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Διπλωματική Εργασία

Ανάπτυξη οικοσυστημικού μοντέλου Ecopath για την περιγραφή του τροφικού πλέγματος του Κορινθιακού κόλπου

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MSc Oceanography and Management of the Marine Environment

Master’s Thesis

Development of an Ecopath ecosystem model for the description of the food web of the Gulf of Corinth

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Περίληψη

Η Μεσόγειος Θάλασσα χαρακτηρίζεται ως σημείο υψηλής βιοποικιλότητας, το οποίο αντιμετωπίζει επιπτώσεις από τους ανθρωπογενείς παράγοντες πίεσης, όπως η υπεραλίευση και η κλιματική αλλαγή, που επηρεάζουν δραστικά το περιβάλλον της. Συγκεκριμένα, ο Κορινθιακός Κόλπος, αντικείμενο μελέτης της εν λόγω έρευνας, φιλοξενεί ένα βαθύ οικοσύστημα με πλούσια βιοποικιλότητα το οποίο όμως δεν έχει μελετηθεί εκτενώς σε σύγκριση με άλλα οικοσυστήματα των ελληνικών θαλασσών. Για την διεξαγωγή της μελέτης, που αφορά στην περίοδο 2014-2016, εφαρμόστηκε ένα τροφικό μοντέλο Ecopath με σκοπό τη σκιαγράφηση της οικολογικής του δομής. Το μοντέλο περιλαμβάνει 39 λειτουργικές ομάδες, ενώ δίνει ιδιαίτερη έμφαση στα δελφίνια, λόγω της υψηλής τους συγκέντρωσης , στα μεσοπελαγικά ψάρια εξαιτίας της αφθονίας τους και στα εμπορικά είδη ώστε να εκτιμηθούν οι επιπτώσεις της αλιείας. Οι ενεργειακές πηγές που βασίζονται στα θραύσματα κυριαρχούν, προωθώντας μια ποικιλόμορφη θαλάσσια κοινότητα, ιδίως στην πελαγική ζώνη. Βασικά είδη, όπως το μεσοζωοπλαγκτόν, τα καλαμάρια, οι καρχαρίες και ο μπακαλιάρος, διαμορφώνουν τις τροφικές σχέσεις στη στήλη του νερού, ενώ βασικές ομάδες θηραμάτων, όπως οι γαρίδες και τα μεσοπελαγικά ψάρια, συμβάλλουν ανάλογα. Παρά την ύπαρξη ορισμένων ιστορικών αναφορών για ρύπανση και έντονες αλιευτικές δραστηριότητες, το οικοσύστημα του Κόλπου της Κορίνθου δεν παρουσιάζει ενδείξεις αλιευτικής πίεσης. Αυτό είναι εμφανές στην εκτιμώμενη πιθανότητα βιώσιμης αλιείας στο οικοσύστημα, η οποία ανέρχεται στο 96%. Το μοντέλο που παρουσιάζεται αναπτύχθηκε για να διευρύνει τις γνώσεις αναφορικά με τις τροφικές σχέσεις των ειδών και τις ροές ενέργειας στο σύστημα, καθιστώντας το ένα κρίσιμο εργαλείο για αποτελεσματικές πρωτοβουλίες διαχείρισης και διατήρησης στον Κορινθιακό Κόλπο.

Λέξεις Κλειδιά

Κορινθιακός Κόλπος, Τροφικό Πλέγμα, Οικολογικό Μοντέλο, Οικοσυστημική Διαχείριση, Είδη Κλειδιά

Abstract

The Mediterranean Sea is characterized as a biodiversity hotspot, which encounters impacts from human-induced stressors, such as overfishing and climate change, which exert pressure on its ecosystem. The Gulf of Corinth hosts a deep ecosystem with a rich biodiversity that has not been extensively studied compared to other ecosystems of the Greek seas. An Ecopath trophic model was applied for the period 2014-2016 to outline its ecological structure. Including 39 functional groups, the model placed particular emphasis on dolphins, given their concentrated presence, mesopelagic fishes due to their abundance, and commercial species to assess the impact of fishing. Detritus-based energy sources dominate, promoting a diverse marine community, particularly in the pelagic zone. Keystone species, such as mesozooplankton, squid, sharks, and hake, shape the trophic relationships in the water column, with keystone prey groups such as shrimps and mesopelagic fish contributing accordingly. Despite some historical reports of pollution and intense fishing activities, the Gulf of Corinth ecosystem shows no evidence of fishing pressure. This is evident in the estimated probability of sustainable fisheries in the ecosystem, which is estimated at 96%. This model was developed to expand knowledge of species trophic relationships and energy flows in the system, making it a critical tool for effective management and conservation initiatives in the Gulf of Corinth.

Keywords

Gulf of Corinth, Food web, Ecological Model, Ecosystem-based Management, Keystone Species

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1. Introduction

The Mediterranean Sea is recognized as a significant hotspot of marine biodiversity, hosting an impressive variety of around 17,000 marine species (Coll *et al.*, 2010). It exhibits notable features of high salinity, temperature, and water density (Tanhua *et al.*, 2013). Geographically, the region occupies a transitional zone between mid-latitude and sub-tropical atmospheric circulation regimes (Cramer *et al.*, 2018). It is divided into two main basins: the western basin with an average depth of approximately 1,600 meters, comprising the Algero Provençal basin and the Tyrrhenian Sea, and the eastern basin, encompassing the Ionian, Aegean, and Levantine Seas (Sardà *et al.*, 2004). Remarkably, the Mediterranean's diverse ecosystem hosts a considerable number of endemic species, amounting to over 25% of the total species found in the basin (Occhipinti-Ambrogi and Savini, 2003).

In recent years, the examination of threats to the Mediterranean Sea has intensified. The Mediterranean Sea's surface temperature rises at 0.4 ºC per decade (Sakallı, 2017), impacting biodiversity. Lessepian species migration constitutes 15% of this impact (Marbà *et al.*, 2015). Indeed, the increased influx of tropical species into the eastern Mediterranean Sea is amplified by oceanic warming (Raitsos *et al.*, 2010). Fish and cnidarian species are the most affected by the above condition, accounting for 53%. These temperature increases have a greater than 50% chance of affecting various aspects of species' lives (Marbà *et al.*, 2015). Urgent action is needed to address these ecological consequences in this vital marine ecosystem. The Mediterranean Sea is also, subject to high fishing pressure due to its proximity to many countries and long history of exploitation. Comprehensive studies conducted on its fish stocks (e.g. Colloca *et al.*, 2017; Hilborn *et al.*, 2020; Vasilakopoulos *et al.*, 2014) reveal an alarming reality of overfishing. Specifically, within FAO fishing area 37 (Mediterranean and Black Sea), a significant 62.5% of stocks are being fished at unsustainable levels, underscoring the urgency for implementing sustainable fishing practices and management strategies (FAO, 2020).

The challenges at hand could be effectively addressed through the application of ecosystem management, a concept that has evolved with various interpretations but rests on several fundamental assumptions (Morishita, 2008). Successful implementation of ecosystem-based management hinges on key prerequisites, including robust data on bycatch, species coexisting within the same ecosystem or interconnected with the target species, and reliable indicators to monitor changes in the ecosystem (Juda, 2009) always in conjunction with good governance (Bundy *et al.*, 2017). For instance, the Common Fisheries Policy (CFP) represents the European Union's (EU) principal mechanism for fisheries management, specifically encompassing the governance of fisheries activities within the Mediterranean Sea and other relevant regions (Jennings and Rice, 2011). To effectively support the demands of an Ecosystem-based Approach to Fisheries (EAF), a scientific program should be structured into three distinct categories (Jennings and Rice, 2011): (i) tactical research aimed at addressing specific issues, (ii) strategic research encompassing fisheries, ecosystems, management, social systems, and governance, and (iii) comprehensive monitoring and assessment endeavors.

The paradigm shift towards an ecosystem approach has generated a demand for robust tools to manage information concerning complex ecosystem interactions. Consequently, trophic network models of aquatic ecosystems are increasingly gaining prominence in scientific literature. These models provide a comprehensive representation of ecosystem structure, functioning, and dynamics, making them indispensable for advancing our understanding of food web theory (Hattab *et al.*, 2013). The fish value chain in the Mediterranean Sea is experiencing a significant increase, leading to notable economic benefits, improved employment rates, and enhanced protein consumption (Liquete *et al.*, 2016). Nonetheless, this intensified fishing activity is exerting considerable pressure on several marine ecosystems, particularly in the Western and Adriatic seas, giving rise to significant sustainability concerns that require urgent attention (Liquete *et al.*, 2016). Similar concerns arise for the rest of the Mediterranean Sea.

To address these concerns ecosystem models have been developed and applied in the basin. Ecopath with Ecosim (Christensen and Walters, 2004) is probably the approach most frequently used in the field of EAF. Presently, numerous ecological models in the central and eastern Mediterranean Sea (e.g., Coll and Libralato, 2012; Corrales *et al.*, 2017; Papantoniou *et al.*, 2021; Tsagarakis *et al.*, 2010) contribute to an enhanced understanding of ecosystems and management strategies in addressing sustainability challenges across the Mediterranean region. Applying models to localized regions within the Mediterranean, such as the Greek seas (e.g. Dimarchopoulou *et al.*, 2019; Keramidas *et al.*, 2022; Papantoniou *et al.*, 2021; Tsagarakis *et al.*, 2022) complements the research and models developed in the wider basin. In addition, local models are used to target specific research challenges (e.g. eutrophication, Papantoniou *et al.*, 2023); cetaceans-fisheries interactions, Carlucci *et al.* (2021)), which are relevant at the local scale rather than the entire basin. Ultimately, a more distinct understanding emerges regarding the pressures on the Mediterranean ecosystems and the necessary actions to be undertaken, encompassing both local and global perspectives (e.g. Piroddi *et al.*, 2017, 2015).

