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Exploring ecosystem dynamics through trophic level analysis in the Aegean Sea

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Abstract

The present study diagnoses the exploitation status of marine resources in the Aegean Sea using EcoTroph, a trophic modelling framework that builds upon ECOPATH outputs to represent biomass distribution as continuous flows across trophic levels (TLs). The model was applied to an updated ECOPATH snapshot for 2021, derived from a time-dynamic ECOSIM model fitted to biomass and catch data from 2006 to 2021. Results showed that biomass was concentrated at intermediate TLs (2.7-3.3), largely dominated by small pelagic fishes, while high-TL predators and low-TL benthic herbivorous and detritivorous groups exhibited signs of depletion under current fishing pressure. Simulations of increasing effort revealed that intermediate levels still retain the capacity for higher yields, although this potential declines as exploitation intensifies. Exploitation thresholds derived from EcoTroph outputs identified the effort levels corresponding to the maximum sustainable yield and a precautionary limit comparable to the $F_{0.1}$ reference point. Results indicated that this precautionary threshold ($E_{0.1}$) has already been exceeded for both low and high TLs, while intermediate TLs remain below it and could sustain limited catch increases before reaching full exploitation. The sensitivity analysis showed that the biomass accessible to fisheries had the strongest influence on catches, whereas top-down control and detritus recycling played smaller roles. Overall, EcoTroph revealed uneven exploitation across the Aegean Sea food web. Mid-trophic species continue to support fisheries, but sustained pressure on predators and benthic groups threatens long-term ecosystem balance.

Keywords: Ecosystem modelling; trophic spectrum; biomass flux; fishing mortality; EcoTroph.

Introduction

Marine ecosystems are characterized by complex interactions between species and energy flows influenced by both natural variability and human activities (Perry & Sumaila, 2007). Understanding these dynamics is essential for effective fisheries management, particularly in regions like the Mediterranean Sea, where biodiversity and multi-gear fisheries coexist within a relatively enclosed marine environment (Colloca *et al.*, 2017). In such contexts, food web modelling tools have become indispensable for capturing ecosystem-wide processes. ECOPATH with ECOSIM (EwE) has emerged as a widely used approach for describing trophic structure, quantifying energy flows, and supporting ecosystem-based management (Polovina, 1984; Christensen & Walters, 2004; Christensen & Walters, 2024). By integrating biological, ecological, and fisheries data, EwE provides a comprehensive framework for evaluating the functioning and resilience of marine food webs (Keramidas *et al.*, 2023).

A key component of such models is the concept of the trophic level (TL), a metric that expresses the position of an organism within the food web based on its feeding relationships (Gascuel, 2005). Historically, the use of TLs was popularized by Lindeman (1942), who introduced the idea of trophic pyramids to describe energy transfer between discrete levels. However, this simplification was soon challenged by Rigler (1975), who emphasized that most organisms feed across multiple TLs, rendering rigid classifications conceptually limited. This criticism led to a conceptual shift, as later studies introduced fractional TLs, which could be empirically estimated from diet composition (Odum & Heald, 1975; Tremblay-Boyer *et al.*, 2011). Additionally, TLs are not fixed for many species, as ontogenetic shifts in diet, where organisms change their feeding preferences during growth, can alter their position within the food web over time (Gascuel *et al.*, 2005). This transition allowed TLs to serve not only as descriptive tools but also as analytical metrics for modelling ecological dynamics (Shannon *et al.*, 2014). It laid the foundation for modern trophic modelling, especially within EwE, which dynamically estimates TLs from species interactions and feeding matrices (Christensen & Pauly, 1992). The development of such modelling approaches, together with the availability of global databases like FishBase (Froese & Pauly, 2025) and extensive research on the ecological impacts of fishing (Pauly *et al.*, 1998), has further consolidated the role of TLs as a central concept in ecosystem science and management (Collie *et al.*, 2016).

Building on these foundations, the EcoTroph model was developed as a trophodynamic framework designed to operate either independently or in conjunction with ECOPATH outputs, allowing for exploration of ecosystem functioning in terms of biomass flows along the continuous TL axis (Gascuel & Pauly, 2009; Gascuel *et al.*, 2009). Rather than modelling individual species or functional groups (FGs), EcoTroph aggregates ecological processes into a synthetic representation of energy transfer, mortality, and productivity across TLs (Gascuel & Pauly, 2009). This makes it particularly well-suited to evaluate the structural impacts of fishing pressure and diagnose inefficiencies in energy transfer within the food web. Unlike mass-balance or species-level models, EcoTroph offers a streamlined, diagnostic perspective that focuses on the emergent properties of trophic structure, such as transfer efficiency, fishing impact gradients, and energy dissipation points (Gascuel *et al.*, 2011; Eddy *et al.*, 2021). These features make it a valuable complement to EwE, especially in regions where fisheries exploit a broad range of species across multiple TLs, as in the Aegean Sea (Touloumis *et al.*, 2025). In recent years, several EcoTroph applications have been developed across the Mediterranean, covering areas such as Port Cros (Valls *et al.*, 2012; Prato *et al.*, 2014), the Gulf of Gabès (Halouani *et al.*, 2015), Portofino (Prato *et al.*, 2016), and the eastern Corsican coast (Vanalderweireldt *et al.*, 2022). These case studies demonstrate the potential of the model to identify TL-specific impacts of fishing and complement broader ecosystem assessments based on ECOPATH models.

This study applied the EcoTroph model to the Aegean Sea ecosystem to evaluate its capacity to diagnose the overall exploitation status of marine resources at the scale of the entire food web. The main objective was to describe how biomass and catches are distributed along the trophic spectrum and to assess the extent to which current fishing pressure has altered this structure compared with the unfished state. Simulations of increasing fishing effort were used to examine changes in biomass and catch across TLs, providing an ecosystem-level diagnosis of exploitation rather than species-specific assessments. Finally, a sensitivity analysis was performed to test the robustness of this diagnosis by evaluating how variations in key EcoTroph parameters influence model outcomes.

