Journal of Marine Systems
November 2022, Volume 235 Pages 103798 (13p.)
https://doi.org/10.1016/j.jmarsys.2022.103798
https://archimer.ifremer.fr/doc/00789/90112/

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Ecosystem modelling of the Eastern Corsican Coast (ECC): Case study of one of the least trawled shelves of the Mediterranean Sea

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Abstract :

The Eastern Corsican Coast (ECC) is distinguished by its shallow sandy shelf, extensive Posidonia seagrass meadows, and the relatively limited exploitation of fish in this region. To understand ECC trophic functioning and the effects of fishing in this region of the Mediterranean Sea, we applied the Ecopath and EcoTroph approaches. Our model encompassed 5 groups of primary producers and detritus, 14 invertebrate groups, two groups of Chondrichthyes, 16 teleost groups, one seabird group, and one group of cetaceans. The ECC ecosystem was structured into five trophic levels, regulated top–down by Sphyraenidae, Epinephelus marginatus, and Dentex dentex. The ecosystem displayed a high degree of benthic–pelagic coupling, confirmed by keystone groups/species located at intermediate trophic levels (Seriola dumerilii, planktivorous teleosts, benthic cephalopods, shrimps, zooplankton). The ECC demonstrated the lowest exploitation rate (F/Z) of all exploited Mediterranean ecosystems, with trawling representing 55% of catches, followed by the lobster net (27%) and fish net (18%) fisheries. Catches often included untargeted groups—often discarded dead—in particular sharks and rays, and several protected species. Moreover, Palinurus elephas, Scorpaena scrofa, and Dentex dentex had elevated F/Z values, highlighting their vulnerabilities to fishing. Although the fishing simulations suggested that the ECC could support a greater exploitation, they also revealed that these fisheries have a marked impact on upper trophic levels. Our study draws attention to the critical habitat the ECC provides for Chondrichthyes, evidenced by the significant biomass for these taxa and the low fishing pressure relative to other exploited Mediterranean systems. This first modelling of the ECC is an initial step towards modelling all Corsican marine ecosystems to serve as a guide for preserving these ecosystems through appropriate management measures.

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Highlights

► The ECC Ecopath model shows a high degree of development as a mature system. ► Fisheries induce a drastic top-down control of top-predator biomass. ► Trawling itself accounts for two-thirds of Chondrichthyes catches, mostly untargeted. ► The East Corsican Coast provides a critical habitat for Chondrichthyes conservation.

Keywords : Ecopath, EcoTroph, fishing impacts, Mediterranean Sea, trawling, trophic structure

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1. Introduction

The Mediterranean Sea is an oligotrophic semi-enclosed basin known to be a key reservoir of biodiversity (Estrada et al. 1985, Coll et al. 2010). Its coast has been inhabited for millennia, and the current marine ecosystems reflect the combination of multiple anthropogenic pressures over time (Durrieu de Madron et al. 2011, Liquete et al. 2016). Moreover, these ecosystems support essential processes and functions that provide valuable ecosystem services and benefits to human societies (Liquete et al. 2016). However, the Mediterranean Sea has been negatively altered in numerous ways, including habitat degradation, the spread of invasive species, water pollution, global environmental change, and the overexploitation of resources (Coll et al. 2012, Du Pontavice et al. 2020). These anthropogenic pressures threaten the ecosystem balance and sustainability, particularly in relation to fishing and its collateral effects, identified as the principal human disturbance of coastal systems (Jackson et al. 2001). In this context, the priority is to assess the overall fishing pressure and the relative impact of fishing activities on ecosystems. In 2008, the European Union adopted the Marine Strategy Framework Directive to boost the overall protection of marine ecosystems around Europe (DSF 2008). The conservation strategies supported by this directive require an initial assessment of the targeted marine ecosystem's current and optimal ecological status and a characterization of the consequences of fishing in the ecosystem.

Since the 1990s, fishery scientists have reconsidered their approach to stock assessment, shifting from single-species or multispecies stock assessments to an understanding of whole-community dynamics when affected by the exploitation activities and the overall consequences for the ecosystem (Pauly et al. 1998, Gascuel 2005, Cury et al. 2008). Stock assessments, supported by statistical models, usually focus on complementary aims, i.e., tactical vs. strategic management planning, including the characterization of fishery impacts

and the environmental drivers in regard to fish stock condition, as well as estimates of the sustainable yield. However, species within an ecosystem are affected by both direct, e.g., predation, and indirect interactions, e.g., competition or underlying trophic links among species assemblages (Corrales et al. 2018). Consequently, the ecosystem-based approach to management (EAM) considers how fisheries target species and affect the populations interacting with the targeted species; this approach allows simulating the exploitation impact on the entire marine ecosystem (Coll and Libralato 2012). Thus, the EAM's holistic approach aims to ensure the sustainable use of marine resources while preserving ecosystem integrity.

With the establishment of the EAM concept and progress in monitoring and computing, much more data have been collected on marine ecosystems. These new inputs have driven the development of ecosystem modelling, i.e., the mathematical representation of systems, and several modelling tools have emerged. For example, OSMOSE, an individual-based model (IBM), focuses on fish species grouped into schools of similar size, weight, age, taxonomy, and geographical location (2D model, Shin and Cury 2001). Atlantis is a 3D ecosystem model with a coarse spatial resolution that accounts for an ecosystem's biophysical, economic, and social components (Fulton 2010).

Among these ecosystem representations, Ecopath is the most common model applied globally, as it is well documented and freely accessible through a user-friendly interface and permits understanding complex marine systems (Christensen and Walters 2004). Ecopath is a mass-balance model that characterizes the trophic structure and functioning among the species groups representing the main ecosystem components (Christensen and Walters 2004, Christensen et al. 2008). These groups are either monospecific or comprise several ecologically similar species in terms of their diet, predators, size, and/or life cycles. The EcoTroph model, based on Ecopath outputs, enables modelling the ecosystem as a continuum

of biomass across trophic levels (TL) ascending the food chain through either predation or ontogenic processes (Gascuel 2005, Gascuel and Pauly 2009). EcoTroph is a trophic level–based model in which the concept of species is no longer explicitly represented, and ecosystem functioning is simplified as a trophic flow of biomass to provide a simple means of rethinking an ecosystem and the impacts of fisheries on these systems.

The application of ecosystem models such as Ecopath or Ecotroph has been recognized as highly relevant for understanding ecosystem functioning and exploring the effects of fishing on an ecosystem of interest (Pauly et al. 2000). Here we apply these integrative tools to the Eastern Corsican Coast (ECC), one of the least exploited marine ecosystems of the Mediterranean Sea (Relini 1999, Coll et al. 2010, Le Manach et al. 2011, Ferrà et al. 2018). Corsica is the fourth-largest island in the Mediterranean Sea and is considered a hotspot for conservation priorities, given its significant biodiversity. For example, coastal Corsica contains one of the most extensive meadows of *Posidonia oceanica* seagrass, classified as a Natura 2000 area (Miniconi et al. 1990, Telesca et al. 2015, INPN-MNHN 2019). In the ECC, marine exploitation is multidisciplinary and includes a wide diversity of small-scale fisheries, including fish nets, spiny lobster nets, longlines, and spiny lobster traps (Le Manach et al. 2011, Bousquet et al. 2022). The ECC is also distinguished by its wide continental shelf that allows trawling by small fishing vessels—perceived as a large-scale or industrial fishery—whereas the rest of the island has remained untrawlable (Ferrà et al. 2018). In addition, the ECC is characterized by one of the lowest fishing intensity rates in the northern Mediterranean Sea, and it can be considered a ‘reference state’ because of its groundfish diversity (Mérigot et al. 2007). Since 1950, the number of fishers has been slowly declining in Corsica, including in the ECC (Le Manach et al. 2011). The decline of fishing as a profession results from both its lack of attractiveness for next-generation candidates and the non-renewal

of licenses for trawling (CRPMEM unpublished data). Even so, the decline of the fishing effort and its resulting impacts on this ecosystem have never been assessed.

To overcome these limitations, we aim to produce relevant tools to guide managers in assessing fishing pressure in the context of ecosystem sustainability within the limits of available knowledge. For this purpose, we develop an ecosystem model to, for the first time, characterize the ECC ecosystem structure, understand its ecosystem functioning, and document the effects of fishing on this marine ecosystem. This ECC modelling offers an unprecedented opportunity to jointly assess the impact of small-scale fisheries and trawling within Corsican coastal waters. We first develop an Ecopath model as a snapshot of the system. We then use Ecopath outputs to develop an EcoTroph model and perform simulations of fishery exploitation to characterize the ECC ecosystem response.

2. Materials and methods

2.1. The Eastern Corsican Coast (ECC): site description and fishery

Because of its diversity of seascapes and habitats, Corsica hosts many fish and invertebrate species and is considered a biodiversity hotspot (Miniconi et al. 1990). The island is inhabited by many emblematic species protected through regulations, including the dusky grouper (*Epinephelus marginatus*), common dentex (*Dentex dentex*), and spiny lobster (*Palinurus elephas;* Bodilis et al. 2003, Marengo et al. 2016, 2020). The island's coastal waters are protected by several marine protected areas (MPAs), including the Scandola Natural Reserve, the Bonifacio Straits Natural Reserve (BNSR), and, more recently, the Cap Corse and Agriate Marine Natural Park (OEC 2011). The ECC forms a singular spatial unit characterized by a continental shelf composed of soft sloping sands and extensive meadows of *Posidonia oceanica* seagrass, a phanerogam species endemic to the Mediterranean Sea. The *P. oceanica*

habitat of the ECC is among the largest classified Natura 2000 areas in relation to its spread and state of conservation (Telesca et al. 2015, INPN-MNHN 2019).

Throughout the ECC, coastal fishery exploitation is limited to artisanal fisheries and consists of a combination of deploying fishing nets and trawling, operated respectively by 26 and 9 fleet vessels. Net fishers, classified as small-scale fisheries, operate with small boats (<12 m long) and use a wide diversity of gears and techniques. This equipment is typically staffed by a single or a pair of fishers. In contrast, trawler vessels are considered large-scale fisheries, having larger boats (>12 m long) handled by several fishers. Three predominant fishing activities are found on the basis of the targeted species, gear, depth, and period during which the gear operates (Radley-Gardner et al. 2016): (i) the spiny lobster fleet, defined as any fishing operation using a trammel or gillnet set at 50–150 m depth for a minimum of 48 h; (ii) the fish net fleet, defined as any fishing operation using a trammel or gillnet set at 15–120 m depth for a maximum of 48 h; and (iii) trawling, defined as fish trawling set for one hour at 50–200 m depth. At a smaller scale, bottom longlines, fishing traps, and recreational fisheries are less widely operated in the ECC relative to fishing nets and trawling, and these fisheries are not sufficiently documented for this period (data from the DACOR project used in Bousquet et al. (2022) and data from the Marte+ project. Hence, these latter activities were not included in the ECC model.

