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Fishing impact in Mediterranean ecosystems: an EcoTroph modeling approach

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ABSTRACT

The EcoTroph modeling approach was applied to five Mediterranean marine ecosystems to characterize their food webs and investigate their responses to several simulated fishing scenarios. First, EcoTroph was used to synthesize the outputs of five pre-existing heterogeneous Ecopath models in a common framework, and thus to compare different ecosystems through their trophic spectra of biomass, catch, and fishing mortalities. This approach contributes to our understanding of ecosystem functioning, from both ecological and fisheries perspectives. Then, we assessed the sensitivity of each ecosystem to fishery, using EcoTroph simulations. For the five ecosystems considered, we simulated the effects of increasing or decreasing fishing mortalities on both the biomass and the catch per trophic class. Our results emphasize that the Mediterranean Sea is strongly affected by the depletion of high trophic level organisms. Results also show that fisheries impacts, at the trophic level scale, differ between ecosystems according to their trophic structure and exploitation patterns. A top-down compensation effect is observed in some simulations where a fishing-induced decrease in the biomass of predators impacts their prey, leading to an increase in the biomass at lower trophic levels. The results of this comparative analysis highlight that ecosystems where top-down controls are observed are less sensitive to variations in fishing mortality in terms of total ecosystem biomass. This suggests that the magnitude of top-down control present in a system can affect its stability.

1. Introduction

Depletion of fishery resources and degradation of marine ecosystems are observed worldwide (Pitcher and Cheung, 2013; Worm et al., 2009). Fisheries can directly and indirectly affect the whole food web and overfishing is a primary threat to ecosystem structure (e.g., species diversity, trophic levels) and dynamics (e.g., stability, resilience) (Daskalov, 2002; Pauly et al., 2002; Travers and Shin, 2010). Thus, it is imperative to properly assess the ecosystem effects of fishing (Cury et al., 2008).

The use of trophic models, such as Ecopath with Ecosim (Christensen and Walters, 2004; Walters et al., 1999), OSMOSE (Shin and Cury, 2001, 2004) and Atlantis (Fulton et al., 2004), is an effective way to describe the trophic structure and functioning of marine ecosystems. These models can provide a comprehensive image of an ecosystem and allow the full complexities of the food web to be considered.

EcoTroph is a more recent trophic model which represents marine ecosystems and assesses fisheries impacts by treating the distribution of biomass or related quantities as a function of continuous trophic levels (TLs) (Gascuel, 2005; Gascuel and Pauly, 2009). An EcoTroph representation of an ecosystem consists of various ecosystem parameters, such as biomass, production, catch or fishing mortality, displayed along trophic spectra (Gascuel, 2005). Unlike the trophic pyramids of Lindeman (1942), where the biomass of each component of ecosystems was shoehorned into a few integer TLs, EcoTroph is based on fractional

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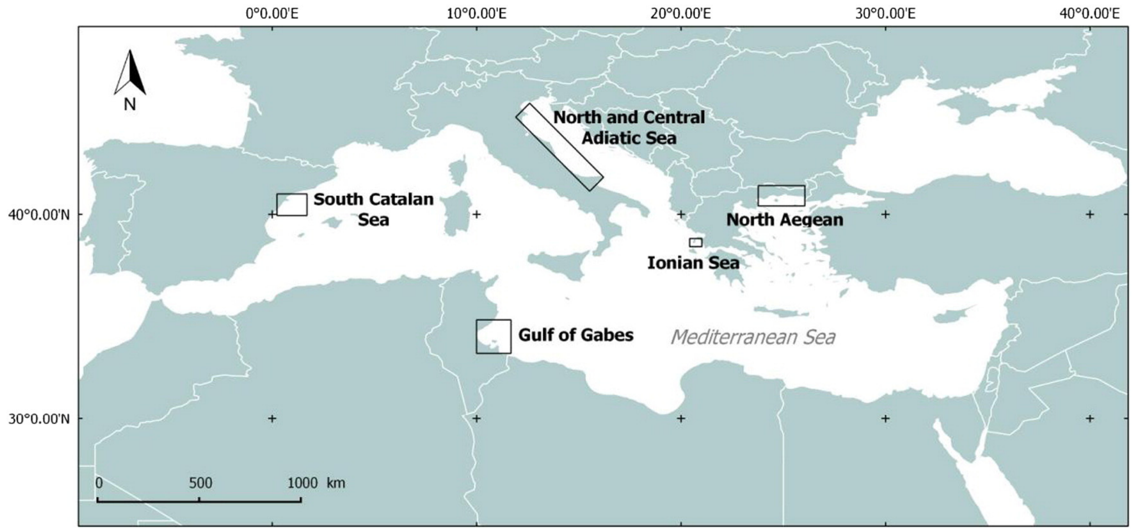

Fig. 1. The locations of each of the five ecosystems studied which correspond with areas previously modeled using Ecopath.

TLs, as most marine animals feed on species from more than one TL (Odum et al., 1975). The specific relevance of this modeling approach lies in the fact that it can take into account the whole trophic spectrum, broadening the focus from individual species. Thus, it offers an overview of the entire ecosystem.

The Mediterranean Sea is both the largest and deepest semi-enclosed seas in the world. Despite the fact that it is characterized by oligotrophic conditions, it is nonetheless considered as an important biodiversity hotspot (Bianchi and Morri, 2000; Coll et al., 2010; Tortonese, 1985). Following a long history of exploitation, the Mediterranean Sea is now experiencing a diverse range of human impacts, many of which are interacting in unexpected ways (Coll et al., 2012; Libralato et al., 2008; Tsagarakis et al., 2010).

By following a comparative approach, this work aims to further our understanding of how commercial fishing can affect marine ecosystems, especially when subjected to differing levels of exploitation. Looking specifically at five exploited ecosystems across the Mediterranean Sea, we compared their trophic structures using trophic spectra, and we used EcoTroph simulations to build ecosystem diagnoses of the impacts of exploitation and explore the effects of different fishing scenarios. As these five systems have been modeled previously using the Ecopath with Ecosim approach (Christensen and Walters, 2004), parameterization of the EcoTroph model was primarily derived from these previous applications.

2. Material and methods

2.1. Pre-existing Ecopath models

Five ecosystems across the Mediterranean Sea were investigated in this study using pre-existing Ecopath models: Gulf of Gabes (Hattab et al., 2013), Ionian Sea (Piroddi et al., 2011), North Aegean Sea (Tsagarakis et al., 2010), Southern Catalan Sea (Coll et al., 2006) and North and Central Adriatic Sea (Coll et al., 2007) (Fig. 1). Four out of these five Ecopath models followed similar structure with around 40 functional groups (Table 1), while the inclusion of the Ionian Sea with 19 functional groups would, among others, serve as an "outgroup" in order to explore whether our results are substantially affected by the structure of the underlying Ecopath model. Outputs from each Ecopath model were used to build the trophic spectra of biomass and catch and to represent the distribution of a fishing mortality parameter across the TLs of each ecosystem.

2.2. The EcoTroph model

The first key idea of EcoTroph is that it deals with the continuous distribution of the biomass in an ecosystem as a function of TL (Gascuel, 2005; Gascuel and Pauly, 2009). The biomass enters the food web at TL 1, generated by the photosynthetic activity of primary producers, and the detritus recycled by the microbial loop (Fig. 2). There is usually no biomass between TLs 1 and 2, all animals being at a TL equal to 2 (for herbivores and detritivores) or higher. At TLs > 2, the biomass is distributed along a continuum of TL values. The diet variability of the different consumers should lead all fractional TLs to be 'occupied'. Thus, the graphical representation of the biomass distribution, expressed as a function of TLs, constitutes what is called a biomass trophic spectrum (Gascuel, 2005).

In the EcoTroph model, a discrete approximation of the continuous distribution of the biomass is used for mathematical simplification and visual representation, based on small trophic classes, each with a conventional width $\Delta_\tau = 0.1$TL.

Table 1
Key details of the Ecopath models previously developed for the five study locations (ecosystems).