Materials and Methods

Study area and base model

The Mediterranean Sea is both the largest and deepest semi-enclosed sea in the world. Despite being characterized as oligotrophic, it is considered a significant biodiversity hotspot (Coll *et al.*, 2010). The Aegean Sea (FAO Division 37.3.1, GSAs 22 and 23), a semi-enclosed water body in the eastern Mediterranean Sea (Fig. 1), supports diverse commercial fisheries, including pelagic

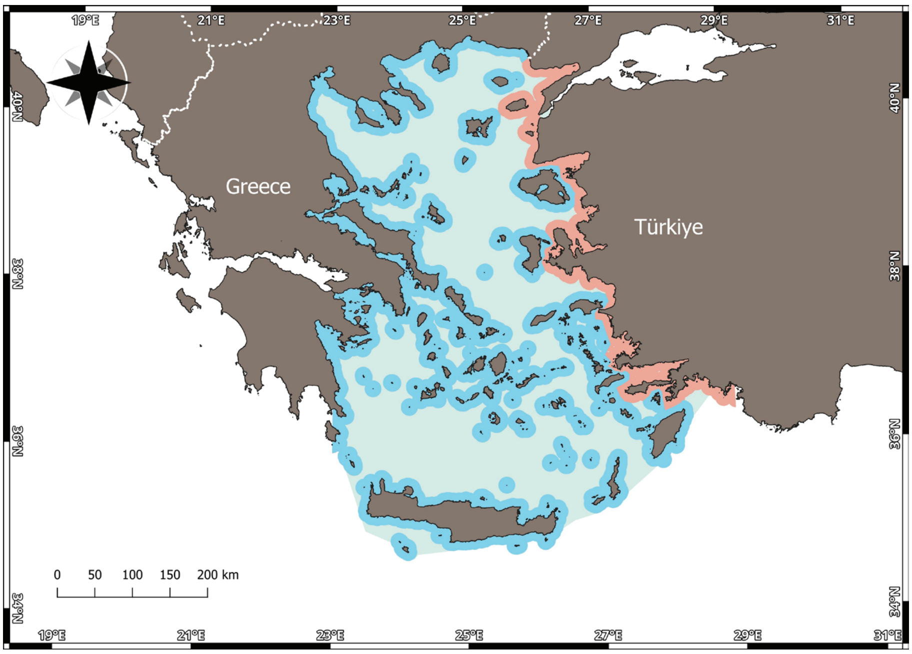

Fig. 1*:* The Aegean Sea modelled area of the base ECOPATH model (defined in Keramidas *et al.*, 2022) where the EcoTroph simulations were based. Blue shaded areas refer to Greek national waters, while red shaded areas are Turkish national waters (both at 6 nautical miles).

species like European pilchard (*Sardina pilchardus*), European anchovy (*Engraulis encrasicolus*), and demersal species like European hake (*Merluccius merluccius*), and red mullet (*Mullus barbatus*). Most of the stocks have been characterized as fully exploited or overexploited (Tsikliras *et al.*, 2015; Colloca *et al.*, 2017; Tsikliras *et al.*, 2021), with a large number of active fishing vessels (> 10,000): the number of recreational fishing vessels is estimated to be twice as high (Keramidas *et al.*, 2018).

The EcoTroph model developed in this study was based on an updated ECOPATH model of the Aegean Sea representing the year 2021. The original ECOPATH model, covering the average period from 2003 to 2006 (Keramidas *et al.*, 2022), consisted of 44 FGs across the food web and four commercial fishing fleets (OTB: bottom trawlers, PS: purse seiners, BS: beach seiners, and SSC: small-scale coastal vessels). This model was subsequently expanded into a time-dynamic ECOSIM model (Keramidas *et al.*, 2024) and a spatially explicit ECOSPACE model (Keramidas *et al.*, 2025), fitted to observed biomass and catch data for the period from 2006 to 2021. For the purposes of the present EcoTroph analysis, we extracted the ECOPATH snapshot corresponding to the year 2021 (Fig. 2), as it was the last year in the fitted time series with complete and validated observed data. This ensured that the EcoTroph model was based on the most recent and robust representation of the ecosystem derived from observed and fitted inputs.

Basic principles of the EcoTroph modelling approach

EcoTroph is a trophic-based modelling framework used to evaluate ecosystem functioning and fishing impacts by describing biomass flows along a continuous trophic axis (Gascuel, 2005; Gascuel & Pauly, 2009). Under steady-state conditions, biomass in each trophic class (τ) is estimated by:

$$B_\tau = \frac{\Phi_\tau}{K_\tau} \cdot \Delta_\tau$$

where B_τ is the biomass in the trophic class (τ), Φ_τ is the average biomass flow passing through this trophic class, K_τ is the average flow rate in class (τ) and Δ_τ is the TL interval, here set to 0.1. Flow kinetics K_τ were derived from *P/B* ratios and reflect how fast biomass transitions to higher TLs through growth, predation, and ontogenetic shifts (Gascuel *et al.*, 2008). Biomass is transferred upward through TLs primarily via predation and ontogenetic dietary shifts, while concurrently reduced by natural losses (respiration, mortality) and fishing (Pranovi *et al.*, 2012).

Fishing was integrated through fishing mortality (F_τ) and fishing loss rate (φ_τ), which quantified the fraction of production harvested at each TL (Worm *et al.*, 2009). Biomass flow at each level is reduced according to:

