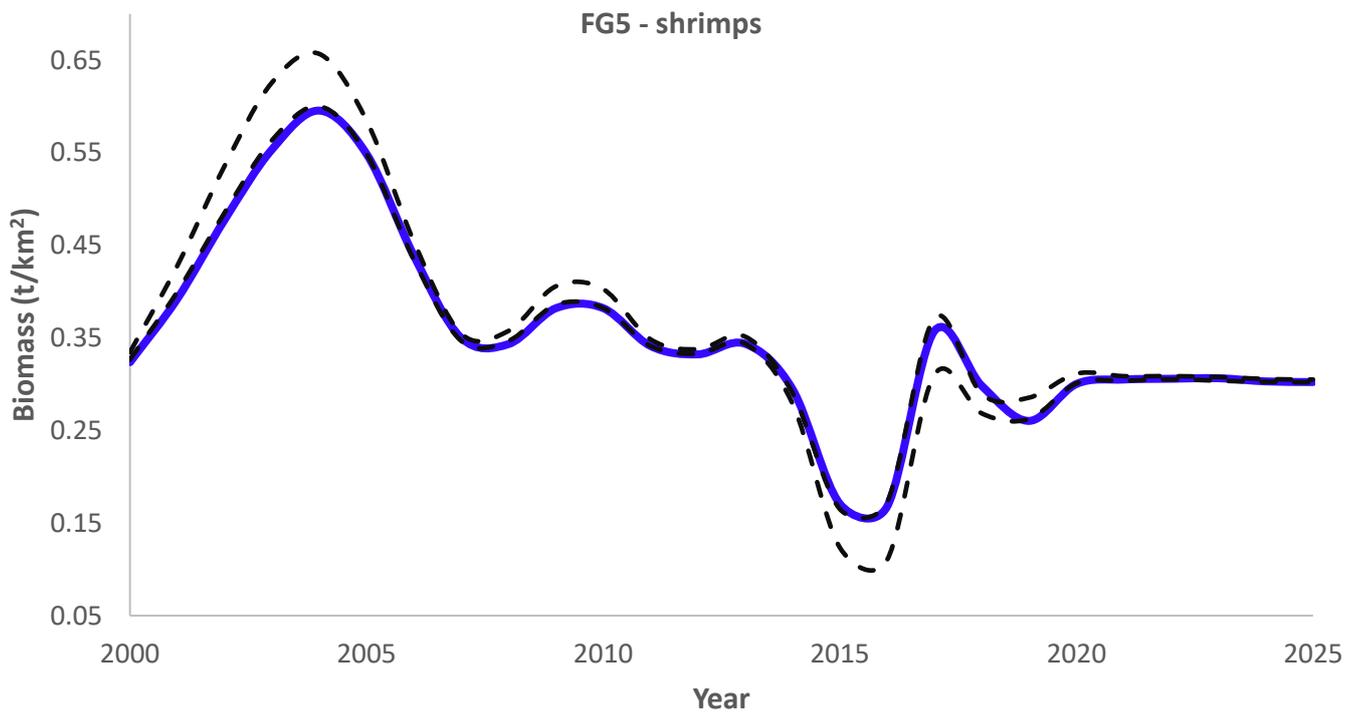
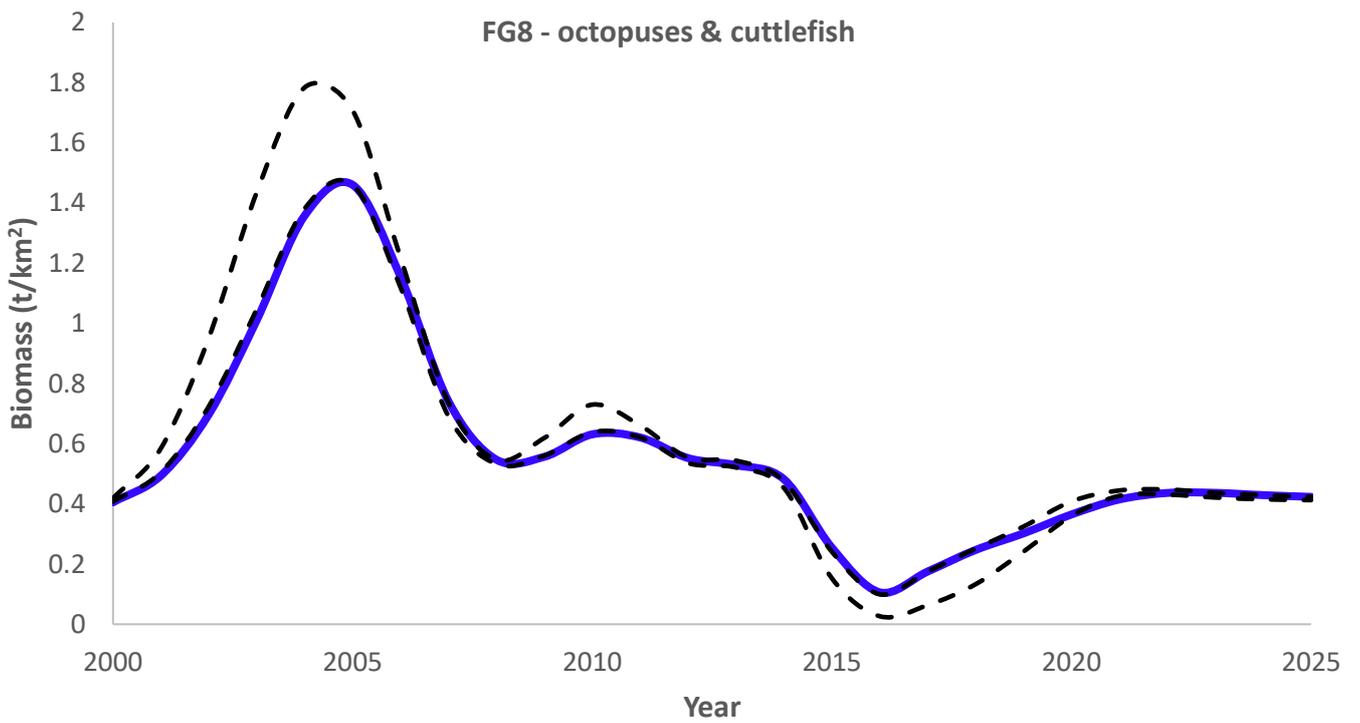
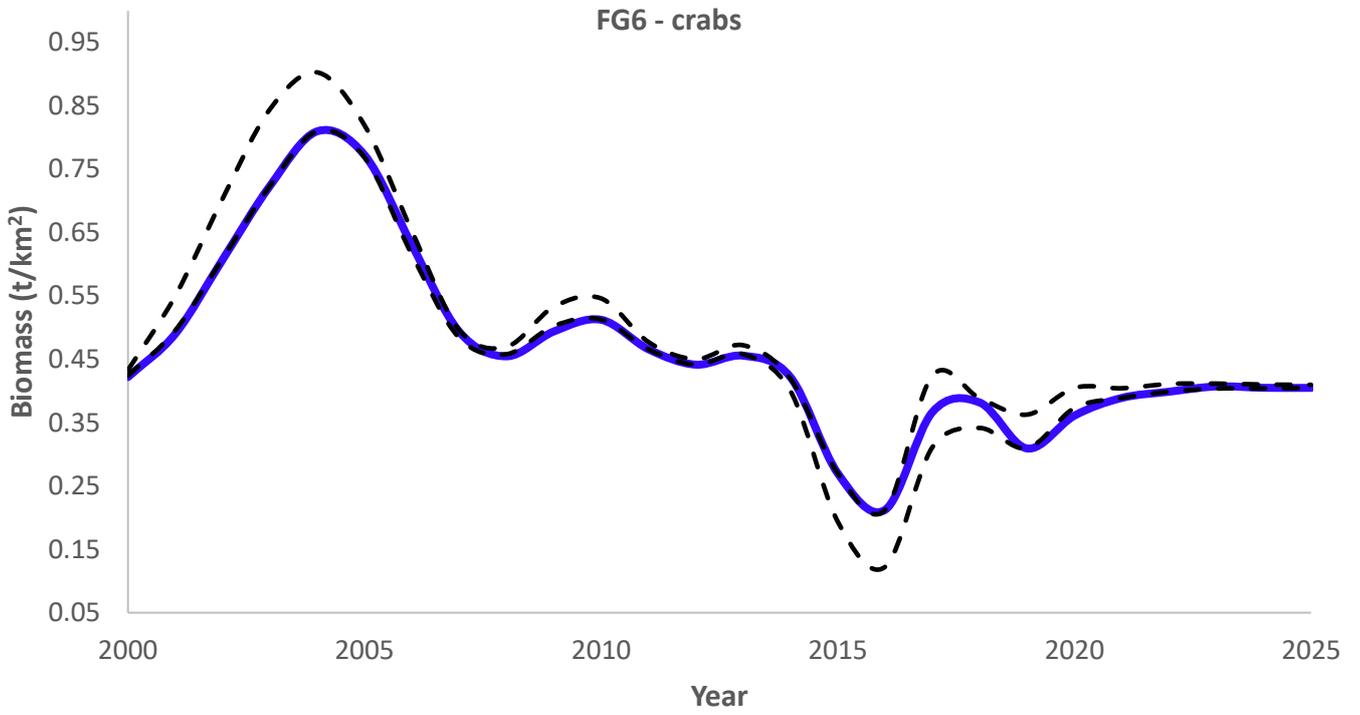
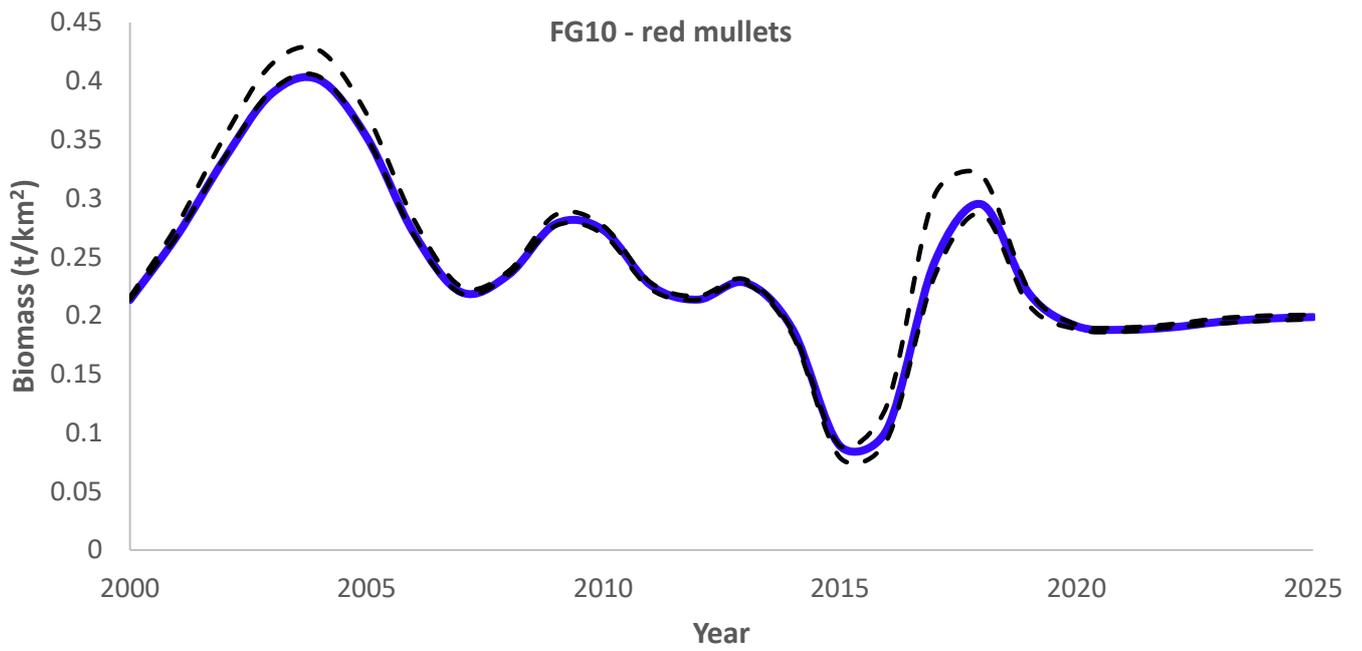
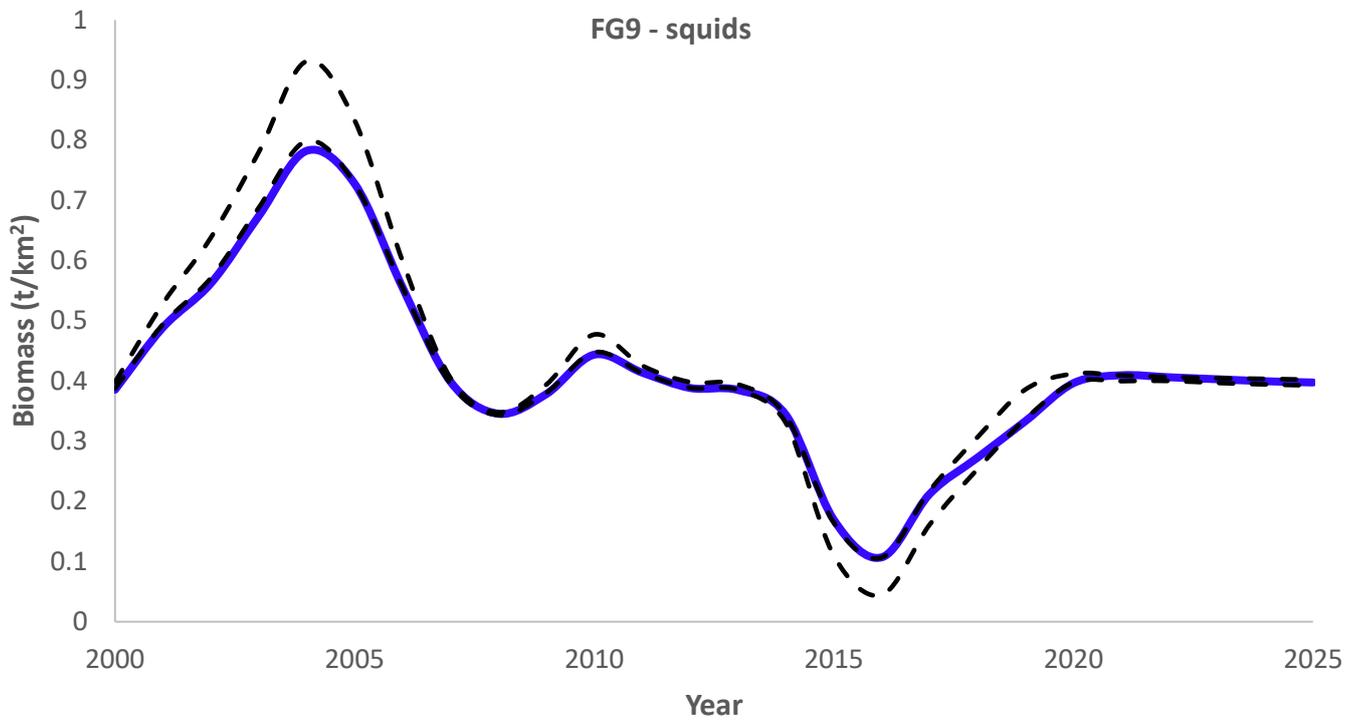
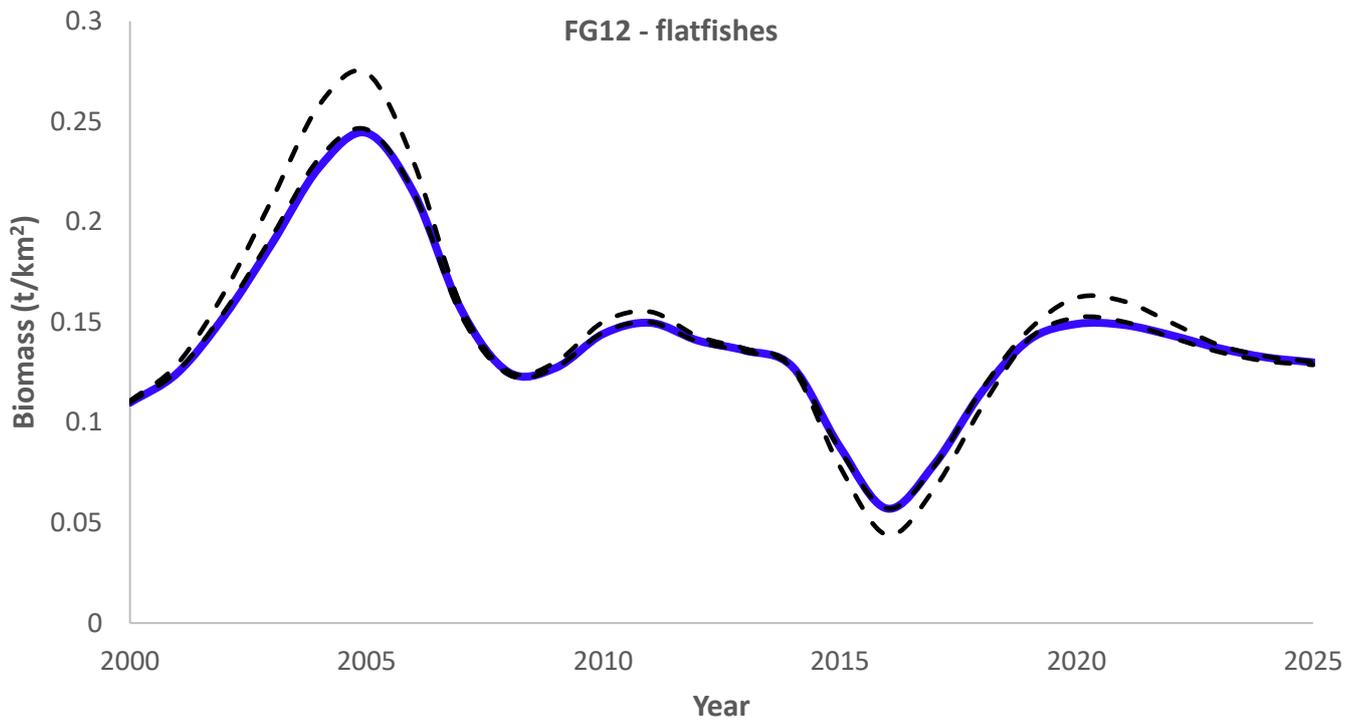
