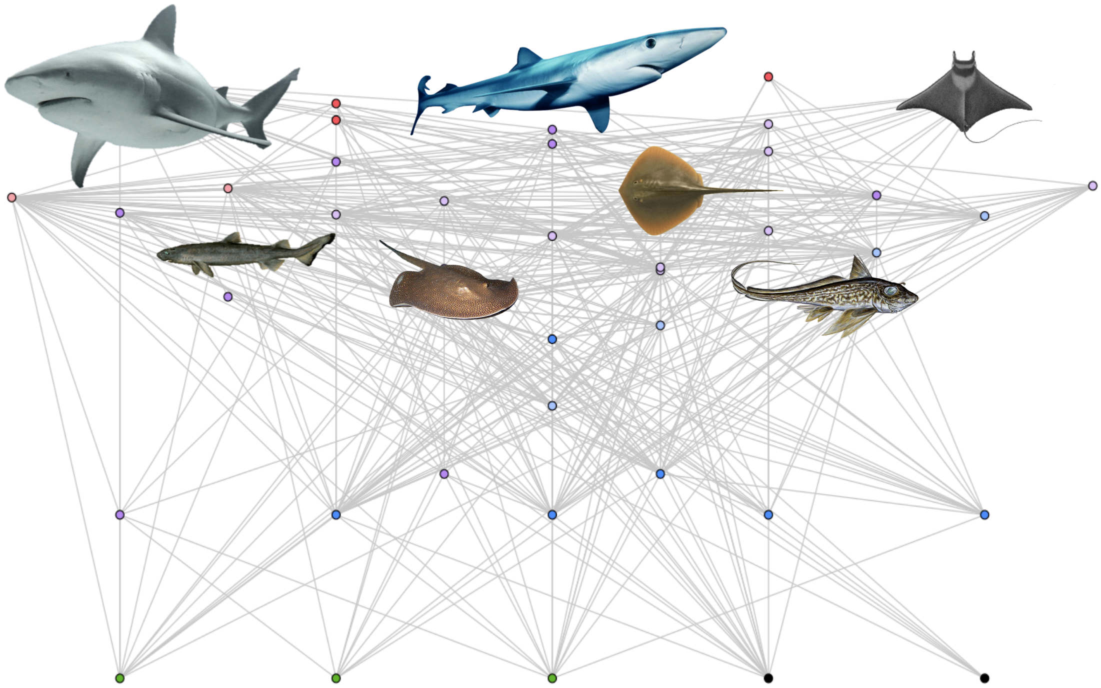
ECOLOGICAL ROLE OF MEDITERRANEAN CHONDRICHTHYANS:

TROPHIC ECOLOGY AND FOOD WEB MODELLING



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Abstract

Fisheries, climate change and habitat degradation are triggering the depletion of marine animal populations worldwide. In particular, the ecological impacts of the removal of keystone species such as chondrichthyans can be far reaching through the food web. In this study, we investigated the trophic ecology of the 81 Mediterranean chondrichthyan species occurring in the basin through a literature review. We found data for 50 species, which highlights research priorities for the future to complement missing information. Regarding the trophic ecology of studied species, prey composition was compared between taxonomic groups (Batoidea, Selachimorpha and Holocephali), habitats (pelagic and demersal) and sizes (small, medium and large). We found significant differences between taxonomic groups, with dissimilarities mainly due to crustaceans and cephalopods consumption between Batoidea and Selachimorpha. We then represented the Mediterranean meta-web by means of a qualitative modelling approach, putting emphasis on the chondrichthyan groups, with a resulting food web network topology of 73 nodes and 1335 trophic links. Finally, we used the qualitative food web representation to test seven extinction scenarios of chondrichthyans extinctions. We found out that large species, pelagic species and sharks had a major contribution to trophic dissimilarity of the ecosystem when compared to small and medium-sized species, demersal species and rays, respectively. Systems with the former species had also higher omnivory rates. Therefore, conservation efforts within the Mediterranean Sea chondrichthyan community seem to be especially important for these groups. This study provides a first overview of the chondrichthyans ecological role in the Mediterranean Sea marine food web and highlights the urgent need to improve available knowledge on these species and to adopt an ecosystem-based management approach in order to decelerate the depletion of chondrichthyans populations and prevent them from local extinctions, with important effects to the marine food web.

Keywords: chondrichthyans, trophic ecology, predator–prey interactions, food web structure, conservation, extinction scenarios, Mediterranean Sea, literature review, qualitative model.

1. Introduction

Humans impact oceanic systems on every scale: in particular, human activities are changing the structure and functioning of marine ecosystems through overexploitation, climate change, ocean acidification and pollution among others (Pascual and Macías, 2021). Furthermore, the rapid expansion of coastal human populations in parallel to the global growth of industrial fishing during the last century are responsible for the decline in many marine species (Jackson et al., 2001; Estes et al., 2011).

The progressive depletion of marine populations around the world is reducing ecosystem connectivity and stability, generating ecological changes that can alter marine ecosystems functioning (Worm et al., 2013; McCauley et al., 2015). As a result, top predators such as chondrichthyans are becoming ecologically extinct in many areas and their abundances and body size are suffering considerable changes (Jackson et al., 2001; Dulvy et al., 2021). These predators can be keystone species in marine habitats, often characterized by strong top-down interactions (Power et al., 2007; Valls et al., 2015), playing central roles in the propagation of impacts through the food web (Baum and Worm, 2009; Bornatowski et al., 2014).

1.1. Chondrichthyans ecology

Sharks, skates, rays and chimaeras comprise one of the oldest extant vertebrate groups on the planet, the chondrichthyan fishes (Class Chondrichthyes), a relatively small (approximately 1,300 species), monophyletic group of predators that originated about 423 million years ago, before any other extant vertebrate predator (Cavanagh and Gibson, 2007; Ferretti et al., 2010; Serena et al., 2020). Their resilience is related to a high evolutionary adaptability and ecological variability among species, which allows them to be among the most wide-ranging predators (Kriwet et al., 2012). Although they initially evolved as small coastal species, natural selection on chondrichthyans favored larger body sizes, continuous growth, delayed age at maturity, and the ability to colonize deep oceanic waters (Ferretti et al., 2010). Thus, chondrichthyans have radiated to fill a range of habitat types and they are found throughout all of the world's oceans, with around 50% of extant species living in coastal and shelf waters (to around 200 m depth), 35% in deeper water (200–2,000 m depth) and the rest are either oceanic (5%), live in freshwater (5%) or occur within several of these habitats (5%) (Compagno, 1990; Compagno et al., 2005; Field et al., 2009).

Population growth rates of chondrichthyans are lower than those for teleosts, which can likely be attributed to the larger body size and older age at maturity (Hutchings et al., 2012). They have a long-lived/ K-selected life history strategy, investing more into adult survival and growth rather than fecundity and having a strong response to changes in both predation and no-natural mortality (Stevens et al., 2000; Ferretti et al., 2010). This is linked to a lower recovery potential after a perturbation and therefore an increased extinction risk, that, added to the global growth of fisheries, the most important threat for these predators, has triggered the progressive depletion of populations of chondrichthyans around the world (Aldebert, 1997; Worm et al., 2013; Walker et al., 2021).

1.2. Threats: fisheries, climate change and habitat loss

Fisheries are altering marine biodiversity, depleting marine resources and weakening ecosystem functioning at a global scale (Worm et al., 2006). Particularly, commercial, artisanal, subsistence and recreational fishing activities are catching chondrichthyans, both as targeting species and as bycatch (Fowler et al., 2005; Dulvy et al., 2014). As a consequence, overfishing is the principal driver of sharks, rays and chimaeras decline and local extinction (Dulvy et al., 2016, 2021). However, there are some difficulties when quantifying the impact of fisheries on these marine predators since fisheries data is often unreported, incomplete or inaccurate (Pauly and Zeller, 2016). Moreover, the reported catches represent only a fraction of total chondrichthyan mortality (Coll et al., 2014b; Pauly et al., 2014; Stevens et al., 2000; Worm et al., 2013; Dulvy et al., 2016), and there is still a significant proportion of chondrichthyan catches that is not reported at the species level (FAO, 2020b).

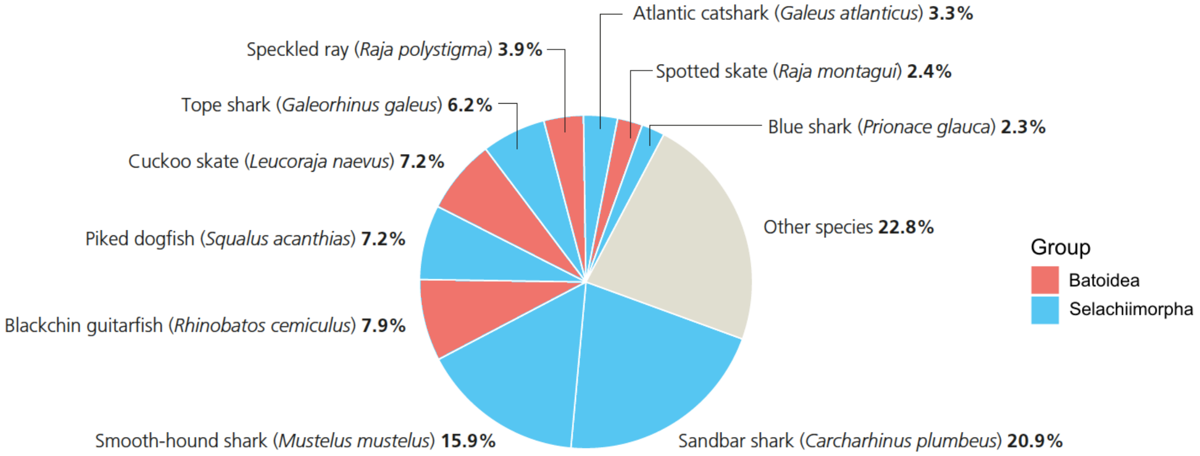

Figure 1. Reported bycatch of the main sharks and rays species in the Mediterranean Sea between 2000 and 2020. Adapted from FAO, 2020a.

The lack of proper catch reports hampers the assessment of population-level consequences for chondrichthyans, particularly when not taking bycatch into account, as it has been reported to be the major threat to chondrichthyan populations nowadays (Dulvy et al., 2021). Furthermore, bycatch is caused by multiple fishing gears, making it even more difficult to assess and impacting a range of different species (Figure 1; Stevens et al., 2000; Dulvy et al., 2014, 2016). For instance, demersal species are particularly vulnerable when interacting with trawl fisheries (Shepherd and Myers, 2005; Ricci et al., 2021), while pelagic and migratory species are more exposed to pelagic long-lines and purse seine nets, which have been reported to cause substantial decreases in their populations (Baum et al., 2003; Ferretti et al., 2008; Pacoureau et al., 2021). Nevertheless, bycatch is not the only impact on chondrichthyan populations, as they are also intentionally targeted for the exploitation of their fins and meat. The practice of finning, where animal fins are removed and the rest of the body is discarded, has spread worldwide due to high demand in the Asian market (Worm et al., 2013). Finning is banned in many countries (e.g., European Union, Regulation 2003/1185 - Removal of fins of sharks on board vessels) but even though the reported chondrichthyan landings seem to be stable or declining, the fin trade is still a major global problem (Worm et al., 2013; Bradai et al., 2018).

Together with south-eastern South America, western Africa, South China Sea and Southeast Asia, and south-eastern Australia, the Mediterranean Sea has been identified as one of the main hotspots where the biodiversity of sharks and rays is particularly threatened (Field et al., 2009; Dulvy et al., 2014). In the Mediterranean, the vulnerability of elasmobranch species to fishing gear is very high (Cavanagh and Gibson, 2007) and their impacts are being reported from small demersal to large pelagic species (Ferretti et al., 2008; Cartes et al., 2013; Nuez et al., 2021). Although there is a decreasing trend in fishing landings, the fishing effort is still growing and the Mediterranean is, in fact, considered one of the areas with the highest percentage of stocks fished at unsustainable levels (62.5% in 2017; FAO, 2020b). Besides the high fishing pressure that Mediterranean waters have supported since the antiquity (Sala, 2004; Lotze et al., 2011), the use of high diversity of fishing gears increases the risk of fishing bycatch. Moreover, although finning is also banned in Mediterranean waters and almost no fishing activity currently targets sharks and rays in this area officially (Serena, 2021), elasmobranch-fishing is still practiced: chondrichthyans represent around the 2% of total official fishing landings (FAO, 2020a), with Libya and Tunisia contributing by more than the 70% of production in between 2010 and 2017, and with other countries such as Spain and Italy still contributing to the supply of global markets (Bradai et al., 2018).