	Gulf of Gabes	South Catalan Sea	Northern and Central Adriatic	North Aegean Sea	Ionian Sea	Unit
Time range	2000–2005	1994	1990s	Mid-2000s	2007	year
Number of trophic groups	41	40	40	40	19	–
Total system throughput	3799	1657	3844	1976	2266	–
Total biomass (excluding detritus)	73.75	58.99	130.3	33.04	44.3	t km^{-2} year^{-1}
Net system production	746.20	59.52	728.76	265.99	161.6	t km^{-2} year^{-1}
Mean trophic level of catches	3.44	3.12	3.07	3.47	3.10	–
Total catches	1.72	5.36	2.44	2.35	1.10	t km^{-2} year^{-1}

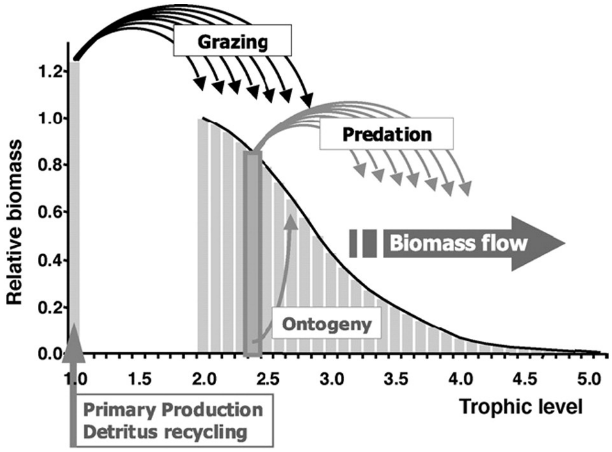

Fig. 2. Diagram of the trophic functioning of an ecosystem according to the EcoTroph model. Theoretical distribution of the biomass by trophic level (TL) and trophic transfer processes, given an arbitrary input of biomass (fixed equal to 1 for TL = 2).
From Gascuel and Pauly (2009).

The second key feature of the EcoTroph model is that the trophic functioning of marine ecosystems can be modeled as a continuous flow of biomass surging up the food web, from lower to higher TLs, through predation and ontogenic processes. Each organic particle moves more or less rapidly up the food web according to continuous processes (ontogenic changes in TLs) and abrupt jumps caused by predation. All particles jointly constitute a biomass flow which is considered together using a continuous model (Gascuel et al., 2008). Thus, this flow of biomass is characterized by two variables: the biomass flow itself, which relates to the quantity of biomass moving up the food web (expressed in t year^{-1}), and the speed of flow (also called the flow kinetics), which quantifies the velocity of biomass transfers in the food web (expressed in TL year^{-1}, i.e. the number of TLs crossed per year).

In steady state conditions, the biomass present in a given trophic class can be derived from these two quantities based on the traditional equations of fluid dynamics:

$$B_\tau = \frac{\Phi_\tau}{K_\tau} \cdot \Delta_\tau \quad (1)$$

where B_τ is the biomass present in the trophic class $[\tau, \tau + \Delta\tau]$, Φ_τ is the mean flow of biomass passing through that trophic class and K_τ is the mean flow speed through that class.

The biomass flow is not conservative and decreases as a function of TL due to natural losses occurring during trophic transfers (e.g., non-predation mortality, respiration and excretion) and to fishing-related losses. Thus, the biomass flow is expressed as:

$$\Phi_{(\tau+\Delta_\tau)} = \Phi_\tau \cdot \exp[-(\mu_\tau + \varphi_\tau) \cdot \Delta_\tau] \quad (2)$$

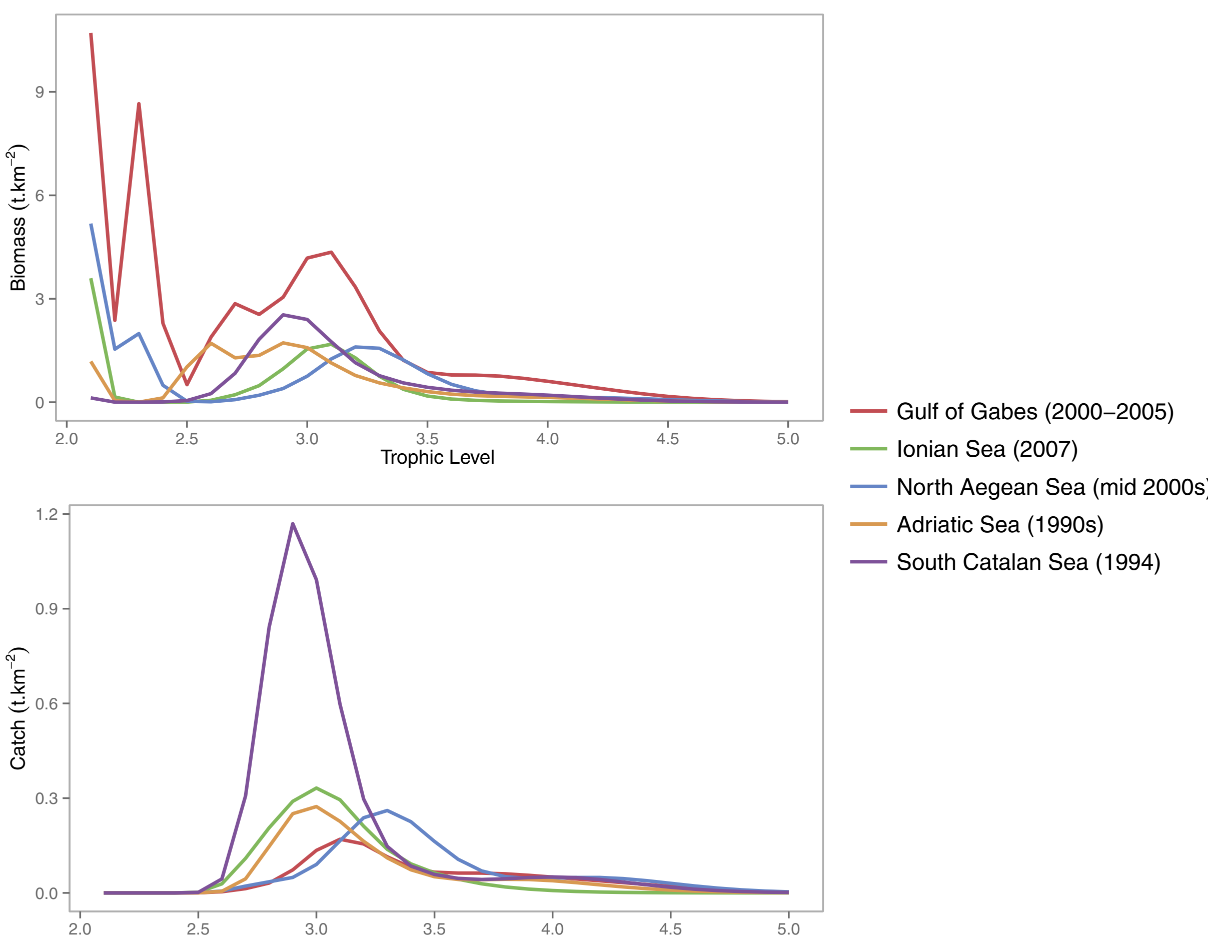

Fig. 3. The trophic spectra of biomass (top) and fisheries catch (bottom) for the five Mediterranean ecosystems examined; note that to achieve a better graphical representation of the biomass, spectra for TLs 1 and 2 were omitted.

where μ_τ is the net natural loss rate of biomass flow and φ_τ is the rate of fishing loss.

The speed of the biomass flow K_τ depends on the turnover of the biomass, while the parameter $1/K_\tau$ is the mean life expectancy of an organism within the trophic class $[\tau, \tau+\Delta\tau]$ (Gascuel et al., 2008). Thus, K_τ depends on both fishing mortality and natural mortality (which itself depends on predator abundance). In EcoTroph, it is expressed using a two step procedure. First, the P_τ/B_τ ratio derived from the underlying Ecopath model (see below) can be used as a measure of $K_{cur,\tau}$ the speed of the flow in the current state of the ecosystem (Gascuel et al., 2008). Then, the speed of flow for a given simulated state is calculated from the current state using the top-down equation:

$$K_\tau = \left[K_{cur,\ \tau} - F_{cur,\ \tau}\right]\cdot\left[1+\alpha_\tau\cdot\frac{B^\gamma_{pred} - B^\gamma_{pred,cur}}{B^\gamma_{pred,cur}}\right] + F_\tau \quad (3)$$

where K_τ is the speed of the flow in any simulated state of the ecosystem, characterized by F_τ; $K_{cur,\tau}$ is the speed of the flow at TL_τ in the current state of the ecosystem, characterized by a fishing mortality $F_{cur,\tau}$; B_{pred} is the predator biomass of trophic groups from $TL_{\tau+1}$; α determines the proportion of natural mortality (between 0 and 1) at TL_τ that is dependent on predator abundance; and γ is a shape parameter (varying between 0 and 1) that defines the functional relationship between prey and predators. A value of $\gamma = 1$ results in the abundance of predators having a linear effect on flow kinetics, while smaller values reflect non-linear effects due to competition between predators.