We developed the Ecopath model of the ECC as an average annual state over two consecutive years (2012–2013), determined by data availability. The ECC ecosystem covers 1930 km^2, extending from the cities of Porto-Vecchio to Bastia, and the marine waters have a maximum depth of 200 m (Fig. 1). As a coastal ecosystem, the area deeper than 50 m only covers 489 km^2, i.e., 25.4% of the total area. The ECC is primarily covered with sand and *P. oceanica* seagrass, accounting respectively for 1668 km^2 and 258 km^2, i.e., 86.4% and 13.4% of the

ecosystem area. Between 2012 and 2013, the mean near-surface sea temperature (NSST) was 18.7 °C, fluctuating between 13.0 and 26.2 °C (NASA 2018).

2.2. The Ecopath model: principles and functioning

We modelled the ECC ecosystem using the Ecopath approach via the open-source software Ecopath with Ecosim v.6.6.5. An Ecopath model is a snapshot of the ecosystem structure produced by applying two master equations separately for each model group, one describing the production term and the other presenting the energy balance (Supplementary data 1). To solve both equations, we required two conditions. First, we had to implement at least three of four basic parameters of each group *i*, i.e., the biomass B ($t \cdot km^{-2} \cdot yr^{-1}$), the production per unit of biomass P/B (yr^{-1}), the consumption rate per unit of biomass Q/B (yr^{-1}), and the ecotrophic efficiency EE (unitless). Second, the model requires implementing parameters involving total fishery catch Y ($t \cdot km^{-2} \cdot yr^{-1}$), the net migration rate E ($t \cdot km^{-2} \cdot yr^{-1}$), the biomass accumulation rate BA ($t \cdot km^{-2} \cdot yr^{-1}$), the assimilation of food intake A ($t \cdot km^{-2} \cdot yr^{-1}$), and the diet composition DC (unitless, Supplementary data 1 and 2). Ecopath can then perform as many linear equations as there are groups implemented within the model to solve for unknown parameters.

2.3. The ECC model

The Ecopath model we developed for the ECC encompasses 39 groups, including 5 groups of primary producers and detritus, 14 invertebrate groups, 2 groups of Chondrichthyes, 16 groups of teleosts, 1 seabird group, and 1 group of cetaceans (Table 1). In addition, 14 of these 39 groups are monospecific, either to isolate species of high interest for fisheries or because of their unique ecological role within the system. Because the model objective is to quantify the effects of fisheries on the ECC ecosystem, groups including exploited species are

more represented than nontargetted groups. An exhaustive list of all species groups (mono- and multispecific groups) inhabiting the ecosystem is provided in Supplementary data 3.

2.3.1. *Primary producers and detritus*

To estimate phytoplankton biomass, we combined satellite ocean colour observations (NASA 2018) and data from the literature (Supplementary data 3). Next, we determined the biomass of *P. oceanica* as the average aboveground biomass per meter (Gobert et al. 2003) and extrapolated to the meadow surface area (Donia Expert 2020, Supplementary data 3). We estimated macroalgal biomass using the average weight per meter from Sargian (1997) and extrapolated to the surface area of rocky bottom (Donia Expert 2020, Supplementary data 3). Then, we assessed the detritus biomass from the empirical equation of Christensen and Pauly (1993) using POC values (IFREMER unpublished data). We collected the P/B estimates for primary producer groups in the literature selected because of the geographical proximity of these studies to Corsica (Supplementary data 3).

2.3.2.Invertebrates

We assessed invertebrate biomass from field data collected for macro- and megafauna (Pelaprat et al. 2013), in addition to the information we extracted from the MEDITS trawling survey data (IFREMER 2019) corrected with catchability parameters (Moutopoulos et al. 2013). We calculated the biomass of the urchin *Paracentrotus lividus* according to Duchaud et al. (2018) and projected to rock surface area below 10 m (Donia expert 2020, Supplementary data 3). We collected the P/B and Q/B parameters either from empirical equations (Eq. 1, Allen 1971; Eq. 2, Brey 2001; Eq. 3, Pauly 1989, Christensen and Pauly 1993) or from published studies selected because of their geographical proximity to Corsica and temporal overlap (Supplementary data 3). We estimated benthic groups' diets from

literature selected once again for their spatiotemporal overlap with this study and weighted each parameter per the relative biomass of each species (Supplementary data 3). Equation 1 states

$$Z = P/B = M + F\ , \qquad (1)$$

where Z represents the total mortality per year, M is the natural mortality per year, and F is the mortality induced by fisheries per year. Equation 2 has

$$log(P/B) = 1.672 + 0.993 \times log(1/A_{max}) - 0.035 \times log M_{max} - 300.447 \times (1/(T + 273))\ , \qquad (2)$$

where A_{max} is the maximum age observed (year), M_{max} is the maximum observed body mass (kJ) converted from wet weight (Mills 1980), and T is the mean water temperature (°C). Equation 3 is

$$log(Q/B) = 7.964 - 0.204 log W_{\infty} - 1.965T' + 0.083A + 0.532h + 0.398d\ , \qquad (3)$$

where W_{∞} is the asymptotic weight (g), T′ is the mean environment temperature expressed as 1000/(°C + 273.15), A is the aspect ratio of the caudal fin (unitless), h and d, two unitless variables, are indicators of herbivory (h = 1, d = 0), detritivory (h = 0, d = 1), and carnivory (h = 0, d = 0). The asymptotic weight W_{∞} was estimated using the length–weight relationship based on the asymptotic length L_{∞} and published allometric coefficients. When L_{∞} was missing, we assumed that the maximum lengths $L_{max}/0.95 = L_{\infty}$. We chose the groups' parameters from the literature for their spatiotemporal overlap with the study. We then weighted the model's input parameters according to each species' relative biomass.

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2.3.3 Fish

We performed cluster analyses on the diet matrix to assign each teleost species to a trophic guild. First, we built the diet matrix from the literature selected for their spatiotemporal overlap, prioritizing the study areas nearest to Corsica and the 2012–2013 period. Second, we conducted cluster analyses on gut-content studies using the average linkage method with Euclidean distance coefficients. The average linkage method provided the highest cophenetic correlation values compared with other clustering methods and was therefore the approach that produced the best clustering model for the distance matrix (Borcard et al. 2011). We selected the optimum number of groups according to silhouette widths and Mantel statistics. Finally, we ensured the consistency between teleost groups by verifying fish length, TL, and water column habitat recognized in the literature, FishBase (Froese and Pauly 2009), and fish landings. We performed the cluster analyses using R software v.3.6.2 (R Core Team 2020) running the vegan (Oksanen et al. 2018), the cluster (Maechler et al. 2018), and the glcus (Hurley 2012) packages.

We calculated the biomass of Chondrichthyes and teleosts from different sources. For the bathymetric stratum (0–50 m), we used the fish net catch data (fishery database cited in Marengo et al. 2016, Pere et al. 2019, Bousquet et al. 2022), and for the bathymetric stratum 50–200 m, we retrieved the information from the MEDITS trawling survey data (IFREMER 2019), corrected by catchability parameters. These latter parameters were extracted from Moutopoulos et al. (2013) by comparing MEDITS data and the biomass used in an Ecopath model for the Calalan Sea (Coll et al. 2006). We estimated the P/B and Q/B parameters from empirical equations (Eq. 1, Allen 1971; Eq. 3, Pauly 1989, Christensen and Pauly 1993; Eq. 4, Gascuel et al. 2008) and weighted the parameters according to the relative biomass of each species. Equation 4 has $P/B = 3.55\tau^{-0.66}K^{0.80}$, where τ is the TL of the group (unitless), and K is the growth coefficient (unitless) extracted from FishBase (Froese and Pauly 2009).

2.3.3. Shags and dolphins

The ECC model encompassed two monospecific groups: the European shag (*Phalacrocorax aristotelis)* and the bottlenose dolphin (*Tursiops truncatus)*. We estimated the parameters B, P/B, and Q/B from visual surveys and the literature chosen because of their geographical proximity to Corsica (Supplementary data 3).

2.3.5 Landings, discards, and fish mortality

Fishing data were collected from March to September 2012–2013 by scientists aboard 14 fleet vessels (fishery database cited in Marengo et al. (2016), Pere et al. (2019), and Bousquet et al. (2022)). Over the last decade, sampling efforts have been deployed to characterize the Corsican fisheries, including the composition of conserved and discarded catches and estimates of annual production. For all fishing activities (spiny lobster fleets, fish net fleets, and trawling), catches including discards were identified to the lowest possible taxonomic level, counted, measured, and the discard mortality recorded. To estimate each catch weight, we used the weight–length relationship (Le Cren 1951) based on published allometric coefficients selected according to their geographical proximity to Corsica. Then, we assessed catches separately for the spiny lobster fleet, fish net fleet, and trawling nets as the product of the biomass per unit effort (BPUE, g·50 m of net) and the total fishing effort (*Et*; Farrugio and Le Corre 1993, Pere et al. 2019, Bousquet et al. 2022; Eq. 5).

$$E_t = N_{fd} \times N_f \times N_n \,, \qquad (5)$$

where Et, in relation to fishing gear, is the total number of either net pieces or trawling hours deployed in one year, N_{fd} is the annual number of fishing day trips (days), N_f represents the annual number of fishers, and N_n is the number of net pieces or trawling hours occurring per

fishing day. We ensured the consistency of the ECC production by comparing our results with Le Manach et al. (2011) and Bousquet et al. (2022).

2.3.4. Balancing the model

To balance the model, we automatically adjusted the diet matrix to reduce the proportion of higher TLs consuming food. Groups' diets were adjusted slightly to account for species' abundances in the ecosystem. In addition, we added diet imports for Sphyranidae, bottlenose dolphin, *Seriola dumerili*, Chondrichthyes, and zooplankton by assuming intra-annual migrations outside of the system (Supplementary data 2). Then, we verified the model's pedigree, estimated at 0.58, and PREBAL diagnostics (Link 2010). PREBAL diagnostics include step-by-step verifications of biomass, biomass ratios, vital rates, vital rate ratios, total production, and total removals across all taxa and TLs (Supplementary data 5).