On the other side, the impacts of fishing activities are, in most cases, intensified by the synergistic impacts of climate change and habitat loss (Dulvy et al., 2014, 2021). The effects of climate change on chondrichthyan populations are diverse, from changes in distribution ranges due to ocean warming and habitat degradation due to bottom trawling, to direct impacts on physiology, behavior and survival of some species because of ocean acidification and other anthropogenic stressors (e.g., increasing chemicals, lights, noise and electromagnetic fields underwater could reduce sensory acuity and, therefore, competitiveness; Walker et al., 2021). These changes have been already documented in the Mediterranean Sea, which is recognized as a climate change hotspot (e.g., changes in dissolved O_2 and decreasing abundance of the velvet belly lanternshark *Etmopterus spinax*; Cartes et al., 2013). On the other hand, habitat degradation, which is likely to increase along the next decade (McCauley et al., 2015), is particularly impacting coastal and estuarine species due to coastal development and pollution (Dulvy et al., 2014).

1.3. Conservation status

Fishers knowledge has been used to reconstruct trends of elasmobranch species that are now scarce in the Mediterranean, indicating their abundances were up to three times higher at the first half of the 20th century (e.g., Maynou et al., 2011; Coll et al., 2014a; Colloca et al., 2020; Nuez et al., 2021). The member governments of the FAO (Food and Agriculture Organization of the United Nations) responded to the alarming declines and presented the International Plan of Action-Sharks in 1999, with the aim of ensuring the conservation and management of sharks, rays and chimaeras, and their long-term sustainable use. Although the European Commission adopted in 2009 the first Action Plan for the conservation and management of elasmobranchs (EU, 2009), relatively few countries have produced assessment reports or developed Elasmobranchs Management Plans (Fowler and Seret, 2010).

Dulvy et al. (2021) estimated in one-third the number of chondrichthyan species threatened worldwide according to the IUCN Red List of Threatened Species, highlighting a risky combination of high threat, low safety and high uncertainty in the threat status of sharks and rays. The regional assessment for the Mediterranean Sea (Dulvy et al., 2016) described 77 chondrichthyan species, 73 of them were assessed, excluding four species (*Carcharhinus brevipinna, Himantura uarnak, Sphyrna mokarran* and *Sphyrna lewini*) considered to be either vagrants or Lessepsian immigrants from the Red Sea. The list was updated by Serena et al. (2020), reporting a total of 88 Mediterranean chondrichthyan species, which included vagrant, rare and species whose presence is questionable.

In the present study, a total of 81 species from 27 different families were considered: 34 species of rays/skates, 46 species of sharks and 1 chimaera (*Chimaera monstrosa*). According to the Mediterranean assessment by the IUCN, half of these species are threatened, with

24.4% of them classified as Critically Endangered (CR, Figure 2a). Squatinidae and Pristidae are the most threatened Families, with 100% of the species inhabiting the Mediterranean classified with the highest extinction threat. A quarter of the species are not assessed or are classified as Data Deficient (DD). In addition, their populations are mostly decreasing (58%) and scarcely 10% are considered stable. Only 15% of the Chondrichthyes species inhabiting the Mediterranean Sea are classified as Least Concern (LC). When comparing to their global status (Figure 2b), the percentage of species threatened is similar (51.2%), but the extinction threat is lower globally, with more species classified as Vulnerable (VU) but less species considered CR (13.4% versus 24.4% at the global and Mediterranean assessment, respectively).

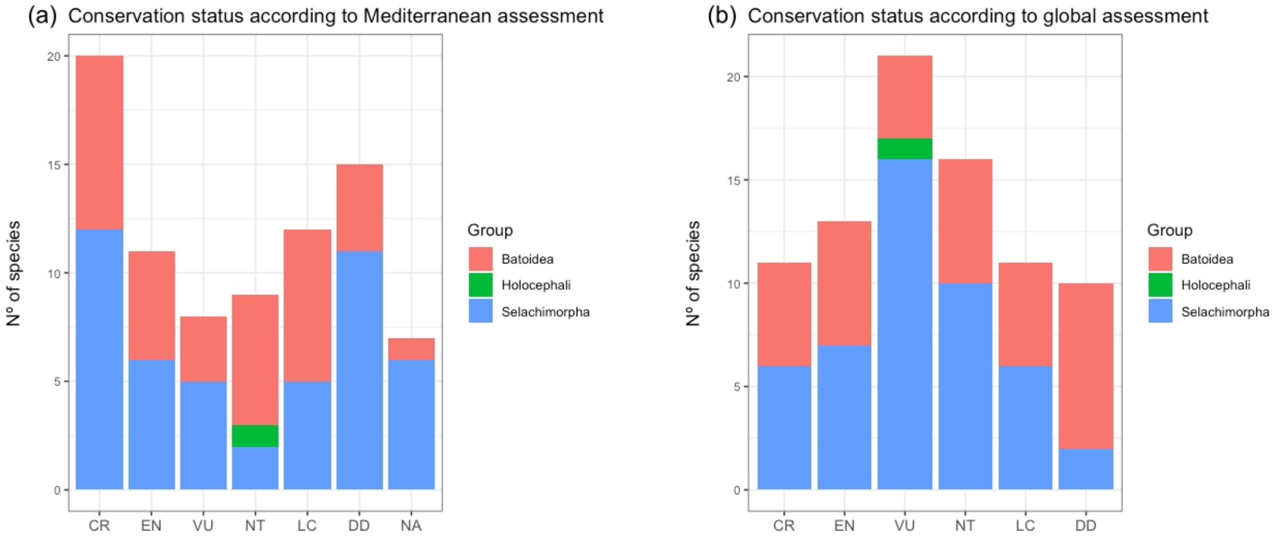

Figure 2. Conservation status of the Mediterranean chondrichthyans by group (Batoidea, Holocephali and Selachimorpha) according to the IUCN (a) Mediterranean and (b) global assessments. CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient, NA: Not Assessed. Source: adapted from IUCN (2021).

No effective chondrichthyan-focused management measures have been successfully implemented or enforced in the Mediterranean basin, and, therefore, there was no sign of improvement in the status of Mediterranean chondrichthyans since they were first assessed (Abdul Malak et al., 2011; Dulvy et al., 2016). In fact, the current number of threatened species reported by Dulvy et al. (2021) has more than doubled the first global assessment in 2014, and three species, the lost shark *Carcharhinus obsoletus*, the Pondicherry shark *Carcharhinus hemiodon* and the Java stingaree *Urolophus javanicus,* are now classified as Critically

Endangered (Possibly Extinct) (CR(PE)), likely representing the first global marine fish extinctions due to overfishing.

1.4. Ecological implications of declines

Marine organisms live as members of populations, assemblages and communities and, thus, they interact with others as a highly connected network (Marbà and Coll, 2021). Most species are close 'neighbors' and therefore negative effects can spread rapidly throughout the food web, although the overall impact can also be dispersed and reduced (Dunne et al., 2004). As a consequence, any change in the abundance and distribution of predators or other keystone species in a particular ecosystem can operate either directly through effects on individual survival and physiology, or indirectly through effects on prey, predators and competitors (Dunne, 2009).

Ecological impacts of eliminating top predators such as large-size sharks can trigger cascading effects that travel both up and down marine food webs (Bornatowski et al., 2014; McCauley et al., 2015) and can be far-reaching, including release of mesopredator prey populations from predatory control and induction of subsequent cascades of indirect trophic interactions (Baum et al., 2003; Shepherd and Myers, 2005; Ward and Myers, 2005; Myers et al., 2007; Field et al., 2009; Ferretti et al., 2010). For example, in some coastal systems, the decline of large sharks has altered the abundance, distribution and behavior of smaller elasmobranch mesopredators that have few other predators and the community became dominated by them (e.g., in the NE Atlantic; Ellis et al., 2005). After the depletion of key species, the likelihood of trophic cascades will depend on the omnivory rate of the system (Bascompte et al., 2005). The role of these indirect effects is crucial to understand the food web energy flow and the ecosystem structure and functioning of natural ecosystems (Bornatowski et al., 2014).

1.5. Food web approach to understand the ecological role of chondrichthyans

Inter- and intra-specific traits variation across marine species plays a fundamental role in understanding population and community functioning and resilience (Kortsch et al., 2021). In fact, the strength of the predator/prey interactions influences the stability of the communities (Bascompte et al., 2005). However, there is a general lack of knowledge about the interactions between species and the spatial-temporal dynamics of population and community structure, functioning and resilience, which prevents us from fully understanding the essential ecological processes and properties of marine ecosystems (Marbà and Coll, 2021). In order to understand the role individual components of the community have on trophic network compartments, further comprehension of the trophic behavior of species is needed to unravel their trophic interactions and quantify the ecological position of species within the marine food web (Bornatowski et al., 2014).

To be able to anticipate the future of marine life in a context of global change, we need to advance our knowledge on marine communities by quantifying the amount of resilience of marine networks in terms of species loss or invasions, and the capacity of organisms to adapt to these changes (Marbà and Coll, 2021). Although food webs have shown to be resilient to the removal of random nodes (Montoya et al., 2006), the loss of species related to anthropogenic stressors tends to be directed towards species that play key roles in the ecosystems and are unable to adapt to the respective pressure (Bascompte et al., 2005), which is the case of chondrichthyans. As they are generally important predators, predicting the effects of their removal is complex (Field et al., 2009). In fact, the effect of predator removal is still poorly understood, particularly for complex trophic webs. An effective management of shark populations should take into account how different decline drivers affect specific species (Field et al., 2009). However, to determine how individual traits and species interactions contribute to community functioning and ecosystem resilience is still a challenge (Marbà and Coll, 2021).

The overall objective of this study was to investigate the ecological role of the different species of chondrichthyans in the Mediterranean Sea, focusing on their trophic (prey-predation) interactions at the food web level. This general objective was divided in three specific ones:

(1) to review the current knowledge and gaps on chondrichthyans trophic ecology in the Mediterranean Sea,

(2) to represent the Mediterranean chondrichthyan species within a Mediterranean food web, and

(3) to quantify the vulnerability degree of the Mediterranean food web to selective removals of different groups of sharks and rays by using a qualitative network approach.

This study contributes knowledge to the urgent need to adopt an ecosystem-based management approach to halt and prevent Mediterranean chondrichthyans populations from local extinction, with large direct and indirect ecosystem effects.

2. Material and methods

To achieve these objectives, we first reviewed all available data regarding feeding habits and conservation status of chondrichthyans in the Mediterranean Sea, followed by an examination of the multivariate structure of chondrichthyans trophic ecology (Figure 3). We then used a Mediterranean meta-web approach previously established to investigate the food web topology of the basin and protected areas (Coll et al., 2019), with an emphasis on chondrichthyan groups. Finally, we tested various extinction scenarios and studied the ecosystem consequences of removing different groups of sharks and rays to identify main effects of their depletion.