This equation allows the EcoTroph model simulations to take into account the indirect ecosystem effects of fishing. By reducing the life expectancy of targeted species, fishing can cause a notable acceleration in an ecosystem's flow kinetics. This equation also introduces top-down control into the model, whose intensity is defined by the α parameter. By reducing the biomass of predators responsible for exerting a top-down control on the system, fishing can slow down the flow of prey to the predator, consequently increasing their life expectancy.

EcoTroph is able to take into account the fact that the biomass flow introduced at TL 1 is partly due to the recycling of detritus. Thus, we may reasonably assume that it depends (at least in part) on the biomass of the whole ecosystem. This process introduces a feedback effect on primary production, called a biomass-input control, which is expressed as:

$$\Phi_1 = (1-\beta).\Phi_{cur,1} + \beta.\Phi_{cur,1}\cdot\frac{B_{tot}}{B_{tot,cur}} \quad (4)$$

where β expresses the amount of biomass-input control, $\Phi_{cur,1}$ is the biomass at TL 1 (in the current state of the ecosystem, i.e., referring to the Ecopath model), and B_{tot} and $B_{tot,cur}$ are the total biomass in the system under the simulated state and the current state, respectively. Therefore, when $\beta = 0$, all secondary production in the ecosystem

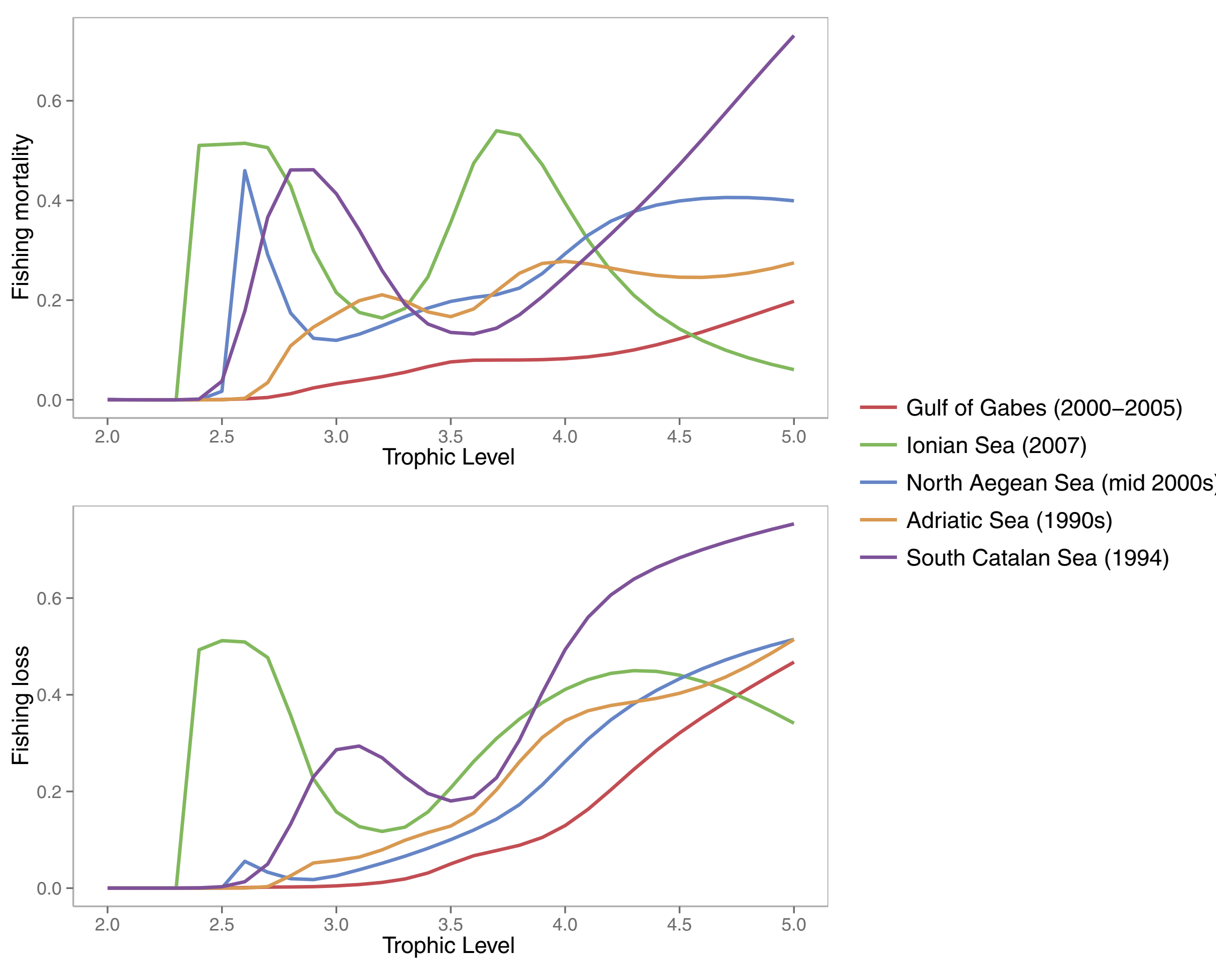

Fig. 4. The trophic spectra of fishing mortality (top) and fishing loss rate (bottom) for each of the five Mediterranean ecosystems examined.

originates from grazing on primary producers, and detritus recycling is insignificant. However, as the value of β moves closer to 1, it increasingly represents an ecosystem where detritus recycling and/or recruitment are major contributors of biomass input.

In EcoTroph (version 1.6), biomass is divided into two compartments: inaccessible and accessible biomasses to the fishery. Eqs. (1) to (3) are applied with different parameters on one hand to the entire biomass (B_τ), and on the other hand to the accessible biomass only (B_τ*). This is because exploited and unexploited trophic groups do not have the same flow kinetics (Gascuel et al., 2011). This is especially the case at low or intermediate TLs where the rate of turnover (and thus the flow kinetics K_τ) is, for instance, much higher for large zooplankton (usually not exploited) than for pelagic finfish.

Finally, catches per trophic class and per time unit are derived from previous equations (see demonstration in Gascuel et al., 2011), as follows:

$$Y_\tau = \varphi_\tau \cdot \Phi_\tau \cdot \Delta_\tau \text{ or } Y_\tau = F_\tau \cdot B_\tau \qquad (5)$$

where F_τ is the usual fishing mortality (year^{-1}), defined as the ratio Y_τ/B_τ and equal to $\varphi_\tau \cdot K_\tau$.

2.3. Building an EcoTroph model

The following parameters are the inputs for the EcoTroph model and are defined for each Ecopath trophic group (i): mean trophic level (TL_i), biomass (B_i), catch (Y_i) and production (P_i). The "ET-Transpose" routine in the EcoTroph R package 1.6 (Colléter et al., 2013) was used to transform the data extracted from Ecopath (for each of the five ecosystems) and convert it into trophic classes. Thus, the "ET-Transpose" routine displays the trophic spectra which represents the current distribution of biomass ($B_{cur,\tau}$), production ($P_{cur,\tau}$) and catch ($Y_{cur,\tau}$) across all the TLs. Additional parameters referring to the current situation are derived from these trophic spectra: the flow kinetics ($K_{cur,\tau} = P_{cur,\tau}/B_{cur,\tau}$), the fishing mortality ($F_{cur} = Y_{cur,\tau}/B_{cur,\tau}$), the fishing loss rate ($\varphi_{cur,\tau} = Y_{cur,\tau}/P_{cur,\tau}$), and the natural loss rate ($\mu_{cur,\tau}$ derived from Eq. (2)). The fishing mortality and fishing loss parameters illustrate current fisheries exploitation patterns by providing a synopsis of fishing pressure across the trophic spectra.

For each Ecopath group, the distributions of biomass, production or catch across the TLs are assumed to follow log-normal curves, defined by the mean TL of the trophic group in question (TL_i) and its standard deviation. The standard deviation (σ_τ; a measure of the TL variability within the group) is conventionally defined according to an empirical model (see Gascuel et al. (2009) for more details). The trophic spectrum is the curve obtained by summing the biomass, production or catch of all the trophic groups.