2.4. Mixed trophic impact analysis and keystoneness

The mixed trophic impact (MTI) analysis quantifies direct and indirect trophic effects that may be caused by a hypothetical increase of the group's biomass, including fishing fleets (Ulanowicz and Puccia, 1990, Christensen et al. 2008). The output of the MTI analysis is an n × n matrix, representing the interaction between the impacting group i and the impacted group j as

$$MTI_{i,j} = DC_{i,j} - FC_{j,i}\ , \qquad (6)$$

where $DC_{i,j}$ is the diet composition term expressing how much j contributes to the diet of i, and $FC_{j,i}$ represents the proportion of the predation on j because of i as a predator. In addition, we supplemented the MTI with the keystoneness (KSi) analysis proposed by Libralato et al.

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(2006). This index has the particularity of attributing high KS values to keystone groups that can have either a low or high biomass proportion in the system.

2.5. The EcoTroph model

Starting from the previous Ecopath balanced model as a reference state, we performed the 'transpose' routine to develop the EcoTroph trophic level–based model (Gascuel 2005, Gascuel and Pauly 2009, Gascuel et al. 2009, Supplementary data 9a). We then undertook a sensitivity analysis on the smooth parameter to obtain a continuous parameter distribution along the TLs (Gascuel et al. 2009, Supplementary data 9b). The smooth parameter is based on the idea that the average TL of a group does not fully reflect its function within an ecosystem, as all species within a given group are exactly the average TL. Using EcoTroph, we first simulated the current exploitation state of the ECC by using the default settings of 0.12 for the smooth parameter, 0.60 for the top–down parameter, and 0.80 for the form-D parameter (Gascuel et al. 2009).

The EcoTroph model assumes that only a fraction of the ecosystem biomass is accessible to fisheries, referred to as the fisheries accessibility (unitless, Table 1). We estimated fisheries accessibility (i) for multispecies groups, as the percentage of fished species within a group; (ii) when fisheries targeted all species of a group, accessibility estimated as the fraction of the inhabited habitat area per the overall ecosystem area; and (iii) by setting the accessibility value to zero for unfished groups (Table 1). Then, we performed the 'diagnosis' routine to simulate the spectral distortions induced by fisheries and changes in the exploitation patterns, applying various multiplying factors to the fishing effort (Gascuel et al. 2009). Using the EcoTroph model, we simulated the current exploitation state and compared outputs to three states of exploitation scenarios: i) an extreme scenario in which the total fishing effort increases fivefold; ii) the cessation of the trawl fishery; and iii) the cessation of the trawl

fishery combined with a two-fold increase in net fishing. We then plotted isopleths of the simulated fishing effort fluctuations on total catches and catch TLs, i.e., a two-dimensional contour graph of two variable functions along which the function has a constant value so that the curve joins points of equal value.

2.6. Comparison of Mediterranean fisheries

We compared the fishing exploitation levels of the ECC to eight Mediterranean models: the Bay of Calvi, Corsica (Pinnegar and Polunin 2004), the Gulf of Lions (Bănaru et al. 2013), the Catalan Sea (Coll et al. 2006), the Adriatic Sea (Coll et al. 2007), the Aegean Sea (Tsagarakis et al. 2010), Port-Cros National Park (Valls et al. 2012), the protected marine areas of Portofino (Prato et al. 2016), and the Gulf of Pagasitikos (Dimarchopoulou et al. 2019). We chose these published models because of their spatial proximity to the ECC and their accessibility on EcoBase, i.e., the open-access database platform (http://ecobase.ecopath.org/). To this end, we selected eight indicators of the fishing pressure: 1) the total catch (Y, $t \cdot km^{-2} \cdot yr^{-1}$); 2) the mean TL of the catches (TL_c); 3) the gross efficiency (GE), defined as the ratio between catch and net primary production (Pauly and Christensen 1995, Pauly et al. 1998); and 4) the probability of an ecosystem being sustainably fished (P_{sust}, Libralato et al. 2008). We also selected 5) the estimated loss in production index (L, Libralato et al. 2008, Eq. 7), defined as

$$L = \frac{-PPR \times TE^{TL_C - 1}}{P_1 \times ln(TE)}, \quad (7)$$

where PPR represents the primary production required to sustain fisheries ($t \cdot km^{-2} \cdot yr^{-1}$), TE is the transfer efficiency ($t \cdot km^{-2} \cdot yr^{-1}$), TL_c is the mean trophic level of catches, and P_1 represents the autotrophic and detritus production within the trophic web ($t \cdot km^{-2} \cdot yr^{-1}$). Finally, we extracted three indicators of the overall fishing pressure from the literature that

were not generated from Ecopath models: 6) the estimated number of operating trawling vessels (FP_{trawl}) or 7) other fishing activities ($FP_{not\ trawl}$, Colloca et al. 2017); and 8) the number of AIS messages (AIS, automatic identification system ship tracking data; Vespe et al. 2016).

AIS messages originated from large trawlers only (bottom otter, beam, and midwater trawls) and contain information on the time, position, direction, and speed of fishing vessels >15 m in length (Vespe et al. 2016). We identified operating trawlers according to speed profiles, which allowed characterizing the fishing grounds and mapping the intensity of use of the offshore fishing areas. We selected the Mediterranean models according to the availability of fishing indicators and used principal component analysis (PCA) to compare the models. PCA was performed using R v.3.6.2 (R Core Team 2020), running the ade4 (Thioulouse et al. 2018) and the factoextra (Kassambara and Mundt 2020) packages (Borcard et al. 2011).

3. Results

3.1. Characterization of the ECC ecosystem

3.1.1. General outputs of Ecopath model

The ECC model was structured into five TLs, ranging from primary producers to top predators, with a TL 4.8 for Sphyraenidae, TL 4.6 for *Epinephelus marginatus*, and TL 4.4 for *Dentex dentex* (Table 1, Supplementary data 6, 7). The group of *Sarpa salpa*, feeding on primary producers, had the lowest TL values for fish at 2.0. Groups of invertebrates obtained TLs from 2.0 for the sea urchin *Paracentrotus lividus* to 3.9 for suprabenthic cephalopods.

The biomass of primary producers dominated the ecosystem model, followed by invertebrates, teleosts, and Chondrichthyes, at 91.6%, 3.8%, 4.2%, and 0.4%, respectively, of the total biomass, excluding detritus (Table 1). *P. oceanica* seagrass alone accounted for

90.1% of total biomass. Planktivorous fish were the most abundant group of vertebrates, followed by invertebrate groups of zooplankton and echinoderm, at 3.4%, 1.4%, and 1.2% of the ecosystem biomass, respectively. The ECC ecosystem supported a high biomass of Chondrichthyes, representing 9% of the total fish biomass.

For many groups, ecotrophic efficiency (EE) from inputs or estimated parameters in the Ecopath model were close to one, especially for low TLs (Table 1). Although the biomass of primary producers was dominated by seagrass, seagrass (EE = 0.3) was less assimilated into the system than phytoplankton (EE = 0.6). In contrast, three groups had efficiency values below 0.1, emphasizing their low exposure to predation and fishing (shag, dolphin, and Sphyraenidae). However, the low EE must be interpreted with caution, given that some groups might be subject to predation, especially during the juvenile stage, or are fished outside the system. Moreover, *Sarpa salpa* is neither fished (its flesh is tasteless) nor hunted, possibly because of its large size and schooling behaviour.

The ratio between production and consumption (P/Q) encompassed expected values (Christensen et al. 2008). The highest values were found for groups of Labridae, benthic crustaceans, followed by shrimps, ranging from 0.3 to 0.4 (Table 1). In contrast, (P/Q) values were very low (0.01) for shags and dolphins.

The system omnivory index (OI), measuring the distribution of the trophic interactions among TLs, was highest for dolphins, *Seriola dumerili*, Sphyraenidae, and benthic sharks, exceeding one (Table 1). In contrast, eight groups had (OI) values below 0.05 (*Chromis chromis*, benthic invertebrate feeders (BIF), planktivorous taxa, *Sciaena umbra*, *Dentex dentex*, worms).

The analysis of the energy fluxes emphasized a main bentho–pelagic pathway, connecting primary producers to the higher TLs in the food web through the benthic invertebrate and

benthic fishes compartments to pelagic fishes (Fig. 2). This group of zooplankton proved to be an essential connector to the energy flow ascent, characterized by a high degree of connections to planktivorous fish. Similarly, the model suggested that shrimps were a major link to connect energy flows towards benthic fishes, cephalopods, and Chondrichthyes (Supplementary data 2 and 6). Groups of zooplankton, *P. oceanica* seagrass, and phytoplankton presented the highest flow values to detritus, at 48.4%, 23.5%, and 19.8%, respectively, of the total flows (Fig. 2).

In the ECC ecosystem, mortality was primarily induced by predation for most groups of lower TLs, especially for phytoplankton and zooplankton (Table 1). Hence, our results emphasized three groups almost unaffected by predation in terms of their status as top predators in the system: *Scorpaena scrofa*, *Dentex dentex*, and *Epinephelus marginatus*.

3.1.2 Analysis of mixed trophic impact (MTI) and keystone groups

The system comprises top–down types of control from top predators, such as *Scorpaena scrofa*, piscivorous fish, and sharks (Fig. 3, Supplementary data 8). Some groups of intermediate TLs had a significant trophic effect on the ecosystem, such as benthic cephalopods, planktivorous fish, and Sparidae. The top–down control of the spiny lobster (*P. elephas*) on the sea urchin *Paracentrotus lividus*, a species limited by macroalgal biomass, illustrated a direct impact. A similar form of trophic cascade occurred for BIF, controlled top–down by benthic sharks and at the same time, bottom–up controlled by shrimps.

Groups of echinoderms and zooplankton exerted a high trophic effect on themselves through cannibalism. Finally, few groups in the system were affected by primary producers groups at the base of the food web, such as macroalgae exerting a bottom–up control on sea urchin *P. lividus* and seagrass *P. oceanica* on *Sarpa salpa*. Following the MTI analyses, analyses of

keystone groups highlighted the leading role of zooplankton, shrimps, benthic cephalopods, and planktivorous fish (Table 1, Fig. 3).