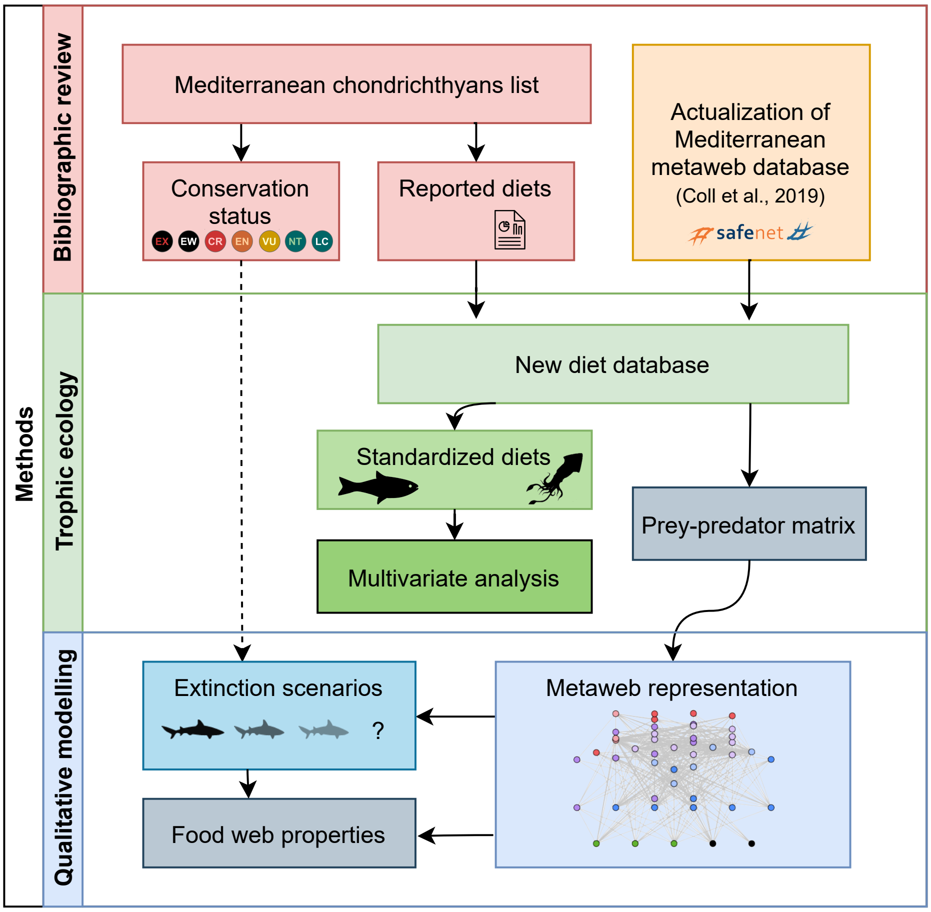

Figure 3. Overview of the methodology followed in the present study to investigate the ecological role of Mediterranean chondrichthyans.

2.1. Bibliographic review and database construction

To assess population status of Mediterranean chondrichthyans, we first classified each species according to their conservation status and population trends both at a Mediterranean and global level evaluations based on the IUCN assessments (IUCN, 2021), including vagrant and rare species.

In order to model the Mediterranean food web, all available information about trophic links among marine species was compiled by an extensive literature review on the foraging ecology and diet of the species inhabiting the Mediterranean Sea. This review updated previous efforts by Stergiou and Karpouzi (2002) and Karachle and Stergiou (2017), and the compilation previously built to develop a Mediterranean meta-web (Coll et al., 2019), which was substantially complemented with additional references (the reports in the databased basically doubled). For each selected publication, we recorded:

1. Species;

2. Information related to the life stage: juveniles or adults;

3. Spatial information: divisions of the Mediterranean Sea were defined following Notarbartolo di Sciara and Agardy (2010): Alboran Sea, Algero-Provençal basin, Tyrrhenian Sea, Adriatic Sea, Strait of Sicily/Tunisian Plateau/Gulf of Sirte, Ionian Sea, Aegean Sea and Levantine Sea;

4. Temporal information: years, season and months of sampling; and

5. Information related to the diet: prey species, diet metrics (contribution by weight, %W; contribution by number, %N; contribution by volume, %V; frequency of occurrence, %F; Index of Relative Importance, %IRI; mean contribution to the stable isotope analysis, SIA hereinafter) and type of analysis (e.g., stomach content analysis or SIA).

Species identified in the literature and coded in the database as prey or predators were also classified in terms of life history and distribution obtaining information from FishBase (Froese and Pauly, 2021) and SeaLifeBase (Palomares and Pauly, 2021). Once the database was completed, the distribution of the chondrichthyans trophic studies was studied by predator species and families, conservation status, area and years of the study, population life stage and methodology used.

2.2. Trophic ecology of Mediterranean chondrichthyans

An overview of chondrichthyan individual species principal prey groups was developed using a quantitative approach. In order to standardize all the reports, we gathered all the indexes: when %W of the prey was not available (the preferred metrics to characterize the trophic information), the % in volume was used, followed by mean contribution to SIA, %IRI,

%F and %N. In the review, studies from all the Mediterranean basin were grouped, hence, prey taxa were aggregated in order to make diet compositions comparable between areas. Prey were grouped into ‘Marine mammals’, ‘Seabirds’, ‘Sea turtles’, ‘Chondrichthyans’, ‘Fish’ (demersal, pelagic and unidentified), ‘Cephalopods’, ‘Crustaceans’, ‘Mollusks’, ‘Annelids’, ‘Gelatinous plankton’, ‘Other invertebrates’ and ‘Detritus and debris’.

Predator species were classified according to the main habitats where the species are present (pelagic or demersal) and their body sizes (small, medium or large). Size classes were defined according to the maximum length (ML) reported in FishBase (Figure A1). We considered as ‘small’ those species with ML <150 cm, ‘medium’ between 150-250 cm and ‘large’ ≥ 250 cm. The analyses were conducted in R (R Core Team, 2020) and all figures were produced using the package ggplot2 (Wickham, 2016).

After a first overview of the chondrichthyan diets composition, we created a prey-predator diet matrix in which columns represent predator species and rows represent main prey groups. Unidentified fish were not excluded from the analysis since they represented a high percentage in many reported diets. Instead, unidentified fish proportion was divided between pelagic and demersal fish according to available reported diets. When only unidentified fish was reported, demersal/pelagic fish proportions of same genera species were applied.

Different statistical approaches were used to compare the trophic ecology of the chondrichthyan species. The diet matrix was forth root transformed and converted into a resemblance matrix using the Bray-Curtis similarity. The multivariate structure of chondrichthyans trophic ecology was examined by means of the non-metric Multidimensional Scaling Analysis (nMDS). A hierarchical cluster analysis based on the “group average” cluster mode was used, providing a dendrogram as a graphic representation in order to look for trophic aggregations between the different species.

Permutational multivariate analyses of the variance (PERMANOVA) were applied to test differences between taxonomic group (Selachimorpha hereinafter referred as sharks, Batoidea hereinafter referred as rays, or Holocephali hereinafter referred as chimaeras), sizes (small, medium or large) and habitats (pelagic or demersal). When significant differences were observed, pairwise tests were performed and we applied a similarity percentage procedure (SIMPER) to identify discriminant prey groups, indicating the average contribution of prey to the dissimilarity between chondrichthyan species. For all PERMANOVA analyses, significance of tests was determined using unrestricted permutation of the raw data with 9999 permutations.

PERMANOVA, SIMPER and nMDS tests were conducted in PRIMER version 7 software (Clarke and Gorley, 2015) and the PERMANOVA+ add-in (Anderson et al., 2015).

2.3. Meta-web construction and analysis

A meta-web is defined as “a compilation of species and their potential feeding interactions within a specific geographical area and time period, which does not represent observed realizations of trophic interactions at a given time step” (Kortsch et al., 2021). In this study, the Mediterranean meta-web was represented following a previously established methodology to develop the meta-web of the Barents Sea (Planque et al., 2014) and its application to the Mediterranean Sea food web (Coll et al., 2019). Due to the heterogeneity in the published information analyzed, we used a binary network model considering only the presence/absence of prey species in predator diets to reduce bias caused by the use of different diet indexes (e.g., %N or %IRI). Qualitative models imply fewer assumptions and have lower data requirement for parametrization than quantitative models (Dunne et al., 2008), and, although they are conservative approaches, results in terms of food web degradation can be informative on ecosystem structure and functioning when used in relative terms (Coll et al., 2008, 2018; Lotze et al., 2011).

Trying to understand all trophic interactions is only practical in simplified communities (Sala, 2004). Therefore, all species identified as predators or prey in the trophic database were classified in different functional groups, which represented all trophic levels of the ecosystem: from primary producers to top predators. This classification was made following previous Mediterranean food web models (e.g., Corrales et al., 2015; Piroddi et al., 2015) and the original Mediterranean meta-web (Coll et al., 2019). As a result, a total of 73 functional groups were described to represent the Mediterranean marine ecosystem with a focus on chondrichthyan species (Table 1). Although fishing fleets *per se* were not included, ‘Fishery discards’ were considered as a group in the model.

In addition to the taxonomic group, the size and the habitat, chondrichthyan species were divided considering their conservation status, separating the groups between low extinction risk (Least Concern, LC, and Near Threatened, NT, species) and high extinction risk (including Vulnerable, VU, Endangered, EN, and Critically Endangered, CR, species). For species classified as Data Deficient (DD), we used the predicted IUCN categorization published by Walls and Dulvy (2020) (Table 1A). Marine mammals were divided into ‘Dolphins’, ‘Toothed whales’, ‘Fin whales’ and the Mediterranean monk seal (*Monachus monachus).* ‘Seabirds’ and ‘Sea turtles’ were grouped in unique functional groups, respectively. Teleosts were classified according their habitat: pelagic, benthopelagic, demersal, bathy/mesopelagic and bathydemersal. Pelagic and demersal teleosts were further divided in ‘small’ (common length <30 cm), ‘medium’ (between 30-89 cm) and ‘large’ (≥ 90 cm) (Coll et al., 2019). Several species (e.g., bluefin tuna *Thunnus thynnus*) or families (e.g., Sparidae) were considered individually due to their important role on the ecosystem as keystone species, abundant species or species with commercial interest. Invertebrates were separated into cephalopods (benthic, benthopelagic and mesopelagic), mollusks (‘Bivalves’ and ‘Gastropods), echinoderms (‘Sea urchins’, ‘Sea cucumbers’ and ‘Starfishes and ophiuroids’), decapods (‘Pelagic decapods’, ‘Shrimps’, the blue and red shrimp *Aristeus antennatus*, the European lobster *Palinurus elephas* and ‘Other decapods’) and ‘Other macro-benthos’ (e.g., sponges). Zooplankton was divided into ‘Micro and mesozooplankton’, ‘Macrozooplankton’ and ‘Suprabenthos’. ‘Gelatinous plankton’ was considered apart from macrozooplankton because of its different trophic role in Mediterranean ecosystems (Corrales et al., 2015). The basal groups were classified into ‘Detritus’ and primary producers, which were divided into three functional groups: ‘Seagrasses’, ‘Algae’ and ‘Phytoplankton’. Detailed description of the functional groups composition is given in Annex B.

The meta-web was represented using the cheddar R package on Analysis and Visualization of Ecological Communities (v0.1-636), which provides a flexible, extendable representation of an ecological community and a range of functions for analysis and visualizations (Hudson et al., 2013, 2020).

Table 1. Functional groups of the meta-web of the Mediterranean Sea. HR: high extinction risk; LR: low extinction risk. Chondrichthyans are represented in red, other vertebrates in purple, invertebrates in blue, producers in green and others in black.