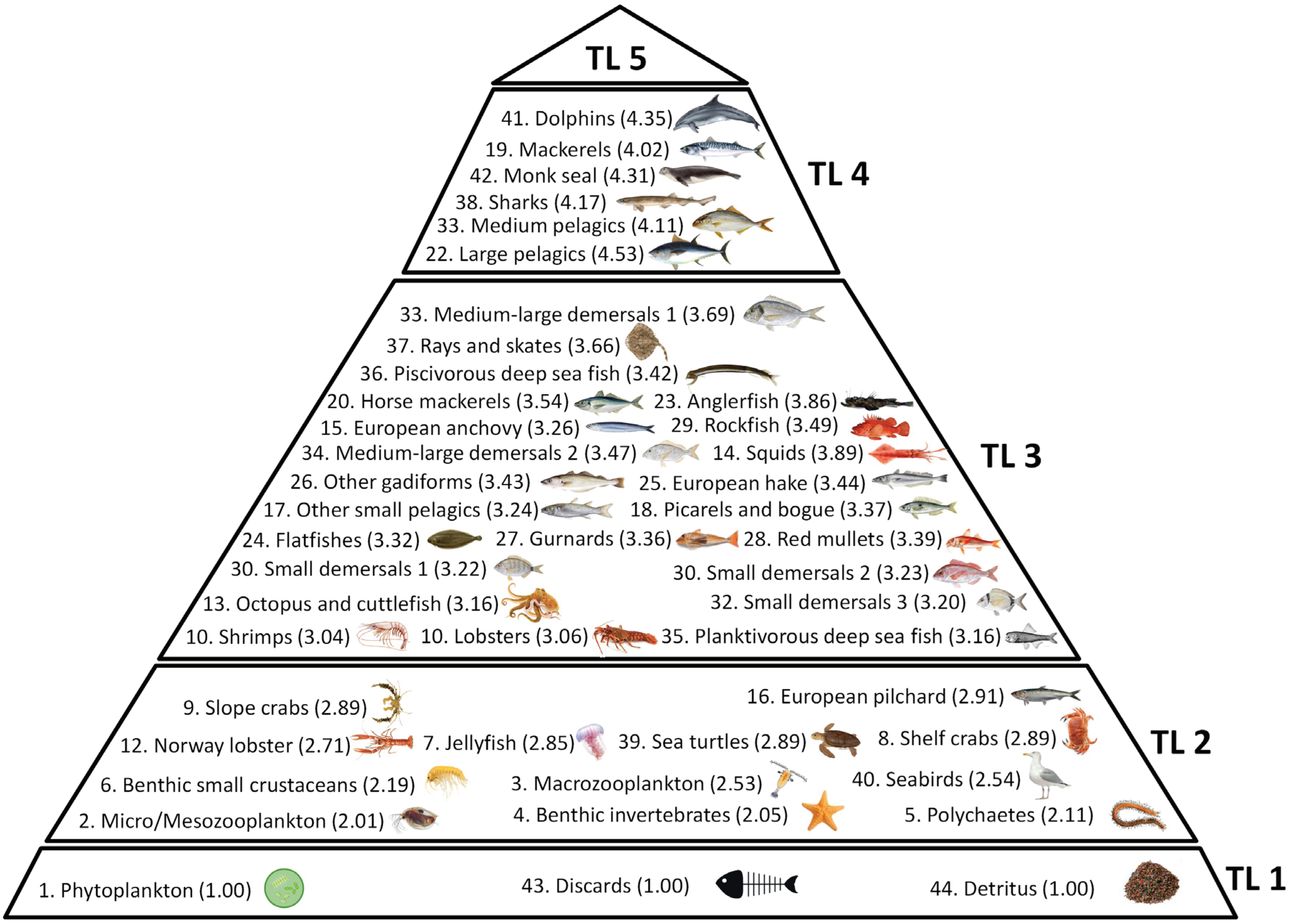

Fig. 2: The trophic pyramid of the ECOPATH model of the Aegean Sea and its corresponding trophic levels. The species composition of the functional groups is provided in Table S1.

$$\Phi_{(\tau+\Delta\tau)} = \Phi_\tau \cdot \exp[-(\mu_\tau + \varphi_\tau) \cdot \Delta_\tau]$$

where μ_τ is the natural loss rate (natural mortality and metabolic waste). These parameters together allow EcoTroph to describe how energy and biomass were transferred and depleted across the ecosystem.

A key parameter in EcoTroph is accessibility (*Acc.*), which defines the proportion of biomass available to fishing under infinite effort (Gascuel & Pauly, 2009). It reflects not only exploitation intensity but also species traits, behavior, and spatial availability. The default EcoTroph value of 0.8 is often considered an upper limit for exploited groups, as a fraction of the population, such as juveniles or individuals distributed outside fishing grounds, remains inaccessible to fisheries. In this model, accessibility values were assigned based on ecological characteristics, spatial distribution, and previous studies (e.g., Lassalle *et al.*, 2012; Bentorcha *et al.*, 2017). Fully exploited groups with high exposure were set closer to 0.8, while others were assigned lower values (Table 1).

Table 1. Input parameters used in the EcoTroph model derived from the ECOPATH model of the Aegean Sea for the year 2021. The table includes functional groups with their corresponding trophic level (TL), biomass (Bi, in t·km^{-2}), production/biomass ratio (P/B, year^{-1}), accessibility coefficient to fisheries (Acc.), and omnivory index (OI).