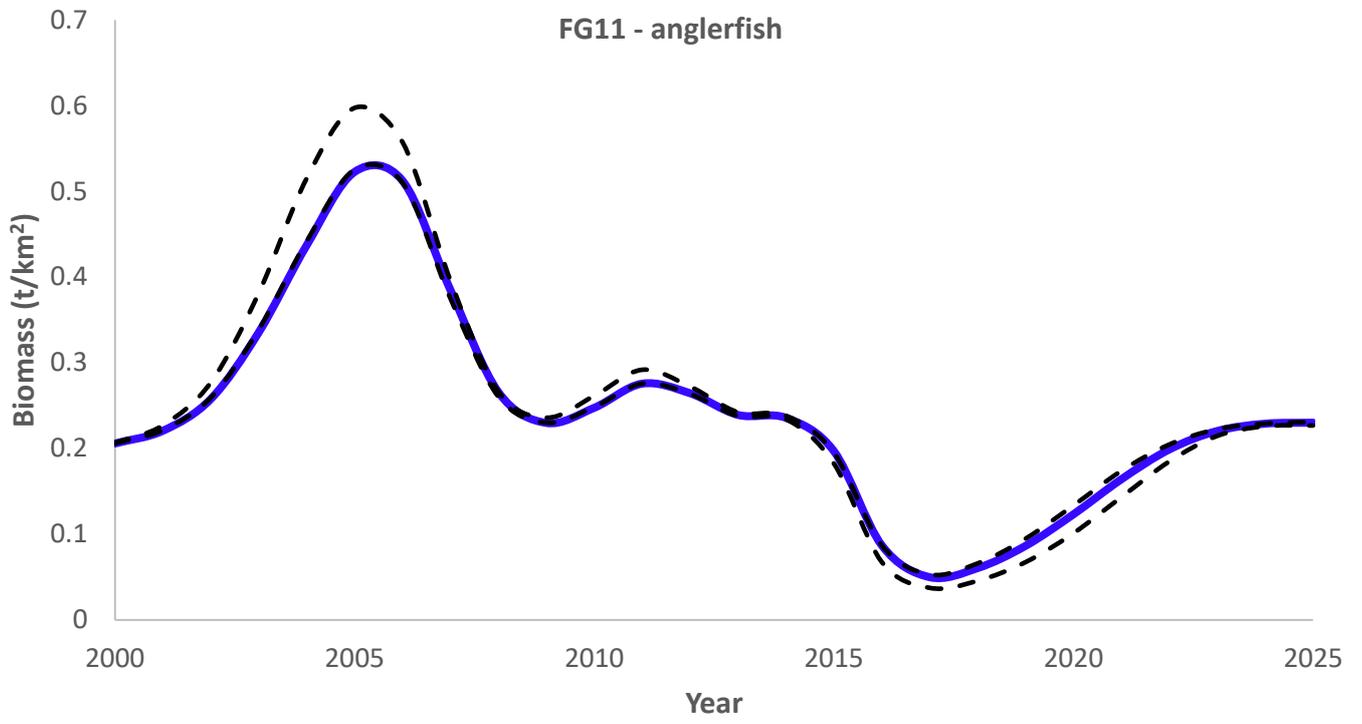


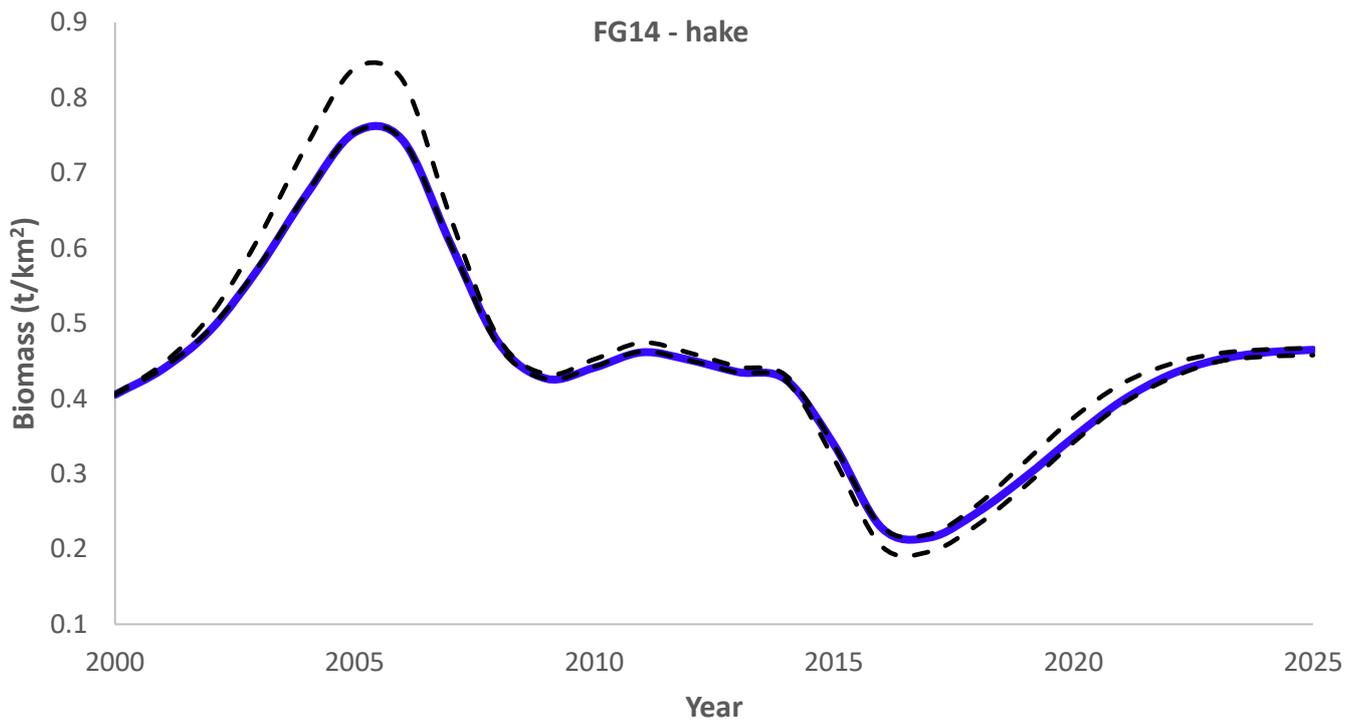
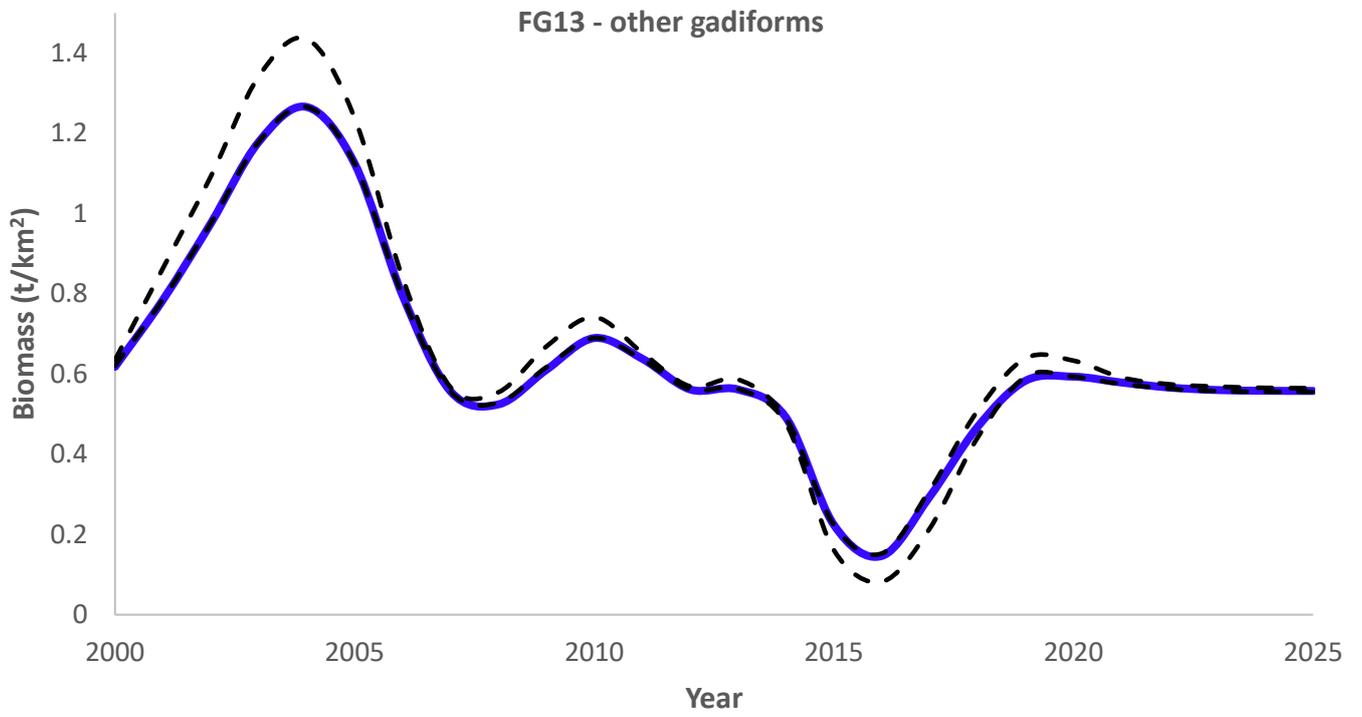
Figure A4 Monthly chlorophyll-a concentration values for the period 2000-2015 in Thermaikos Gulf that were derived from the biogeochemical validated model of the Copernicus Marine Environmental Service (CMEMS: MEDSEA_REANALYSIS_BIO_006_008) and were used to force the biomass of the primary producer (phytoplankton) during the fitting procedure (the year label refers to January).