Nº	Functional group	Organism type	Nº	Functional group	Organism type
1	HR Large pelagic sharks	Chondrichthyans	38	Blue whiting	Fish
2	HR Large demersal shark	Chondrichthyans	39	Sparidae	Fish
3	HR Medium demersal shark	Chondrichthyans	40	Scorpaenidae	Fish
4	HR Small demersal shark	Chondrichthyans	41	Groupers	Fish
5	HR Large pelagic rays	Chondrichthyans	42	Labridae and Serranidae	Fish
6	HR Medium pelagic rays	Chondrichthyans	43	Flatfishes	Fish
7	HR Large demersal rays	Chondrichthyans	44	Medium demersal fishes	Fish
8	HR Medium demersal rays	Chondrichthyans	45	Small demersal fishes	Fish
9	HR Small demersal rays	Chondrichthyans	46	Salema	Fish
10	LR Large demersal shark	Chondrichthyans	47	Mugilidae	Fish
11	LR Medium demersal shark	Chondrichthyans	48	Bathydemersal (deep sea) fishes	Fish
12	LR Small demersal shark	Chondrichthyans	49	Coastal benthic cephalopods	Invertebrates
13	LR Small pelagic rays	Chondrichthyans	50	Other benthic cephalopods	Invertebrates
14	LR Medium demersal rays	Chondrichthyans	51	Benthopelagic cephalopods	Invertebrates
15	LR Small demersal rays	Chondrichthyans	52	Mesopelagic cephalopods	Invertebrates
16	Chimaeras	Chondrichthyans	53	Bivalves	Invertebrates
17	Dolphins	Mammals	54	Gastropods	Invertebrates
18	Baleen whales	Mammals	55	Blue and red shrimp	Invertebrates
19	Toothed whales	Mammals	56	Shrimps	Invertebrates
20	Monk seals	Mammals	57	European lobster	Invertebrates
21	Seabirds	Seabirds	58	Pelagic decapods	Invertebrates
22	Sea turtles	Sea turtles	59	Other decapods	Invertebrates
23	Bluefin tuna	Fish	60	Suprabenthos	Invertebrates
24	Swordfish	Fish	61	Sea urchins	Invertebrates
25	Sunfish	Fish	62	Sea cucumbers	Invertebrates
26	Large pelagic fishes	Fish	63	Starfishes and ophiurans	Invertebrates
27	Mackerels and horse mackerels	Fish	64	Other macro-benthos	Invertebrates
28	Medium pelagic fishes	Fish	65	Gelatinous plankton	Invertebrates
29	Anchovy and sardine	Fish	66	Micro and mesozooplankton	Invertebrates
30	Other small pelagic fishes	Fish	67	Macrozooplankton	Invertebrates
31	Benthopelagic fishes	Fish	68	Seagrass	Plant
32	Meso/bathy pelagic fishes	Fish	69	Algae	Algae
33	Angler fish	Fish	70	Phytoplankton	Algae
34	European conger	Fish	71	Detritus	Organic matter
35	European hake	Fish	72	Debris	Organic matter
36	Large demersal fishes	Fish	73	Discards	Organic matter
37	Poor cod	Fish			

2.3.1. Extinction scenarios

We tested seven scenarios of the functional extinction of chondrichthyan groups by using qualitative modelling (Hudson et al., 2013). In order to quantify the changes on community's structural complexity, we calculated linkage density (n° of links/ n° of nodes) and connectance (n° of links/ n° of nodes^2). In addition, omnivory and trophic similarity indexes were also included, which measure the proportion of nodes that consume two or more species and have a non-integer trophic level, and the trophic overlap between nodes in the community, respectively.

The extinction simulations used in the study were as followed:

Simulation 1: Extinction of threatened demersal sharks and rays;

Simulation 2: Extinction of threatened pelagic sharks and rays;

Simulation 3: Extinction of threatened rays;

Simulation 4: Extinction of threatened sharks;

Simulation 5: Extinction of threatened large sharks and rays;

Simulation 6: Extinction of threatened small and medium sharks and rays;

Simulation 7: Extinction of all threatened chondrichthyan species.

3. Results

3.1. Bibliographic review

Trophic ecology information was available for 50 of the 81 chondrichthyan species reported in the Mediterranean, with a total of 114 reports examined in the present study (Annex B). Information available was balanced between major groups, with 52%, 44% and 4% of them studying sharks, rays/skates and chimaeras, respectively. The most studied Families were the rays of the family Rajidae and the sharks of the family Scylorhinidae (Figure 4). The most studied species were the small-spotted catshark *Scyliorhinus canicula*, the blackmouth catshark *Galeus melastomus* and the thornback ray *Raja clavata* (Figure 5).

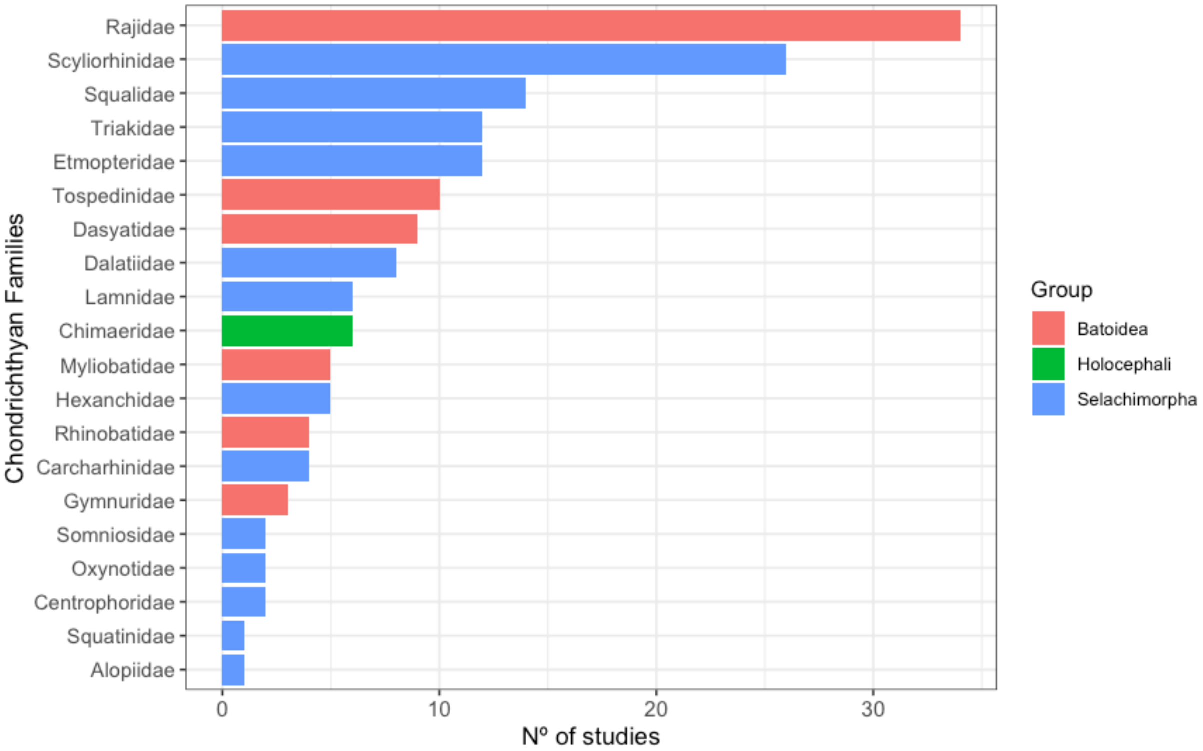

Figure 4. Number of studies grouped by the different chondrichthyan families present in the Mediterranean Sea.

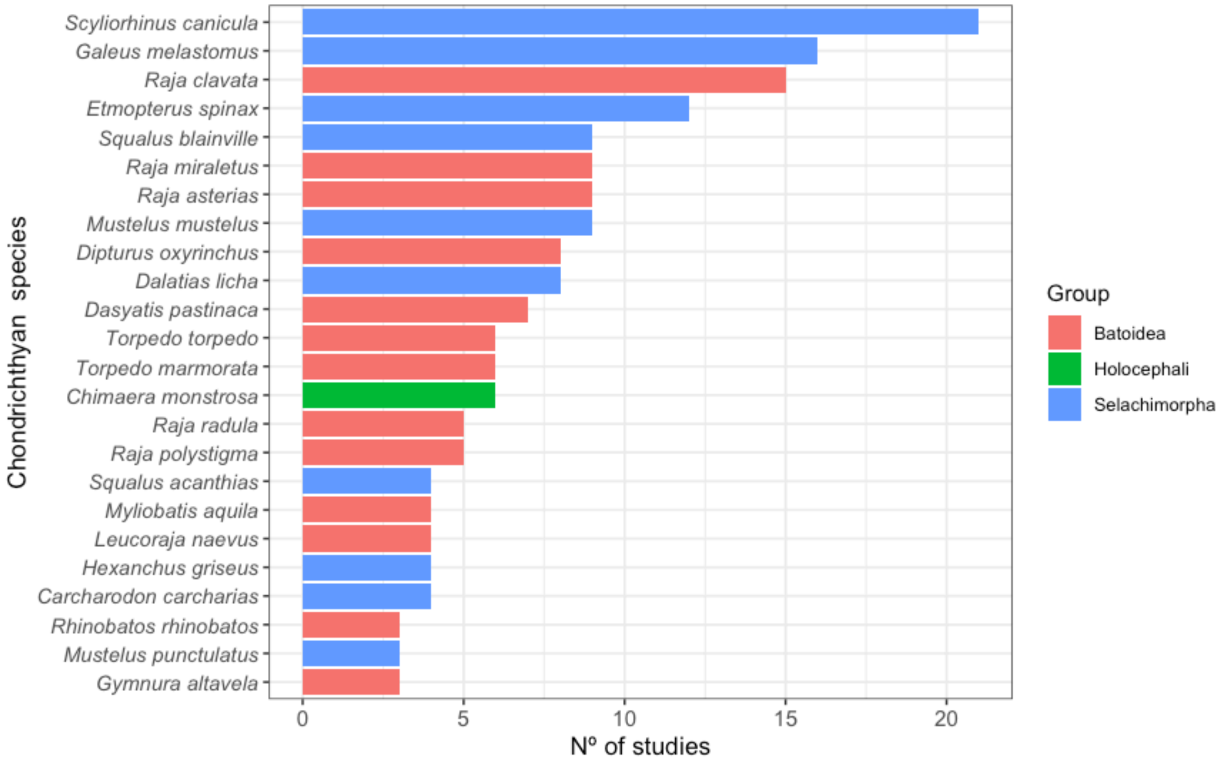

Figure 5. Number of studies per chondrichthyan species in the Mediterranean Sea. Only species with three or more reports are represented.

Relating to the IUCN category, we found that low risk species were more studied than endangered ones, which only accounted for 39% of the reported diets (Figure 6).

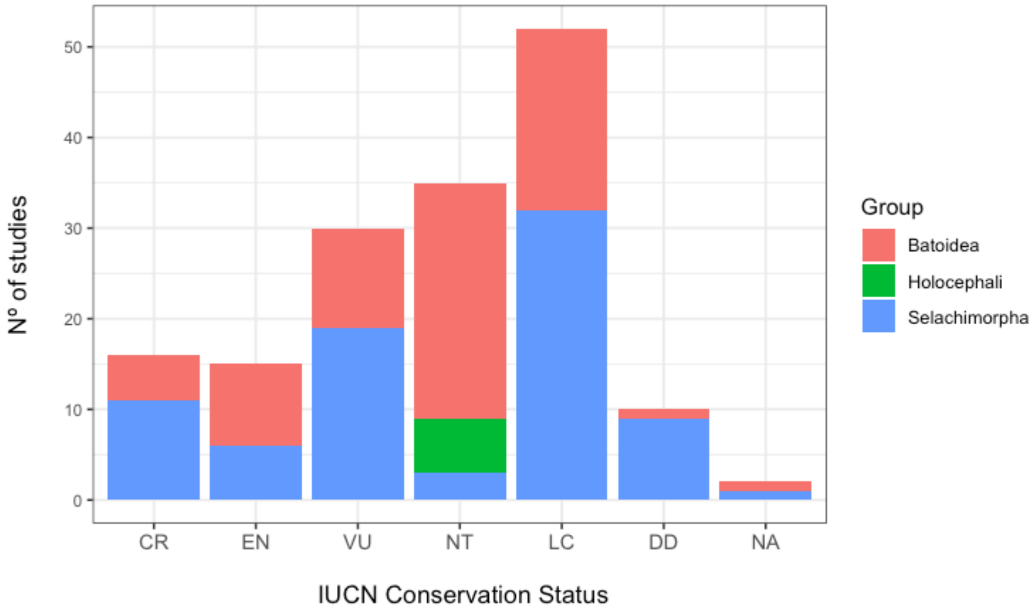

Figure 6. Number of studies per IUCN Conservation Status according to the Mediterranean assessment (IUCN, 2021).

Chondrichthyan trophic information was heterogeneously distributed between Mediterranean areas, with most studies focusing in four main areas (Figure 7): the Strait of Sicily/Tunisian Plateau/Gulf of Sirte, the Algero-Provençal basin, the Aegean and the Adriatic Seas. Information was scarce regarding the Alboran Sea, with less than five diet reports published.