The Gulf of Corinth is a deep-sea basin located in the eastern Mediterranean Sea (Greece) and is an area of high ecological importance. This work focuses on the application of an Ecopath food-web model dedicated to the description of the food web of the Gulf of Corinth. As the Western Mediterranean region, including this area, has insufficient data (Albano *et al*., 2020), this study should prove to be a valuable contribution to improving our understanding of the region's marine ecosystem. Although some studies have been conducted on the geological features (e.g. Beckers et al., 2016; Poulos et al., 1996) of the bay, and the unique dolphin population it hosts (e.g. Bearzi et al., 2016; Bonizzoni et al., 2019; Carlucci et al., 2021; Frantzis and Herzing, 2002), no research has been done on the bay as a whole. We aim to provide a detailed picture of ecosystem structure and function, including biomass and trophic flows. Our focus is on quantifying emergent ecosystem properties, examining the interplay among the trophic levels of the food web, and identifying the ecological role of keystone species. To maintain the health of the Gulf, it is essential to understand and monitor its food web (Bearzi et al., 2011; Kapelonis et al., 2023; Santostasi et al., 2021). Moreover, we will assess the direct and indirect effects of local fishing fleets on the food web by incorporating fishing activities within an ecosystem context, utilizing exploitation indicators. Finally, the comparison with areas that have been extensively researched and have reliable data will help to ensure that the results are accurate and trustworthy. Furthermore, studying well-researched areas can help identify gaps in knowledge and highlight specific scientific areas that need further exploration. The development of an Ecopath ecosystem model is an important tool in this effort.

2. Materials and Methods

2.1 Study area

The study area, the Gulf of Corinth (Fig. 1), is a semi-enclosed marine system at the easternmost part of the Ionian Sea. It stretches from west to east at 120 km, from south to north at 30 km, and at a depth approaching 930 m (Beckers *et al.*, 2016). The Gulf of Corinth, owing to its remarkable depth relative to its small size, harbors biodiversity of considerable importance. The total area considered for modeling was estimated at 2166.5 km^2 based on GIS tools. The Gulf of Corinth is linked with the Ionian Sea through the Patraikos Bay and with the Aegean Sea through an artificial connection (Corinth canal) at the Isthmus of Corinth. In the Northern part of the gulf, there are some embayments where the shelf extends to 200 m with smooth slopes. In contrast, in the southern part, the slopes are quite steep. In the central part of the bay, there is an abyssal plain which for the most part maintains a flat area with slight variations in slopes and depths of up to 800 m or even more, as mentioned above (Poulos *et al.*, 1996).

The marine ecosystem of the study area is highly understudied compared to other areas of Greece. Nevertheless, the bay hosts, around its shores, several rural populations that engage in fishing and aquaculture activities. The northern part of the Gulf hosts 24 fish farms (Beriatos *et al.*, 2019), a fact that is worth mentioning because they are associated with the coastal activity of bottlenose dolphins (Rossi *et al.*, 2022). During the summer season, the Gulf of Corinth is of tourist interest as it is only a few hours away from the metropolitan center of Athens, a fact that potentially stresses its marine ecosystem. The studies that have been carried out in the area mainly concern its geology as it is geologically a quite active area (e.g. Beckers *et al.*, 2016; Poulos *et al.*, 1996), while ecological studies focus on the dolphin populations that the bay hosts, which number over 1400 individuals (e.g. Bearzi *et al.*, 2016; Bonizzoni *et al.*, 2019; Carlucci *et al.*, 2021). A plethora of organisms are hosted in the Gulf of Corinth, from commercial pelagic to intertidal bony fishes, sharks, turtles, etc. It is worth mentioning that the bay is a Natura 2000 site of interest for the protection of biodiversity(Natura 2000, 2020).

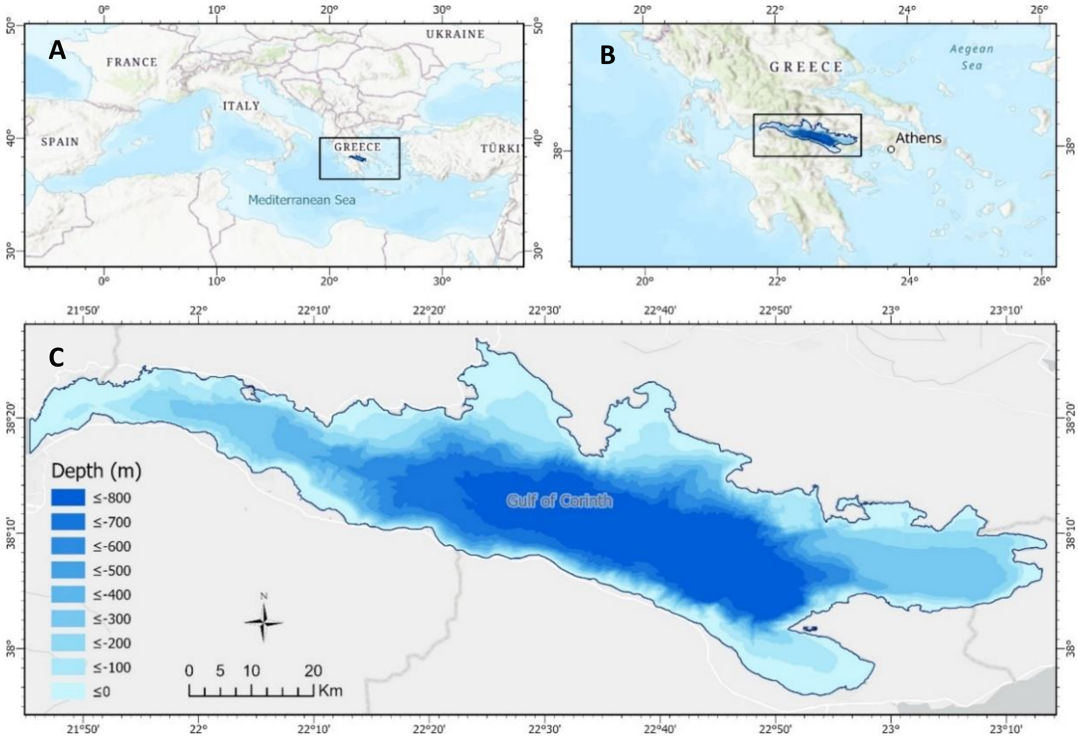

Figure 1: Study area: the Gulf of Corinth's position to the Mediterranean (A) and Greece (B), as well as its bathymetry (C).

2.2 Model approach

An ecosystem model for the Gulf of Corinth was developed and parameterized using the Ecopath with Ecosim (EwE) approach (software v. 6.6), which is widely used for the analysis of food web dynamics (Christensen and Walters, 2004b). The model was set up to analyze the trophic relationships in the Gulf of Corinth. To obtain a comprehensive quantitative assessment of the average annual flows (in t km^{-2} yr^{-1}) among the wet biomasses (in t km^{-2}) of the functional groups (FG) present in the Corinthian Gulf ecosystem, a static Ecopath model was developed, integrating environmental, biological and fishery data. The functional groups represent the structural components of the food web as defined in our model; they are either single species or groups of species and are compiled along the lines of common characteristics, their habitat, or even their feeding habits or importance for fisheries. The Ecopath component describes a static snapshot of the ecosystem, while the Ecosim component simulates the dynamics of the ecosystem over time, taking into account factors such as trophic interactions, fishing, and environmental variability. The model can be used to explore the impacts of different management strategies and environmental changes on the ecosystem and its components (Christensen and Walters, 2004b; Heymans *et al.*, 2016). The method of operation of the Ecopath model is discussed in detail by Christensen and Walters (2004). Ecopath utilizes two master linear equations to describe and parameterize the trophic interactions among FGs. For any functional group, production is a function of natural and fishing mortality so that the corresponding equation follows (Christensen and Walters, 2004b; Heymans *et al.*, 2016):

Production = catch + predation + net migration + biomass accumulation + other mortality

$$P_i = Y_i + B_i \cdot M2_i + E_i + BA_i + P_i \cdot (1 - EE_i) \quad (1)$$

In more detail: The initial equation describes the total production (Pi) for each group i, assuming a mass balance for a given length of time. Total production depends on predation mortality (M2i), which is driven by factors such as diet composition (DC), consumption (Qi), predator biomass (Bj), as well as ecosystem exports due to fishing (Yi), net migration rate (Ei), biomass accumulation (BAi) and other forms of mortality (1-EE). Herein, EE represents the ecotrophic efficiency of a group, indicating the proportion of the group's output used within the system. The second equation then ensures energy balance for each group, defining balance when a group's consumption (Qi) equals the sum of production energy (Pi), respiration (R), and unassimilated food (U/Q) i. For the functionality of the model, the key parameters for each group include diet composition (DC), unassimilated food (U/Q) i, catch (Yi), exports (Ei), and three fundamental parameters: Bi, (Q/B) i and EEi.