Functional Group	TL	Bi	P/B	Acc.	OI
1. Phytoplankton	1.00	2.66	120.22	0	0.00
2. Micro/Mesozooplankton	2.01	4.99	28.39	0	0.01
3. Macrozooplankton	2.53	1.00	20.26	0	0.29
4. Benthic invertebrates	2.05	10.71	1.90	0.4	0.06
5. Polychaetes	2.11	6.19	2.85	0	0.12
6. Benthic small crustaceans	2.19	1.37	9.29	0	0.17
7. Jellyfish	2.85	1.31	15.75	0	0.17
8. Shelf crabs	2.89	0.08	2.85	0.6	0.18
9. Slope crabs	2.89	0.00	1.49	0	0.18
10. Shrimps	3.04	0.45	3.48	0.6	0.17
11. Lobsters	3.06	0.01	2.48	0.4	0.16
12. Norway lobster	2.71	0.01	1.35	0.5	0.46
13. Octopus and cuttlefish	3.16	0.44	2.55	0.6	0.06
14. Squids	3.89	0.62	2.79	0.7	0.26
15. European anchovy	3.27	1.97	2.81	0.7	0.11
16. European pilchard	2.91	2.20	2.54	0.7	0.14
17. Other small pelagics	3.24	1.15	1.35	0.6	0.15
18. Picarels and bogue	3.37	0.78	1.84	0.6	0.15
19. Mackerels	4.02	0.10	2.15	0.7	0.28
20. Horse mackerels	3.54	0.23	1.02	0.7	0.17
21. Medium pelagics	4.12	0.25	0.71	0.6	0.12
22. Large pelagics	4.53	0.05	0.25	0.6	0.47
23. Anglerfish	3.86	0.17	0.66	0.5	0.43
24. Flatfishes	3.32	0.07	0.72	0.6	0.51
25. European hake	3.44	0.57	1.23	0.6	0.28
26. Other gadiforms	3.43	0.62	0.41	0.5	0.12
27. Gurnards	3.36	0.14	0.50	0.5	0.15
28. Red mullets	3.49	0.07	1.81	0.6	0.18
29. Rockfish	3.50	0.05	0.44	0.4	0.31
30. Small demersals 1	3.22	0.10	1.23	0.4	0.13
31. Small demersals 2	3.23	0.16	0.61	0.4	0.46
32. Small demersals 3	3.20	0.04	0.29	0.4	0.14
33. Medium-large demersals 1	3.69	0.06	0.56	0.6	0.42
34. Medium-large demersals 2	3.47	0.07	0.96	0.6	0.38
35. Planktivorous deep sea fish	3.16	0.51	0.34	0.3	0.02
36. Piscivorous deep sea fish	3.42	0.22	0.25	0.3	0.15
37. Rays and skates	3.67	0.15	0.24	0.3	0.41
38. Sharks	4.17	0.21	0.08	0.2	0.49
39. Sea turtles	2.89	0.08	0.17	0.01	0.38
40. Seabirds	2.54	0.00	5.05	0.01	0.77
41. Dolphins	4.35	0.02	0.08	0.01	0.09
42. Monk seal	4.31	0.00	0.13	0.01	0.08
43. Discards	1.00	0.11	0.00	0	0.00
44. Detritus	1.00	29.86	0.00	0	0.19

To evaluate uncertainty, a sensitivity analysis was performed by varying accessibility coefficients for exploited groups within a range of 0.2 to 0.8. This analysis explored how different assumptions about biomass availability to fisheries influenced model outputs and the estimation of fishing impacts. Comparing results across this range allowed the assessment of the robustness of EcoTroph diagnoses and defined both optimistic and pessimistic exploitation scenarios along the trophic spectrum.

EcoTroph model and parameterization

To analyze trophic structure and fishing impacts, the EcoTroph model was implemented using the R-based EcoTroph 1.6 package (Colléter *et al.*, 2013). Two main routines were used: "ET-Transpose", which converted the ECOPATH outputs into trophic spectra of biomass, production, and catch across continuous TLs, and "ET-Diagnosis", which simulated fishing pressure across TLs (Gascuel *et al.*, 2009). Biomass, production, and catch for each FG were distributed using lognormal curves centered at the mean TL of each group, with a constant standard deviation ($\sigma_{ln} = 0.12$) to account for intra-group trophic variability (Gascuel, 2005; Colléter *et al.*, 2013).

To assess the ecosystem's response to exploitation, we simulated incremental increases in fishing effort using effort multipliers (mE) from 0 to 5, evaluating changes in biomass, catch, flow rates, and transfer efficiency at each TL. These simulations allowed for the diagnosis of fishing impact patterns along the trophic continuum. The baseline scenario corresponded to current fishing levels (mE.1)

Biomass flow through TLs was shaped by three parameters: the top-down control coefficient (α), the input control coefficient (β), and a shape parameter (γ), based on the flow kinetics equation:

$$K_\tau = [K_{cur,\tau} - F_{cur,\tau}] \cdot \left[1 + \alpha_\tau \cdot \frac{B^\gamma_{pred} - B^\gamma_{pred,cur}}{B^\gamma_{pred,cur}}\right] + F_\tau$$

where $K_{cur,\tau}$ is the flow rate in the current state, defined by the ECOPATH model and affected by the corresponding fishing mortality ($F_{cur,\tau}$), and B_{pred} is the biomass of predator FGs in trophic class (τ). The recommended values of the EcoTroph application were used; $\alpha = 0.4$ to reflect mixed control in the oligotrophic Aegean Sea (Siokou-Frangou *et al.*, 2002), $\beta = 0.1$ for limited detritus recycling, and $\gamma = 0.5$ to represent moderate predator-prey relationships. A sensitivity analysis was also carried out to assess the influence of the top-down control coefficient (α), the detritus recycling coefficient (β), and accessibility to fisheries on model outputs.

To define exploitation thresholds, we used the EcoTroph simulations to identify the effort level (E_{MSY}) that would theoretically correspond to the Maximum Sustainable Yield (MSY), defined as the maximum catch obtainable at equilibrium for each TL (Gasche *et al.*, 2012; Tsikliras & Froese, 2019). Additionally, a precautionary reference point ($E_{0.1}$) was calculated, defined as the effort multiplier at which the slope of the catch curve dropped to 10% of its initial value, following the $F_{0.1}$ approach commonly used in single-species stock assessments (Deriso, 1987), where it is generally considered to represent the limit of full exploitation. These thresholds were used to assess the risk of overexploitation across the food web of the Aegean Sea under increased fishing effort scenarios.