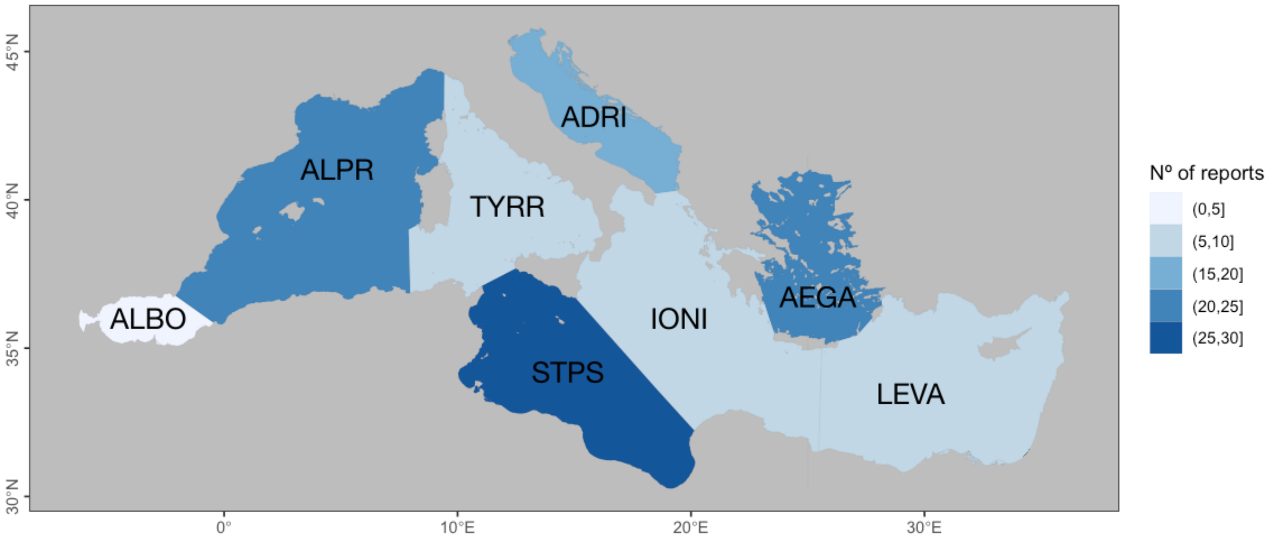

Figure 7. Number of studies reporting chondrichthyans diet information per area. Divisions of the Mediterranean Sea were defined following Notarbartolo di Sciara and Agardy (2010): Alboran Sea (ALBO), Algero-Provençal basin (ALPR), Tyrrhenian Sea (TYRR), Adriatic Sea (ADRI), Strait of Sicily/Tunisian Plateau/Gulf of Sirte (STPS), Ionian Sea (IONI), Aegean Sea (AEGA) and Levantine Sea (LEVA).

Regarding temporal distribution, most of the sampling of Mediterranean sharks and rays published diet reports started between 2000 and 2010, with the first study beginning in 1973 and last one in 2019 (Figure 8). Only few articles included trophic information about chondrichthyans before the 1990s.

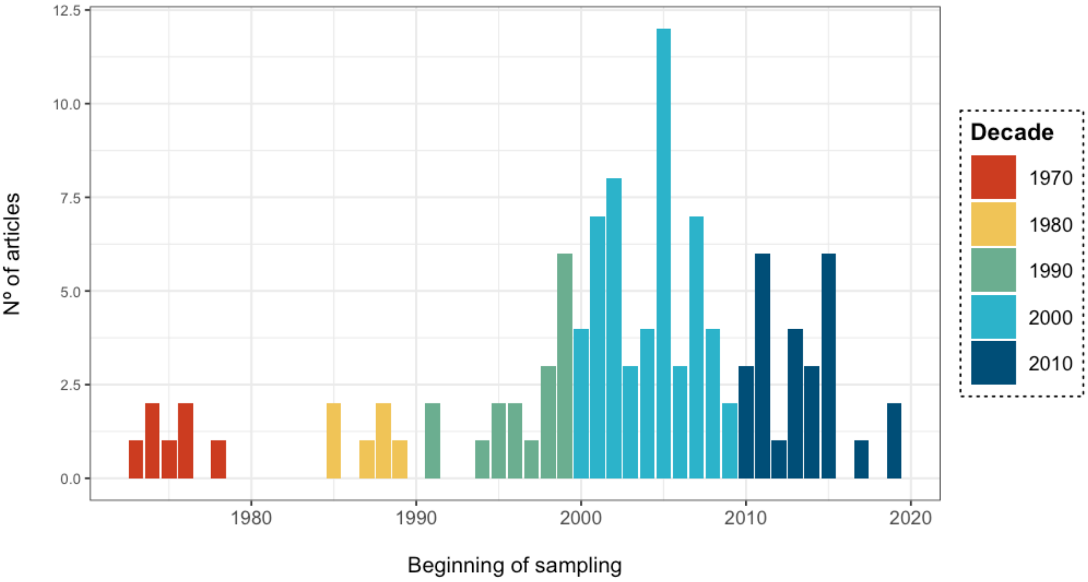

Figure 8. Number of studies reporting chondrichthyans diet information per year.

3.2. Trophic ecology of Mediterranean chondrichthyans

All prey group categories considered were recorded in the diet of at least one species. On a presence-absence basis, cephalopods were the most frequent prey, being present in 90% of the species' diets, followed by demersal fishes (82%) and crustaceans (78%). On the contrary, marine mammals, seabirds and sea turtles were present in less than 10% of the diets.

Trophic differences were observed between demersal sharks and demersal rays, with crustaceans being more important for rays, while cephalopods being more important for demersal sharks (Figure 9). Cephalopods also made up an important part of pelagic sharks' diets (Figure 10), except for the great white shark *Carcharodon carcharias*, whose diet contained mostly fish, marine mammals and sea turtles*.* All pelagic ray species, the bull ray *Aetomylaeus bovinus*, the devil fish *Mobula mobular* and the pelagic stingray *Pteroplatytrygon violacea,* had at least one trophic report in the Mediterraenan Sea, with the first two preying mainly on fish and the third including benthic invertebrates such as mollusks and annelids (Figure 10). The diet of rabbitfish *Chimaera monstrosa*, the only chimera present in the Mediterranean Sea, was dominated by crustaceans (Figure 11).

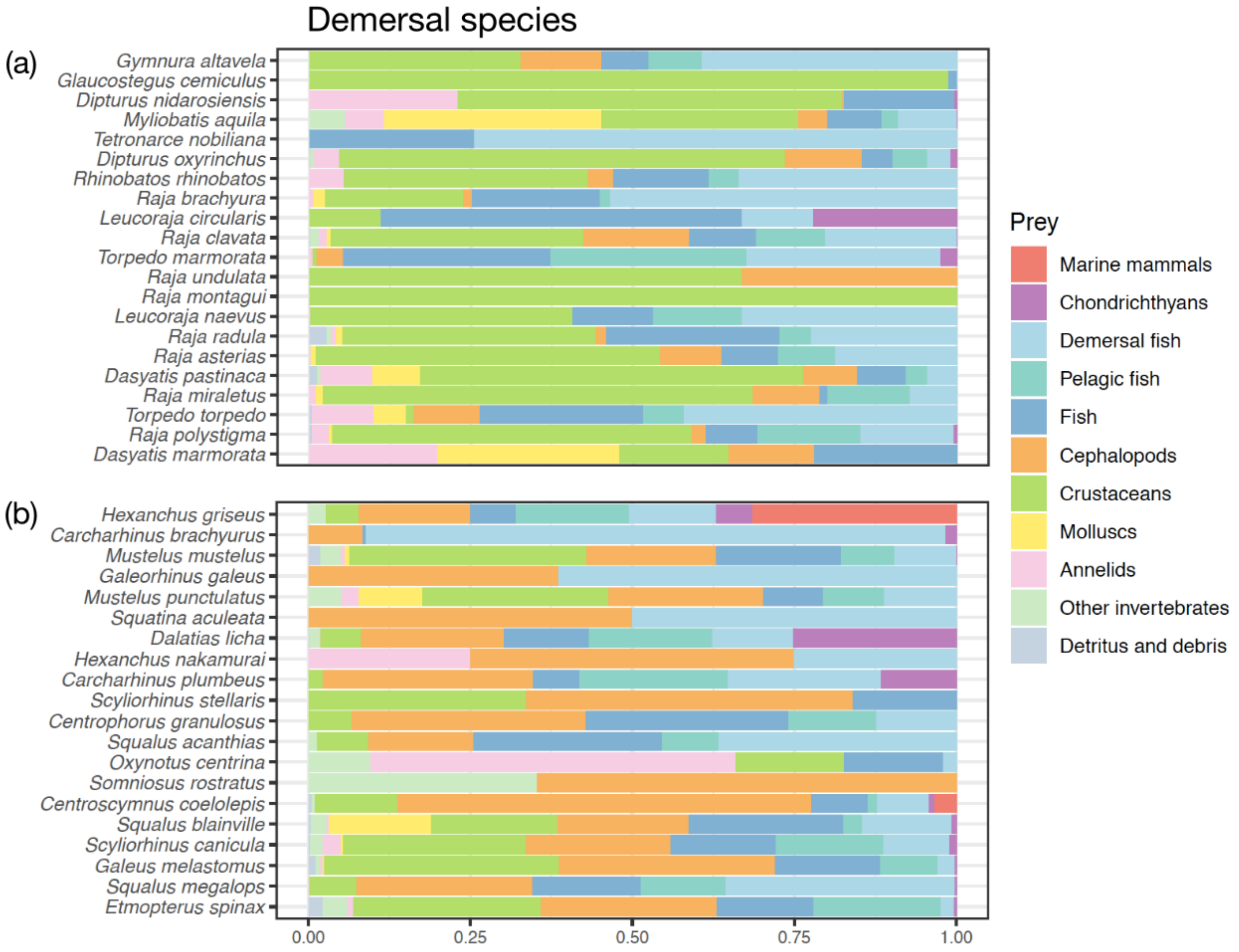

Figure 9. Prey category contributions to the standardized diets of demersal species of (a) rays and (b) sharks. Species are ordered by decreasing size. Prey category ‘Fish’ referred to unidentified fish (thus unclassified between demersal and pelagic).

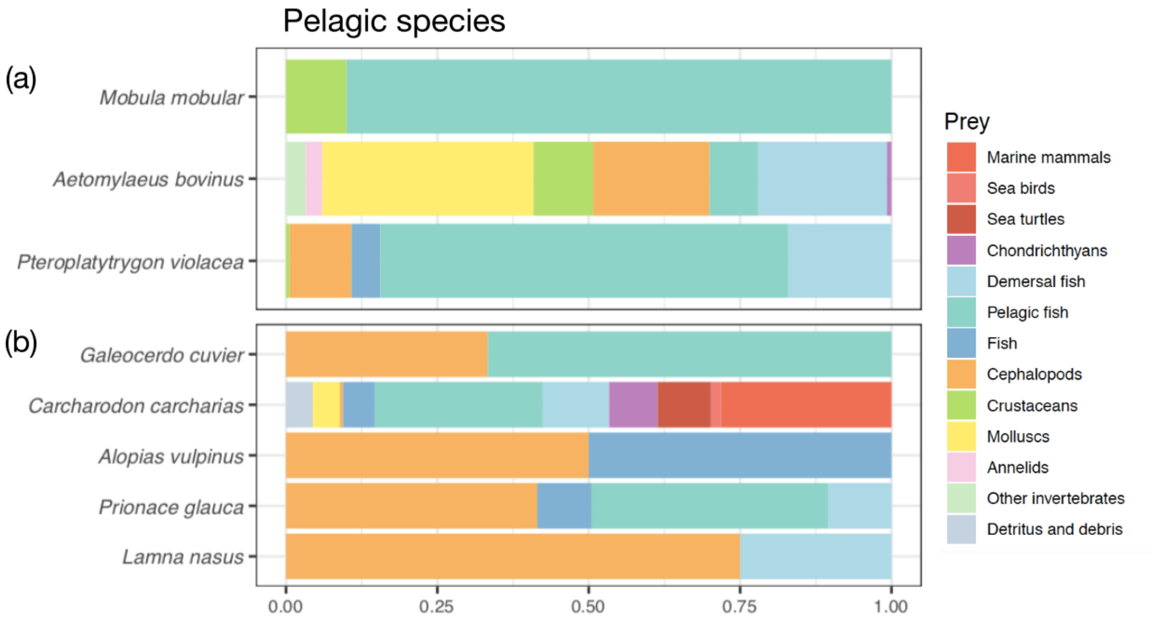

Figure 10. Prey category contributions to the standardized diets of pelagic species of (a) rays and (b) sharks. Species are ordered by decreasing size. Prey category ‘Fish’ referred to unidentified fish (thus unclassified between demersal and pelagic).