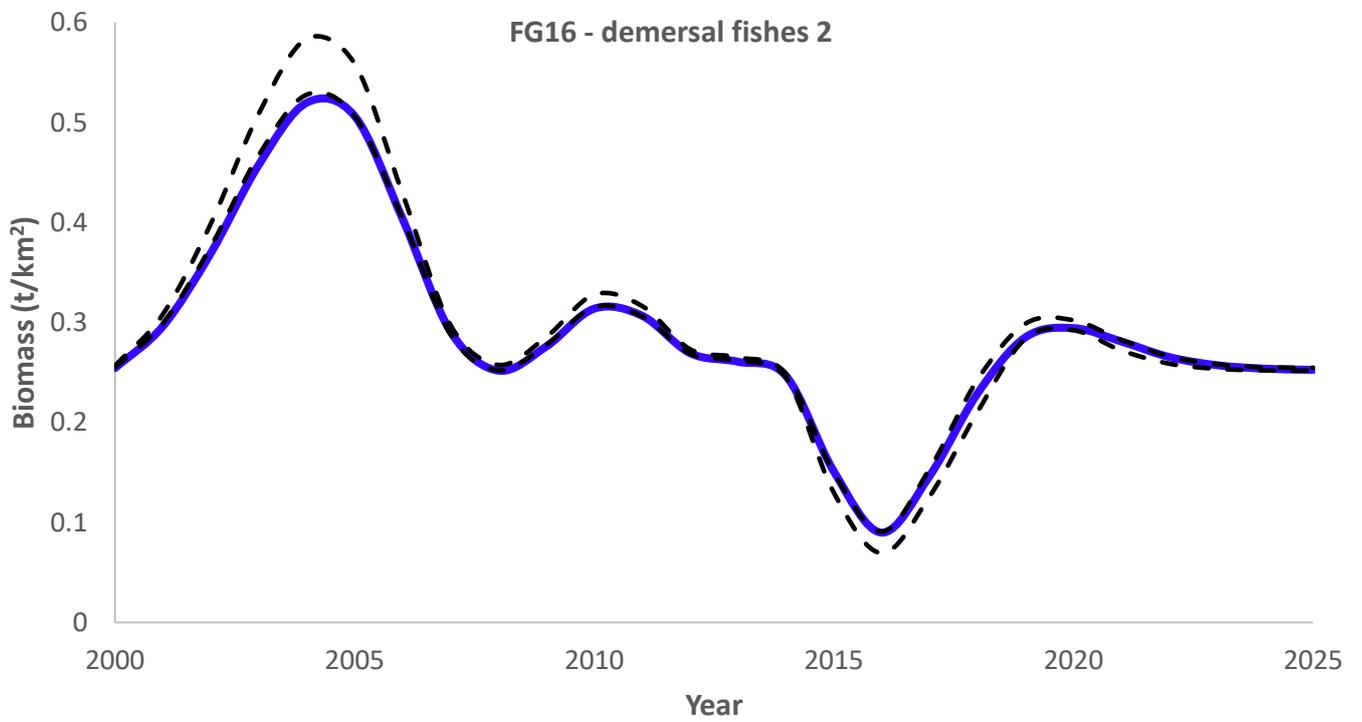
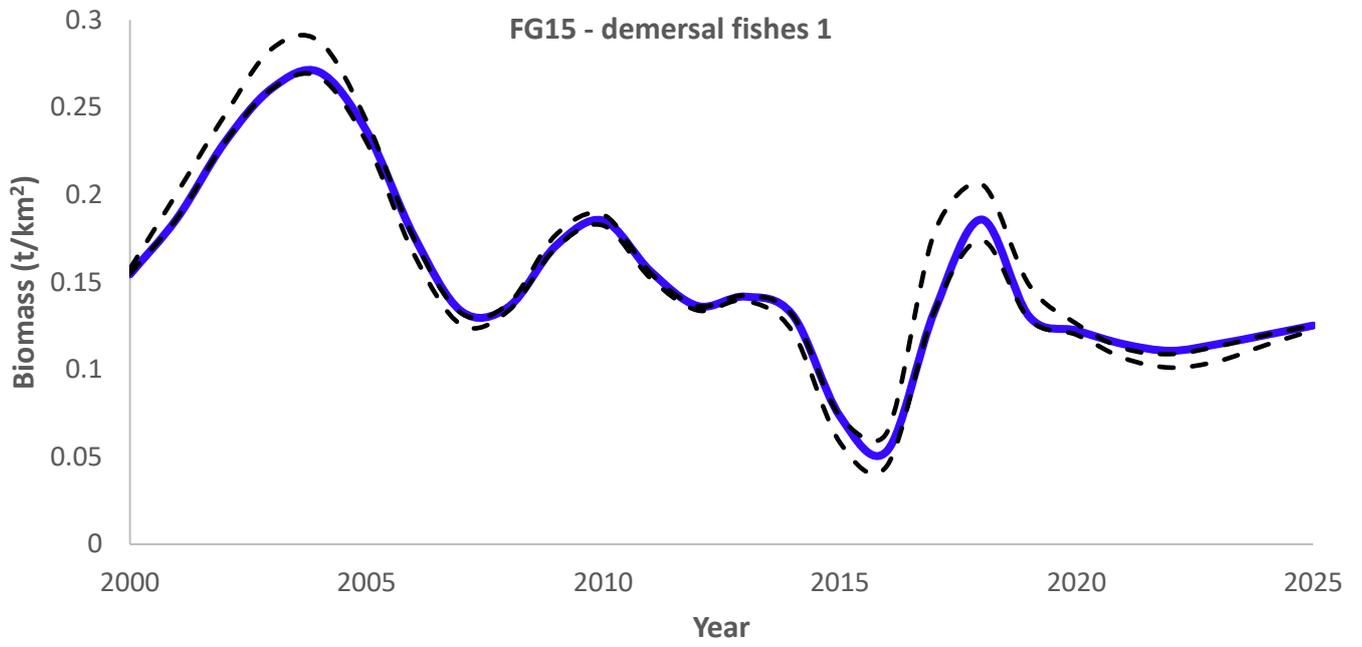


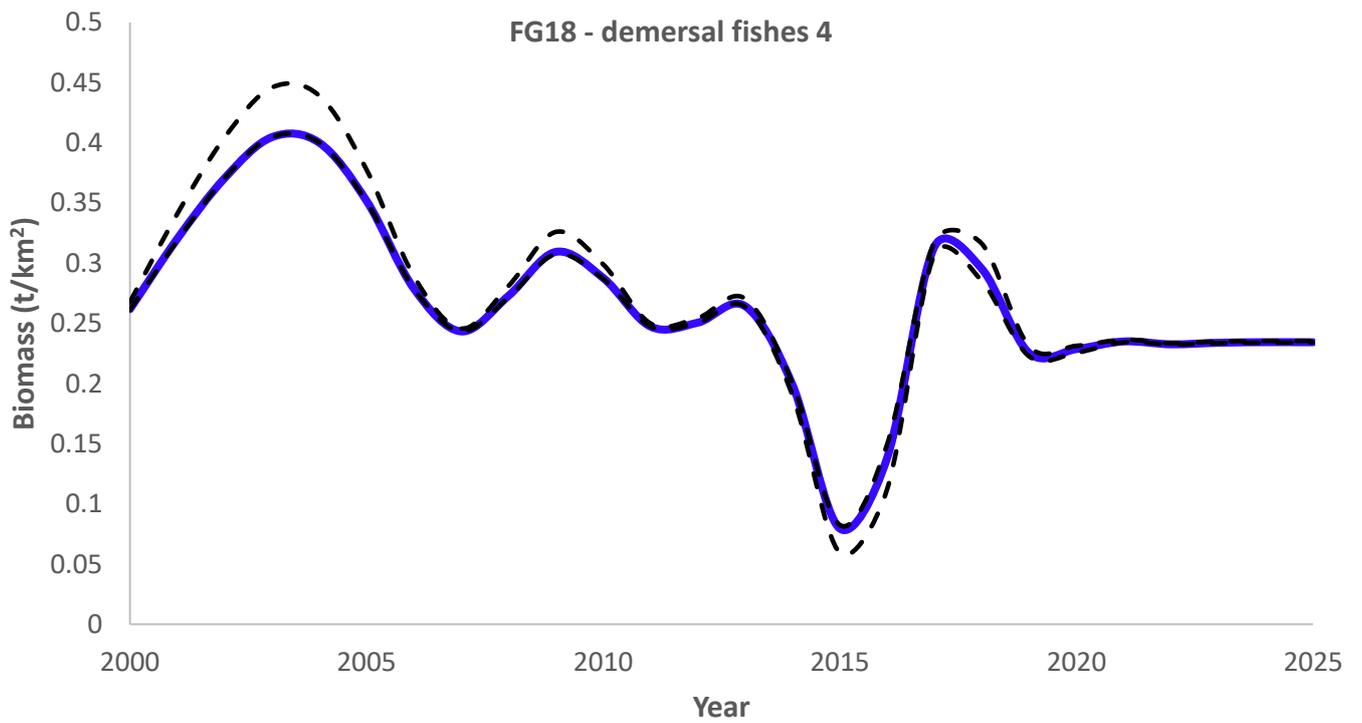
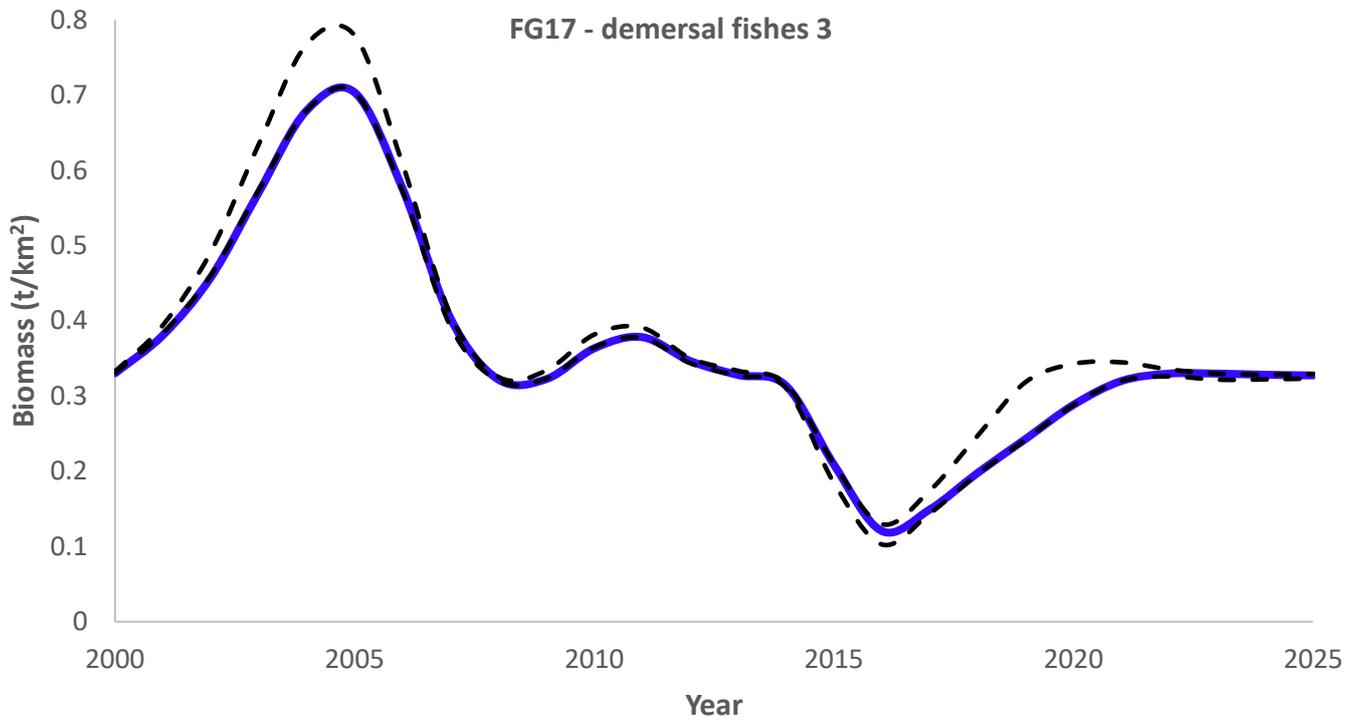