At first, we used default values for the parameters which quantified the top-down control effect (α and γ) and the biomass-input control (β) in all five ecosystems. To facilitate the simulations of changing fishing effort, these parameters were assumed to be constant throughout the trophic spectrum. Afterwards, we performed sensitivity analyses to test a wide range of values for each parameter.

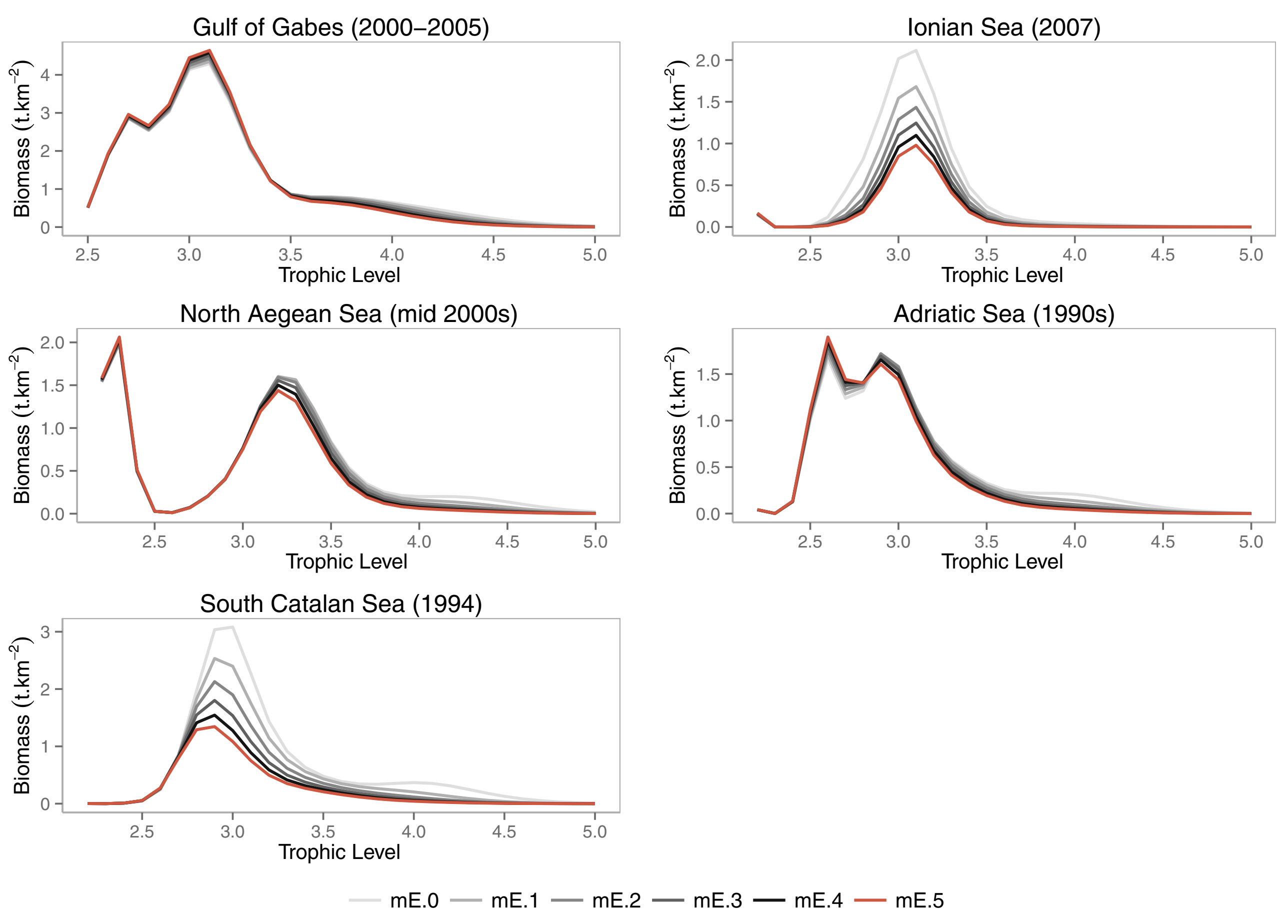

Fig. 5. The simulated biomass trophic spectra for fishing mortality multipliers (mEs; range: 0–5) for each of the five Mediterranean ecosystems examined.

2.4. Simulations of different levels of fishing effort

EcoTroph was used to simulate the impacts of a range of different levels of fishing pressure on the trophic spectra. This was achieved by modifying fishing mortality levels, assuming that the natural loss rates μ_τ and the α, β, and γ EcoTroph coefficients remain unchanged whatever the fishing pressure is. Simulations were conducted for each of the five ecosystems using the "ET-Diagnosis" routine in the EcoTroph R package (Gascuel et al., 2009). This routine simulates the same changes in fishing mortality across all the TLs by using a fishing mortality multiplier (mE) whose value ranges from 0 to 5. A 0 value represents an unexploited ecosystem, values between 0 and 1 represent a decrease in fishing mortality and, finally, values above 1 represent an increase in fishing mortality.

For each value of the fishing mortality multiplier mE, the ET-Routine successively calculates the simulated fishing mortalities ($F_\tau = \text{mE} \cdot F_{\text{cur},\tau}$), the fishing loss rates ($\varphi_\tau = F_\tau / K_\tau$), and then: the biomass flow at TL 1 (Φ_1) and across all the TLs (Φ_τ), the kinetics (K_τ), the biomass (B_τ) and the catch (Y_τ) from Eqs. (4), (2), (3), (1), and (5) respectively. As some parameters are interdependent (B_τ and K_τ on one hand, B_τ and Φ_1 on the other hand), the system of equations needs to be solved iteratively, starting with the reference values of $K_{\text{cur},\tau}$ and $\Phi_{\text{cur},1}$, estimating K_τ and Φ_1 for a given F_τ, then estimating B_τ, and iterating until K_τ, Φ_1 and B_τ estimates stabilize. The outputs of simulations were compared to the current state where $mE = 1$.

Finally, sensitivity analyses were performed to characterize the functioning of each ecosystem and compare their respective responses to changes made to the user-defined parameters, α and β. The coefficients were tested individually, while all other parameters remained constant. For α, we tested values by increments of 0.1 between 0 and 1. For β, we tested values by increments of 0.05 between 0 and 0.3 (values exceeding 0.3 are very unlikely to be found in marine ecosystems).

3. Results and discussion

3.1. Current biomass and catch trophic spectra

The highest values of the current biomass over TL 2 were observed for the Gulf of Gabes ecosystem, followed by the Southern Catalan Sea and North and Central Adriatic Sea ecosystems (Fig. 3). A possible explanation for this finding is the high productivity found at the continental shelves and more broadly, the productivity patterns across the Mediterranean Sea (i.e., higher productivity in the western and northern regions, and lower productivity in the eastern and southern regions) (Bosc et al., 2004). We also noted that for all five ecosystems, medium trophic level species (~TL 3) represented the largest proportions of total biomass. This result reflects the fact that small pelagic fish are the main component of fisheries catches across the Mediterranean Sea (Palomera et al., 2007; Papaconstantinou and Farrugio, 2000), followed by benthic invertebrates (both ~TL 3).