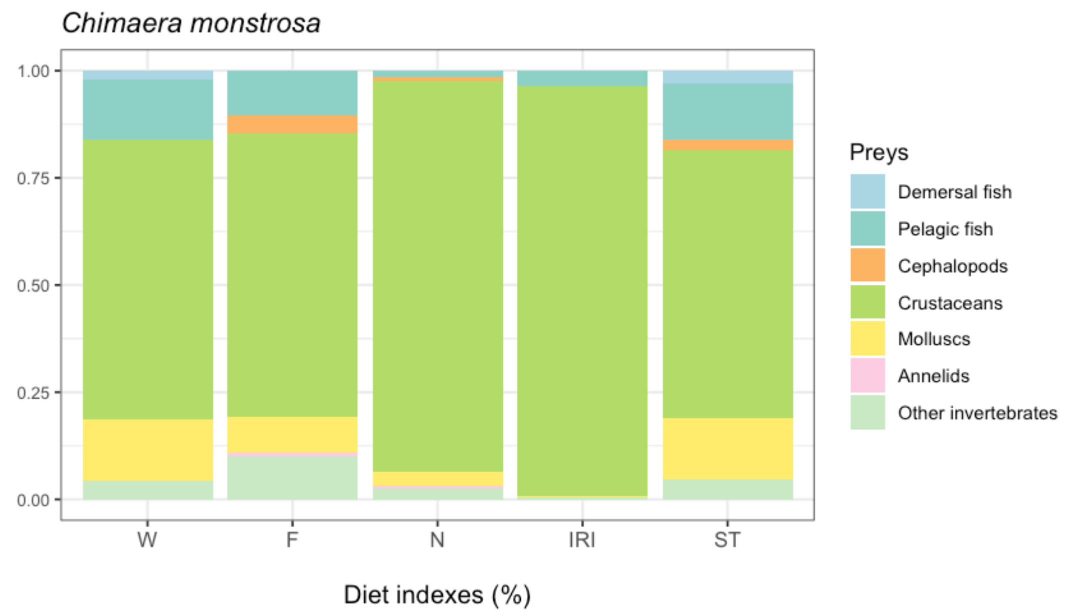

Figure 11. Rabbitfish *Chimaera monstrosa* diet proportions according to different diet indexes.

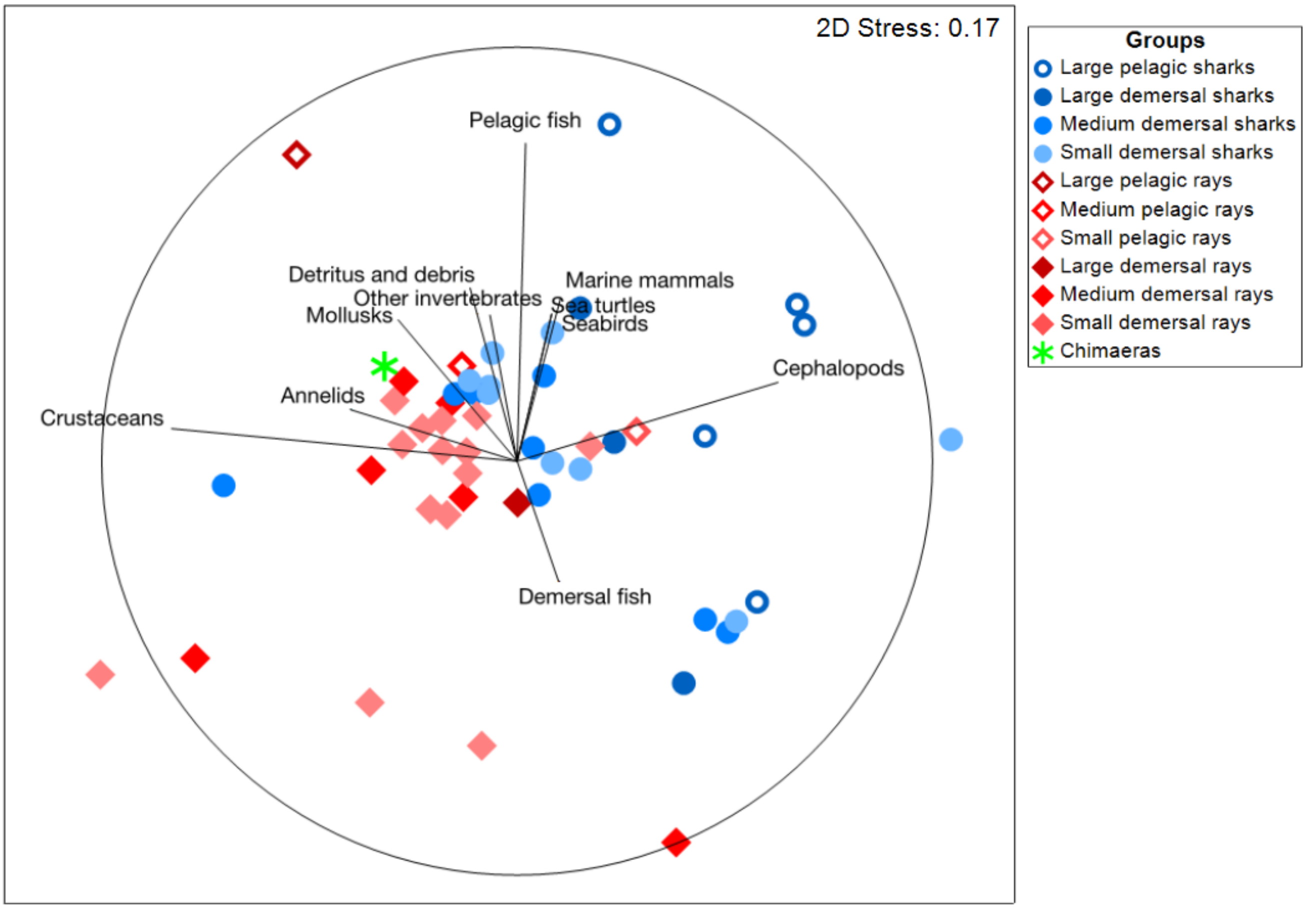

Figure 12. NMDS plot of 50 chondrichthyan species grouped according to size, habitat and taxonomic group. A biplot with prey groups with correlation > 0.3 is presented. The plots were generated using Bray-Curtis similarity (2D-stress = 0.17). Species names are represented in Figure 2A.

The results of the multidimensional scaling analysis showed no well-defined clusters (Figure 12). However, shark species were more represented by a diet composed by cephalopods and less by crustaceans than rays, except for the angular roughshark *Oxynotus centrina,* in which annelids played a major trophic role (Figure 9). This is in accordance to the SIMPER test results (Table 2), which highlighted crustaceans and cephalopods as the main groups contributing to dissimilarity between sharks and rays. Chimaeras were grouped next to medium and small demersal rays which mainly preyed on mollusks (e.g., the common eagle ray *Myliobatis aquila).* Mollusks were the main prey causing dissimilarity between chimaeras from one side and sharks and rays from the other (Table 2).

Table 2. Percentage contribution of prey to dissimilarity between taxonomic groups (SIMPER analysis; cut-off for low contribution at 70%). Average abundance (Av. Abund.), percentage contribution to the dissimilarity (Contrib.) and percentage contribution to the accumulated dissimilarity (Cum.) are shown.

Average dissimilarity = 42.99

Prey	**Batoidea** (Av.Abund.)	**Selachimorpha** (Av.Abund.)	**Contrib.** (%)	**Cum.** (%)
Crustaceans	0.7	0.37	16.65	16.65
Cephalopods	0.4	0.71	15.99	32.64
Pelagic fish	0.47	0.48	12.76	45.4
Demersal fish	0.62	0.61	11.53	56.93
Annelids	0.28	0.16	10.65	67.57
Other invertebrates	0.09	0.2	9.25	76.82

Average dissimilarity = 35.25

Prey	**Batoidea** (Av.Abund.)	**Holocephali** (Av.Abund.)	**Contrib.** (%)	**Cum.** (%)
Mollusks	0.21	0.61	20.5	20.5
Other invertebrates	0.09	0.47	17.9	38.4
Demersal fish	0.62	0.41	14.73	53.13
Pelagic fish	0.47	0.6	11.09	64.22
Annelids	0.28	0.17	9.79	74

Average dissimilarity = 41.42

Prey	**Selachimorpha** (Av.Abund.)	**Holocephali** (Av.Abund.)	**Contrib.** (%)	**Cum.** (%)
Mollusks	0.1	0.61	19.4	19.4
Crustaceans	0.37	0.89	16.95	36.35
Cephalopods	0.71	0.38	13.36	49.72
Demersal fish	0.61	0.41	11.17	60.89
Other invertebrates	0.2	0.47	10.14	71.03

Accordingly, the results from PERMANOVA showed significant differences between species diets regarding taxonomic group (Selachimorpha, Batoidea and Holocephali), but suggested that the prey composition did not differ significantly between habitats (pelagic and demersal) and sizes (small, medium and large; Table 3). Pairwise comparisons showed highly significant differences between Selachimorpha and Batoidea ($p < 0.01$). The interaction between factors was not significant (Table 3).

Table 3. Summary of PERMANOVA tests examining differences between taxonomic group, habitat and size (and their interactions) in prey composition of 50 chondrichthyan species diet.

Factor	df	Pseudo-F	*P* (perm)
Taxonomic group	2	2.676	**0.029**
Habitat	1	1.496	0.208
Size	2	1.052	0.397
Tax. group x Habitat**	1	0.564	0.618
Tax. group x Size**	2	0.173	0.976
Habitat x Size	2	0.899	0.484
Tax. group x Habitat x Size**	0	No test	

** Term has one or more empty cells.

Cluster analysis of standardized diets revealed four major trophic clusters for rays (Figure 13, cophenetic correlation = 0.90) and eight clusters for sharks (Figure 14, cophenetic correlation = 0.86). For rays, the first cluster was formed by species that mainly feed on demersal fish, the sandy ray *Leucoraja circularis* and the electric ray *Tetronarce nobiliana* (cluster a). The devil fish *Mobula mobular*, whose main prey were pelagic fish, formed its own cluster (cluster c). The remainder species were divided in species which feed on both demersal and pelagic fish (cluster b), and species with almost no fish in their diet (cluster d). In the case of sharks, eight clusters were defined, with the little sleeper shark *Somniosus rostratus,* the angular roughshark *Oxynotus centrina* and the Great white shark *Carcharodon carcharias* conforming their own clusters (clusters a, b and c). Cluster d was composed by shark species that do not prey on pelagic fish and cluster e with species that do not prey on demersal fish. The Portuguese dogfish *Centroscymnus coelolepis* and the bluntnose sixgill shark *Hexanchus griseus*, which include marine mammals on their diet, are grouped together in cluster f. Clusters g and h had high percentage of similarity (> 75%), with similar prey proportions in their reported diets.

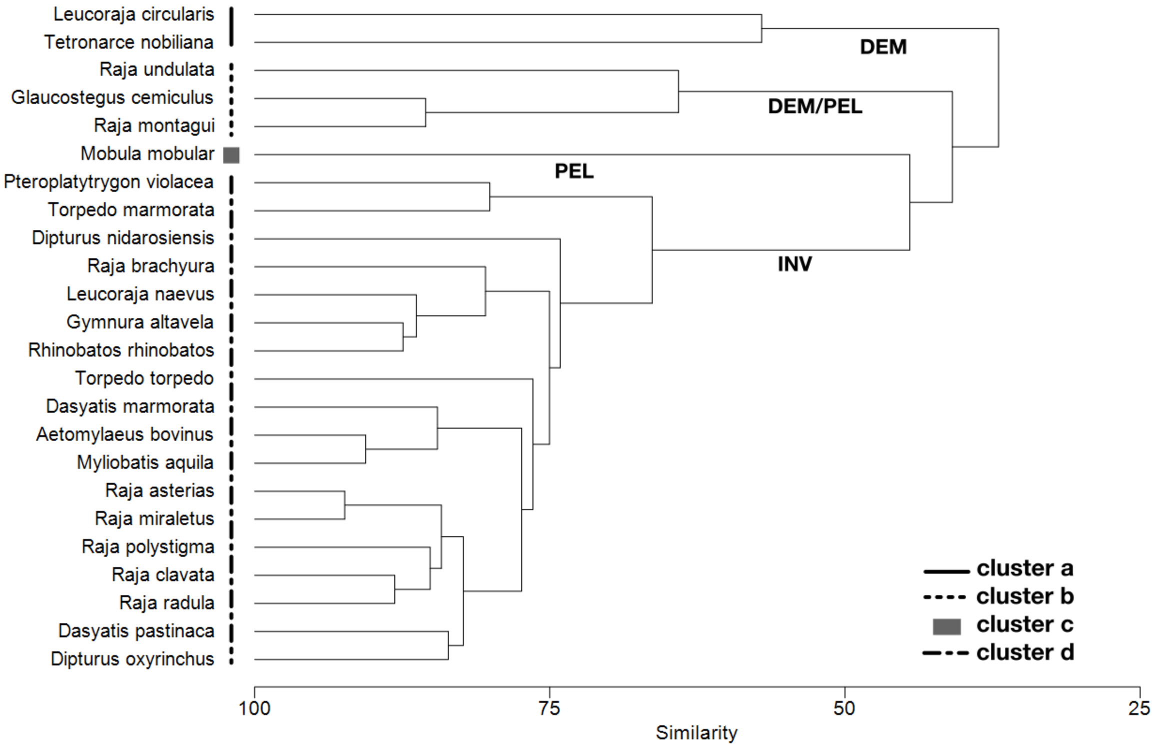

Figure 13. Cluster analysis of standardized diet compositions for ray species. DEM: Demersal fish; PEL: Pelagic fish; INV: Invertebrates.