Consumption=production + respiration + unassimilated food. (2)

For model parameterization, input includes diet composition, catches (landed and discarded), and three of the four following parameters: biomass (B), production/biomass (P/B), consumption/biomass (Q/B), and Ecotrophic Efficiency (EE), while the fourth is estimated by the software based on the model equations(Christensen and Walters, 2004b).

2.3 Input

For the needs of the system, 39 FGs (Appendix, Table A1) were created, specifically, four plankton groups, one non-commercial benthic invertebrate group, three decapod groups, two cephalopod, and 22 fish functional groups, while marine megafauna were represented by two dolphin groups, sea turtles, seals, and seabirds. Finally, two non-living groups were included, i.e., discards and detritus. The model was built with data from the period 2014-2016.

The fish and commercial invertebrates' FGs were built using as a basis the ones defined for the Saronikos Gulf model (Papantoniou *et al.*, 2021) where multivariate analysis was applied to species diets, after making the modifications required for the Gulf of Corinth ecosystem. The list of fish species was taken from bottom trawl (MEDITS; Spedicato *et al.*, 2019) and acoustic (MEDIAS; Leonori *et al.*, 2021) surveys, the Hellenic Statistical Authority (ELSTAT, 2021) and from other HCMR field survey data (e.g., MESOBED project; Kapelonis *et al.*, 2023). Commercial species such as hake (*Merluccius merluccius*), sardine (*Sardina pilchardus*), and anchovy (*Engraulis encrasicolus*) were included as individual functional groups. In addition, sufficiently abundant species, such as Mueller's pearlside (*Maurolicus muelleri*) were also included as single-species functional groups. Special focus was given to dolphins, which were represented by two groups, one consisting of Striped (*Stenella coeruleoalba*) and Common dolphins (*Delphinus delphis*), which are known to form mixed groups in the region (Bearzi *et al.*, 2016; Frantzis and Herzing, 2002) and a second group consisting of bottlenose dolphins (*Tursiops truncatus*).

Stock assessments, field ecological studies, and literature are the main data sources used to build the model. For biomasses, bottom trawl data (MEDITS; (Spedicato MT *et al.*, 2019), acoustic data (MEDIAS; Leonori *et al.*, 2021), and in the case of dolphins (Bearzi *et al.*, 2016), seals (Azzolin *et al.*, 2020) and turtles (DiMatteo *et al.*, 2022), data from observational studies were used. The dolphins' observational data combined with the estimation of the average individual size in the study area, provided biomass data for the corresponding number of individuals (Appendix, Table A1). For benthic and demersal fish, biomass data from bottom trawl surveys were used to estimate biomass in t/km^2 in four bathymetric strata after applying the swept area method and weighing with the area occupied by each stratum (Spedicato *et al.*, 2019). Of small pelagic and mesopelagic species, biomass estimation was based on acoustic and pelagic trawl data collected in HCMR surveys(Kapelonis *et al.*, 2023; Leonori *et al.*, 2021). For other species (e.g. Benthic Invertebrates, Appendix Table A1) that there was insufficient information, biomass was obtained from other sources (Moutopoulos *et al.*, 2018; Papantoniou *et al.*, 2021).

The P/B and Q/B parameters were added to the model mainly after calculation through empirical equations. For fish, the empirical equation for P/B was the one by Pauly (1980) and for Q/B by Pauly *et al.*(1990), while additional empirical equations were used to calculate these factors for dolphins (Innes *et al.*, 1987; Trites *et al.*, 1997) (Appendix, Table A1). For some functional groups (e.g. seabirds, gelatinous plankton), the specific variables were retrieved from other models from adjacent areas (Ionian Sea: Moutopoulos *et al.*, 2018; Saronikos Gulf: Papantoniou *et al.*, 2021) due to shortage of information for the Gulf of Corinth (Appendix Table A1). The diet composition (DC) of the species was mainly derived from the literature and thus a relevant database was created. For each FG, the diet composition was estimated after weighing each species' diet preferences with the relative biomass contribution of the species in the group.

Fishing activities in the Gulf of Corinth were included in the model and divided into four main categories: trawlers, purse seines, boat seines, and a category concerning various other small artisanal fishing gears referred to as scale small-scale fisheries (SSF). For landings, we obtained data from ELSTAT (2022), specifically the quantity of each species caught in each gear for the years 2014 to 2016. Data from commercial vessels in an area of similar characteristics (Ionian Sea) were used to calculate the discard ratio (discards/landings) for each FG in each gear and, therefore, to estimate total discards based on landings data (CINEA, 2022). A detailed description of the data sources and parameterization of all functional groups is provided in Appendix Table A1.

2.4 Balancing

For an Ecopath model to be considered ecologically and thermodynamically balanced, it must meet the following requirements for all functional groups: EE<1, P/Q values between 0.1 and 0.35 excluding fast-growing groups, respiration/feed assimilation ratio <1, respiration/biomass ratio between 1 and 10 for fish and above this limit for smaller organisms, net efficiency of food conversion (NE) > gross efficiency for food conversion (GE) and ultimately production/ respiration rate <1 (Christensen *et al.*, 2005; Christensen and Walters, 2004b). Upon implementing the data into the model, it was observed that the conditions for the model to be in equilibrium were unmet, as 19 functional groups had EE>1. To balance the model, a manual approach with stepwise modifications in input parameters was followed, mainly starting from high trophic levels and working downwards, following the guidelines provided in the literature (Heymans *et al.*, 2016). Parameters with high uncertainty in the data were reconfigured, mainly diets but also other inputs (e.g. biomass, EE), where needed. Once the model was parameterized and balanced, the PREBAL diagnostics (Appendix Figure 1) described in detail by Link (2010) was applied to ensure that the model adheres to ecological principles. The pedigree routine, which attributes a score to each input parameter according to its origin and resolution, was utilized ultimately to assess the quality of input parameters and evaluate the quality of data sources.

2.5 Data analysis

A series of analyses was applied and indicators (Table 1) were estimated to describe the structure and functional characteristics of the Gulf of Corinth, mainly based on flows among functional groups. Most of these were direct outputs of the software, such as the Mixed Trophic Impact (MTI) plot, the flow diagram, the Lindeman spine, and the keystone index diagram, while others were calculated externally (e.g., fractions of flows and biomasses in the pelagic and demersal systems, SURF and Connectance Index). The sum of all key flows in the system is expressed through the total system throughput index and essentially presents the whole system in the form of flows. The MTI shows how a small increase in one group's biomass affects another group's biomass. It can reveal direct predator-prey effects and indirect effects on the prey's prey or competitor (Christensen *et al.*, 2005). A keystone species in a food web refers to the species that, in proportion to its biomass, has a very high impact on the system; the keystone index proposed by Libralato *et al.* (2006) was used. The exploitation rate (F/Z), denoting the fraction of total mortality (Z) ascribed to the impact of fishing activities (F), was computed individually for every distinct Functional Group (FG). To assess the level of exploitation of stocks and the sustainability of fishing activities, we calculated the %PPR (Primary Production Required) both from primary production and from primary production and detritus, as well as the probability of sustainable exploitation (Psust, Table 1).

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

Index	**Description**
Total system throughput	Expresses the total flows within the system and is expressed in units of $t \cdot km^{-2} \cdot year^{-1}$(Christensen *et al.*, 2005)
Total primary production/ total respiration	The ratio of total primary production to total respiration is known as the ecological efficiency ratio, and it is an essential measure of the maturity of a system, as noted by Christensen *et al.* (2005), who based their work on the earlier research of Odum (1971). A value below 1 indicates a stressed

	environment, while a value above 1 suggests that the system is still in its early stages of development, and therefore, immature.
Net system production	The difference between total production and total respiration gives values that place the system closer to maturity (as the production value tends towards 0) or respectively to immaturity (Christensen *et al.*, 2005).
Total primary production/ total biomass	System maturity can be determined by the primary production to total biomass ratio. Immature systems accumulate biomass as production exceeds respiration (Christensen *et al.*, 2005)
System Omnivory Index	The omnivory index measures the diversity of prey consumed by a predator across trophic levels. A higher value indicates greater variation in the prey consumed (Christensen and Pauly, 1992).
Finn's Cycling Index	The 'cycling index,' introduced by Finn (1976), quantifies the proportion of an ecosystem's throughput that undergoes recycling.
Shannon diversity index	Shannon's diversity index (Shannon, 1948), estimates species diversity by considering the quantity of species present in a habitat and their respective abundance.
PPR	Introduced by Pauly and Christensen (1995) it is a metric utilized to assess the sustainability of fisheries, which expresses the primary production needed to maintain the catch.
Psust	The concept of the mean annual probability of sustainable fishing (Psust) has been recently devised as a method to evaluate the extent of overfishing within an ecosystem. This assessment is based on the estimation of the total depletion of secondary production about reference levels derived from ecosystem models, as established by Coll *et al.* (2008) and Libralato *et al.* (2008).

To establish which species has a regulatory role in the ecosystem, the SURF (SUpportive Role to Fishery ecosystems; Plagányi and Essington, 2014) and Connectance (Smith *et al.*, 2011) indicators were used.