Results

The EcoTroph model results for the Aegean Sea revealed that FGs at intermediate TLs (ranging from 2.7 to 3.3) accounted for the largest biomass concentrations (Fig. S1, Fig. S2). These groups primarily consisted of small pelagic fish, such as European pilchard. Total biomass showed a clear decreasing trend as TL increased. Similarly, the catch trophic spectra by fishing fleet showed that all major fleets operating in the Aegean Sea primarily target FGs at intermediate TLs, generally between TL 3.0 and 3.5 (Fig. S3, Fig. S4, Fig. S5, Fig. S6). Bottom trawlers and small-scale coastal fisheries displayed the widest targeted trophic range, extending toward lower demersal levels, whereas purse and beach seiners focused almost exclusively on small pelagic species. This convergence of fleet activity around mid-trophic groups indicated that fishing pressure is concentrated in the same range where biomass and catches are most abundant. Accordingly, total catches and the cumulative harvesting capacity of the ecosystem also peaked at intermediate TLs (Fig. S7). Simulations of increasing fishing effort, applied as effort multipliers, altered the structure of the biomass trophic spectrum (Fig. 3). The sensitivity of biomass accessible to fisheries to each multiplier varied across certain TLs. Although fishing mortality was higher at higher TLs (Fig. S8), the increase of the mE had a more pronounced effect on intermediate TLs. Specifically, the biomass of small pelagic FGs like European anchovy (TL = 3.2) appeared to have the highest sensitivity to changes in fishing effort, a characteristic associated with their relatively high P/B ratio. Conversely, the effects of simulated biomass relative to the initial state exhibited an opposite trend in terms of sensitivity.

As TL increased, the relative impact of fishing became more pronounced, with biomass at higher TLs already strongly depleted under current effort conditions in the Aegean Sea (Fig. 3). Increasing fishing effort led to stronger biomass reductions at higher TLs in comparison with the reference biomass (Fig. 4A). TL 5 was the most affected, dropping to about 75% of its reference biomass at mE.5, while TL 4.5 declined by more than half. The biomass accessible to fisheries (Fig. 4B) showed a sharper response, with TL 5 declining by ~60% at mE.2 and approaching depletion at mE.5.

Regarding catch, it was observed that higher mE can lead to an increase in catch. At the same time, at TLs above 4.4, there is a threshold beyond which the maximum possible catch can no longer be achieved, even with higher mE, whereas the opposite effect may occur with lower multipliers (Fig. 5). This implies that an increase

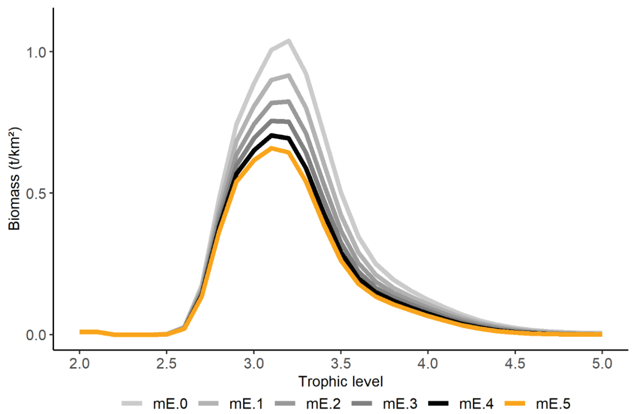

***Fig. 3**:* Simulated trophic spectra of biomass accessible to fisheries under fishing effort multipliers (mE) ranging from 0 to 5. The current state of the ecosystem is represented by mE.1.

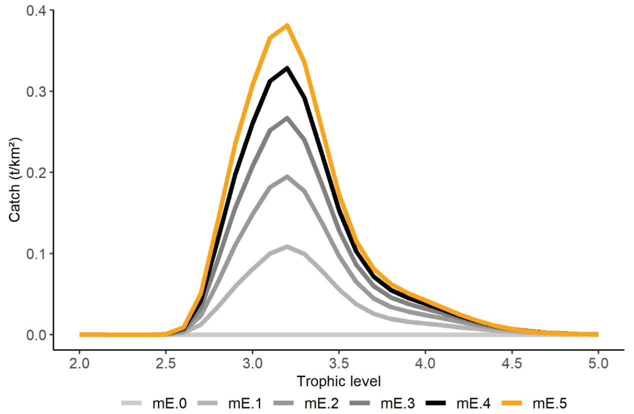

Fig. 5: Simulated catch trophic spectra under fishing effort multipliers (mE) ranging from 0 to 5. The current state of the ecosystem is represented by mE.1.

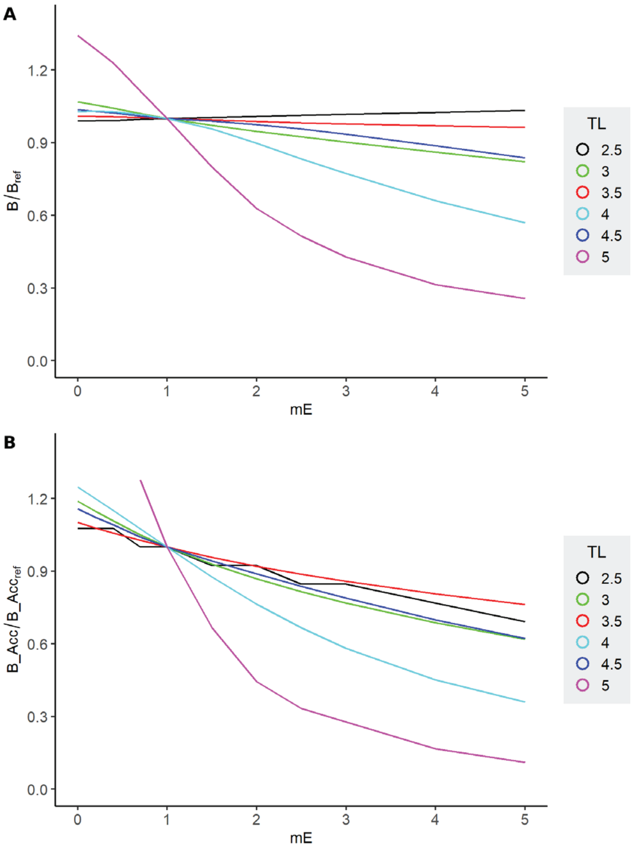

Fig. 4: Simulated relative biomass (A) and relative biomass accessible to fisheries (B) of six trophic levels of the Aegean Sea EcoTroph model.

in fishing effort poses an elevated risk of overexploitation for species at higher TLs. The increase in total catch was not linear and reached a maximum value before beginning to decline. Catches at lower TLs did not reach their maximum possible values with any of the examined mE, as they continued to increase with each multiplier. Meanwhile, catches of small pelagic species (i.e., TL = 3.2) approximately doubled with the doubling of fishing effort. The effects of simulated catch relative to the initial catch indicated that at TLs near 5, catch could only increase by approximately 10% with a doubling of fishing effort before beginning to decline (Fig. 6). In contrast, catch levels at other trophic tiers did not reach a peak within the tested range of mE.