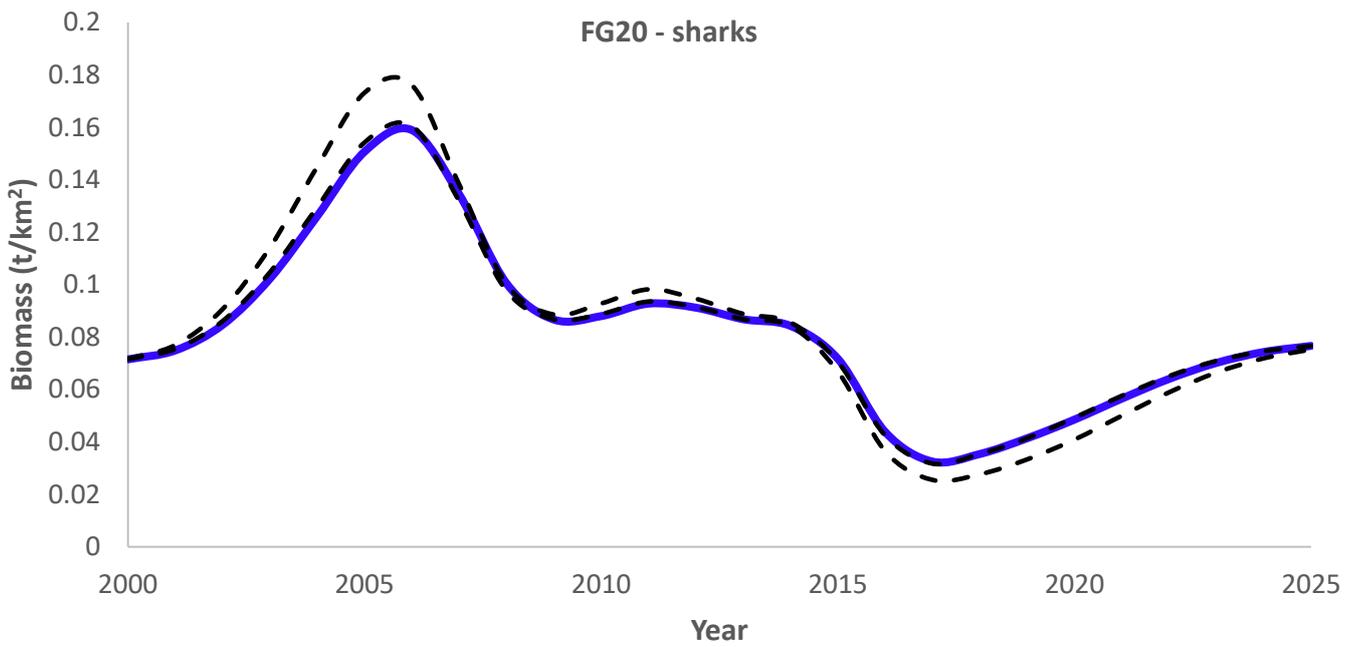
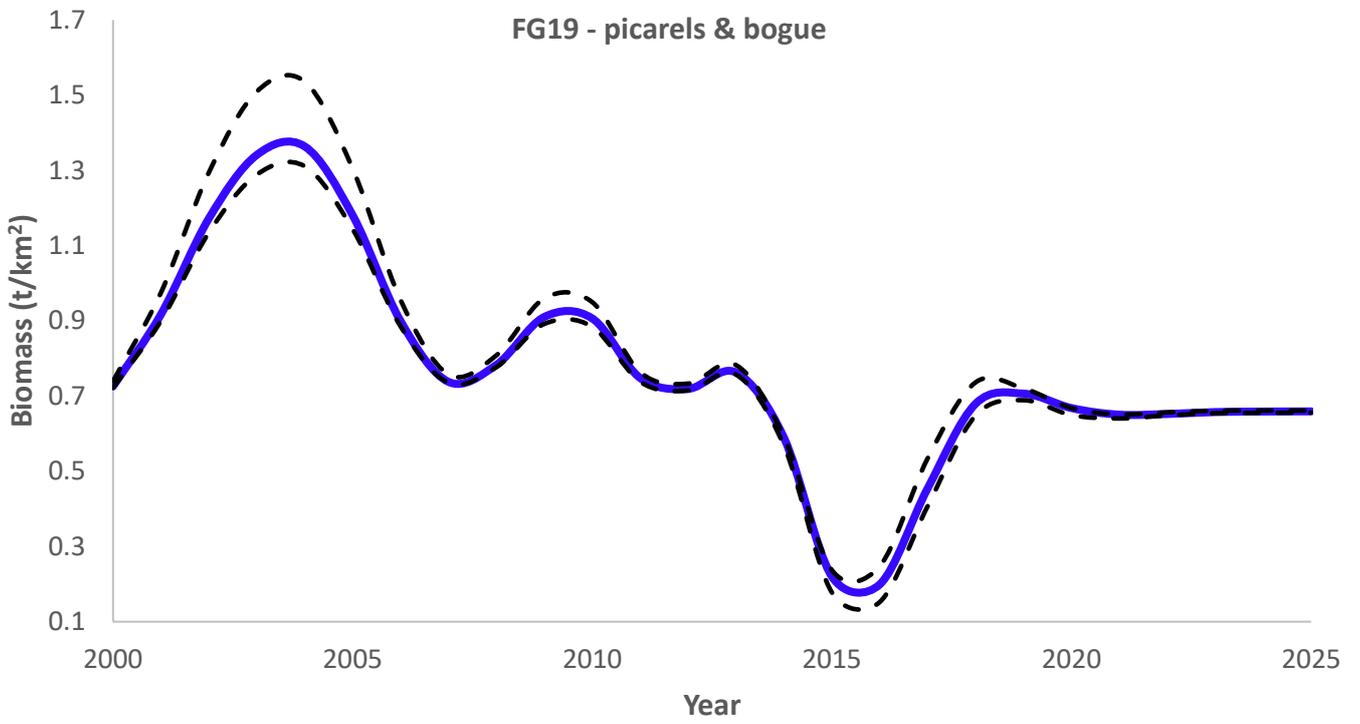


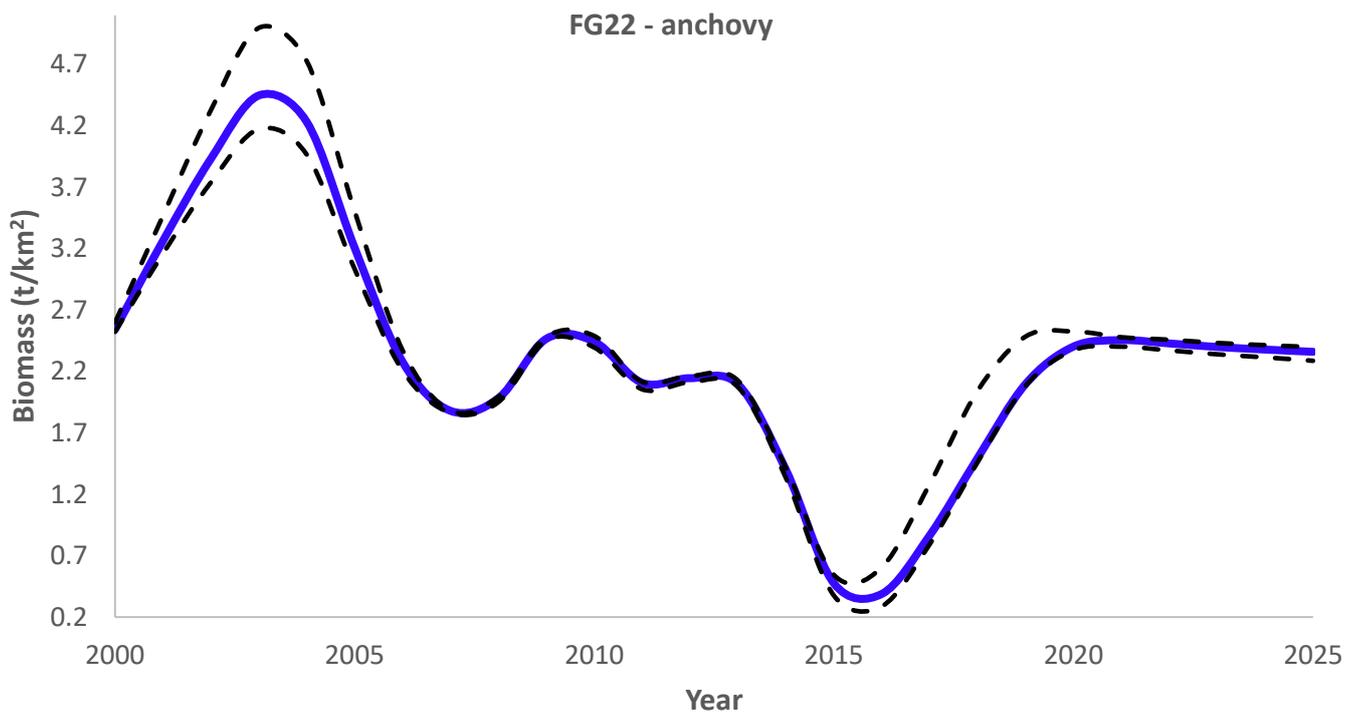
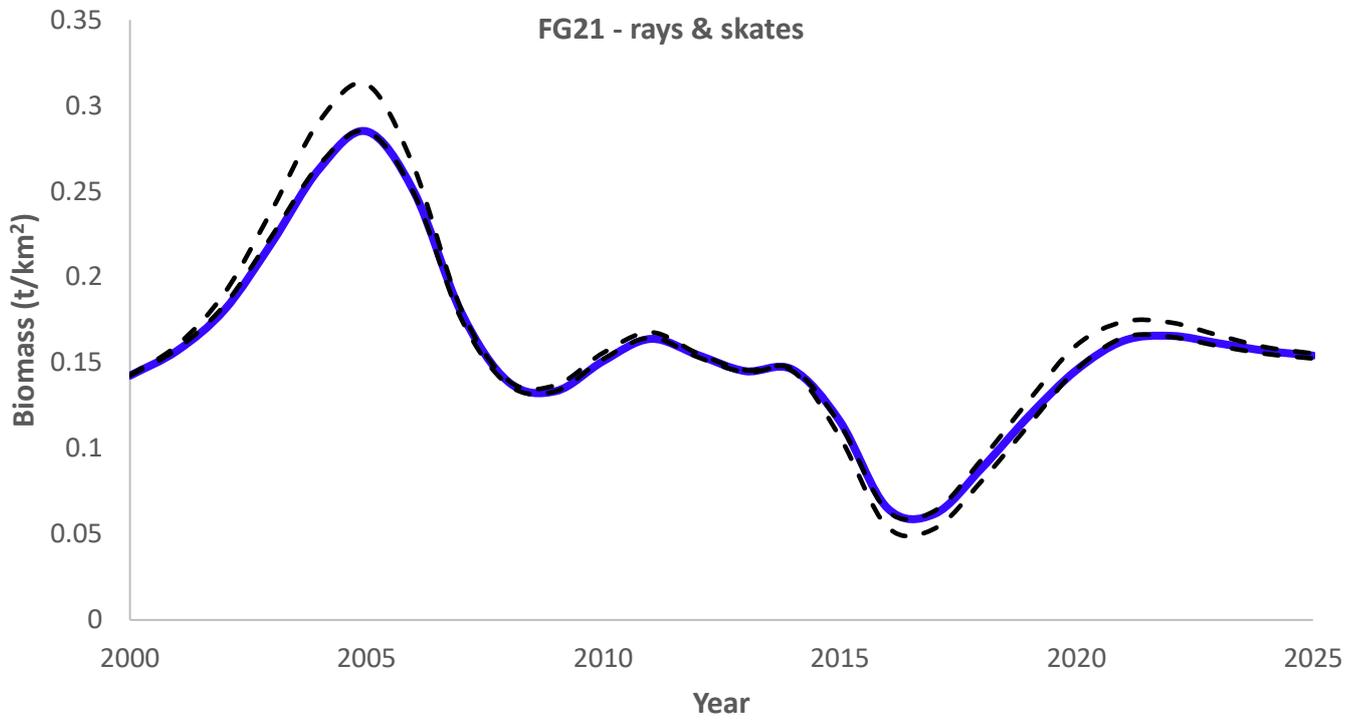