The equation for calculating SURF index is:

$$SURF_i = \frac{\sum_{j=1}^{S} p_{ij}^2}{L} \quad (3)$$

with S predators and pij to stand for the diet of the predator j on prey i among the total number of linkages in the food web which is L. The scaled SURF index is a measure used to determine the importance of a prey species in an ecosystem. It takes into account the diet fraction of predators on the prey species and the total number of connections in a food web and is consistent with the analysis of Connectance. When all the values in the pij matrix are either 0 or 1, the Connectance measure used by Smith *et al.* (2011) is equal to the scaled SURF index. This means that Connectance is a specific scenario within the broader framework of the SURF index. Values closer to zero indicate that the species is not very important, while larger values indicate that it is (Plagányi and Essington, 2014). We calculated and plotted these metrics with respect to the consumer biomass proportion, which is the fraction of total consumer biomass consisting of a given species relative to the summed biomass of all species with a trophic level greater than 2 (Plagányi and Essington, 2014).

2.6 Comparison of outputs

We compared the ecological indicators generated by our model with seven other models developed for the Greek seas' ecosystems. This allowed us to present our findings within a more comprehensive framework. Specifically, we compared the Gulf of Corinth model results with those of models from the North Aegean Sea (Thracian Sea and Strymonikos gulf: Tsagarakis *et al.*, 2010; Thermaikos gulf: Dimarchopoulou *et al.*, 2022), the central Aegean Sea (Pagasitikos gulf: Dimarchopoulou *et al.*, 2019; Saronikos gulf: Papantoniou *et al.*, 2021), the entire Aegean Sea (Keramidas *et al.*, 2022) and the Ionian Sea (Northeastern Ionian Sea: Piroddi *et al.*, 2010: entire Ionian Sea: Moutopoulos *et al.*, 2018). Most of these models have been developed using similar methods to form FGs and estimate input data, resulting in comparable ecological structures. To prevent issues arising from structural differences in comparing these models, we only compared robust indicators that are not much affected by the model's structure (such as statistics and flows, or exploitation indices).

3. Results

The main results and the graphical representation of the interaction between functional groups, as well as the pedigree index indicating sufficient data but room for further research. The system shows higher production than consumption, suggesting an immature state. Several indicators, such as Finn's cyclic index and the Shannon diversity index, provide insights into the recycling of energy and species diversity in the Gulf of Corinth. MTI analysis reveals trophic interactions in the bay ecosystem. Low trophic groups positively affect many species, especially pelagic species. The analysis of keystoneness and connectivity indicators, as well as positive and negative interactions between species, highlight the importance of the different groups in the food web. At the same time, the impact of fisheries is also shown, which is limited.

3.1 Model input and trophic dynamics assessment

The initial data and resulting output parameters of the balanced model are presented in Table 2. The production/consumption ratios (P/Q), respiration/assimilation ratios (R/A), and net food conversion efficiencies for all functional groups were found to be within the expected range, as described by Christensen and Walters (2004). The pedigree index of the model is 0.566, denoting that the data available for the Gulf of Corinth is relatively sufficient but there is room for further research in the area. Based on the model's results, it was found that bottlenose dolphins, large pelagic fish, and seals were the species with the highest trophic levels (TLs) (Figure 2), with values of 4.43, 4.40, and 4.35, respectively. Following closely were stripped and common dolphins with a TL of 4.34, and hake with 4.10. Figure 2 displays the trophic transfers between different functional groups, including the fishing fleets. The arrangement of groups in the flow diagram is based on their TLs as provided in Table 2, while the arrows indicate the flow of energy between different groups. In terms of trophic interactions, there are several arrows that connect different trophic levels. The diagram reveals several species involved in multiple trophic interactions, for example zooplankton and pelagic fish (e.g. Planktivorous Fish, Bogue, Anchovy), which are consumed by several different species at higher trophic levels.

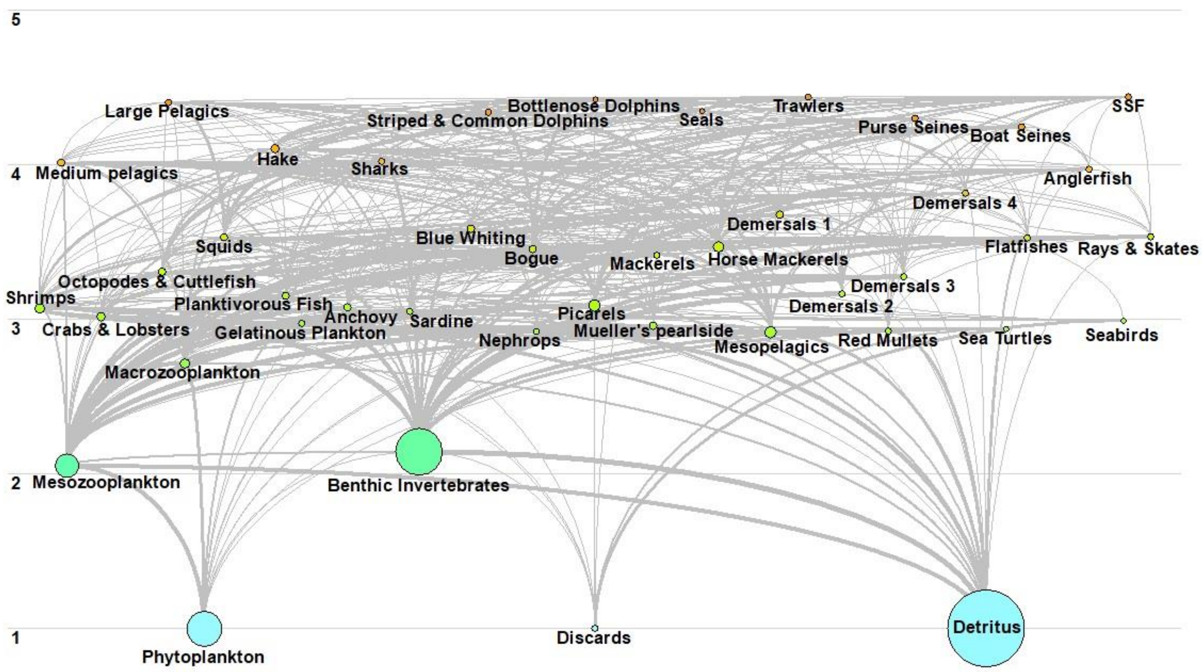

Figure 2: Flow diagram: the organization of the Gulf of Corinth food web by functional groups, arranged by increasing trophic level (y-axis). The size of each circle corresponds to the relative biomass of its respective functional group, while the lines denote the trophic connections between the groups.

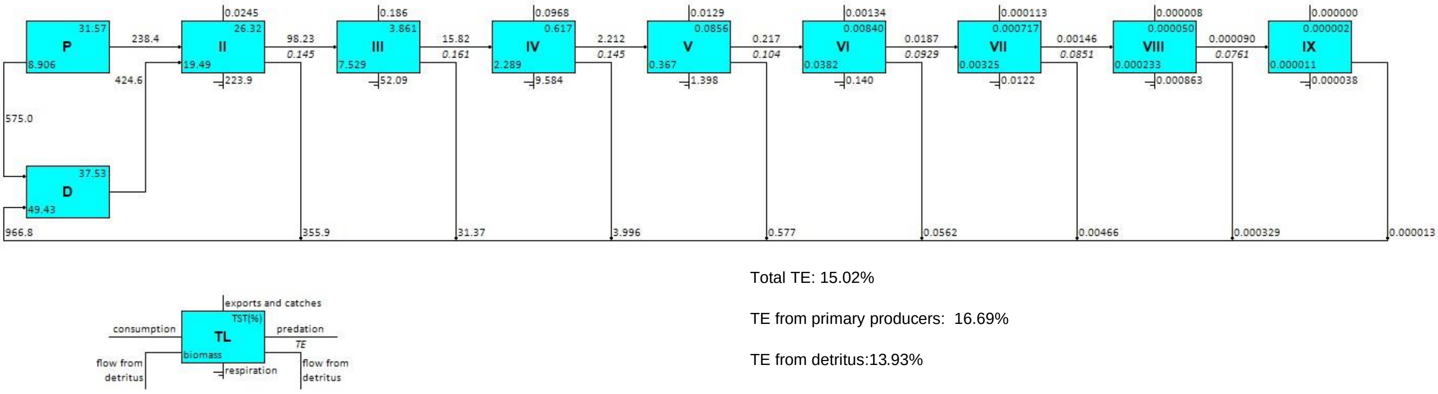

Figure 3: The ecosystem of the Gulf of Corinth has been organized based on integer trophic levels using a Lindeman spine to represent the trophic flows. Trophic level I has been divided into primary producers (P) and detritus (D) to assess the transfer efficiency (TE) and total system throughput (TST).

3.2 Transfer efficiency changes and comparative ecosystem analysis

An illustration of the flows among integer trophic levels using a Lindeman spine, as proposed by Lindeman (1942) and further developed by Ulanowicz (1990), is presented in Figure 3. The first trophic level encompasses primary producers and detritus, enabling the evaluation of the importance of autotrophic and heterotrophic flows. The total transfer efficiency for all the trophic levels in the Gulf of Corinth was 15.02%. The TE related to detritus (13.93%) was by almost 3% lower than the respective from the primary producers (16.69%). The transfer efficiency reached its highest value (16.1%) between TL III and IV and decreased in paths among higher TL, where flows were in any case very low (Fig. 3).