3.2. Fisheries effect on the ECC ecosystem

Along the ECC, biomass extracted by fishing activities represented 463.2 t annually for the entire ecosystem, i.e., 0.5% of the system biomass of combined vertebrates, cephalopods, and crustaceans (Table 1). Total catches of fisheries, estimated at 0.2 t $km^{-2} \cdot yr^{-1}$, were primarily through trawling (56.1%), lobster net (22.7%), and fish net (21.1%, Table 1; Fig. 4) activities. When all fishery activities were combined, catches included mainly groups of benthic sharks (23.6%), planktivorous fish (21.0%), rays (12.7%), and piscivorous fish (12.2%, Fig. 4a). Fishing fleets targeted distinct ecosystem groups, reflected in the average TLs of total catches (fish net: 3.7, lobster net: 3.7, trawling: 3.5, Table 1).

Trawling in the area primarily involved planktivorous fish (37.2%), sharks (27.0%), and Sparidae (11.3%, Fig. 4b). The fish netting was marked by high landings of rays (27.0%), piscivorous teleosts (22.4%), *Dentex dentex* (15.5%), and sharks (14.1%, Fig. 4c). The spiny lobster net fishery affected mainly groups of rays (29.7%), piscivorous teleosts (28.7%), and sharks (24.7%, Fig. 4d). Moreover, two monospecific groups, of *Scorpaena scrofa* and *Palinurus elephas*, showed high exploitation rates (F/Z > 0.2) (Table 1). However, our results also highlighted the moderate effect of fisheries, as gross efficiency (GE) was below 0.01%.

MTI analysis confirmed the strong control of trawling currently exercised within the ECC system (Fig. 3). Indeed, trawling has a significant top–down impact on both Sphyranidae and sharks as the top predators of rays and BIF, with consequences continuing down the food chain. MTI analysis also emphasized that fishing nets have lower trophic impacts than

trawling. Important top–down controls were noted for fish nets on *Dentex dentex* and lobster nets on *P. elephas* (Supplementary data 8).

Comparing the ECC to an unfished state, using the EcoTroph model, our simulation emphasized that the biomass of TLs >3.5 was most affected by fishing—leading to a gradual biomass decrease as TL increased (Fig. 5a). The extreme scenario of a fivefold increase in fishing effort showed the most pronounced response relative to the reference state. In the extreme scenario, the biomass flow increased from TL 2.5 to 3.5 and then dropped by half for TLs greater than 3.5. Simulations also suggested that the suppression of trawling resulted in a clear improvement of top-predator abundance. In contrast, the trawling ban and the doubling of net effort resulted in a decrease in top-predator biomass relative to the current state.

Fishing effort fluctuations illustrated using isopleths showed that total catches increased uniformly with fishing pressure and that trawling and net fishing did not compete with one another (Fig 5b, c). The isopleths produced by EcoTroph indicated that enhanced trawling and net fisheries had a low effect on the mean TL of catches (Fig. 5d).

3.3. Comparison of Mediterranean fisheries

Overall, the PCA performed on fishing indicators was explained by the first two components, and Mediterranean models were correctly represented in the two-level factorial design (i.e., 68.1%, Fig. 6). The PCA highlighted the importance of four fishing variables: the FP_{trawl}, TLc, P_{sust}, and L. FP_{trawl}, the estimated number of operating trawling vessels, and TLc, the mean TL of catches, explained most of the first component (PC1: 45.0%). The right factorial plane included the Catalan Sea, Portofino, and the Adriatic Sea, areas highly frequented by trawlers. In contrast, the right part of the graph, composed of the ECC, Calvi, and Port-Cros models, corresponded to less-trawled systems. TLc is a proxy indicator of the exploitation

level that an ecosystem faces. Hence, TLc decreased in highly exploited ecosystems, as fisheries target primarily top predators having high TLs. PC1 emphasized along its axis the high values of TLc in the ECC, Calvi, and Port-Cros systems. Moreover, the second axis was driven by P_{sust}, the probability of the system being in a sustainable fishing situation, and L, the loss in production index (PC2: 23.1%). P_{sust} and L values were lowest for the Gulf of Lions model and highest for the ECC model.

4. Discussion

4.1. Ecosystem functioning

The Ecopath model of the ECC reveals a high degree of development, reflecting a mature ecosystem. The model statistics indicate a developed system on the basis of (i) its high value of total system throughput (TST = 3598.56 $t \cdot km^{-2} \cdot yr^{-1}$), representing 'the size of the entire system in terms of flow' (Ulanowicz 1986), (ii) its ratio between primary production and respiration approaching 1 (Pp_{tot}/R_{tot} = 1.73, Odum 1971); (iii) its high biomass and low production rates (P_{tot}/B_{tot} = 1.77), suggesting a high abundance of slow-growing groups (Christensen and Pauly, 1993), and (iv) the development of the ecosystem network to the uppermost trophic levels (Table 1, Supplemental material 7). When comparing these results with other Mediterranean ecosystems—selected for their proximity and similarities—we note that the TST values are similar to those of the Gulf of Gabes model (TST = 3798.99 $t \cdot km^{-2} \cdot yr^{-1}$, Halouani et al. 2016). Both models present similar, gently sloping continental shelves and a maximum depth not exceeding 200 m. In regard to previous Corsican region models, the Pp/R and P/B of the ECC ranged between values recorded for Calvi (Pp/R = 0.62, P/B = 1.56; Pinnegar and Polunin, 2004) and those for the Bonifacio Straits Natural Reserve (BSNR, Pp/R = 1.12, P/B = 8.91; Albouy et al. 2010). Although these systems share very similar biodiversity values, the Calvi and BSNR systems differ from the ECC by the former

Journal Pre-proof

systems' rocky coasts and dominant species. Species inhabiting soft substrates, such as Chondrichthyes, are favoured in the ECC and are more prominent than observed for the Calvi and BSNR regions (Pinnegar and Polunin, 2004, Albouy et al. 2010, Lauria et al. 2015). The dissimilarity between these systems may involve significant changes in trophic cascades affecting the overall system balance. The top TLs of the ECC are consistent with the range of previous models developed for the Mediterranean Sea, as the highest TLs were >4.00 for Port-Cros (Valls et al. 2012), the Gulf of Lions (Bănaru et al. 2013), the Gulf of Gabes (Halouani et al. 2016), and Portofino (Prato et al. 2016). The Corsican models of Calvi and BSNR had Sphyraenidae and pelagic and piscivorous fish as the top predators, having TLs from 4.30 to 4.96 (Pinnegar and Polunin 2004, Albouy et al. 2010).

In the mature ecosystem of the ECC, we identified several TL controls, including a top–down control exercised by top predators, a wasp–waist control at intermediate TLs, and a bottom–up control of primary producers. The mixed trophic analysis (MTI) emphasizes that top predators, including red scorpionfish (*Scorpaena scrofa*), piscivorous fish, and sharks, shape their prey dynamics; these prey are striped red mullet *(Mullus surmuletus)*, brown meagre (*S. umbra*), BIF, and rays. The MTI also suggests that benthic cephalopods exert a wasp–waist control in the ECC, their abundance affecting positively dusky grouper (*Epinephelus marginatus)* and negatively lobster (*Homarus gammarus)*. Moreover, over the last decades, the imposed fishing moratorium on grouper around Corsica prohibits recreational fishing, both spearfishing and hook-and-line fishing (Arrêté nº 2013,357–0001). In agreement with Prato et al. (2016), we suggest that benthic cephalopods could provide an effective monitoring tool for conservation considering that their biomass could become—or already is—a limiting food item for the dusky grouper. However, using benthic cephalopods as an indicator for management must be undertaken with caution given the short lifespan, fast growth, and opportunist feeding behaviour of these species can lead to marked population fluctuations

(Arkhipkin et al. 2021). The observed benthic cephalopod increase could also involve the decrease of *Homarus gammarus*, as the exploited stock of European lobster is suspected to be low and vulnerable around Corsica (Pere et al. 2019).

MTI also highlights a bottom–up control of *P. oceanica* seagrass that controls the abundance of the sparid teleost *Sarpa salpa*, its most important grazer (Buñuel et al. 2021). Similar to Albouy et al. (2010), we had previously assumed that the foraging activity of *S. salpa* induced a top–down control of the seagrass. Our results suggest that the seagrass meadows are so well developed in the ECC that herbivory does not threaten their expansion. Moreover, we suspect that the ECC provides an optimum habitat for *S. salpa* with its shallow habitats of mixed meadows/sand cover. Because *S. salpa* is not targeted by fisheries or predation, we assume that this population has already reached the asymptotic stage, probably limited by the ecology of its young stages, growth rates, its strategy of monandric protogyny, or even the number of eggs. Considering these points, it is unlikely that the top–down control of *S. salpa* on *Posidonia* meadows would increase unless the meadows were to decline.

Keystone groups/species revealed by the model highlight the importance of zooplankton, shrimps, benthic cephalopods, and planktivorous teleosts for maintaining ecosystem balance. Zooplankton, the most abundant group of animals in the ECC model, include a wide range of phyla, sizes, and functions, e.g., ichthyoplankton, thereby explaining its keystone function. As expected, we noted widespread cannibalism within the zooplankton and a notable MTI effect on this group. Shrimps, as the third-most abundant group of animals, include a wide diversity of suprabenthic species of crustaceans and provides a key food to forage fish species, favouring the rapid transfer of energy to higher TLs. However, these results should be interpreted with caution, given that both zooplankton and shrimp biomass were estimated by the model, thereby involving a high degree of uncertainty in terms of the related energy flows.

Journal Pre-proof

In the ECC model, benthic cephalopods also play a crucial role as opportunists, feeding on 12 different benthic groups. Benthic cephalopods are also preyed upon mainly by higher TLs—with benthic cephalopods also preying on a wide range of TLs. As revealed by MTI, the benthic cephalopods exercise a wasp–waist control, and their biomass fluctuation thus has a marked impact on coastal food webs. Cephalopods also have high keystone index values in the Portofino (Prato et al. 2016), Port-Cros (Valls et al. 2012), and the Gulf of Lions (Bănaru et al. 2013) models. Finally, the planktivorous group was dominated by *Spicara smaris* and *S. maena,* in agreement with Mérigot et al. (2007). Recently, Andromède Océanologie identified the ECC as one of the largest habitats for *Spicara* spp., containing many hectares of spawning grounds. The ECC model emphasizes planktivorous fish as a key group probably because of its dominance in biomass, i.e., 43.34% of the total animal biomass of the model.