In all five ecosystems, an important decrease in total biomass was observed from the lower to higher TLs. In every ecosystem, significant peaks in biomass were observed between TLs 2.6 and 3.3. Broadly,

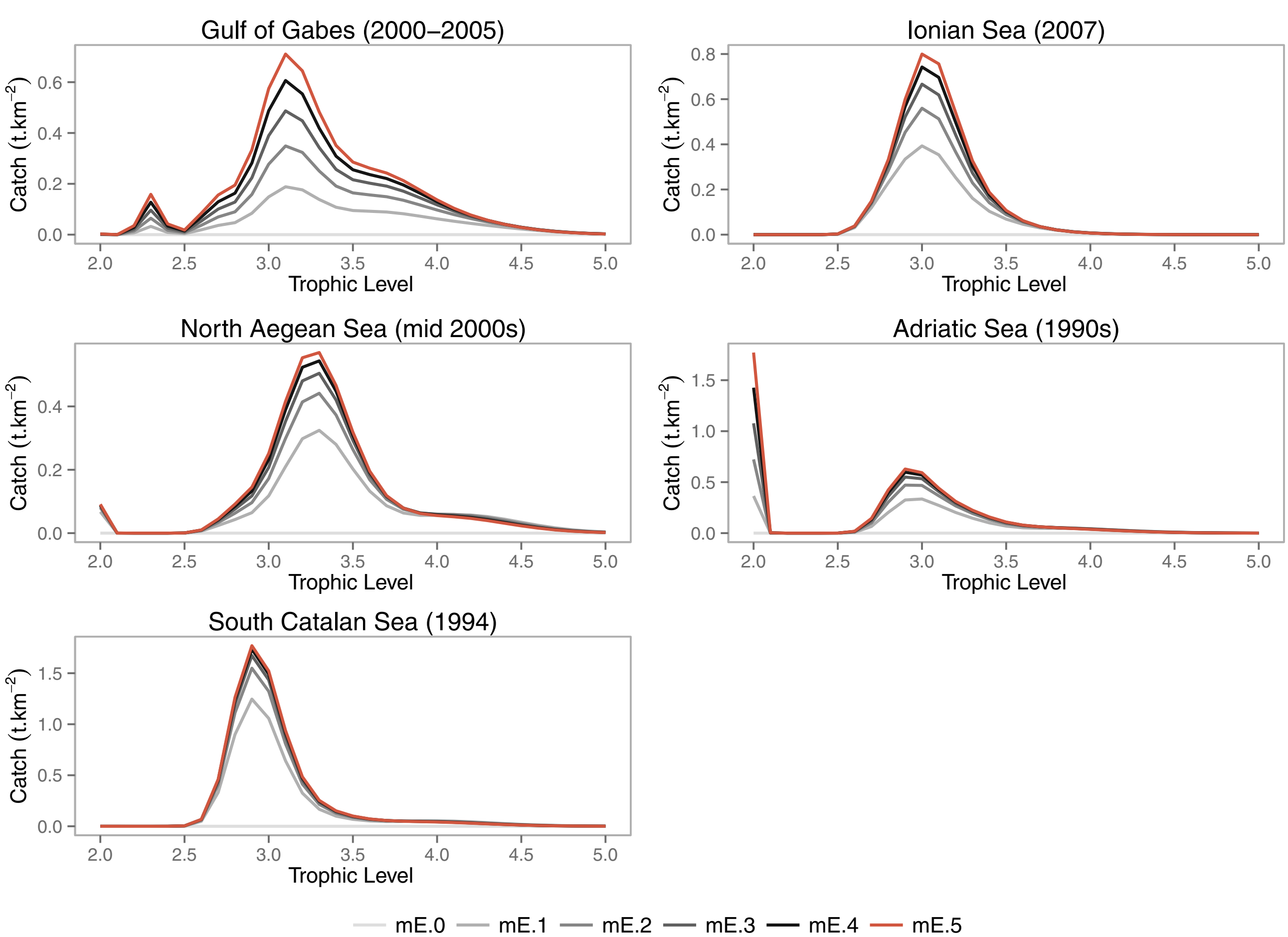

Fig. 6. The simulated trophic spectra of catch for fishing mortality multipliers (mEs) ranging from 0 to 5, for each of the five Mediterranean ecosystems considered.

these peaks correspond to small pelagic fish, such as sardine *Sardina pilchardus* and anchovy *Engraulis encrasicolus*. At around TL 2.2, another significant peak occurs, corresponding to mesozooplankton, benthic mollusks and other benthic invertebrates. This may be driven by the low availability of biomass estimates for some non-commercial species or due to the fact that similar trophic groups may have slightly different TLs across the different ecosystem models (e.g., in the North Aegean Sea model, mesozooplankton is estimated to be TL 2.3, while in the South Catalan Sea model it is TL 2.05) (Coll et al., 2008; Tsagarakis et al., 2010). Around TL 2.5, a gap was observed in all biomass spectra due to the small number of trophic groups present at this point.

A significant finding of this study is that the Mediterranean Sea is highly affected by the depletion of high TL fishes, a fact that is clearly shown in the trophic spectra of biomass at each of the study sites. What is particularly striking about this finding is that it appears to be unusual in comparison with other ecosystems, which show high predator biomasses (≥ TL 4) relative to the Mediterranean Sea, such as the Southern Benguela (Gasche et al., 2012), the Guinean ecosystem (Gascuel et al., 2011),the Celtic Sea and Bay of Biscay (Lassalle et al., 2012) or the Mediterranean marine protected areas of Port-Cros and Bonifacio (Colléter et al., 2014). The results from this study reflect what is actually occurring in the Mediterranean Sea, namely the depletion of large fish species (Lotze et al., 2011; Maynou et al., 2011) and secondarily of marine mammals.

The trophic spectra of fisheries catch are roughly the same shape for all five ecosystems with the exception of the South Catalan Sea whose peak at TL 2.9 is particularly prominent. This is because the fishery there mainly targets small pelagic and juvenile demersal fishes (Fig. 3). These differences in the TL peaks are related to the fact that the TL of any given trophic group can vary slightly between ecosystems.

3.2. Exploitation patterns: trophic spectra of fishing mortality and fishing loss rate

The fishing mortality spectrum reflects which TLs in an ecosystem are currently being targeted. An analysis of the different spectra (across the five study sites) revealed that in most of the ecosystems, high TL organisms (TL > 3.5) are targeted by fishers and fishing mortalities are generally higher than 0.2 year^{-1}. In the case of the Ionian Sea, fishing mortality was up to 0.5 year^{-1} due to the heavily exploitation of hake (Fig. 4). The mid-TLs (around 3.0) are characterized by intermediate fishing mortality values (between 0.1 year^{-1} and 0.2 year^{-1}), except in the South Catalan Sea (F close to 0.5 year^{-1}) due to the intense exploitation of sardine. The Gulf of Gabes was also an exception, exhibiting relatively low fishing mortality values (i.e., F < 0.1 year^{-1}) for all TLs.

The fishing loss rate (φ_τ) measures the proportion of production caught each year. As the impacts that can arise from targeting any given species depend on its productivity, this parameter can be a