Statistics for the Gulf of Corinth (Central Greece) are presented in Table 3. In comparison, the Gulf of Corinth surpasses the entire Aegean Sea and the oligotrophic deep Ionian Sea ecosystems in terms of system flows (TST 2637 t/km^2/year), yet falls below other gulfs and enclosed seas. Notably, the Gulf of Corinth exhibits a significant number of trophic compounds, as indicated by the omnivory index (0.252). This pattern is consistent with other Greek seas systems, such as the Ionian Sea (Moutopoulos *et al.*, 2018), the Gulf of Pagasitikos (Dimarchopoulou *et al.*, 2019), and the Saronikos Gulf (Papantoniou *et al.*, 2021). The total production (1044 t/km^2/year) was found to be higher than the total consumption (840 t/km^2/year), thus in agreement with some models of the Greek seas such as those of the Saronikos Gulf and the Ionian Sea (Table 3). The total biomass (excluding detritus) in the Gulf of Corinth is 38.62 t/km^2, a value similar to that of the Saronikos Gulf (38.94 t/km^2), the Aegean Sea (39.9 t/km^2) and the Thermaikos Gulf (40 t/km^2). During the early phases of system development, the assumption is that production will exceed respiration, resulting in a ratio of more than 1 (Table 1). The ratio of primary production to system respiration projects an immature system as the value is 2.8 (Table 3). Finn's cyclic index in the Gulf of Corinth has a value of 13.92 % of the total system throughput, and expresses the percentage of energy recycled in the system. Finn's index is slightly higher than that of the Saronikos Gulf, slightly lower than the North Aegean system and slightly higher than that of the Ionian. The Shannon Diversity Index, which takes into account the number of species and the relative abundance of each species, has a value of 2.09, i.e., lower than the value estimated in the model for the entire Aegean Sea (2.574, Table 3).

Table 2: Input (in bold) and output parameters for the Gulf of Corinth Ecopath model. Bi, biomass (t km^{-2}); P/B, production/biomass (yr $^{-1}$); Q/B, consumption/biomass (yr $^{-1}$); EE, ecotrophic efficiency; landings and discards (t km^{-2} yr $^{-1}$); TL, trophic level; F, fishing mortality (yr^{-1}); M2, predation mortality (yr^{-1}); M0, other mortality (yr $^{-1}$); F/Z, exploitation rate; OI, Omnivory Index; FD, flow to detritus (t km ^{2} yr $^{-1}$).

No.	Fuctional Group	Bi	P/B	Q/B	EE	P/Q	Landings	Discards	TL	F	M2	M0	F/Z	OI	FD
1	Phytoplankton	**8.906**	**91.32**	-	0.29	-	**-**	**-**	1.000	0.00	26.77	64.56	0.00	0.00	574.96
2	Mesozooplankton	**4.387**	**36.51**	91.51	0.63	0.40	**0.0000**	**0.000**	2.053	0.00	23.02	13.49	0.00	0.05	219.75
3	Macrozooplankton	0.756	**18.00**	49.90	**0.90**	0.36	**0.0000**	**0.000**	2.717	0.00	16.20	1.80	0.00	0.30	8.91
4	Gelatinous Plankton	**0.140**	**26.67**	35.59	0.13	0.75	**0.0000**	**0.000**	2.974	0.00	3.36	23.31	0.00	0.22	4.26
5	Benthic Invertebrates	**15.189**	**2.51**	20.90	0.89	0.12	**0.0004**	**0.011**	2.143	0.00	2.22	0.29	0.00	0.14	140.89
6	Shrimps	0.667	**2.32**	7.85	**0.98**	0.30	**0.0156**	**0.003**	3.074	0.01	2.25	0.05	0.01	0.30	1.08
7	Nephrops	**0.079**	**1.38**	4.97	0.99	0.28	**0.0025**	**0.000**	2.920	0.02	1.33	0.02	0.02	0.71	0.08
8	Crabs & Lobsters	0.466	**2.19**	5.16	**0.98**	0.42	**0.0020**	**0.001**	3.016	0.00	2.14	0.04	0.00	0.27	0.50
9	Octopodes & Cuttlefish	**0.257**	**2.80**	5.78	0.98	0.48	**0.0108**	**0.000**	3.304	0.02	2.71	0.05	0.02	0.36	0.21
10	Squids	**0.351**	**3.25**	15.00	0.99	0.22	**0.0130**	**0.000**	3.527	0.01	3.17	0.04	0.01	0.42	2.05
11	Planktivorous Fish	**0.224**	**2.05**	10.29	0.99	0.20	**0.0089**	**0.001**	3.149	0.02	2.00	0.01	0.02	0.06	0.69
12	Anchovy	**0.279**	**1.74**	6.37	0.98	0.27	**0.0079**	**0.002**	3.073	0.02	1.67	0.03	0.02	0.01	0.54
13	Sardine	**0.105**	**1.29**	10.42	0.99	0.12	**0.0115**	**0.001**	3.051	0.09	1.16	0.01	0.09	0.02	0.33
14	Blue Whiting	**0.310**	**0.90**	8.16	0.99	0.11	**0.0103**	**0.000**	3.583	0.04	0.86	0.00	0.04	0.22	0.51
15	Bogue	**0.240**	**1.73**	7.41	0.98	0.23	**0.0364**	**0.009**	3.451	0.11	1.50	0.04	0.11	0.10	0.36
16	Picarels	**1.192**	**1.45**	9.50	0.75	0.15	**0.0097**	**0.002**	3.085	0.01	1.07	0.37	0.01	0.02	2.70
17	Mackerels	0.097	**0.92**	6.94	**0.90**	0.13	**0.0042**	**0.000**	3.414	0.05	0.78	0.09	0.05	0.21	0.14
18	Horse Mackerels	**1.056**	**1.22**	6.66	0.92	0.18	**0.0322**	**0.016**	3.469	0.04	1.08	0.10	0.04	0.18	1.51
19	Mueller's pearlside	**0.255**	**2.39**	20.96	0.99	0.11	**0.0000**	**0.000**	2.954	0.00	2.37	0.02	0.00	0.21	1.07
20	Mesopelagics	**1.280**	**2.15**	12.98	1.00	0.17	**0.0000**	**0.000**	2.913	0.00	2.15	0.00	0.00	0.38	3.32
21	Medium pelagics	**0.268**	**0.66**	4.12	0.28	0.16	**0.0053**	**0.000**	4.010	0.03	0.17	0.47	0.03	0.18	0.35

22	Large Pelagics	**0.149**	**0.58**	2.33	0.09	0.25	**0.0023**	**0.000**	4.403	0.03	0.03	0.53	0.03	0.11	0.15
23	Demersals 1	**0.364**	**0.86**	6.05	0.99	0.14	**0.0100**	**0.001**	3.674	0.04	0.82	0.01	0.04	0.19	0.44
24	Demersals 2	**0.092**	**0.90**	6.05	0.99	0.15	**0.0158**	**0.001**	3.164	0.20	0.71	0.01	0.20	0.17	0.11
25	Demersals 3	**0.098**	**1.01**	8.37	0.98	0.12	**0.0015**	**0.001**	3.275	0.03	0.96	0.02	0.03	0.16	0.17
26	Demersals 4	**0.192**	**1.44**	5.90	0.93	0.24	**0.0136**	**0.004**	3.816	0.06	1.25	0.10	0.06	0.36	0.25
27	Red Mullets	**0.053**	**1.44**	8.75	0.99	0.16	**0.0108**	**0.000**	2.924	0.14	1.22	0.01	0.14	0.58	0.09
28	Hake	**0.610**	**0.76**	4.47	0.92	0.17	**0.0313**	**0.001**	4.104	0.07	0.65	0.06	0.07	0.36	0.58
29	Flatfishes	**0.080**	**0.96**	9.37	0.97	0.10	**0.0042**	**0.001**	3.526	0.07	0.87	0.03	0.07	0.49	0.15
30	Anglerfish	**0.171**	**0.58**	4.91	0.71	0.12	**0.0024**	**0.000**	3.970	0.02	0.40	0.17	0.02	0.47	0.20
31	Rays & Skates	**0.190**	**0.46**	4.39	0.65	0.10	**0.0005**	**0.001**	3.534	0.02	0.29	0.16	0.02	0.27	0.20
32	Sharks	**0.041**	**0.84**	6.47	0.95	0.13	**0.0002**	**0.000**	4.022	0.02	0.78	0.04	0.02	0.39	0.05
33	Striped & Common Dolphins	**0.065**	**0.08**	14.53	0.58	0.01	**0.0000**	**0.000**	4.340	0.00	0.05	0.03	0.00	0.13	0.19
34	Bottlenose Dolphins	**0.006**	**0.08**	11.59	0.00	0.01	**0.0000**	**0.000**	4.425	0.00	0.00	0.08	0.00	0.21	0.01
35	Sea Turtles	**0.003**	**0.27**	2.81	0.00	0.10	**0.0000**	**0.000**	2.940	0.00	0.00	0.27	0.00	0.60	0.00
36	Seals	**0.000**	**0.12**	12.59	0.00	0.01	**0.0000**	**0.000**	4.350	0.00	0.00	0.12	0.00	0.67	0.00
37	Seabirds	**0.001**	**5.00**	69.34	0.00	0.07	**0.0000**	**0.000**	2.994	0.00	0.17	4.83	0.00	1.13	0.02
38	Discards	**0.059**	**-**	-	1.00		-	-	1.000	-	-	-	0.00	0.00	0.00
39	Detritus	**49.372**	**-**	-	0.44		-	-	1.000	-	-	-	0.00	0.36	0.00

Table 3: Comparing the statistics, flows, and ecological indicators of the Gulf of Corinth with models from the two main Greek Seas. Ionian Sea: Gulf of Corinth (GoC, current study), entire Ionian Sea (IOS, Moutopoulos et al. 2018), Northeastern Ionian Sea (NIOS, Piroddi et al. 2010). Aegean Sea: Saronikos Gulf (SG, Papantoniou et al. 2021), Pagasitikos Gulf (PG, Dimarchopoulou et al. 2019), the entire Aegean Sea (AS, Keramidas et al. 2022), Thermaikos Gulf (TG, Dimarchopoulou et al. 2022), North Aegean (Strymonikos Gulf & Thracian Sea) (NA, Tsagarakis et al. 2010).