4.2. Fisheries pressure on the ECC

Our results underline the moderate impact of fisheries on the ECC, one of the least exploited ecosystems of Mediterranean systems. These findings also emphasize the unequal fishing pressure among groups, with fisheries having a particular impact on TLs >3.50 and untargeted groups, including benthic sharks and rays.

The biomass value extracted by fisheries (0.24 $t \cdot km^{-2} \cdot yr^{-1}$) is close to the estimates for the BNSR (0.19 $t \cdot km^{-2} \cdot yr^{-1}$; Albouy et al. 2010) and Port-Cros (0.32 $t \cdot km^{-2} \cdot yr^{-1}$; Valls et al. 2012) and are distinctly lower than for other Mediterranean models (Pinnegar and Polunin, 2004, Bănaru et al. 2013, Coll et al. 2006, Tsagarakis et al. 2010, Prato et al. 2016, Dimarchopoulou et al. 2019, Michailidis et al. 2019). Fishing pressure in the ECC model, however, proved to be unequal among groups as: (i) sharks, planktivorous fish, rays, and piscivorous fish represent the highest catches, and (ii) exploitation rates ($F/Z > 0.20$) are notable for *Scorpaena scrofa* and *Palinurus elephas*. In addition, most catches include

untargeted groups, particularly sharks, rays, and planktivorous fish, primarily discarded dead because of their low market value and poor resistance to stress when entangled in nets. Chondrichthyes, caught dead, remain essentially unexploited in the present state throughout the Mediterranean Sea (Guijarro et al. 2012). Caught Chondrichthyes in the ECC encompass protected species classified as vulnerable (*Myliobatis aquila*, *Dasyatis pastinaca*, Serena et al. 2016a, b) and even endangered (*Rostroraja alba*, Ellis et al. 2016). Moreover, the Chondrichthyes biomass estimated for the ECC (2.75 $t \cdot km^{-2} \cdot yr^{-1}$) is much higher than for other Mediterranean systems—from 0.02 $t \cdot km^{-2} \cdot yr^{-1}$ in the Ionian Sea (Moutopoulos et al. 2013) to 0.69 $t \cdot km^{-2} \cdot yr^{-1}$ in the Gulf of Gabes (Halouani et al. 2016) from studies where Chondrichthyes are included, as this is not always the case (Albouy et al. 2010, Valls et al. 2012, Corrales et al. 2018, Dimarchopoulou et al. 2019). The high abundance of Chondrichthyes in the ECC is probably because of vast expanses of sandy bottom (Lauria et al. 2015) and low fishing pressure, especially from trawlers (Walls and Dulvy 2021), leading to their high catch rates.

By comparing the exploited EEC to an unfished state, our simulation emphasizes that all exploitation activities combined affect, in particular, groups and species having a TL above 3.50, reducing the abundance of these groups/species by nearly 30%. These results can be explained by the fact that fisheries value and retain resources of high TL, thereby shaping the structure of marine ecosystems. In the EEC, the mean TL of catches is 3.60, whereas it ranges from 3.07 (Adriatic Sea, Coll et al. 2007) to 3.94 (Aegean Sea, Tsagarakis et al. 2010) in the Mediterranean Sea (Bănaru et al. 2013, Coll et al. 2006, Valls et al. 2012, Prato et al. 2016, Dimarchopoulou et al. 2019). Previous models developed for Corsica show higher values of TL catches, i.e., 3.75 for the Calvi model (Pinnegar and Polunin 2004) and 3.94 for the BSNR (Albouy et al. 2010). This difference may be explained by the unselective gear used by trawling fisheries included in the ECC model; this significantly reduces the mean TL of

catches. Considering only the catches by fish net and spiny lobster net, values for TL catches ranged between 3.71 and 3.77. In addition, the other two existing Corsican models are based on different fishing data sources. The BNSR model distinguished itself by integrating recreational fishing activities (spearfishing, boat fishing, and shore fishing), which may justify this contrast. Yet the ECC model encompasses three species of intermediate TLs having a high economic value: *Palinurus elephas*, *Homarus gammarus*, and *Paracentrotus lividus*. Catches of spiny lobster *P. elephas,* are often discarded alive, as regulations prohibit catches of spiny lobsters carrying eggs, individuals captured outside the fishing season (October–February), and lobsters below a size limit (Marengo et al. 2020). These three species are poorly represented within the ECC, as their ecological niche of rocky habitats is scarce (Pere et al. 2019, Duchaud et al. 2018), explaining their low catch rates. Finally, the structure of the models themselves may lead to attribute distinct TLs to the same groups, explaining the difference.

Trawling, accounting for half of the total catches, was the most non-selective gear with the broadest ranging impact on the ecosystem. This activity exerts the strongest top–down control on the ecosystem, followed by a significant trophic cascade, as revealed by MTI. Yet in recent years, the number of trawl licences has been reduced continuously, with expectations that trawling exploitation will likely cease over the next decades (CRPMEM, unpublished data). Simulations also suggest that the trawling fisheries removal induces a noticeable improvement in the abundance of top predators, which can be counterbalanced or even enhanced by an increase in net fishing effort. It is worth noting that trawling was responsible for 64% to 92% of Chondrichthyes catches; hence, dealing with trawling issues is critical for managing their conservation. Furthermore, our study confirms that trawling does not compete with the lobster net and fish net fisheries, given that the increase in one fishery will not impact the landings from another. Our results also suggest that the current exploitation rate only

marginally influences mean-catch TLs. We expect the ecosystem TL to diminish in an overexploited system as fisheries eliminate the top TL predators.

When comparing fishing exploitation in the Mediterranean Sea, PCA—driven by the density of trawlers (FP_{trawl}), the mean TL of catches (TLc), the probability that the system would be in a sustainable fishing state (P_{sust}), and the loss in production index (L)—confirmed the ECC as one of the least exploited Mediterranean ecosystems. Our PCA designates the Catalan Sea (Coll et al. 2006), the Adriatic Sea (Coll et al. 2007), and the Gulf of Lions (Bănaru et al. 2013) as the most exploited systems. The ECC is a unique system in the Mediterranean Sea and is distinguished from the Corsican model of Calvi (Pinnegar and Polunin 2004), despite the two models having the same artisanal fishing pressure. However, our PCA results have some caveats given that (i) Mediterranean models differ in their periods of simulation, development, and compartment structure; (ii) the availability of the models' database forced us to omit some models having characteristics similar to the ECC, such as the Gulf of Gabes (Halouani et al. 2016), Cyprus Island (Michailidis et al. 2019), and the BNSR (Albouy et al. 2010); and (iii) some fishing activities of the ECC model are missing, including bottom longlines, fishing traps, and recreational fisheries (CRPMEM unpublished data).

5. Conclusions

- The Ecopath model of the Eastern Corsican Coast (ECC) shows this mature ecosystem to have a high degree of development.

- Four groups represent critical links in the ecosystem for moving biomass from primary producers to predators: zooplankton, shrimps, benthic cephalopods, and planktivorous teleosts. Benthic cephalopods exercise a wasp–waist control, and fluctuations in their biomass

thus have significant consequences on the coastal food web, including for their predator *Epinephelus marginatus*.

- MTI analysis emphasizes that trawling fisheries induce significant controls on top-predator biomass and thus substantially alter the ecosystem balance.

- Benthic sharks, planktivorous fish, and rays represent the most important groups in terms of catch, despite often not being targeted or even kept by fisheries. Trawling fisheries accounted for 64% to 92% of Chondrichthyes catches; therefore, trawling issues are critical for managing Chondrichthyes conservation, especially considering that some Chondrichthyes species are classified as vulnerable or endangered. Furthermore, our study suggests that the ECC waters, among the least harvested of the Mediterranean Sea, provide a suitable habitat and a shelter for Chondrichthyes development as reflected by their high biomass. These results raise into question the contribution of the ECC as a sink of Chondrichthyes and whether populations from nearby areas may supply this system.

- Fishery indicators confirm that fishing pressure on the ECC ecosystem is low to moderate, although being at the same time one of the least exploited trawlable shelves in the Mediterranean Sea. Simulations performed using the EcoTroph model suggest that the ecosystem would eventually be able to support an increase in the fishing effort as a whole system, although impacting more drastically high trophic levels. However, these results must be taken with caution, given that we did not include bottom longlines, fishing traps, and recreational fisheries in our model.

- This first ecosystem model of the ECC is an initial component of a more far-reaching project that aims to model the entire Corsican coast. This research will provide a relevant tool for managers, offering guidance for future decisions and conservation measures.

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Acknowledgments

This work forms part of the MoonFish project (Modelisation tOOls for the management of FISHeries resources in Corsica) sponsored by the 'Collectivité Territoriale de Corse (CdC)' within the funding framework of the European project PO-FEDER 2014–2021. The MoonFish project is a consortium involving the University of Corsica/CNRS (project leader), the Environmental Office of Corsica (OEC), STARESO, and GRPMEM. We thank all data providers: IFREMER for the MEDITS data, Dr. Nathalie Marot (IFREMER) for the POC data, Gilles Faggio (OEC) for the marine bird data, Dr. Dimitrios K. Moutopoulos (University of Patras) for help regarding trawling catchability, and the Projet GDEGeM for the Tursiop data. We are also especially grateful to all Corsican fishermen for their tremendous goodwill and kindness in welcoming scientific observers onboard their boats. A special thanks to Dr. Murray Hay from Maxafeau Editing Services for linguistic revisions.

Figure 1. Map of the Eastern Corsican Coast (ECC) ecosystem in the north-western Mediterranean Sea. The two heavy lines delimit the northern and southern boundaries of the eastern shelf ecosystem, and the 200 m isobath demarks the eastern border.

Figure 2. Flow diagram of the ECC ecosystem aggregated into a Lindeman spine and organized by integer trophic level (TL) and detritus (D). TST, total system throughput; TE, transfer efficiency.

Figure 3. Mixed trophic impact (MTI) analysis of the Eastern Corsican Coast (ECC). We included only the absolute values of MTI >0.5. Arrow thickness is in function of impact value

for both positive (*dotted grey arrows*) and negative (*solid red arrows*) impacts. SIF, suprabenthic invertebrate feeders; BIF, benthic invertebrate feeders; Benth. ceph., benthic cephalopods; Zoopl., zooplankton. Keystone groups/species (represented in *bold green*) were identified according to Libralato et al. (2006).