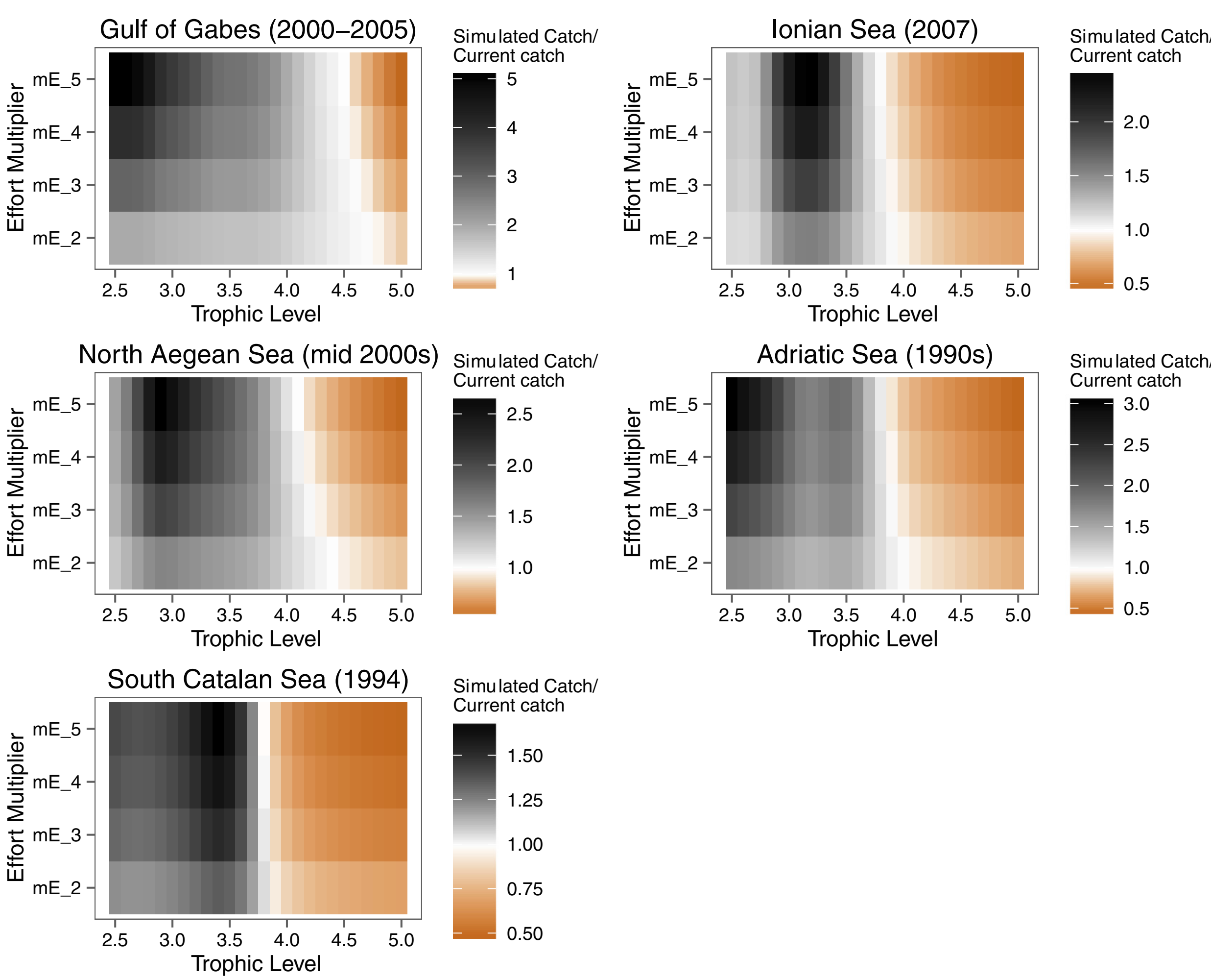

Fig. 7. The simulated relative fisheries catches (simulated catch/current catch) for fishing mortality multipliers (mEs) ranging from 1 to 5, for each of the five Mediterranean ecosystems considered.

more appropriate indication than *F*, as concerns which TLs are being most impacted by fishing activities. Consequently, the corresponding trophic spectrum of fishing loss rate can more accurately reflect fisheries impacts on the ecosystem by TL. In this study, predators with high TLs appear to be most affected by fishing pressure, since the maximum fishing loss rate suggested that for the majority of ecosystems, 40% of the production of high TL species (≥ TL 4, represented by demersal and large pelagic fish) is caught every year in Mediterranean ecosystems (Fig. 4). This result is in line with previous findings from within and outside of the Mediterranean Sea (Coll et al., 2008; Gasche et al., 2012; Gascuel and Pauly, 2009). In contrast, this proportion is estimated to be lower than 10% for small pelagic fish. This suggests that currently, for most of the studied ecosystems, the TL that mainly corresponds to small pelagics would be the least impacted. An exception is in the South Catalan Sea, where the fishing loss rates of small pelagic fish equals 0.3 TL^{-1}.

3.3. Simulations of changes in the level of fishing pressure

3.3.1. Impact on ecosystem biomass

Simulating increasing or decreasing fishing effort allowed us to evaluate the sensitivity of each ecosystem to fishing pressure. Modifications of the fishing mortality multiplier mE led to changes in the shape of the biomass trophic spectra. These changes were due to differences in the structures of the food webs between the five ecosystems and differences in their fisheries exploitation patterns (Table 1). In this analysis, the Gulf of Gabes and the North and Central Adriatic Sea ecosystems appeared to be less affected by the simulated fishing effort than the South Catalan or Ionian Seas (Fig. 5). The biomass sensitivity to mE differed substantially between the TLs. Indeed, the biomass of small pelagic fish in the South Catalan and Ionian Seas seems to be sensitive to fishing pressure, despite their relatively high production/biomass ratio. Essentially, this is due to the nature of the fisheries operating in these areas (i.e., which mainly target small pelagic species) and the fact that both ecosystems are already intensively fished (Coll and Libralato, 2012; Libralato et al., 2008).

3.3.2. Impact on catch

According to the trophic spectrum of catch for each of the five ecosystems studied, total fisheries catches would increase as fishing mortality increases (Fig. 6). However, for the Adriatic Sea and the South Catalan Sea ecosystems, the potential increase in total catch appears very limited, and it only results from higher catch at intermediate TLs (~3). In these two ecosystems, trophic spectra simulated using $mE = 1$ (referring to the current state of the ecosystem) exhibit almost the highest values, while for the three other ecosystems, the Gulf of

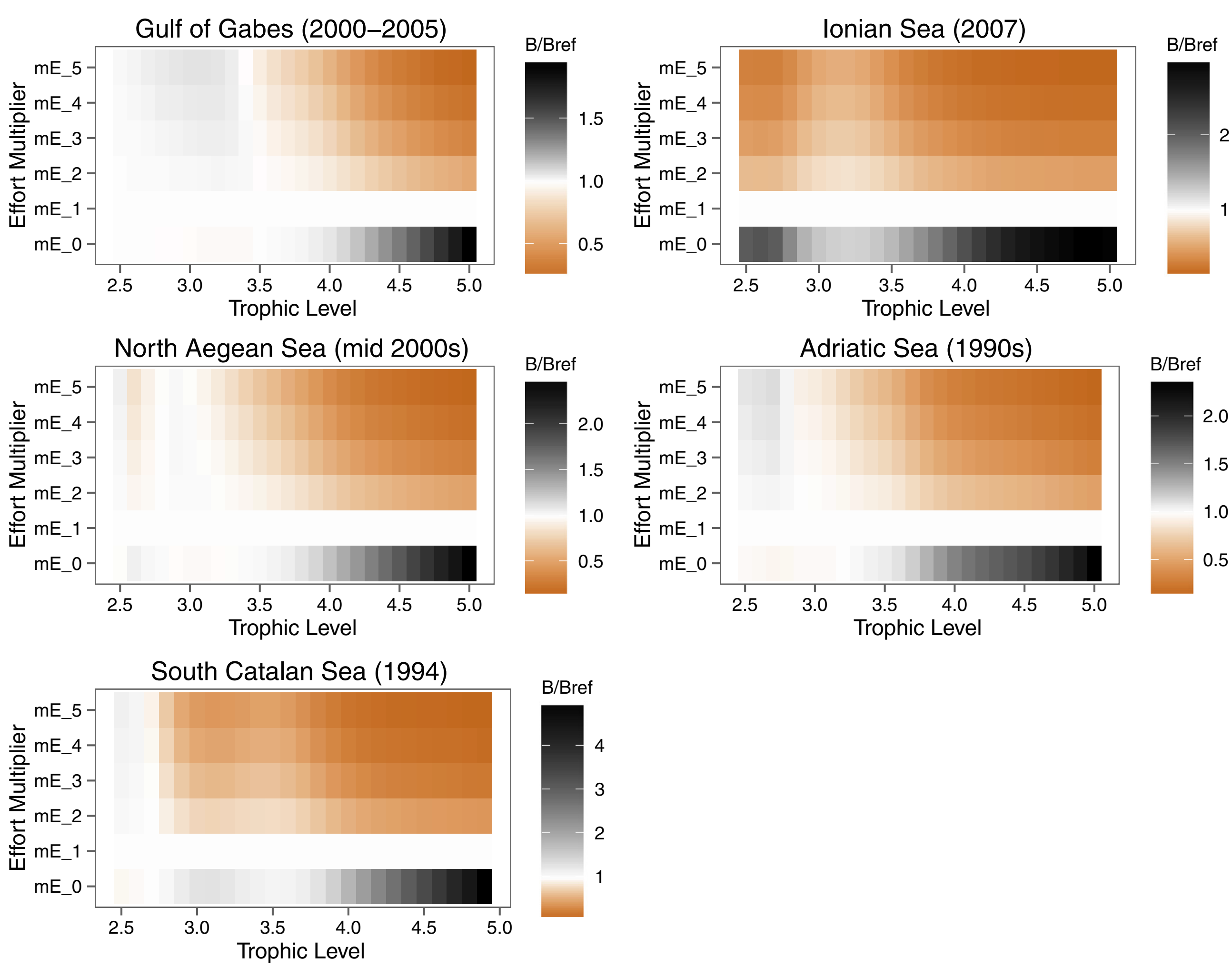

Fig. 8. Simulated relative biomass (B/B_{ref}: simulated biomass/current biomass) for fishing mortality multipliers (mEs) ranging from 0 to 5, for each of the five Mediterranean ecosystems considered.

Gabes, the Ionian Sea and the North Aegean Sea, spectra simulating an increase in the fishing effort (i.e. base on mE > 1) provide greater total catch. This seems to be especially true for the Gulf of Gabes where this increase in catch is observed for all TLs.