	IONIAN SEA			**AEGEAN SEA**					**UNITS**
Indicators	GOC	IOS	NIOS	SG	AS	NA	PG	TG	
Years	**2014-2016**	1998	1964	1998-2000	2003-2006	2003–2006	2008	1998-2000	
Depth Range	**10-930**	50-1100	100-200	20-450	20-2250	20–300	0-102	0-100	m
Area Modeled	**2167.5**	49149	1021	2665	201535	8374	639	3339	km^2
Number of fuctional groups	**39**	43	22	40	44	40	31	33	
Number of primary producers	**1**	2	2	1	1	1	1	1	
Number of all living FG	**37**	41	20	38	42	38	29	31	
Nature of the system	**semi-enclosed**	open sea	semi-closed	semi-enclosed	open sea	semi-closed	semi-enclosed	semi- closed	
Sum of all consumptions (TQ)	**840**	564.6	851.9	1369	874.87	868.83	1456	1386	$t/km^2/year$
Sum of all exports	**543**	178	162.1	686	41.63	274.81	249	514	$t/km^2/year$
Sum of all respiratory flows	**287**	321	503.3	571	291.78	269.48	486	417	$t/km^2/year$
Sum of all flows to detritus	**967**	548.6	748.8	1297	364.16	562.53	761	868	$t/km^2/year$
Total system throughput (TST)	**2637**	1612.3	2266.1	3925	1572.44	1976	2951	3185	$t/km^2/year$
Sum of all production	**1044**	626.1	813.6	1521	574.71	791	1114	1350	$t/km^2/year$
Calculated total net primary production	**813**	495.4	664.9	1243	320.25	535.48	712	923	$t/km^2/year$
Total primary production/ total respiration	**2.8**	1.543	1.3	2.17	1.1	1.99	1.47	2.21	
Net system production	**526**	174.4	161.6	672	28.47	265.99	227	506	$t/km^2/year$
Total primary production/ total biomass (Pp/B)	**21**	15.02	15	2.17	8.03	16.21	9.1	23	
Total Biomass/ TST	**0.015**	0.021	0.02	0.01	0.02	0.02	0.03	0.01	/year
PP to sustain fisheries (%PPR)	**3.962**	27.41	-	4.66	4.74	3.45	3.55	3.38	
Ecosystem's sustainable fishing probability (Psust)	**96**	-	-	65	-	70.54	-	-	%
Finn’s cycling Index (of total throughput) (FCI)	**13.92**	10.60	-	12.53	-	14.6	-	-	% of TST
Shannon diversity index	**2.09**	-	-	-	2.574	-	-	-	
Connectance Index (CI)	**0.336**	0.233	0.22	0.332	0.18	-	-	-	

System Omnivory index (SOI)	**0.252**	0.3	0.1	0.23	0.21	0.18	0.25	0.2	
Total Biomass (excluding detritus)	**38.62**	32.99	44.3	38.94	39.9	33.04	78	40	$t/km^2/year$
Ecopath pedigree index	**0.566**	0.539	-	0.65	0.53	0.61	0.53	0.497	

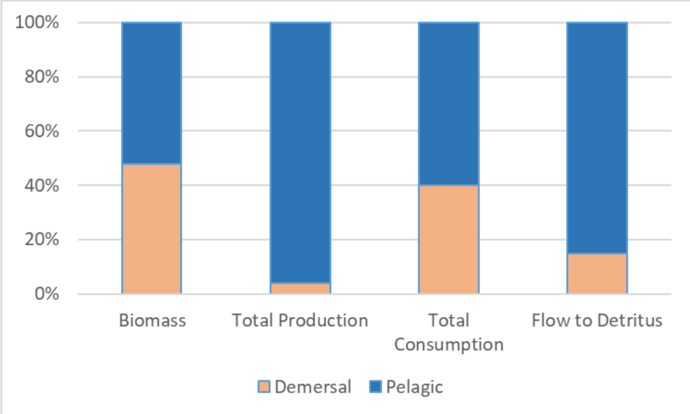

Figure 4: The pelagic and demersal components' share in the overall biomass (excluding detritus), production, consumption, and flow to detritus in the Gulf of Corinth ecosystem.

Despite an equal distribution of the food web biomass between the pelagic and demersal components (52% and 48% of the total biomass, respectively), the pelagic FGs exhibited higher levels of production (95.9%) and consumption (59.8%), as well as flows to detritus (85%) (Fig. 4).

3.3 Mixed trophic impact, fishing influence, and keystoneness

The MTI analysis predicts how changing one species' biomass affects others in the food web, revealing direct and indirect effects of trophic interactions within the ecosystem. Fig. 5 shows that low trophic level FGs have a positive effect on many other FGs, especially pelagic ones, while high trophic level groups such as hake and sharks impact several other low and high TL FGs. More specifically, we distinguished the three most negative relationships and the three most positive relationships based on the numerical representation of the Mixed Trophic Impact. The study reveals three prominent positive interactions: sharks have a positive effect on the bogue group (0.434), mesozooplankton positively influence anchovy (0.407) and picarels exhibit the most substantial positive impact on boat seines (0.517). Conversely, notable negative associations involve the squid group, exerting adverse effects on octopodes and cuttlefish (-0.559), as well as on mackerel (-0.57). Notably, sharks show the highest negative influence in terms of predation in the combined group of striped and common dolphins (-0.677). Fisheries do not seem to have high impact on the system, with the exception of small-scale fisheries (SSF) which have a negative effect on the large pelagic and Demersal 2 fish groups. The only high positive effect on fisheries is that of Picarels on the Boat seines that was mentioned above. In addition, a positive effect of discards on seabirds is highlighted (Fig. 5).

Regarding fishing impact, the system has relatively low fishing activity. The ratio of fishing mortality to total mortality (F/Z) appears to have low values in the system, but some of them stand out and tell us which species are fished more often and more consistently to the extent of overfishing. The top catches come from bogue and red mullets, with Demersals 2 being the most caught species in the system (see Table 2). This assessment matches the mean annual probability of sustainable fishing (Psust) concept. Psust (Table 3) helps us evaluate overfishing in an ecosystem, calculated by comparing secondary production reduction to reference levels from ecosystem models, following Coll *et al.* (2008) and Libralato *et al.* (2008).

According to the keystoneness analysis presented in Figure 6, squids, sharks, and hake can be considered key species because while they have a small biomass, they have a large total impact on the food web. Mesozooplankton is the group with the highest relative total impact and keystoneness, while Benthic invertebrates, phytoplankton, macrozooplankton, cephalopods, and the group of striped and common dolphins also play an important role (Fig. 6). At the lowest level are the functional groups of sea turtles and seals, which have neither high biomass nor a high impact on the ecosystem. Two indicators that come to complement the Keystone index as for prey species, the Connectance and SURF indicators, are observed to have commonalities in how the key species are positioned. The shrimp group is involved in 4.9% of the connections in the food web (Fig. 7), occupying the largest proportion. The group of mesopelagic fish (Fig. 7) stands out in both indices as it constitutes 4.5 % of the biomass of consumers (Bspecies/Bconsumers), has a connectance index of 0.037 so it's a considerable species in terms of importance in the food web. Other groups that stand out are those of picarels, horse mackerels, octopodes and cuttlefish, squids, and the group of crabs and lobsters.