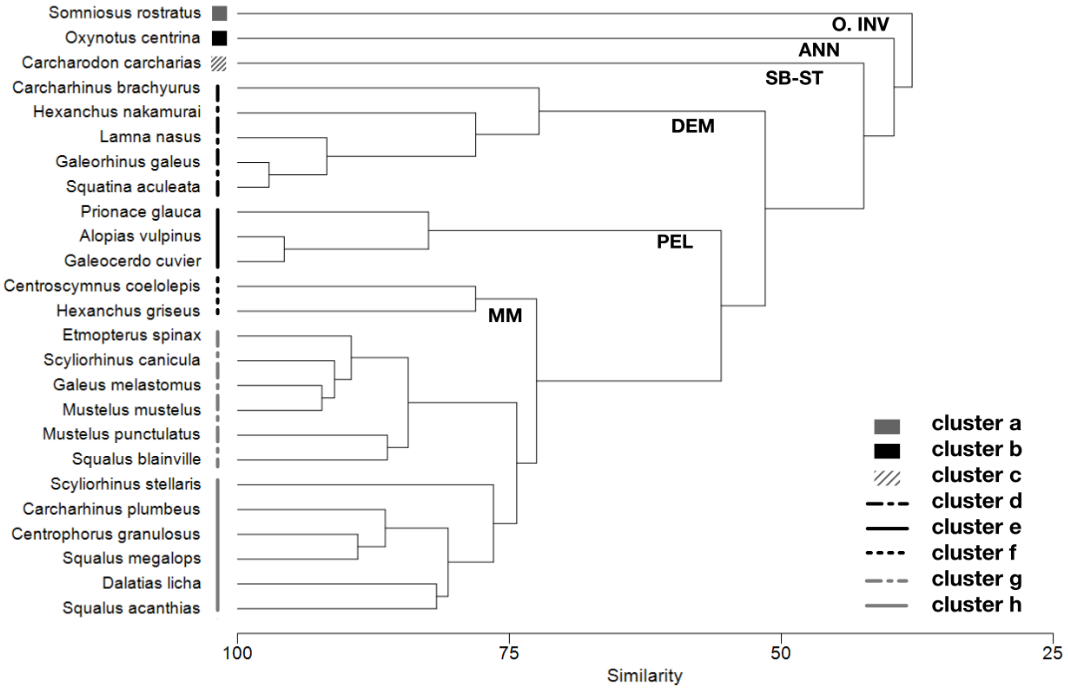

Figure 14. Cluster analysis of standardized diet compositions for shark species. MM: Marine Mammals; SB: Seabirds; ST: Sea Turtles; DEM: Demersal fish; PEL: Pelagic fish; ANN: Annelids; O. INV: Invertebrates.

3.3. Mediterranean meta-web and extinction scenarios

A total of 602 studies were included in the Mediterranean meta-web. The resulting meta-web included information of 399 different predator species and a total of 1720 taxa were identified as prey, with the resulting topology of 73 nodes and 1335 trophic links (Figure 15).

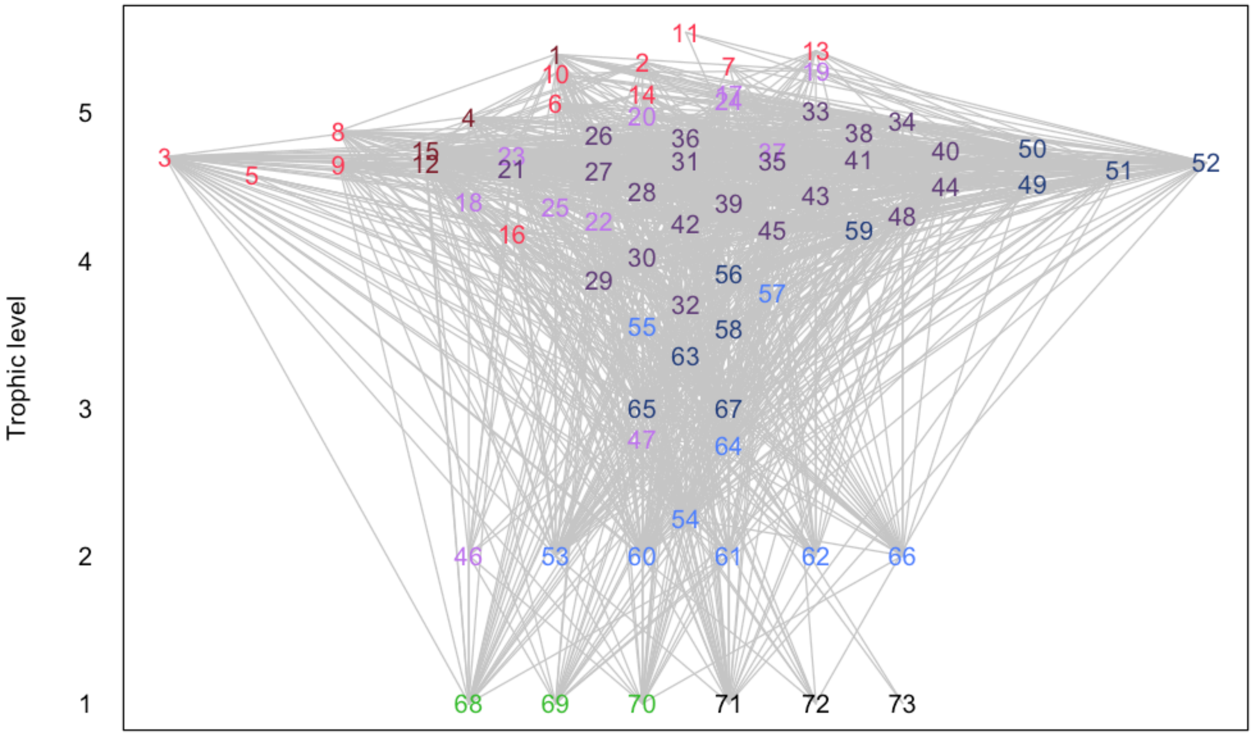

Figure 15. Graphical representation of the Mediterranean Sea meta-web with emphasis on chondrichthyan species. Functional groups codes are presented at Table 1. Chondrichthyans are represented in red, other vertebrates in purple, invertebrates in blue, producers in green and others in black colors. Nodes with cannibalism (i.e. predation inside the node) are presented in darker colors.

Different extinction simulations and the correspondent indexes are presented in Table 4 (see Figure 1B for the resultant meta-web topologies of the extinction simulations). Major changes were detected when all threatened chondrichthyans were removed (simulation 7), resulting in a food web with higher connectance and trophic similarity, and lower density and omnivory than the non-extinction scenario food web. When comparing between the extinction of demersal and pelagic species (simulations 1 and 2), although more nodes were eliminated from the web in simulation 1, changes in trophic similarity were greater for simulation 2. Although the extinction of rays (simulation 3) reduced the number of nodes more than the extinction of sharks (simulation 4), the reduction of trophic links and, therefore, of density, was greater when sharks were removed. Trophic similarity was also higher in simulation 4. The removal of large chondrichthyans (simulation 5) had a higher impact on trophic similarity and connectance than the removal of medium and small groups (simulation 6), even though more nodes were removed in simulation 6.

Table 4. Structural and complexity descriptors (without units) of the different extinction scenarios.

Simulation	Nodes	Trophic links	Density	Connectance	Omnivory	MeanMax Trophic Similarity
0 No extinction	73	1335	18.29	0.251	0.822	0.639
1 Threatened demersal spp.	67	1184	17.67	0.264	0.806	0.642
2 Threatened pelagic spp.	70	1280	18.29	0.261	0.814	0.648
3 Threatened rays	68	1245	18.31	0.269	0.809	0.646
4 Threatened sharks	69	1219	17.67	0.256	0.812	0.649
5 Threatened large spp.	70	1285	18.36	0.262	0.814	0.651
6 Threatened small/medium spp.	68	1184	17.41	0.256	0.809	0.635
7 All threatened groups	64	1131	17.67	0.286	0.797	0.653

4. Discussion

4.1. Bibliographic review

Limited demographic and trophic data is available for most of Mediterranean chondrichthyan species and the major part of this information is obtained by fisheries-related captures. Since most of the species are not primary targeted by fishing fleets in the Mediterranean Sea, they are mainly caught as bycatch and, therefore, underreported (Coll et al., 2013; Bradai et al., 2018). In fact, the central Mediterranean, which reported more than twice elasmobranchs incidental catch than the rest areas of the Mediterranean (FAO, 2020a), was also the area with more chondrichthyans' diets studies (e.g., Saïdi et al., 2007; Kara et al., 2019). Nevertheless, the most reported as bycatch species did not match with the most studied species. For example, the Strait of Sicily/Tunisian Plateau/Gulf of Sirte (STPS) was the area with more published papers, with the smooth-hound shark *Mustelus mustelus* being the most studied species; yet, the Algero-Provençal basin was the area that contributed with more species diets (27 different species versus 23 in STPS) due to multispecific studies. The most studied species correspond to the most abundant species in the western Mediterranean (e.g., blackmouth catshark *Galeus melastomus* and velvet belly lantern shark *Etmopterus spinax*; Giménez et al., 2020), two species commonly captured by bottom trawl survey campaigns such as the MEDITS (Bertrand et al., 2002; Follesa et al., 2019).

As Stevens et al. (2000) and Bradai et al. (2018) pointed out, the commercial value of species conditions research priorities, and thus scientific knowledge, is less extensive for species which are legally protected, such as the blue skate *Dipturus batis*, whose fishing is prohibited in the Mediterranean by the SPA/BD Protocol and no diet reports were found. Besides, more threatened species tend to be scarce and, therefore, less likely to be fished. The lack of trophic ecology information for an important proportion of chondrichthyan species hardens the representation of these endangered species in ecosystem models, with the consequent underrepresentation of their role. Scientific campaigns targeting these species could help understand their trophic ecology, however, the impacts on their already low abundances could be detrimental.

4.2. Trophic ecology of Mediterranean chondrichthyans

Trophic ecology studies usually rely on stomach content analysis, which require large sample sizes to obtain an accurate representation of prey composition, especially in chondrichthyan species, which often present empty stomachs (Navarro et al., 2014 and references therein). These samples are difficult to obtain, particularly for threatened species, and species such as the little sleeper shark *Somniosus rostratus,* were only reported in one study that analyzed only 3 individuals (Barría et al., 2015). In addition, the lack of samples force many studies to analyze both juveniles and adults together, even though ontogenetic shifts in the diet have been already reported in sharks (Barría et al., 2018) and rays (Consalvo et al., 2010). For the same reasons, few studies take into account seasonal variability on chondrichthyans trophic ecology (e.g., Romanelli et al., 2006; Filiz, 2009). Besides, soft prey like gelatinous plankton are usually underestimated because of their rapid degradation (Cardona et al., 2012), and prey with hard structures (e.g., cephalopods beaks) can accumulate and be overrepresented in number. These limitations could be overcome with the combined use of stable isotope analyses (SIA), which allows to estimate the relative contribution of each prey in their predator diet without the need of a lethal approach (Barría et al. 2018).