The sensitivity analysis indicated that, among the parameters tested, total biomass was most responsive to variations in the top-down control coefficient (Fig. 7). Higher α values slightly reduced the impact of increased fishing effort on biomass, while lower α values led to a steeper decline. In contrast, accessibility (*Acc.*) had the strongest effect on catch, with higher accessibility values consistently producing greater yields, particularly at effort multipliers above the current level (Fig. 7). Changes in the detritus recycling coefficient (β) had minimal influence on catch and only a modest effect on biomass, with higher β values maintaining slightly greater biomass under high fishing pressure (Fig. 7).

The degree of exploitation was observed using E_{MSY} and $E_{0.1}$ indicators. Simulations indicated that under current conditions, $E_{0.1}$ is exceeded both in low (below 2.7) and high TLs (above 4.5). Interestingly, while E_{MSY} does not fall within the tested range of multipliers for small pelagic species, $E_{0.1}$ was comparatively much higher for these species, indicating their catch could increase significantly before reaching full exploitation. Among all TLs, the highest $E_{0.1}$ was observed between TLs 3 and 3.5 (European anchovy and commercially important demer-

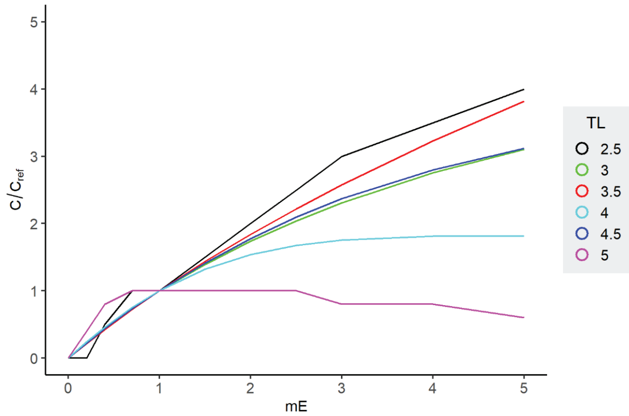

***Fig. 6**:* Simulated relative catch of six trophic levels of the Aegean Sea EcoTroph model.

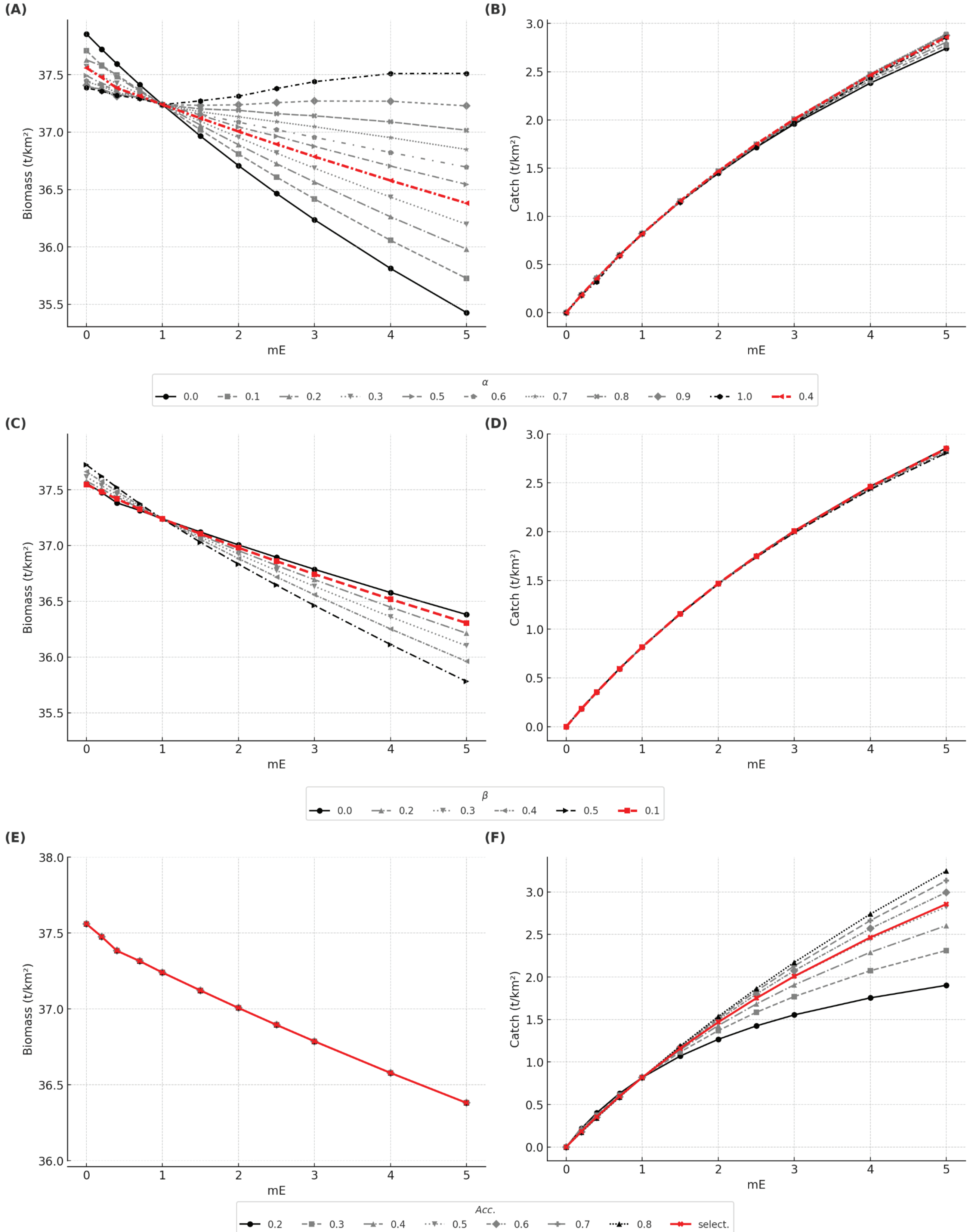

Fig. 7: Sensitivity analysis in relation to key EcoTroph parameters: top-down control (α) for biomass (A) and catch (B), input control for biomass recycling (β) for biomass (C) and catch (D), and accessibility to fisheries (*Acc.*) for biomass (E) and catch (F). The parameters used in the current model are highlighted in red for reference.