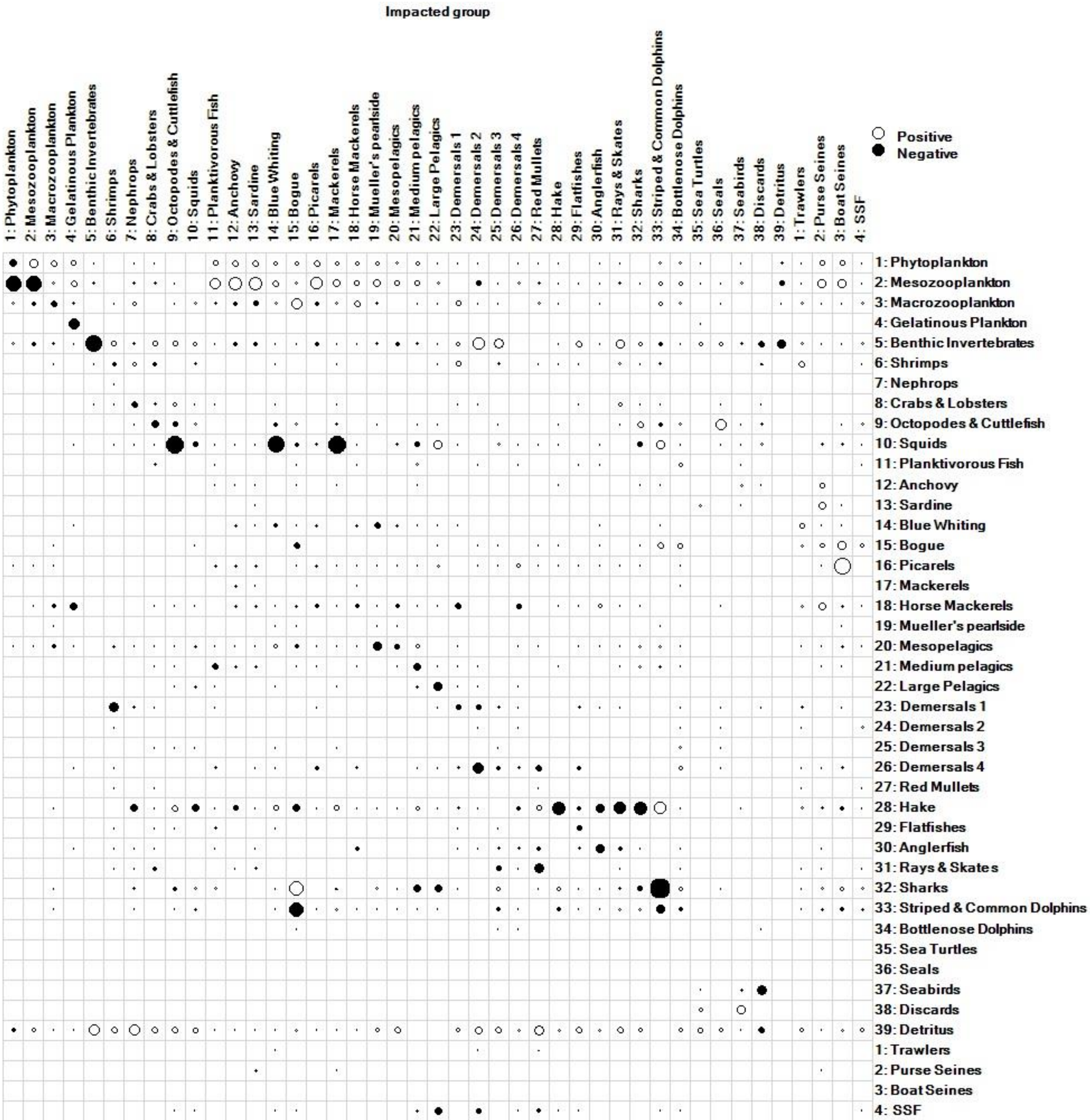

Figure 5: The Gulf of Corinth food web was analyzed using Mixed Trophic Impact (MTI) analysis. In this analysis, the functional groups were black and white circle-coded according to the size of their trophic impact, with white indicating a positive impact and black indicating a negative impact. The x-axis listed predators, while the y-axis listed prey. The model included four fishing fleets and was represented at the bottom of the figure. Please refer to the web version of the article for more information on interpreting the colors in the legend of this figure.

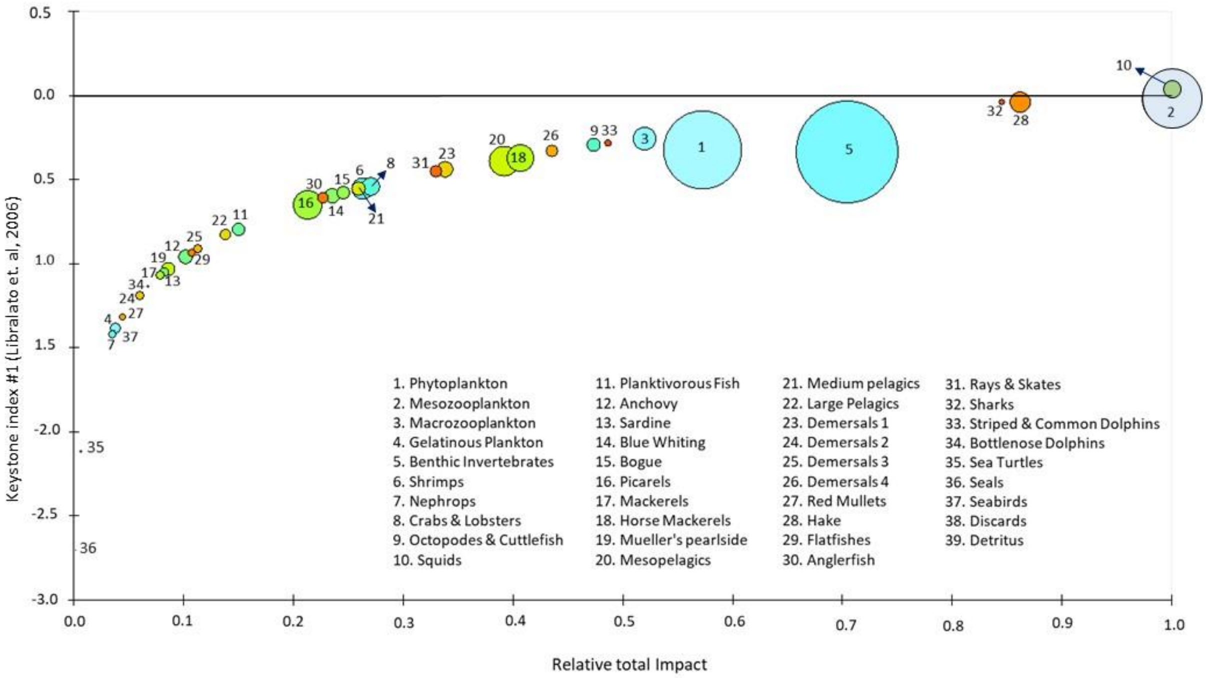

Figure 6: Keystone index for Gulf of Corinth according to Libralato et al. (2006) definition. The circles' dimensions correspond to the relative biomass of each functional group.

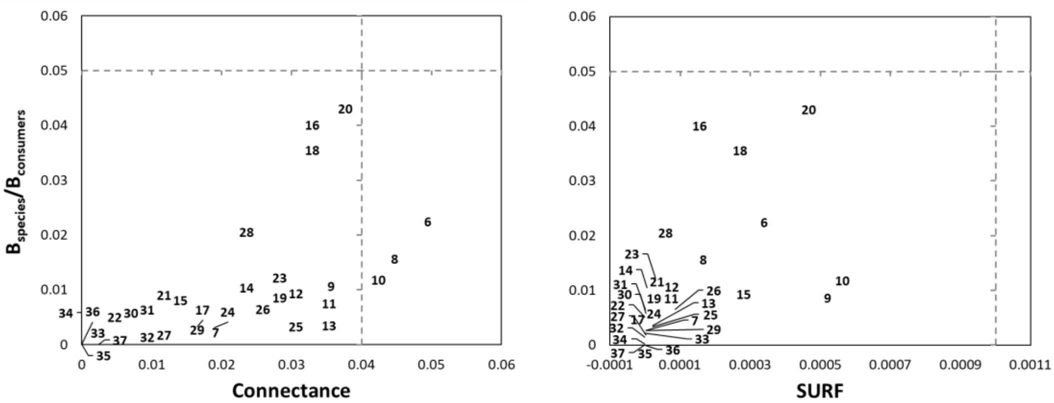

Figure 7: Relationship between consumer biomass proportion and Connectance (on the left) and SURF (on the right) indices. The threshold values for designating a species as "key" are indicated by the horizontal and vertical dashed lines. These threshold values are based on the guidelines proposed by Smith et al. (2011) for Connectance and Plagányi & Essington (2014) for the SURF index (where SURF > 0.001). The plot does not include the functional groups of micro- and mesozooplankton.

4. Discussion

The model developed for the Gulf of Corinth offers a depiction of the energy flows and their distribution in the food web using as baseline the period 2014-2016, which was selected mainly based on data availability. The Gulf of Corinth is an important region from an ecological perspective as it represents a unique, enclosed, deep ecosystem (Kapelonis *et al.*, 2023) that sustains substantial populations of PET species and simultaneously supports fishing activities, especially SSF. Therefore, the model developed here is a tool that can provide information on the structure and functioning of the ecosystem to be used for management and conservation purposes.

The outcomes of the model provide a comprehensive insight into the ecosystem's developmental stage and potential stressors. An effective gauge of maturity is the total primary production to total respiration ratio, as per Odum (1971), which is an indicator of system maturation. This is linked to the concept of Net System Production, according to which higher values indicate system immaturity, as indicated by Christensen *et al.* (2005). In the case of the Gulf of Corinth, these values are 2.8 and 526 t km^{-2} $year^{-1}$, respectively, indicating an ongoing developmental stage. Despite this, the ecosystem's high biodiversity is evident according to the Shannon Index.