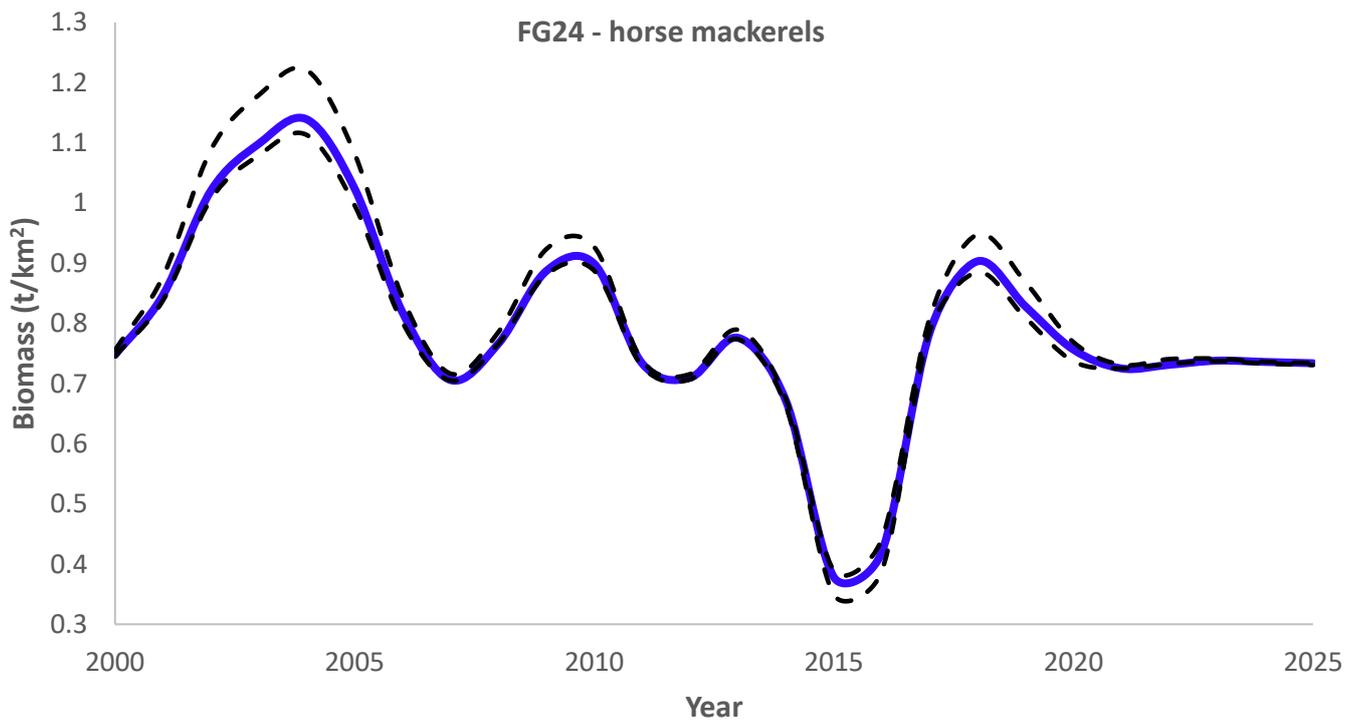
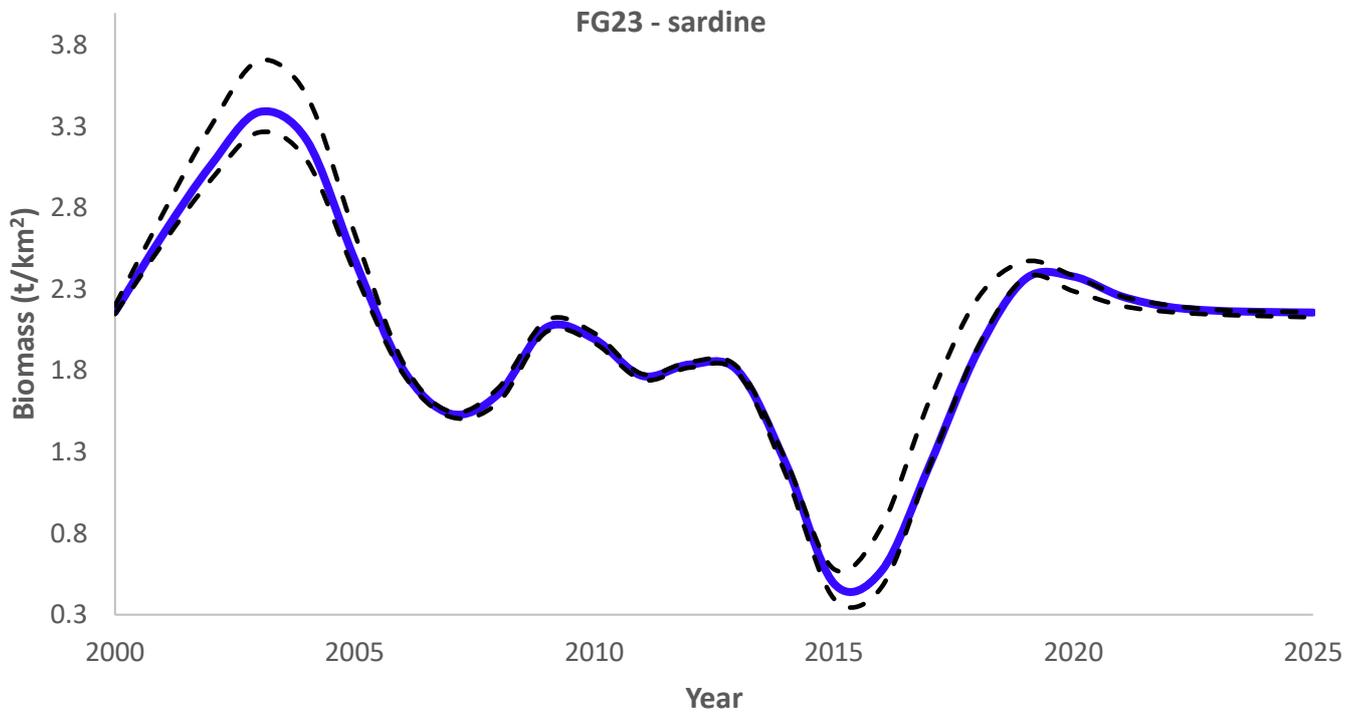


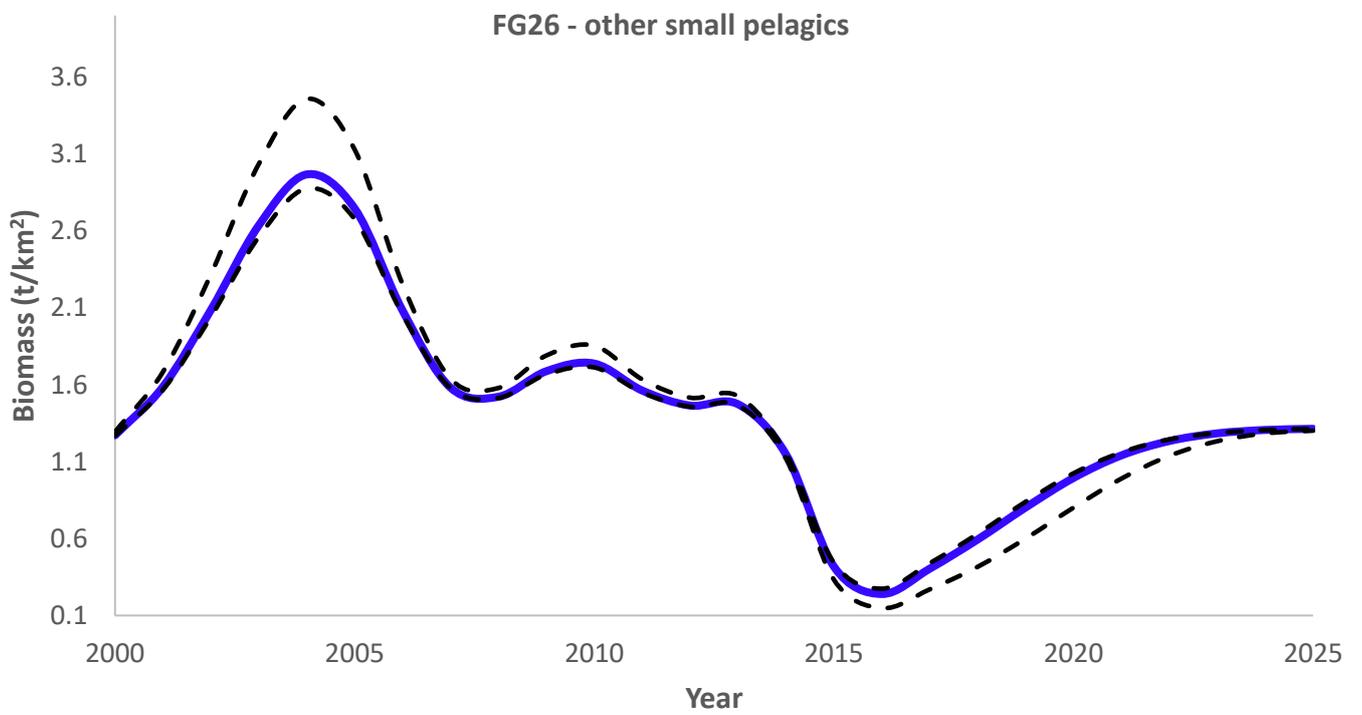
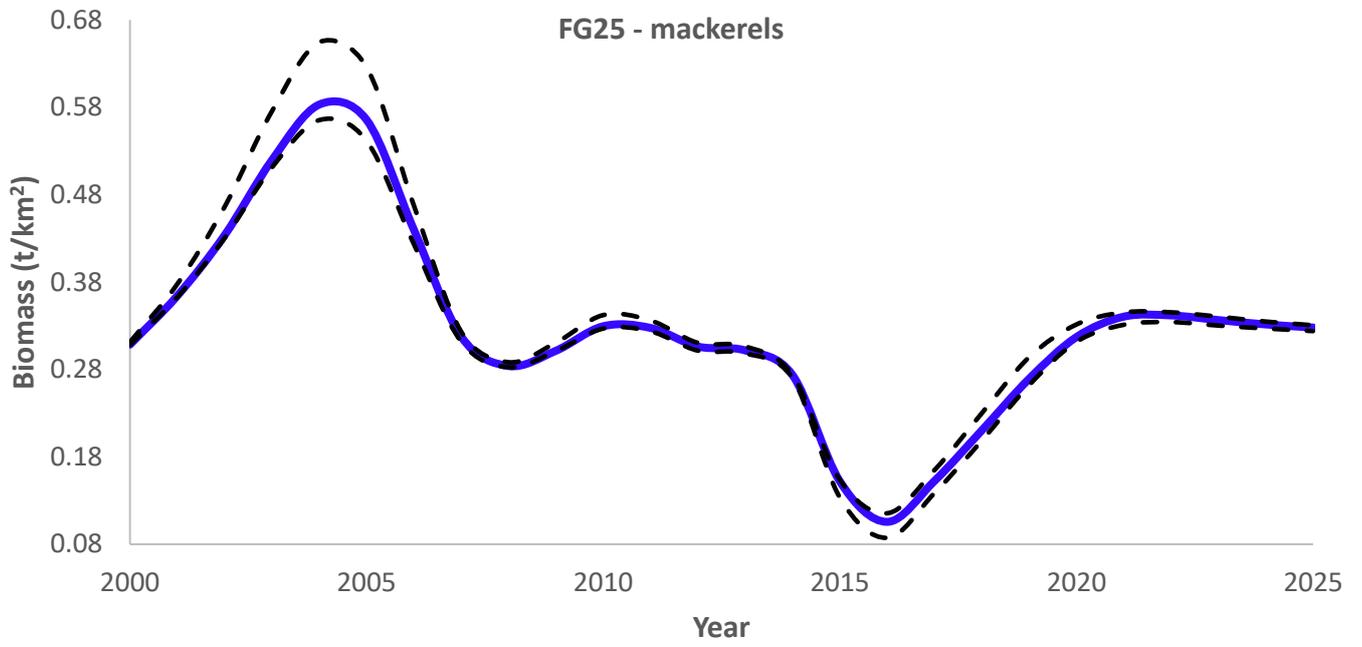