sal species), confirming their high potential for increased catch (Fig. 8). The slight increase between TLs 3.6 and 4 can be attributed to the higher catch of mackerels and squids in the model. Thus, a moderate exploitation rate was assumed at intermediate TLs, even though overexploitation can occur if fishing effort intensifies significantly with even higher multipliers. On the other hand, predatory FGs such as sharks and large pelagics, along

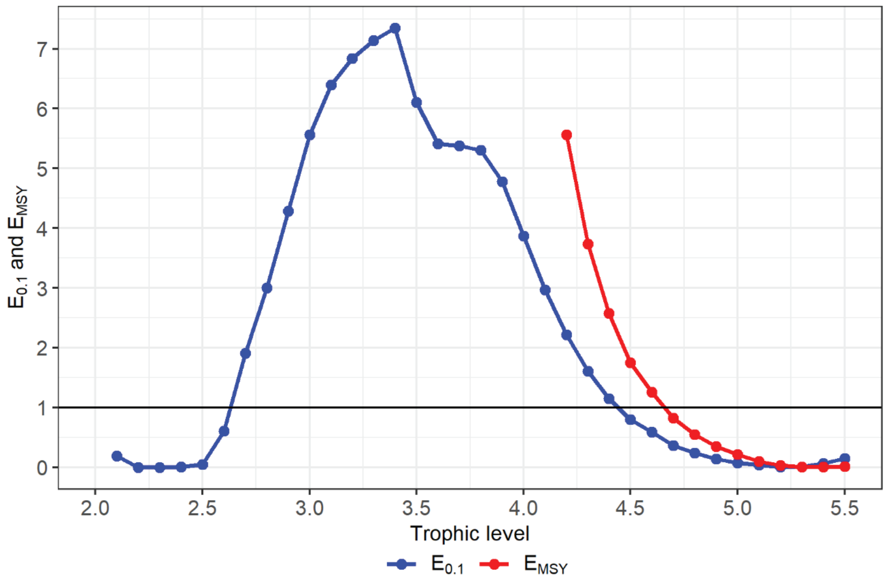

Fig. 8: Indicators of the current status of the ecosystem, including exploitation rates $E_{0.1}$ and E_{MSY} per trophic level in the Aegean Sea ecosystem.

with commercially important detritivorous/scavenger groups such as Norway lobster, were fully exploited or overexploited in terms of catch.

Discussion

The EcoTroph model of the Aegean Sea revealed that the ecosystem is characterized by the depletion of top predators (FGs at higher TLs), a pattern consistently reported across the Mediterranean Sea (Halouani *et al.*, 2015). The trophic spectrum of biomass accessible to fisheries showed low biomass concentrations above TL 4, in contrast to ecosystems such as the southern Benguela (Gasche *et al.*, 2012), the Guinea coast (Gascuel *et al.*, 2011; Gasche & Gascuel, 2013), and the Bay of Biscay (Lassalle *et al.*, 2011; Lassalle *et al.*, 2012), where top predators remain more abundant. The decline of large pelagic fishes (Dimarchopoulou *et al.*, 2021), sharks (Ferretti *et al.*, 2008), and marine mammals (Maynou *et al.*, 2011; Lambert *et al.*, 2025) has been well documented, and the Aegean Sea results fit within this regional trend.

The catch trophic spectrum, peaking between TLs 3 and 3.5, agreed with other Mediterranean EcoTroph applications (Halouani *et al.*, 2015; Prato *et al.*, 2016) and reflected the dominance of lower-TL small pelagic fishes (European anchovy, European pilchard) and demersal species (flatfishes, red mullets). Catches at intermediate TLs could still increase with higher effort multipliers, whereas those at higher TLs rapidly reached thresholds beyond which they declined. This confirms the limited productive potential of top predators and highlights the dependence of Aegean fisheries on mid-trophic groups (Keramidas *et al.*, 2022; Touloumis *et al.*, 2025), consistent with findings from the Gulf of Gabès (Halouani *et al.*, 2015).

Simulations of increasing fishing effort showed that the Aegean Sea biomass spectrum was less affected compared to more productive systems such as the southern Catalan and Ionian Seas (Halouani *et al.*, 2015). This may result from the lower sensitivity of small pelagic species in the Aegean Sea, whose short life spans, high natural mortality, and environmentally driven recruitment lead to rapid fluctuations (Ramírez *et al.*, 2021). In the southern Catalan and Ionian Seas, where small pelagics dominate the catches (Giannoulaki *et al.*, 2013) and exploitation is intense (Coll & Libralato, 2012), catches peaked mainly at intermediate TLs (Shannon *et al.*, 2014). In contrast, in the Aegean Sea and the Gulf of Gabès, lower exploitation levels allowed catches to rise across most TLs as effort increased.

FGs at both low and high TLs were more sensitive to fishing than those at intermediate TLs. High-TL species, already overexploited in most Mediterranean systems, declined with increasing effort (Froese *et al.*, 2018), whereas low-TL species showed moderate catch increases due to their high reproductive potential (Smith *et al.*, 2011). Intense fishing at low and intermediate TLs can reduce prey availability, alter predator diets, and reshape competition (Rehren & Gascuel, 2020), leading to cascading effects that ultimately reduce catches of mid- and high-trophic predators such as mackerels and large pelagics (Touloumis *et al.*, 2025). Catches at TLs 4-4.5 did not increase despite greater effort, indicating that harvesting capacity has already been reached (Halouani *et al.*, 2015). This likely reflects reduced predation mortality caused by the decline of top predators (du Pontavice *et al.*, 2021) and the cascading impacts of long-term fishing pressure in the Mediterranean Sea (Dimarchopoulou *et al.*, 2021), leading to lower biomass and body size (Piroddi *et al.*, 2021; Touloumis *et al.*, 2025).