The impact of fishing on the trophic spectra of catch was clearer when we compared the simulated catches to the current state catches for each TL (Fig. 7). Simulating an increase in fishing mortality illustrated that fisheries catches at low and high TLs are more sensitive than those at medium TLs. Indeed, for the five ecosystems considered in this study, the high TLs are already overexploited and thus, simulated catches decreased when fishing effort was intensified. However, since their biomasses are less affected at high exploitation levels (in comparison to high TL species), catches of low TL species increased with fishing pressure. This is because these trophic groups have a relatively high production/biomass ratio. High fishing mortality on both low and medium TL species can also have significant direct and indirect ecosystem effects, both at the predatory level and overall ecosystem level. These effects need to be taken into account (Cury et al., 2011; Libralato et al., 2008) and are considered within EcoTroph. Thus, the decrease in the biomass of prey contributes to limit the catch of predators, when the fishing mortalities increase.

A comparison of the relative catch across the five ecosystems showed that their responses to an increase in fishing mortality were quite similar. For all five ecosystems, there is a range in the trophic spectra (between TL 3.7 and TL 4.5) where the trophic groups were not affected by a moderate increase in fishing mortality (Fig. 7). This may be driven by a lessening in predation-related mortality due to the declines in the biomass of high TL species. When fishing mortality is increased further, we observed that this range shifted to incorporate lower TLs, while catches at low TLs increased. This modification can be seen as evidence that Mediterranean ecosystems are experiencing the ‘fishing down the food web’ phenomenon (Pauly et al., 1998).

3.4. Top-down control and ecosystem stability

According to the simulated trophic spectra of biomass, the ecosystem impacts of increasing fishing mortality in the Gulf of Gabes and the Adriatic Sea suggest the possible presence of top-down control. The spectra of both ecosystems showed that the increase in fishing mortality stimulates a decrease in predator abundance (≥ TL 3.5) and an increase in biomass at low and medium TLs due to the release of predation (Fig. 8). This outcome agrees with previous findings that examined ecosystem regime shifts related to a system-wide trophic cascade triggered by overfishing (Daskalov et al., 2007). For the South Catalan and Ionian Seas, the impact of predator biomass levels on their prey groups can be seen more clearly through the top-down effect when we simulated an ecosystem with no fishing. Similar findings have already been discussed in the literature related to the functioning of Mediterranean marine ecosystems (Coll et al., 2009; Hattab et al., 2013).

Total ecosystem biomass appears to be less sensitive to the level of fishing mortality when a top-down control is observed (in the Gulf of Gabes and the North and Central Adriatic Sea). This is because an increase in prey's abundance creates positive effects which compensate, at least partially, the fishing impact on predators. For these two ecosystems, the mean path length (i.e. the average number of trophic compartments that an inflow or outflow passes through) is shorter than in the South Catalan or Ionian Sea (Hattab et al., 2013). This suggests that the stability of the ecosystem's biomass is related to the degree of top-down control and that the mean path length may have a role in influencing the top-down effects. Moreover, the sensitivity analyses we completed for the α parameter showed that it was much more stable in the Gulf of Gabes and North and Central Adriatic Sea models (both of which experienced an important top-down control) than it was in the South Catalan and Ionian Sea ecosystems (Appendix B).

3.5. Sensitivity analyses of biomass and catch to input parameters

The sensitivity analyses that we conducted on the parameters α and β illustrated the effects of modifying the parameters on the simulated biomasses. Looking at the variations in total biomass, the sensitivity graphs show that the choice of β did not affect global results (Appendix A) and further, the total biomass changed by less than 3%. Note, however, that the ecosystem response to high values of β differs between locations. The α parameter has a more significant impact on total biomass for all five ecosystems (Appendix B). For the South Catalan Sea, when fishing mortality was multiplied by five (i.e., mE = 5), total biomass was modified by 12 t km^{-2}. In a current state, this represents approximately 25% of total biomass. The level of sensitivity differed considerably across the five ecosystems.

3.6. The EcoTroph approach: thinking about modeling limitations

Comparing ecosystems using EcoTroph is a particularly relevant modeling approach for highlighting differences in ecosystem functioning. However, there are some limitations associated with its use that relate to the input data. These limitations must be considered when constructing EcoTroph models. In this study, our EcoTroph models likely inherited some limitations from the Ecopath model inputs or outputs due to the use of different methodologies and assumptions when parameterizing the Ecopath models. These model limitations can be broadly summarized as:

- Data availability: typically, there is more and with higher resolution data for commercial and/or charismatic species than for lower TL species. This can create ‘fake gaps’ in the modeled trophic spectra of biomass, especially at lower TLs, if some trophic groups are missing and/or over-aggregated and can lead to biomass underestimations (with resultant consequences for mortality estimates). In this study, this issue predominantly affected species between TL 2 and TL 3 and therefore, our EcoTroph models should be considered more efficient for the medium and high TLs.
- The trophic groups considered in the Ecopath models were composed of both commercial and non-commercial species and consequently, the effects of overfishing in some TLs may be underestimated.
- The estimation of catches: this differed between the five ecosystems due to the nature of the available data (i.e., official data versus data from reconstructed catch). In several instances, the official data used did not take into account discards, by-catch or other sources of fishing mortality (e.g., recreational, and illegal, unreported and unregulated catches).
- The level of aggregation of Ecopath groups: The aim of the EcoTroph approach is to omit the notion of species (or trophic group) to facilitate the comparison between ecosystems. However, when the level of aggregation is too high it will affect the accuracy of EcoTroph outputs due to a loss of information. In this study, the Ecopath models have similar level of aggregation (40 trophic groups) except for the Ionian Sea (19 trophic groups). However, the Ionian Sea was kept in this analysis for comparison to the other ecosystems. This comparison suggests that the behavior of the model was not altered and the EcoTroph outputs from the Ionian Sea were consistent with other results. This is due to the fact that the 19 trophic groups of the model are well distributed throughout the trophic spectrum.

In light of these issues, it is important to understand that the uncertainty associated with the input data used in this study may differ between the five ecosystems. This is important as the relevance of the EcoTroph approach depends primarily on the degree of uncertainty associated with these data.

Despite these limitations, however, the approach set out in this study illustrates a novel application for Ecopath outputs. Further, incorporating Ecopath outputs into EcoTroph models can be used as a tool to identify problems or poorly-estimated parameters in the initial Ecopath model. For example, in this study, we showed that the over optimistic diagnoses of these EcoTroph models may reflect an underestimation in the fisheries mortality estimates for small pelagic fish species, as deduced from some of our Mediterranean Ecopath models. This is especially true in the Gulf of Gabes, where the low fishing mortalities suggested by EcoTroph do not match stock assessment results, indicating that the Ecopath model should be revised.

4. Conclusion

The development of Ecopath in 1984 for modeling marine ecosystems made a substantial contribution to this area of research: TLs (as model outputs) were able to be used to describe food webs and develop indicators that facilitated evaluations of marine ecosystem health. Examples of its application include the development of the marine trophic index (Pauly and Watson, 2005), determining balanced fishing levels (Christensen, 2000) and the development of the L index (Libralato et al., 2008). In EcoTroph, TLs are inputs used to build trophic spectra which provide a summary of an ecosystem. Such an approach ensures that a number of food web characteristics are considered (e.g., biomasses, catches and mortalities of trophic groups). Thus, EcoTroph is a useful tool for developing ecosystem-based indicators, supporting one of the core requirements of effective ecosystem management (Rombouts et al., 2013).

As EcoTroph does not actively consider individual species, it is a relevant tool for both comparing the trophic structures of marine ecosystems and analyzing the functioning of ecosystems in terms of trophic flows, in both an ecological and a fisheries context (Gascuel and Pauly, 2009). In addition, it appears that EcoTroph can be an appropriate tool for exploring ranges of different levels of fishing pressure, which is very useful for understanding some food web properties (e.g., sensitivity to fishing, the intensity of the top-down control and ecosystem stability). This can be achieved by comparing ecosystem responses throughout the trophic spectrum. The comparisons undertaken in this study reveal common features between the five ecosystems we considered. This information will then allow us to link these features to some observed patterns and ecosystem properties; for example, the relationship between the magnitude of top-down control and ecosystems stability. The EcoTroph approach can also be applied to reveal analogies between ecosystems, in terms of their responses to fishing pressure. This type of analysis is useful for highlighting and predicting patterns of ecosystem behavior.