The ratio of total primary production to total respiration, (Christensen *et al.*, 2005; Odum, 1971) serves as an indicator that may reflect a system's vulnerability to organic pollution, where values below 1 suggest burdened conditions. Despite indications of pollution, as reported in the marine environment of the Gulf of Corinth (Papatheodorou *et al.*, 1999; Tsangaris *et al.*, 2010), particularly with heavy metals causing contamination, the corresponding indicators contradict this observation. The ecosystem's present immaturity likely stems from historical factors, including past pollution and possibly historical fishing pressures. To gain comprehensive insights, long-term data collection is essential. While existing data provides some understanding, additional data could offer a clearer understanding of the region's human-induced impacts. In the future, the accumulation of data regarding past and present human activities within this area could significantly enhance our comprehension.

When comparing ecosystems, such as the Aegean, we observe a consistent alignment between two key metrics, the connectance index and the Pp/R ratio, in gauging their maturity. Specifically, in the Aegean, these metrics yield values of 0.18 and 1.1, respectively. Similarly, in the case of the Saronikos Gulf and Thermaikos Gulf, which are categorized as immature ecosystems, the values recorded are 2.17 and 2.21 respectively. Moreover, our analysis extends to the P/B ratio, a measure that relates primary production (Pp) to total biomass (B). Notably, the Gulf of Corinth, the focal point of our study, demonstrates a P/B value of 21, aligning with the maturity levels deduced from the Pp/R ratio. This congruence is further corroborated by the maturity assessments, evident in the values derived for the Thermaikos Gulf where the P/B ratio is 23.

The TE in the system has a value of 15.02% while the world average is 10% (Pauly & Christensen, 1995). The value varies depending on the system and its peculiarities. The PPR% is at 3.962, a value similar to models from other Greek gulfs (ranging from 3.38% to 4.66%); despite differences in productivity, these regions share similar conditions and fishing practices, and seem to be under similar exploitation status with their total catches probably being affected by patterns in productivity. The stronger divergence in values is found in the open sea systems (e.g. Moutopoulos *et al.* 2018) and in the highly exploited ecosystems such as the North Aegean Sea in the early 1990s (Tsagarakis *et al.* 2022).

Specific values of the exploitation rate (F/Z) indicate that three Functional Groups (FGs), namely Bogue, Red mullets, and Demersals 2, exhibit moderate catches without implying overfishing. Further insight emerges from the Mixed Trophic Impact (MTI) which demonstrates the low impact of fishing on the ecosystem. The MTI also highlights the positive influence of picarels on boat seines and, to a lesser extent, bogue, sardines, and horse mackerels on purse seines, along with shrimps on trawlers. So, the conclusion is that there are no particular pressures and that catches are perhaps at a balanced level for the area, so fishing is not a stressor of particular concern for the system.

As mentioned above, this is a system which, as suggested by the model, is not much affected by fishing activities. The results of the model showed that the fisheries interact most with the TLIII trophic level, which includes commercial species in the area. Note that the predominant fishing activity is in the SSFs, so there is the possibility of data misalignment. More extensive and reliable fisheries data can contribute to the management of stocks and the impacts of fisheries on PET species. The study highlights that the Gulf of Corinth is a system not subjected to severe fishing pressures, potentially owing to its status as a partially protected area (designated as a Natura 2000 site) with temporal fishing restrictions, particularly aimed at semi-industrial fisheries. The legislation strictly prohibits fishing activity near the coast of the bay which is considered to be busy in terms of visitors. In particular, throughout the bay, trawling is prohibited from April to November, and purse seine fishing increases its activity mainly in the summer months as it is prohibited from 15 December to February (Hellenic Coast Guard, 2022). While in the case of open seas, there is the problem of constant movement of species which creates difficulties in conservation (Fortuna *et al.*, 2018), the Gulf of Corinth with the natural structure of the closed bay, which makes it easier to protect and conserve.

If effectively implemented for a prolonged period, the current fishing bans and additional regulations will prevent future adverse effects of overfishing, competition within the food chain, and unintended catches. Although the fishing operations in the Gulf of Corinth are primarily of a small-scale nature, there is also the occurrence of a few semi-industrial fishing vessels, accompanied by instances of illegal fishing in banned areas, as reported by Bearzi *et al.* (2016) although overall illegal fishing in the Gulf of Corinth is quite small in terms of intensity and size (Moutopoulos *et al.*, 2020). Employing ecosystem modeling techniques would prove invaluable in exploring the interrelationships between FGs and the ecological disturbances caused by fisheries-related activities (Piroddi *et al.*, 2011, 2010).

The study of the Gulf of Corinth ecosystem revealed some interesting features that are commonly seen in Mediterranean ecosystems. These features provide insights into how the ecosystem functions. The ecosystem heavily depends on detritus as a crucial source of energy, with 57% of the energy flows in the Gulf of Corinth specifically relying on detritus. This complex interaction also simplifies the seamless exchange of energy and nutrients between the seabed and the water column, essential for the ecosystem functioning. This dynamic relationship is emphasized by the fact that detritus transfers from the pelagic zone to detritus account for 85% of the total flows. This transfer pattern significantly benefits the benthic species within the ecosystem. Notably, the MTI reinforces the positive influence of detritus across various FGs. This influence is particularly pronounced in Demersal FGs, as well as in shrimps and zooplankton FGs showing that detritus positively impacts a wide spectrum of species and further highlighting the connection between different ecosystem components. The organisms in the pelagic compartment, such as phytoplankton, zooplankton, and fish, play a dominant role in the transfer and distribution of energy within the Gulf of Corinth ecosystem. This means that most of the energy flows through these organisms, highlighting their importance in the ecosystem. Lastly, the transfer of energy from one level of the food web to the next is efficient in the Gulf ecosystem as shown by the high value of estimated TE. This is in line with other Mediterranean ecosystems and is probably related to the relatively oligotrophic nature of the region (Tsagarakis *et al.*, 2010).

Two of the most impacting FGs, i.e. sharks and dolphins (stripped and common) are top predators. Top predators are often classified as keystone species, however, sharks are not among the usual ones, at least in the Mediterranean Sea (Coll and Libralato, 2012). With a significant presence, dolphins in the Gulf of Corinth are certainly one of the trademarks of the region as ~1400 individuals are observed (Bearzi *et al.* 2016). In the system, they are an important component as they are highly ranked in the keystone index (Libralato *et al.* 2006). Another important group in the system is the mesopelagic fishes; represented by more than 15 taxa in the region (Kapelonis *et al.*, 2023), they have a significant contribution to the Gulf of Corinth's biomass of consumers (i.e., groups with TL>2) (Figure 7). Mesopelagic fish have a significant ecological function as they link primary consumers to top predators (Woodstock and Zhang, 2022). This includes commercially valuable pelagic and demersal fish species, as well as protected, endangered, and/or threatened species (Catul *et al.*, 2011), such as the striped and common dolphins in the case of the Gulf of Corinth. As a result, they play a vital role in the energy flow of the open ocean and greatly contribute to the transportation of organic carbon from the surface to the deep sea through their daily vertical migrations (Kaartvedt *et al.*, 2019). Other important FGs in the Gulf of Corinth system include basic prey groups such as mesozooplankton and benthic invertebrates, a usual feature for Mediterranean ecosystems (Coll & Libralato, 2012).

The model was developed using data for the period 2014-2016, and the information from that timeframe was considered sufficient for constructing the ecosystem model. This work is the first attempt to visualize an ecosystem that is relatively unexplored compared to other marine ecosystems of Greece. The overall limited scientific surveys and the fact that SSF - the key fishing fleet in the region – are not so well monitored compared to semi-industrial fisheries, are some of the weaknesses that may hinder a reliable representation of the ecosystem. In the broader context, although the model development benefitted from scientific surveys realized in the area, the data for the Gulf of Corinth are limited compared to other regions. However, complementing data from adjacent areas of similar characteristics (Moutopoulos *et al.* 2018; Papantoniou *et al.* 2021), it was possible to fill gaps in the modeling approach. Nevertheless, EwE helped analyze and correlate data on different aspects of the ecosystem giving an in-depth picture of its structure and dynamics. The model outputs provide a scientific basis for initiating more extensive research aimed at understanding the system and its organisms to an even greater extent in light of the questions raised by the above results. It is important to continue the model at the simulation level, both in time and space, to create a powerful tool for management and research. This general system approach through the model can provide the Integrated Ecosystem Assessment (IEA) as a tool to conduct a more comprehensive Ecosystem-based management (EBM) analysis from a socio-economic perspective aiming at the sustainability of the marine environment (Levin *et al.* 2009). Ecosystem-based management is of paramount importance for an ecosystem that may not as a whole be experiencing severe problems at the moment but contains organisms that are threatened (e.g. the common dolphins in the area which are critically endangered; Santostasi *et al.*, 2021) and this threat may intensify. The challenges the marine environment and its organisms are facing are now more clearly defined than ever before, and the challenge now is to manage and provide the right tools to ensure that biodiversity conservation is best achieved (Kirkfeldt, 2019; Levin *et al.*, 2009).

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Supplementary Material

Appendix_GulfOfCorinth_SupplementaryMaterial

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