Accessibility to fishing activity was another major factor shaping exploitation patterns (Jennings & Collingridge, 2015). Fishing exerts stronger effects on the biomass accessible to fisheries than on total biomass, highlighting localized overexploitation of specific stocks

(Froese *et al.*, 2016; Froese *et al.*, 2017). These effects are reinforced by the multi-gear nature of Mediterranean fisheries (Stergiou *et al.*, 2016) and the spatial concentration of fleets in certain areas (Colloca *et al.*, 2017). High fishing mortality can further alter species balance, favoring non-target species that benefit from the depletion of competitors (Tsikliras *et al.*, 2021). In extreme cases, this can lead to structural shifts in ecosystem composition, as observed in the northern Benguela (Heymans *et al.*, 2004), the coast of Senegal (Colléter *et al.*, 2012), the Black Sea (Akoglu, 2023), and more recently in the Aegean Sea (Touloumis *et al.*, 2025).

The sensitivity analysis confirmed that the top-down control coefficient (α) primarily affected biomass through compensatory feedback within the food web (Lynam *et al.*, 2017). Higher α values buffered biomass decline by allowing prey release after predator removal (Colléter *et al.*, 2013), while lower α values led to a steeper decline. Accessibility (*Acc.*) had the strongest effect on catch, determining the proportion of biomass available for harvest, while the detritus recycling coefficient (β) had little influence, consistent with results from the Guinea coast (Gasche *et al.*, 2012). Overall, accessibility largely governs catch outcomes, whereas α and β modulate energy redistribution and the balance between trophic feedback and ecosystem productivity (Vasconcellos *et al.*, 1997).

The bimodal pattern in exploitation risk reflected two main mechanisms. High-TL predators, which grow slowly and have low productivity (Young *et al.*, 2015), are vulnerable even to moderate fishing, while benthic and detritivorous groups are exposed through spatial overlap with trawl grounds (González-Irusta *et al.*, 2018). High accessibility, bycatch, and chronic disturbance keep these groups near precautionary thresholds. Intermediate TLs display greater resilience due to faster turnover and broader diets but can lose this buffer if fishing intensifies (Kaplan *et al.*, 2013). Management should therefore aim to limit overexploitation of predators, reduce benthic disturbance, and treat mid-TL capacity as temporary rather than as an opportunity for increased effort (Fenberg & Roy, 2008).

EcoTroph provides a synthetic TL perspective that complements other ecosystem models. A potential caveat arises from the steady-state Ecopath input, which simplifies temporal variability, and from uncertainties in input data that can propagate through trophic spectra (Gascuel & Pauly, 2009). These aspects underline that EcoTroph results should be interpreted alongside dynamic and species-specific approaches (Bourdaud *et al.*, 2016). Despite these constraints, EcoTroph offered a valuable ecosystem-wide diagnosis of fishing impacts in the Aegean Sea and highlighted the need for management strategies that integrate TL insights with species-based and spatially explicit analyses.

Conclusions

This study demonstrated the usefulness of EcoTroph as a trophic modelling tool for assessing ecosystem structure and fishing impacts in the Aegean Sea. Biomass accessible to fisheries was concentrated at intermediate TLs, dominated by small pelagic fishes, while high TL predators were shown to be particularly vulnerable to fishing pressure. Simulations indicated that moderate effort could maintain biomass stability and support yields, but increasing effort beyond precautionary thresholds could lead to rapid depletion, especially at the upper and lower ends of the trophic spectrum. These results highlighted the importance of an ecosystem-based fisheries management. Protecting high TL predators is essential for maintaining ecosystem structure and balance, while the apparent capacity of mid-trophic species to support catches should be treated as conditional and time-limited rather than sustainable in the long term. Although EcoTroph is limited by its steady-state assumptions and lack of spatial or species-specific resolution, it provides a valuable complementary perspective to other modelling approaches. By diagnosing exploitation patterns across the trophic continuum, it can inform management strategies aimed at balancing fisheries productivity with biodiversity conservation in the Aegean Sea.

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Supplementary Data

The following supplementary information is available online for the article:

Table S1. Species synthesis of functional groups in the ECOTROPH model of the Aegean Sea ecosystem. For further details on species composition parameters, the reader may refer to Keramidas *et al.* (2022).

Fig. S1: The biomass trophic spectrum of the Aegean Sea EcoTroph model by functional group. The black line represents the total biomass. For a clearer graphical illustration, some functional groups (i.e., Benthic invertebrates, Detritus, Micro/Mesozooplankton, Phytoplankton) were excluded.

Fig. S2: The trophic spectrum of the biomass accessible to fisheries for the Aegean Sea EcoTroph model, by functional group. The black line represents total accessible biomass.

Fig. S3: The bottom trawling (OTB) catch trophic spectrum of the Aegean Sea EcoTroph model by functional group. For a clearer graphical illustration, trophic spectra lower than TL 2.5 were excluded.

Fig. S4: The purse seining (PS) catch trophic spectrum of the Aegean Sea EcoTroph model by functional group. For a clearer graphical illustration, trophic spectra lower than TL 2.5 were excluded.

Fig. S5: The beach seining (BS) catch trophic spectrum of the Aegean Sea EcoTroph model by functional group. For a clearer graphical illustration, trophic spectra lower than TL 2.5 were excluded.

Fig. S6: The small-scale coastal fisheries (SSC) catch trophic spectrum of the Aegean Sea EcoTroph model by functional group. For a clearer graphical illustration, trophic spectra lower than TL 2.5 were excluded.

Fig. S7: The cumulative catch by fleet trophic spectrum of the Aegean Sea EcoTroph model. The black line represents total catch. For a clearer graphical illustration, trophic spectra lower than TL 2.5 were excluded.

Fig. S8: The trophic spectra of fishing mortality and fishing loss rate of the Aegean Sea EcoTroph model.