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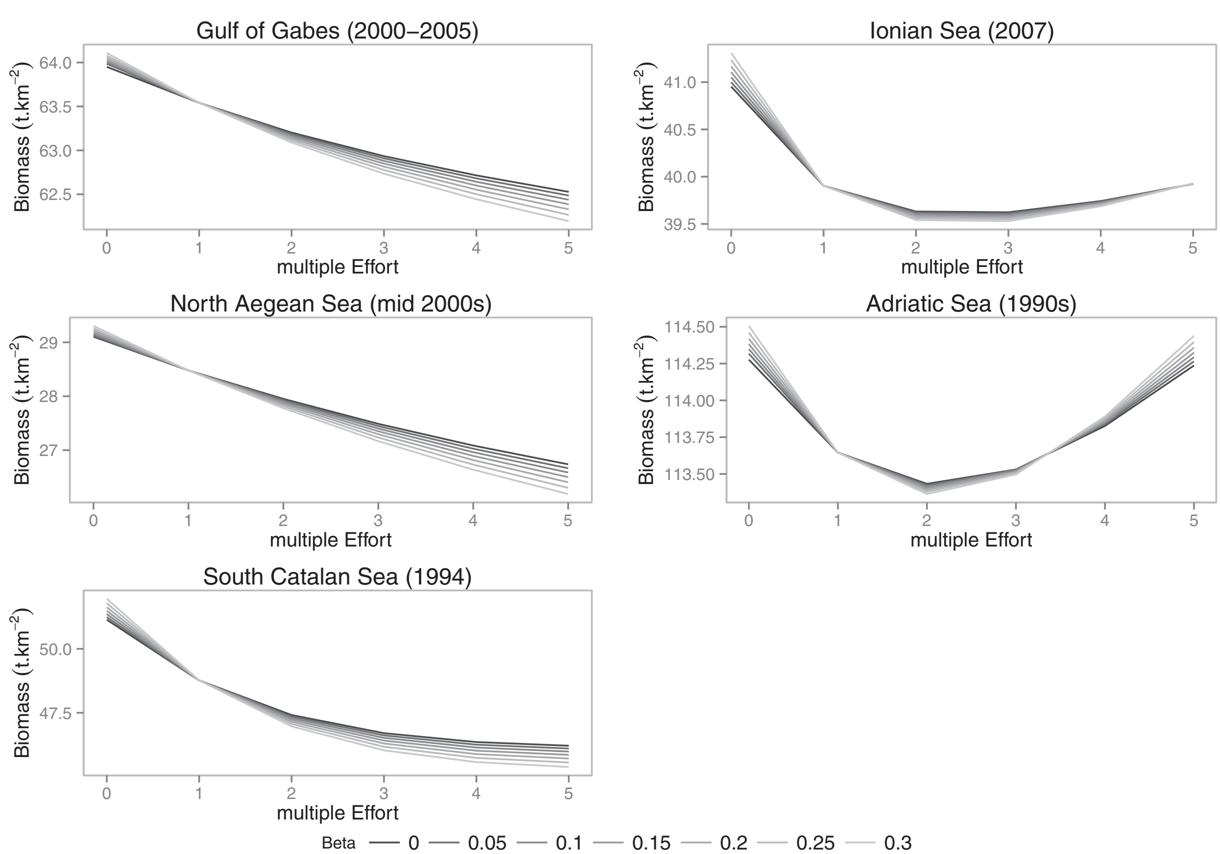
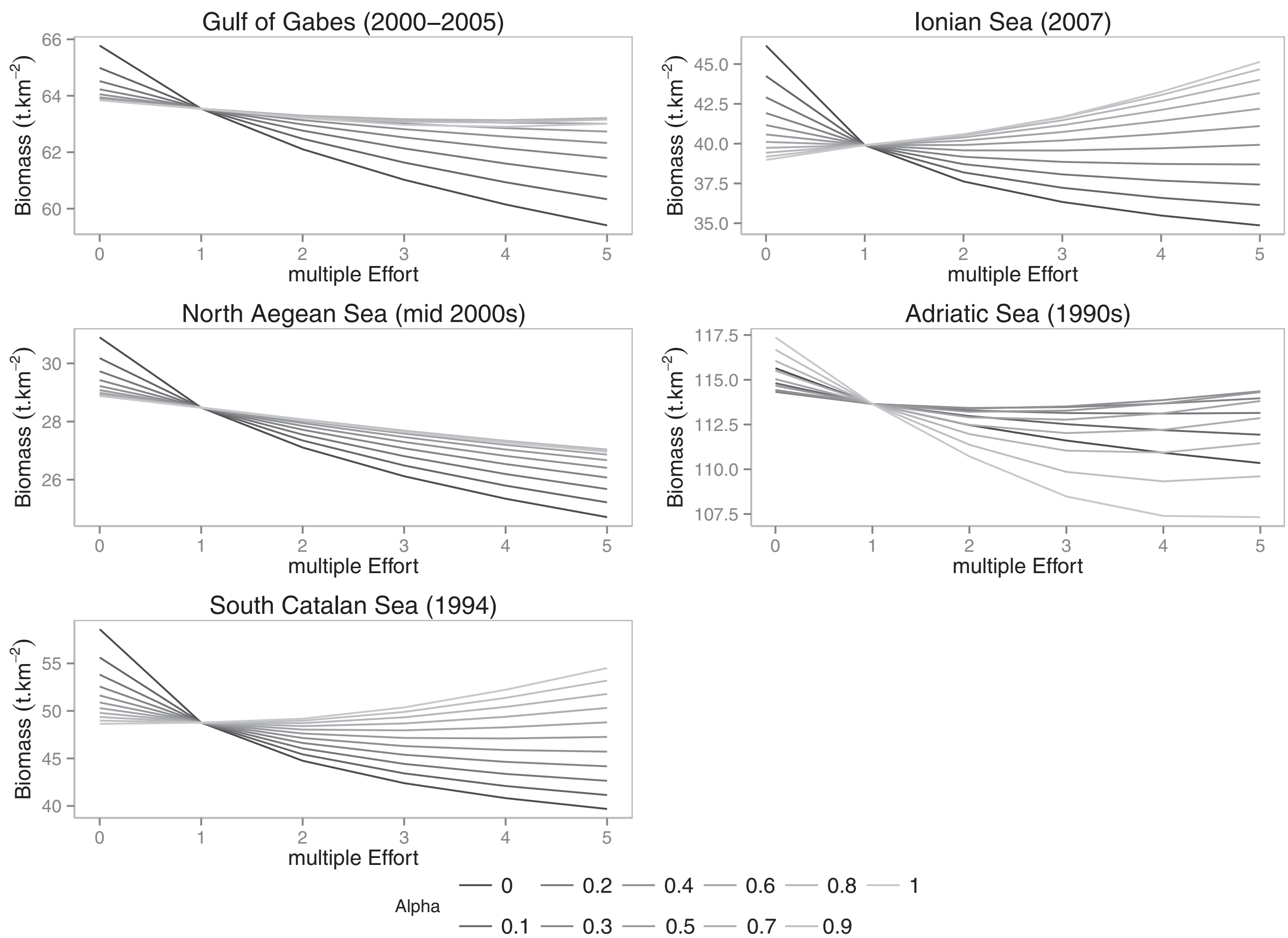
Appendix A. Analyses of the sensitivity of biomass by ecosystem to the intensity of biomass recycling (β) in Mediterranean Sea ecosystems



Appendix B. Analyses of the sensitivity of biomass by ecosystem to the intensity of top down control (α) in Mediterranean Sea ecosystems



Glossary: Input parameters of the EcoTroph model

Variable	Parameter definition	Value or formula	Units
B	Biomass	B	t km^{-2}
Y	Catch	Y	t km^{-2} year^{-1}
P	Production	$K \cdot B$ or $\Phi \cdot \Delta\tau$	t km^{-2} τ year^{-1}
F	Fishing mortality	$F = Y/B$	year^{-1}
K	Flow kinetic	$K = P/B$	TL year^{-1}
μ	Natural loss rate of biomass flow	$\mathrm{LN}(P_\tau/(P_\tau + \Delta\tau))/\Delta\tau - \varphi_\tau$	τ^{-1}
φ	Fishing loss rate of biomass flow	Y/P	τ^{-1}
β	Coefficient of biomass input control	0.2	
α	Coefficient of top-down control	0.4	
γ	A shape parameter defining the functional relationship between prey and predators	0.7	

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