Figure 4. Composition of total catches (%) of the Eastern Corsican Coast (ECC) ecosystem of (a) all combined fleets, (b) trawling, (c) fish net, and (d) spiny lobster net catches.

Figure 5. (a) Trophic spectra of relative biomass (unitless) by fishing scenario of the Eastern Corsican Coast (ECC) ecosystem. We calculated the relative biomass as the ratio between biomass values of the simulated fishing scenario and unexploited state. The horizontal line of relative biomass equal to one corresponds to the unexploited state. Isopleths of scenarios simulating the fluctuation of fishing effort of the ECC ecosystem on (b) the trawling catches ($t \cdot km^{-2} \cdot yr^{-1}$), (c) the net catches ($t \cdot km^{-2} \cdot yr^{-1}$), and (d) the catch trophic level (TL). Net fisheries included the spiny lobster and fish netting; mE is a multiplier of the fishing effort.

Figure 6. Principal component analysis (PCA) of fishing pressure indicators estimated in the models of the Mediterranean Sea: the Bay of Calvi, Corsica (Pinnegar and Polunin, 2004), Gulf of Lions (Bănaru et al. 2013), Catalan Sea (Coll et al. 2006), Adriatic Sea (Coll et al. 2007), Aegean Sea (Tsagarakis et al. 2010), Port-Cros National Park (Valls et al. 2012), protected marine areas of Portofino (Prato et al. 2016), and the Gulf of Pagasitikos (Dimarchopoulou et al. 2019). Y, total catch of all fisheries combined ($t \cdot km^{-2} \cdot yr^{-1}$), TL_c, mean TL of catches; GE, gross efficiency; P_{sust}, probability of an ecosystem being sustainably fished; L, loss of production index; FP_{trawl}, estimated number of trawling vessels; $FP_{not\ trawl}$ estimated number of vessels engaged in other fishing activities; AIS, density of AIS messages classified as 'fishing'.

Journal Pre-proof

Table 1. Parameters of the Ecopath model of the Eastern Corsican Coast (ECC) ecosystem by species or group (Ecopath-estimated values in bold). TL, trophic level (unitless); B, biomass ($t \cdot km^{-2} \cdot yr^{-1}$); P/B, production/biomass (yr^{-1}); Q/B, consumption/biomass (yr^{-1}); EE, ecotrophic efficiency (unitless); P/Q, production/consumption (unitless); OI, omnivory index (unitless); Z, total mortality (yr^{-1}); M2, predation mortality (yr^{-1}); KS, keystone index (unitless, Libralato et al. 2006); Y, landings ($t \cdot km^{-2} \cdot yr^{-1}$); F/Z, ratio between fishing mortality F and total mortality Z; Acc, the fisheries accessibility (unitless). Groups/species are presented ordered by trophic level. Supra ceph, suprabenthic cephalopods; Benth sharks, benthic sharks; Benth ceph, benthic cephalopods; BIF, benthic invertebrate feeders; SIF, suprabenthic invertebrate feeders.

	Group/Specie	TL	B	P/B	Q/B	EE	P/Q	OI	Z	M2	KS	Y	F/Z	Acc
1	Sphyraenida	**4.8**	0.04	0.53	5.48	**<0.0**	0.1	**1.0**	**0.53**		**−0.0**	<0.00	**<0.0**	0.5
2	*Epinephelus*	**4.5**	<0.01	0.21	2.13	**0.10**	0.0	**0.1**	**0.21**	**0.02**	**−1.3**			
3	*Dentex*	**4.4**	0.12	0.43	4.39	**0.14**	0.1	**0.0**	**0.43**	**0.01**	**−0.1**	0.006	**0.13**	0.7
4	Bottlenose	**4.2**	<0.01	0.09	3.56	**<0.0**	0.0	**1.2**	**0.09**		**−1.2**			
5	*Scorpaena*	**4.2**	0.02	0.60	4.71	**0.53**	0.1	**0.0**	**0.60**	**<0.0**	**−0.2**	0.006	**0.53**	0.6
6	European	**4.1**	<0.01	0.68	5.86	**<0.0**	0.0	**0.0**	**0.68**		**−2.5**			
7	Piscivorous	**4.1**	0.63	0.44	4.62	**0.40**	0.1	**0.0**	**0.44**	**0.14**	**−0.0**	0.029	**0.07**	0.7
8	*Seriola*	**3.9**	0.22	0.36	3.48	**0.56**	0.1	**1.1**	**0.36**	**0.20**	**−0.1**			
9	Supra ceph	**3.9**	0.06	2.48	8.50	**0.68**	0.2	**0.1**	**2.48**	**1.60**	**−1.1**	0.004	**0.03**	0.5
1	Benth sharks	**3.8**	1.50	0.44	4.45	**0.12**	0.1	**1.0**	**0.44**		**−0.0**	0.080	**0.12**	0.5
1	Benth ceph	**3.7**	0.19	1.60	9.83	**0.81**	0.1	**0.2**	**1.60**	**1.28**	**0.05**	0.003	**0.01**	0.5
1	Serranidae	**3.6**	0.12	0.63	5.84	**0.57**	0.1	**0.2**	**0.63**	**0.33**	**−0.7**	0.004	**0.05**	0.7
1	Rays	**3.5**	0.56	0.56	3.86	**0.34**	0.1	**0.8**	**0.56**	**0.13**	**−0.4**	0.032	**0.10**	0.5
1	BIF	**3.4**	0.37	0.93	7.44	**0.70**	0.1	**0.0**	**0.93**	**0.66**	**−0.5**	<0.00	**<0.0**	0.6
1	Labridae	**3.3**	**0.21**	2.64	6.83	0.90	0.3	**0.2**	**2.64**	**2.37**	**−0.2**	0.001	**<0.0**	0.1
1	*Mullus*	**3.3**	0.19	0.82	5.27	**0.18**	0.1	**0.0**	**0.82**	**0.11**	**−0.7**	0.008	**0.05**	0.3
1	Sparidae	**3.2**	0.69	0.58	4.34	**0.53**	0.1	**0.1**	**0.58**	**0.29**	**−0.1**	0.013	**0.03**	0.6
1	SIF	**3.2**	0.57	0.70	6.22	**0.89**	0.1	**0.0**	**0.70**	**0.62**	**−0.4**	0.002	**0.01**	0.1
1	*Sciaena*	**3.1**	**0.02**	0.41	3.73	0.40	0.1	**0.0**	**0.41**	**0.16**	**−2.0**	<0.00	**<0.0**	0.8
2	Planktivorous	**3.1**	16.83	0.75	7.36	**0.61**	0.1	**0.0**	**0.75**	**0.45**	**0.02**	0.046	**<0.0**	0.2
2	*Chromis*	**3.1**	**0.02**	0.99	8.10	0.95	0.1	**0.0**	**0.99**	**0.94**	**−1.5**			
2	*Palinurus*	**3.1**	0.02	0.36	6.17	**0.62**	0.0	**0.2**	**0.36**	**0.05**	**−0.1**	0.003	**0.47**	0.8
2	*Homarus*	**3.0**	**<0.01**	1.22	6.17	0.38	0.2	**0.1**	**1.22**	**0.46**	**−2.4**			
2	Gelatinous	**2.6**	**0.15**	15.04	54.75	0.30	0.2	**0.3**	**15.04**	**4.51**	**−1.3**			
2	Shrimps	**2.5**	**3.51**	3.34	10.37	0.99	0.3	**0.3**	**3.34**	**3.31**	**0.05**			
2	Cnidaria	**2.3**	0.31	1.08	9.11	**0.67**	0.1	**0.3**	**1.08**	**0.72**	**−0.2**			
2	Gasteropods	**2.2**	0.08	1.94	10.92	**0.92**	0.1	**0.1**	**1.94**	**1.78**	**−0.2**			
2	Bivalvia	**2.2**	0.25	2.10	8.97	**0.79**	0.2	**0.2**	**2.10**	**1.66**	**−0.1**			
2	Zooplankton	**2.1**	**7.01**	48.69	165.5	0.95	0.2	**0.2**	**48.69**	**46.2**	**0.12**			
3	Echinoderms	**2.1**	6.13	0.49	2.70	**0.56**	0.1	**0.1**	**0.49**	**0.27**	**−0.2**			
3	Benthic	**2.0**	0.64	11.44	33.81	**0.72**	0.3	**0.0**	**11.44**	**8.23**	**−0.0**	0.005	**<0.0**	0.3

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	Group/Specie	TL	B	P/B	Q/B	EE	P/Q	OI	Z	M2	KS	Y	F/Z	Acc
3	Worms	**2.0**	0.53	7.59	40.57	**0.83**	0.1	**0.0**	**7.59**	**6.28**	**−0.5**			
3	*Sarpa salpa*	**2.0**	0.87	0.72	3.67	0.30	0.2		**0.72**	**0.22**	**−0.4**	<0.00	**<0.0**	0.3
3	*Paracentrotu*	**2.0**	0.10	0.19	1.26	**0.68**	0.1		**0.19**	**0.13**	**−0.9**			
3	Macroalgae	**1.0**	0.43	13.33		**0.22**			**13.33**	**2.91**	**−0.1**			
3	Phytobentho	**1.0**	**2.22**	6.52		0.90			**6.52**	**5.87**	**−0.4**			
3	Seagrass	**1.0**	449.1	0.74		**0.30**			**0.74**	**0.22**	**−1.0**			
3	Phytoplankto	**1.0**	4.83	109.6		**0.63**			**109.6**	**68.8**	**−0.4**			
3	Detritus	**1.0**	74.90			**0.33**		**0.4**						

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Highlights

- The ECC Ecopath model shows a high degree of development as a mature system.
- Fisheries induce a drastic top-down control of top-predator biomass.
- The ECC ecosystem is one of least exploited trawlable shelves in the Mediterranean.
- Trawling itself accounts for two-thirds of Chondrichthyes catches, mostly untargeted.
- The East Corsican Coast provides a critical habitat for Chondrichthyes conservation.