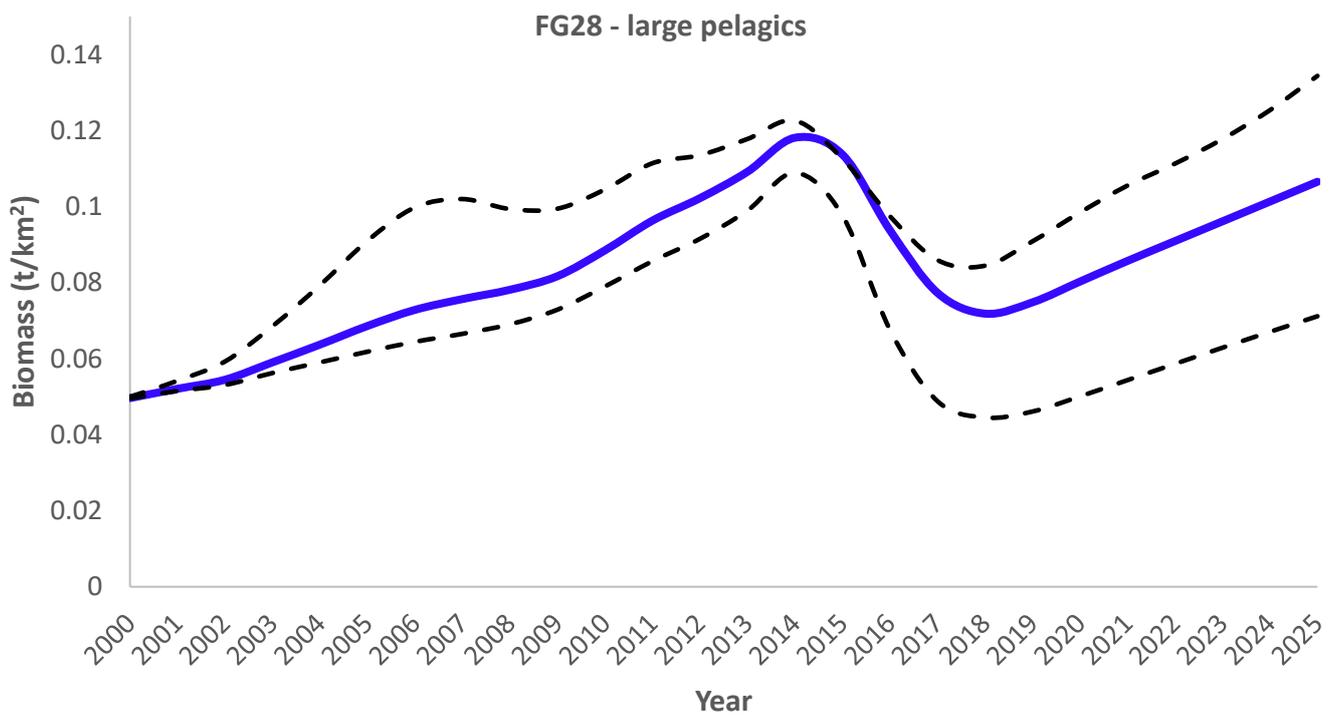
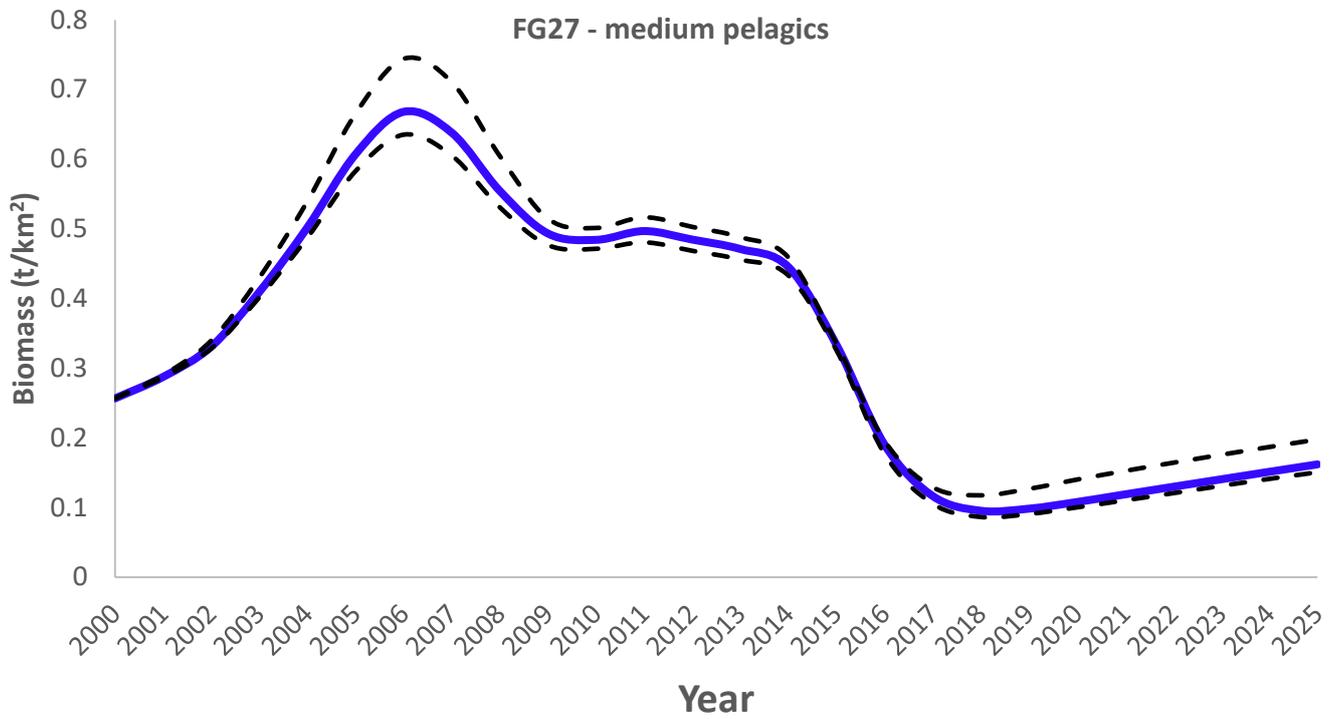


Figure A5 Biomass predicted by the Ecosim model for each functional group (FG) of the Thermaikos Gulf from 2000 to 2025, according to the business-as-usual scenario (blue line). The dashed lines represent the 5% and 95% percentiles obtained using the Monte Carlo routine (20 simulations).