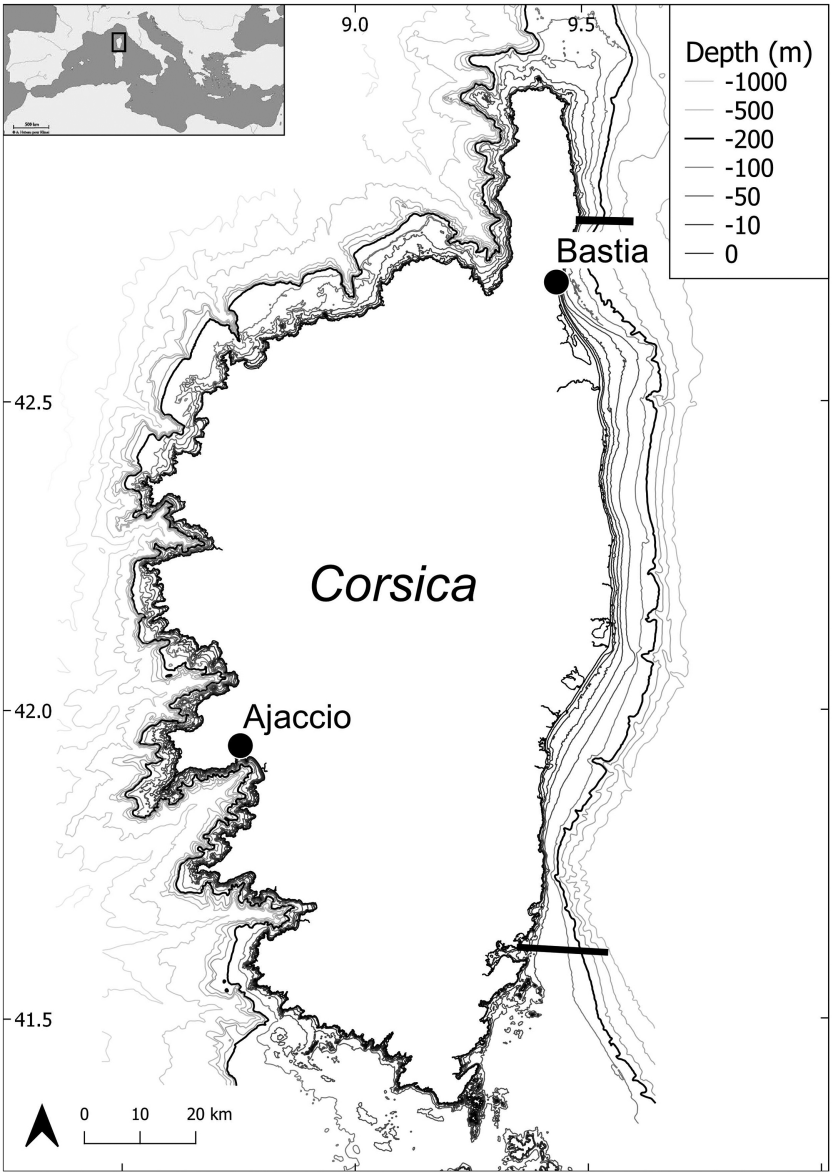
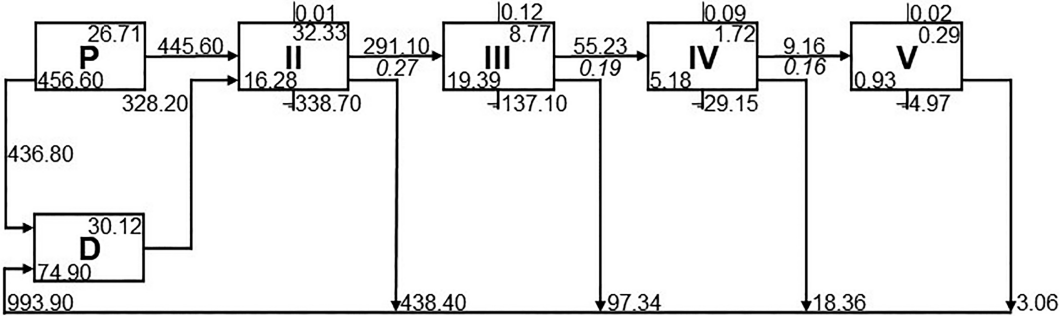

9.0
9.5
Depth (m)
-1000
-500
-200
-100
-50
-10
0
Bastia
42.5
Corsica
42.0
Ajaccio
41.5
0
10
20 km

Figure 1


P
26.71
456.60
445.60
II
0.01
32.33
16.28
291.10
0.27
III
0.12
8.77
19.39
55.23
0.19
IV
0.09
1.72
5.18
9.16
0.16
V
0.02
0.29
0.93
328.20
338.70
137.10
29.15
4.97
436.80
D
30.12
74.90
993.90
438.40
97.34
18.36
3.06

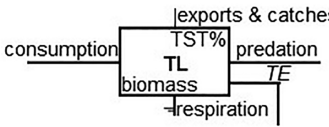

exports & catches
consumption
TST%
TL
biomass
predation
TE
respiration

Figure 2

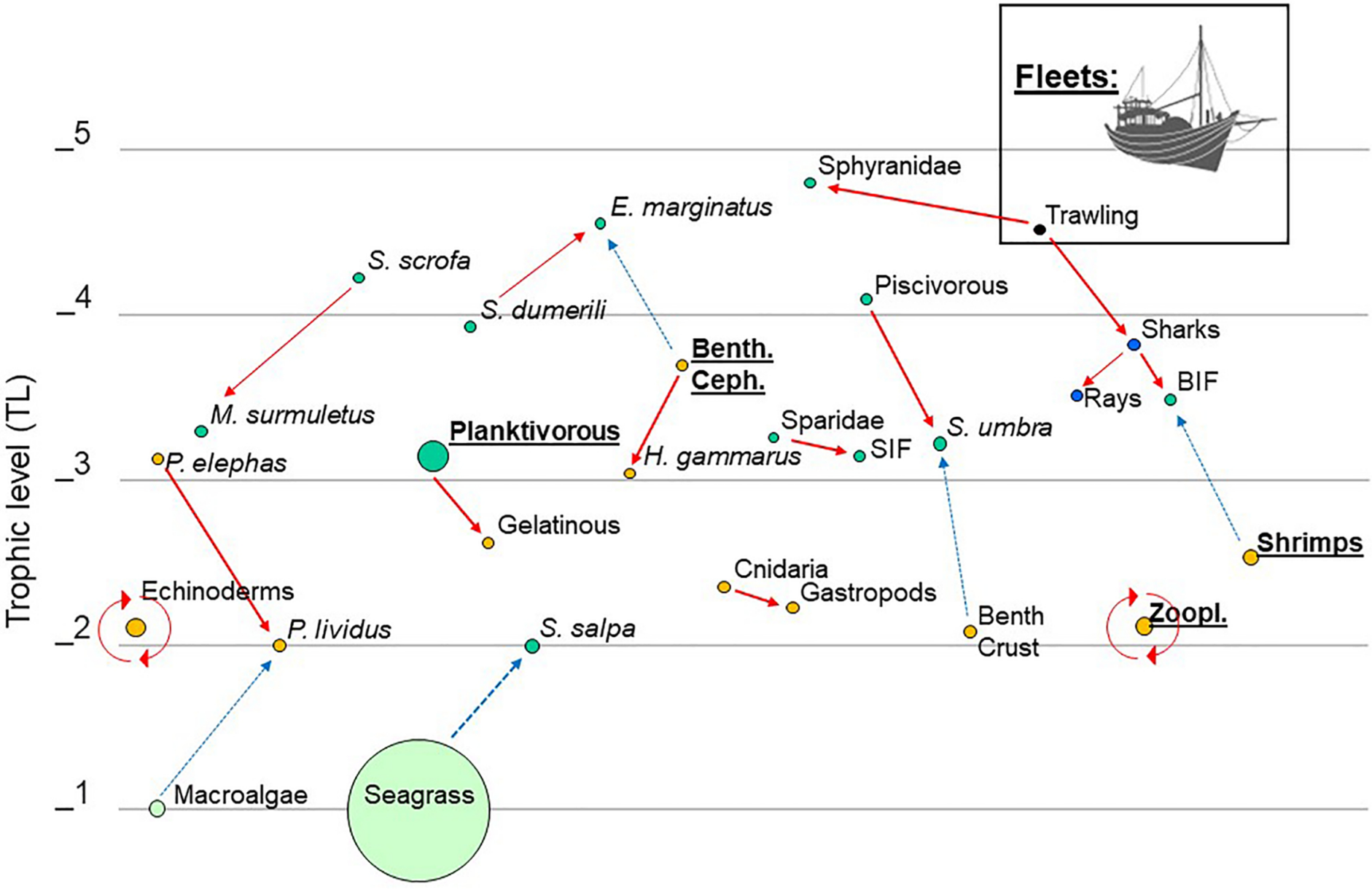

Fleets:
Trophic level (TL)
5
4
3
2
1
Sphyranidae
E. marginatus
Trawling
S. scrofa
S. dumerili
Piscivorous
Sharks
Benth.
Ceph.
Rays
BIF
M. surmuletus
Planktivorous
Sparidae
S. umbra
P. elephas
H. gammarus
SIF
Gelatinous
Shrimps
Cnidaria
Gastropods
Echinoderms
Benth
Crust
Zoopl.
P. lividus
S. salpa
Macroalgae
Seagrass

Figure 3

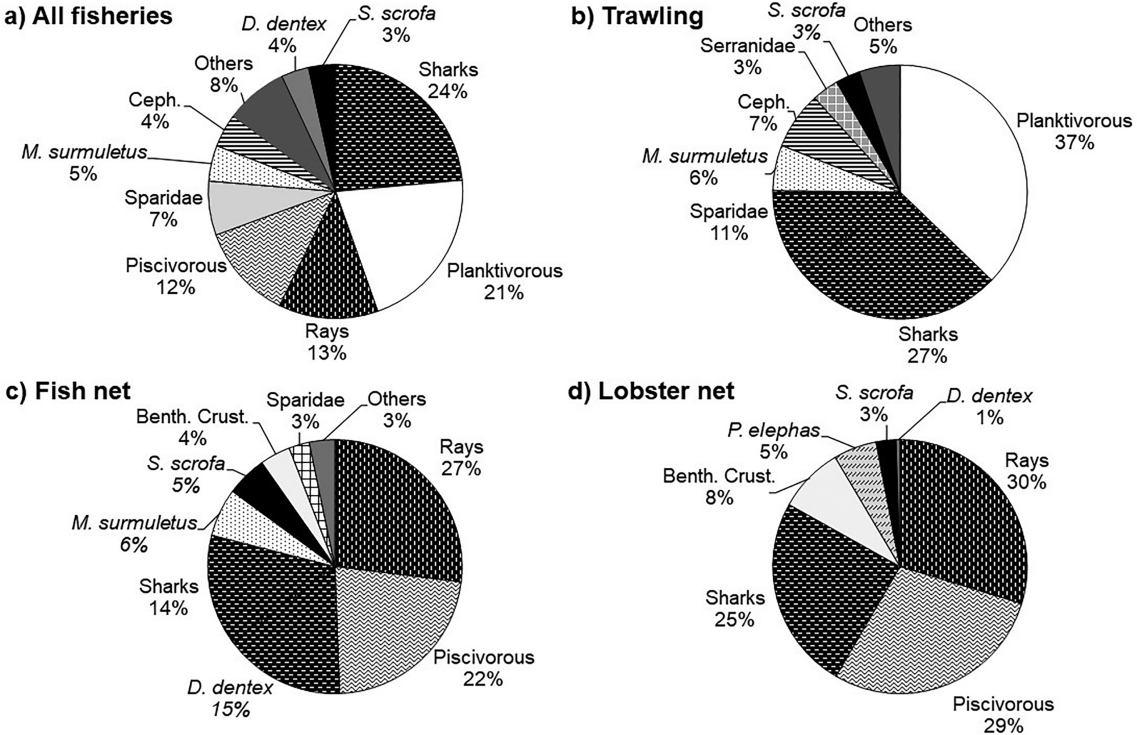

a) All fisheries
D. dentex 4%
S. scrofa 3%
Others 8%
Sharks 24%
Ceph. 4%
M. surmuletus 5%
Sparidae 7%
Piscivorous 12%
Planktivorous 21%
Rays 13%
b) Trawling
S. scrofa 3%
Others 5%
Serranidae 3%
Ceph. 7%
Planktivorous 37%
M. surmuletus 6%
Sparidae 11%
Sharks 27%
c) Fish net
Benth. Crust. 4%
Sparidae 3%
Others 3%
Rays 27%
S. scrofa 5%
M. surmuletus 6%
Sharks 14%
Piscivorous 22%
D. dentex 15%
d) Lobster net
S. scrofa 3%
D. dentex 1%
P. elephas 5%
Rays 30%
Benth. Crust. 8%
Sharks 25%
Piscivorous 29%

Figure 4

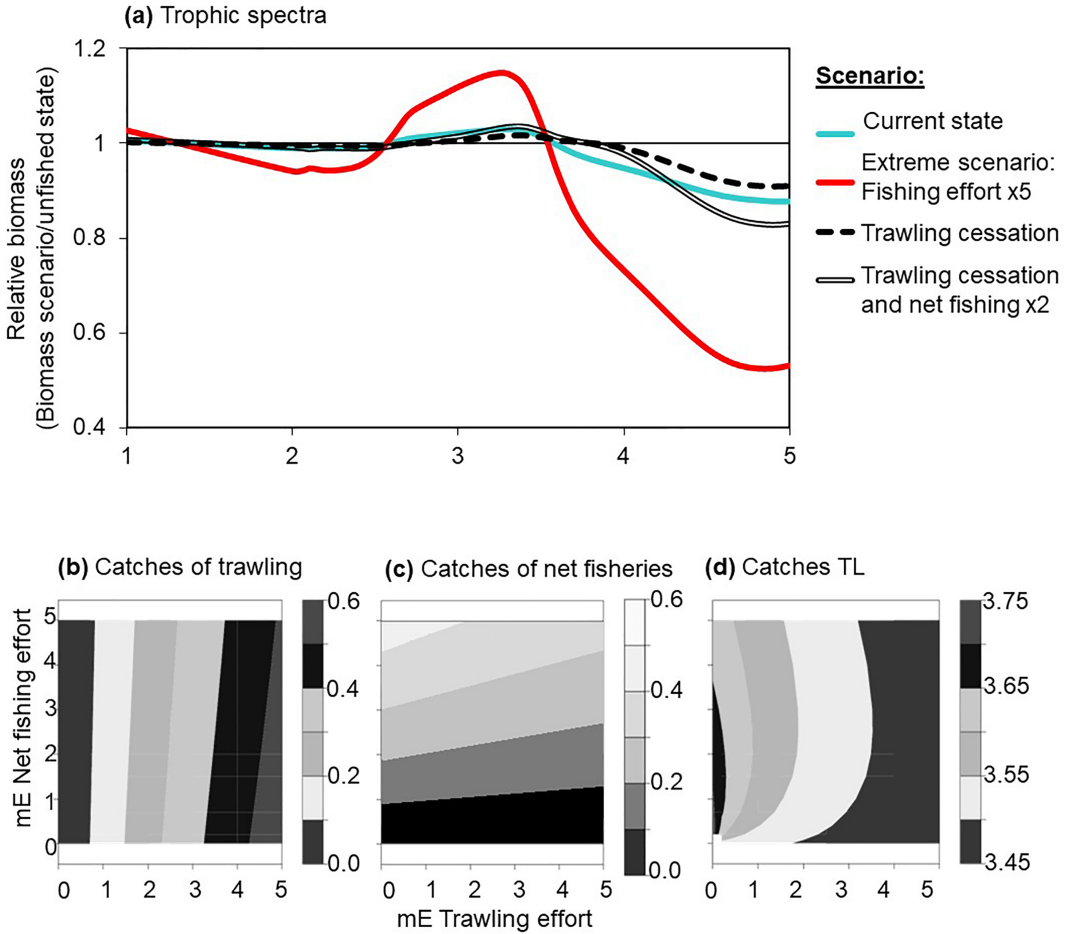

(a) Trophic spectra
Relative biomass
(Biomass scenario/unfished state)
1.2
1
0.8
0.6
0.4
1
2
3
4
5
Scenario:
Current state
Extreme scenario:
Fishing effort x5
Trawling cessation
Trawling cessation
and net fishing x2
(b) Catches of trawling
(c) Catches of net fisheries
(d) Catches TL
mE Net fishing effort
mE Trawling effort
0.6
0.4
0.2
0.0
3.75
3.65
3.55
3.45

Figure 5

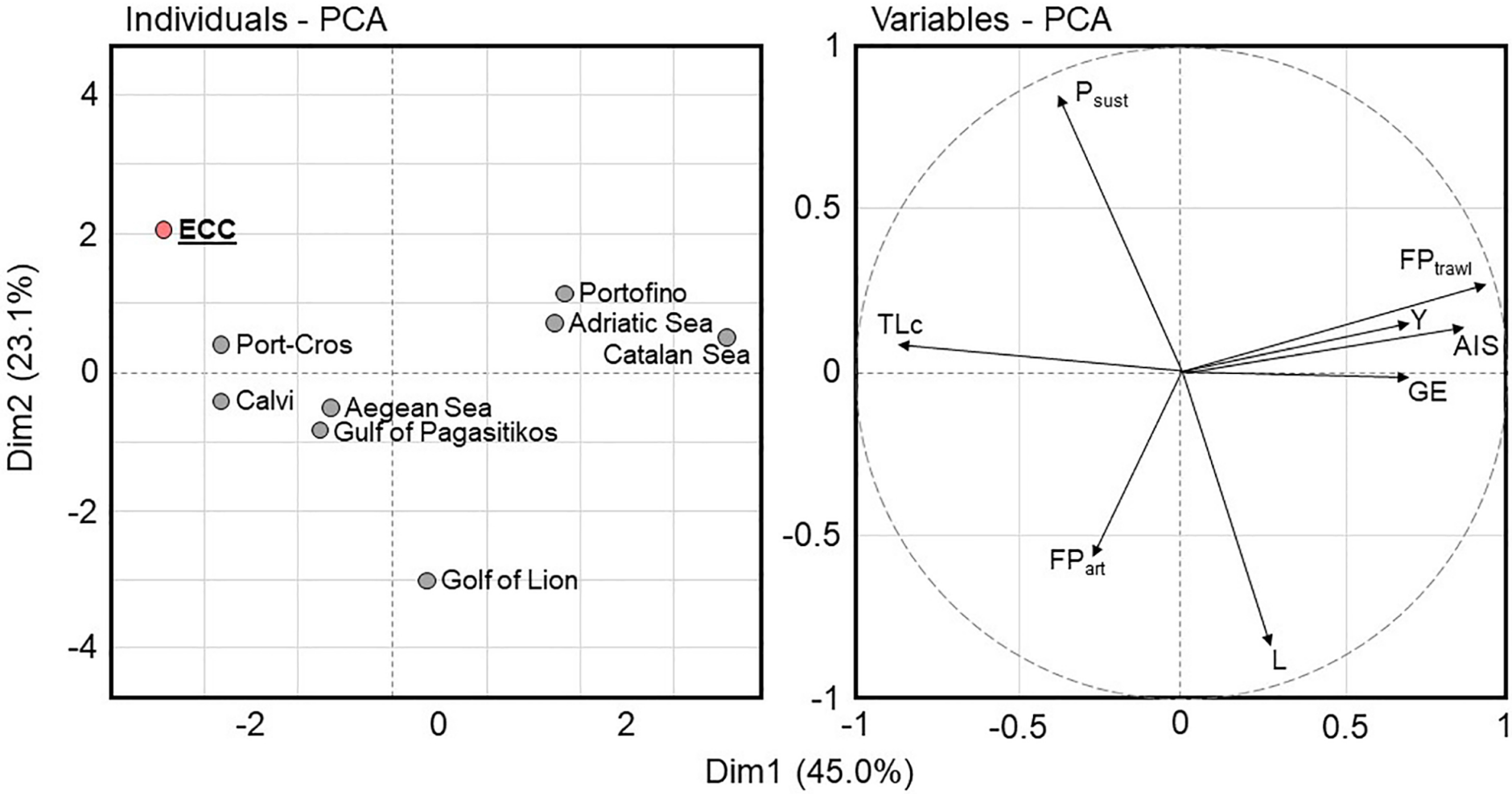

Individuals - PCA
Variables - PCA
ECC
Portofino
Adriatic Sea
Catalan Sea
Port-Cros
Calvi
Aegean Sea
Gulf of Pagasitikos
Golf of Lion
Dim2 (23.1%)
Dim1 (45.0%)
P sust
FP trawl
Y
AIS
TLc
GE
FP art
L
4
2
0
-2
-4
1
0.5
0
-0.5
-1

Figure 6