Although stomach content allows higher taxonomic resolution than other methods like SIA, we found high percentages of unidentified prey or low taxonomic resolution (e.g., Teleosts) in some studies using stomach contents, such as in the case of the nursehound *Scyliorhinus* *stellaris* (Yemisken et al., 2019). The difference in prey taxonomic resolution, together with the different number of reports per species and the use of different metrics when presenting prey proportions, hinders standardization of species trophic ecology.

Since the aim of the study was to obtain an overview of the ecological role of sharks, rays and chimaeras in the Mediterranean food web, we used a low taxonomic resolution of the diet composition. This low resolution is likely conditioning our results, where trophic segregation between different sizes and different habitats was not clear. However, a division between sharks, rays and chimaeras was found and we were able to aggregate shark and ray species in different clusters according to their main prey. For most marine predators, prey is conditioned by mouth size (Morlon et al., 2014), thus, although prey group proportions showed no differences between sizes, specific composition of the diet does: e.g., small demersal sharks showed different specific trophic links than large demersal sharks. Besides, size and habitat do relate to conservation status, with larger species being more likely to be threatened than smaller ones (Dulvy et al., 2021) and pelagic species suffering higher extinction risk (Walls and Dulvy, 2021).

4.3. Mediterranean meta-web and extinction scenarios

Sub-tropical and tropical marine food webs, such as the ones from the Mediterranean Sea, are particularly complex, with small scale variations in their topology (Sala, 2004). Since species with low extinction risk tend to be more abundant and, therefore, easier to study, they usually have a better characterization of their diet. Relying in these species may serve as a good approach to use for those less abundant species with similar ecological requirements (Navarro et al., 2016; Giménez et al., 2020).

Chondrichthyans can alter prey diversity and size distributions, and even foraging behavior of prey, altering ecosystem functions such as nutrient recycling and structural habitat complexity (Field et al., 2009). Indeed, the depletion of endangered species could also trigger the depletion of similar not-threatened species: co-extinctions represent a synergistic process in which species loss occurs more rapidly than otherwise expected (Field et al., 2009) and non-Red-Listed species could be extinct alongside their listed symbionts due to interspecific dependencies (Koh et al., 2004). Nonetheless, our scenarios of extinction of sharks and rays were tested by means of qualitative modelling and, since biomasses nor abundances were taken into account, trophic cascade effects could not be investigated. Therefore, our analysis of the extinction consequences was limited to the qualitative topological changes, such as changes in connectance and omnivory of the system. Overall, levels of omnivory found in this study were around 80%, which is in accordance with Dunne et al. (2004), who found that marine food webs have high levels of omnivory, although they discuss whether it can be an artifact of poor resolution of primary producers and their trophic links. According to our scenarios, extinction of threatened chondrichthyans would lead to a reduction in omnivory, increasing the likelihood and magnitude of trophic cascades, that is reduced in the presence of strong omnivory (Bascompte et al., 2005).

Higher values of connectance, which are related to lower structural complexity (Bornatowski et al., 2014), were found when removing threatened chondrichthyans. Changes in connectance were greater when more nodes were removed with the exception of the removal of the large species (simulation 5) when compared with the removal of small and medium groups. These alterations produced by species loss constitute a decrease in robustness, which relates to the maintenance of network integrity and also has consequences for stability (Sánchez-Carmona et al., 2013). Therefore, food web robustness could be more impacted by the extinction of large-sized chondrichthyans. On the other hand, pelagic species, large species and sharks showed greater contribution to trophic dissimilarity when compared to demersal species, small and medium species and rays, respectively. Therefore, our results suggest that a special focus on the conservation of pelagic species, large species and sharks groups is need: higher similarity between nodes could enhance competence and lead to a less diverse system (Morlon et al., 2014). In fact, all Mediterranean large pelagic sharks are considered endangered or critically endangered (Table 1A; IUCN, 2021), and species composition is changing: larger sharks such as the thresher shark *Alopias vulpinus* and hammerhead sharks *Sphyrna* spp. which were frequently reported by fishers in the past, have been replaced by smaller species such the blue shark *Prionace glauca* (Coll et al., 2014a). This is in line with historical change of populations of large sharks in the Mediterranean Sea (Ferretti et al. 2008).

5. Conclusions

Whether is due to an increase of scientific knowledge, to a genuinely worsened status, or a combination of both, the number of threatened chondrichthyans keeps growing (Dulvy et al., 2021). Actual exploitation rates are unsustainable over the long term, suggesting that the majority of chondrichthyan populations will continue to decline under current fishing pressure (Worm et al., 2013; Dulvy et al., 2021). Overall, there is an urgent need to preserve oceans biodiversity and ecosystem properties with their associated services is order to achieve a resilient, healthy ocean (Pascual and Macías, 2021). Within this context, the protection of key species as chondrichthyans can serve as a proactive strategy to conserve the whole marine food web (Giménez et al., 2020). According to Nuez et al. (2021), since chondrichthyans are not frequently targeted directly by fisheries, reducing bycatch by means of operational changes or the designation of marine protected areas (MPAs) are the only real alternatives. However, chondrichthyans species are not explicitly accounted for in current Mediterranean Sea MPA design, thus they lack representation in existing marine protected areas (Giménez et al., 2020). Besides, for long-lived species such as sharks, it may take decades to recover their abundance when management regulations are applied, especially under unfavorable environmental conditions (Bradai et al., 2018; FAO, 2020b; Walls and Dulvy, 2021).

This study represents a first step towards the analyses of foodweb complex interactions were Mediterranean chondrichthyan species intervene. Overall, our analysis showed an increment of trophic similarity and a reduction of omnivory with the extinction of threatened chondrichthyans, highlighting the contribution of pelagic species, large species and shark species to a more resilient and diverse system. It therefore underlines the need of a drastic improvement of fisheries management focused on chondrichthyans protection to prevent regional species extinctions, which are already happening in the Mediterranean Sea (Dulvy et al., 2021; Nuez et al., 2021; Walls and Dulvy, 2021); and to preserve ecosystem diversity, complexity and resilience (Field et al., 2009).

Future iterations of the work can be used to test additional typologies of sub-systems within the Mediterranean meta-web and additional extinction scenarios. For example, conservation threat categories were only considered for chondrichthyan species when developing the extinction scenarios. But direct protection of chondrichthyans may not be sufficient neither to stop their abundance decreasing nor to recover their populations since the fate of their prey should also be taken into account. Therefore, future analyses could include the extinction scenarios of main chondrichthyans prey, both commercial and non-commercial. This study also highlights that further studies of trophic ecology on Mediterranean chondrichthyans are need in order to consider all the species and incorporate the seasonality and ontogenetic variations of their diets, which could lead to a better comprehension and representation of their key role in marine food webs.

6. Description of the tasks performed by the student

I was involved in the following tasks:

- A bibliographic review in order to upgrade the previous Mediterranean meta-web (Coll et al., 2019) with all the chondrichthyan diets available for the Mediterranean.

- Screening of the reports and introduction of diet tables into the database with a resulting database with more than 25,000 entries (vs the initial 8,000).
- Introduction of taxonomy, life history and distribution of the new species introduced both as prey and predators in the database from WoRMs (https://www.marinespecies.org/), FishBase and SeaLifeBase.
- Adjustment of the previous functional groups of the Mediterranean meta-web to meet the objective of our study to focus on the chondrichthyan community, and classification of the new species into their groups.
- Diet description of chondrichthyans: I summarized the data in different prey categories and represented the diet composition in R with package ggplot2. I used this diet composition table to perform the multivariate analyses with PRIMER.
- Meta-web construction: I generated the predators-prey matrix with R to obtain the trophic links and nodes tables needed to run the Cheddar R package in order to represent the meta-web. I added two food web indicators to the ones already used in Coll et al. (2019) and tested novel extinction simulations.

7. Acknowledgments

First, I would like to thank my supervisors, Dr. Marta Coll and Dr. Joan Navarro, for their help and support during the development of the work. I would also like to highlight the implication of PhD. Jazel Ouled-Cheikh in this work, whose help with the bibliographic review and the R scripts was essential, many thanks for your time and your helpful comments. Finally, I would also like to thank Marc and all my colleges from the research group and the Department of Renewable Marine Resources for all their encouragement and patience.

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ANNEX A: Supplementary material

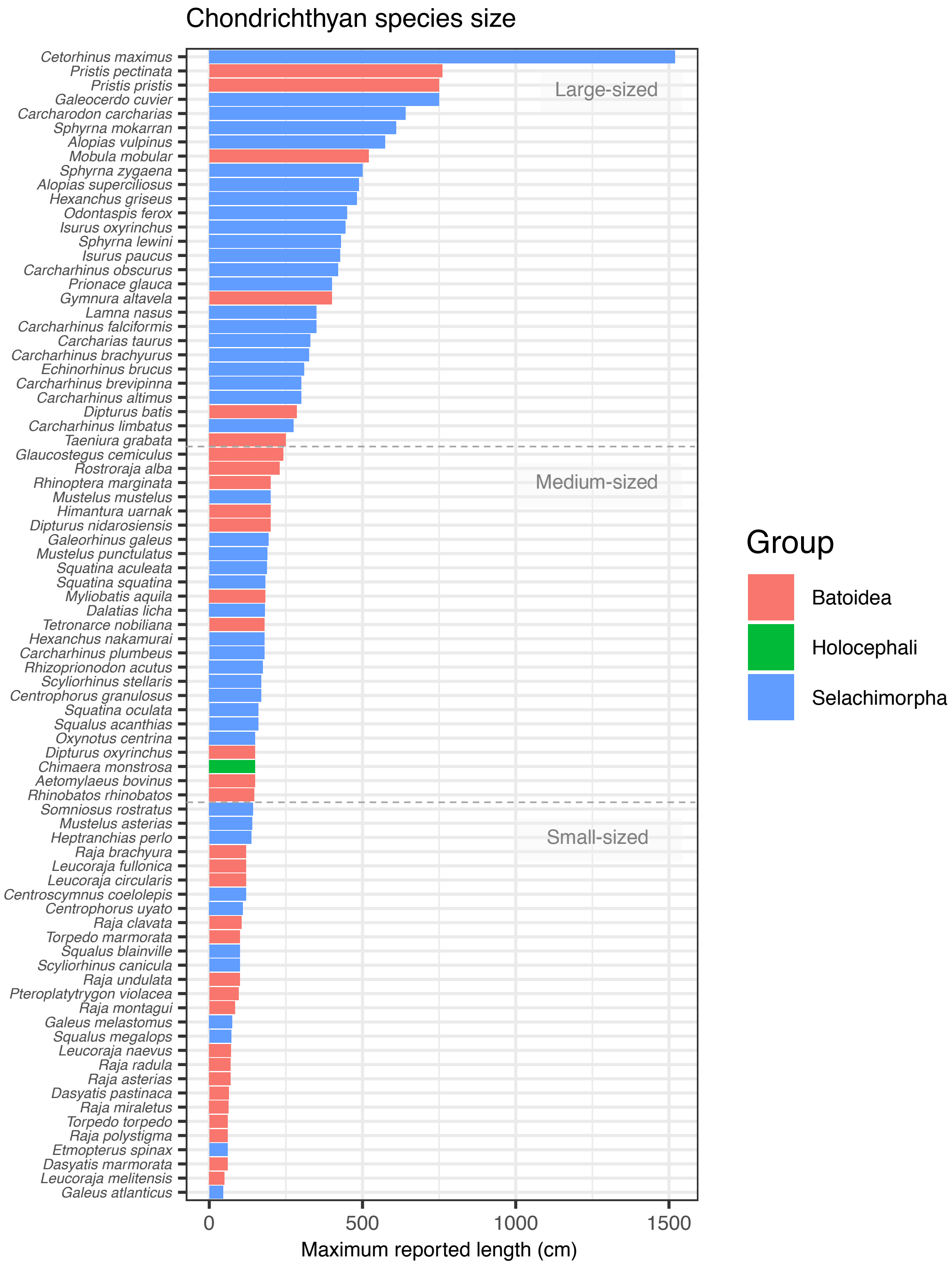


Figure 1A. Maximum reported length (ML) used in this study. Source FishBase (Froese and Pauly, 2021).

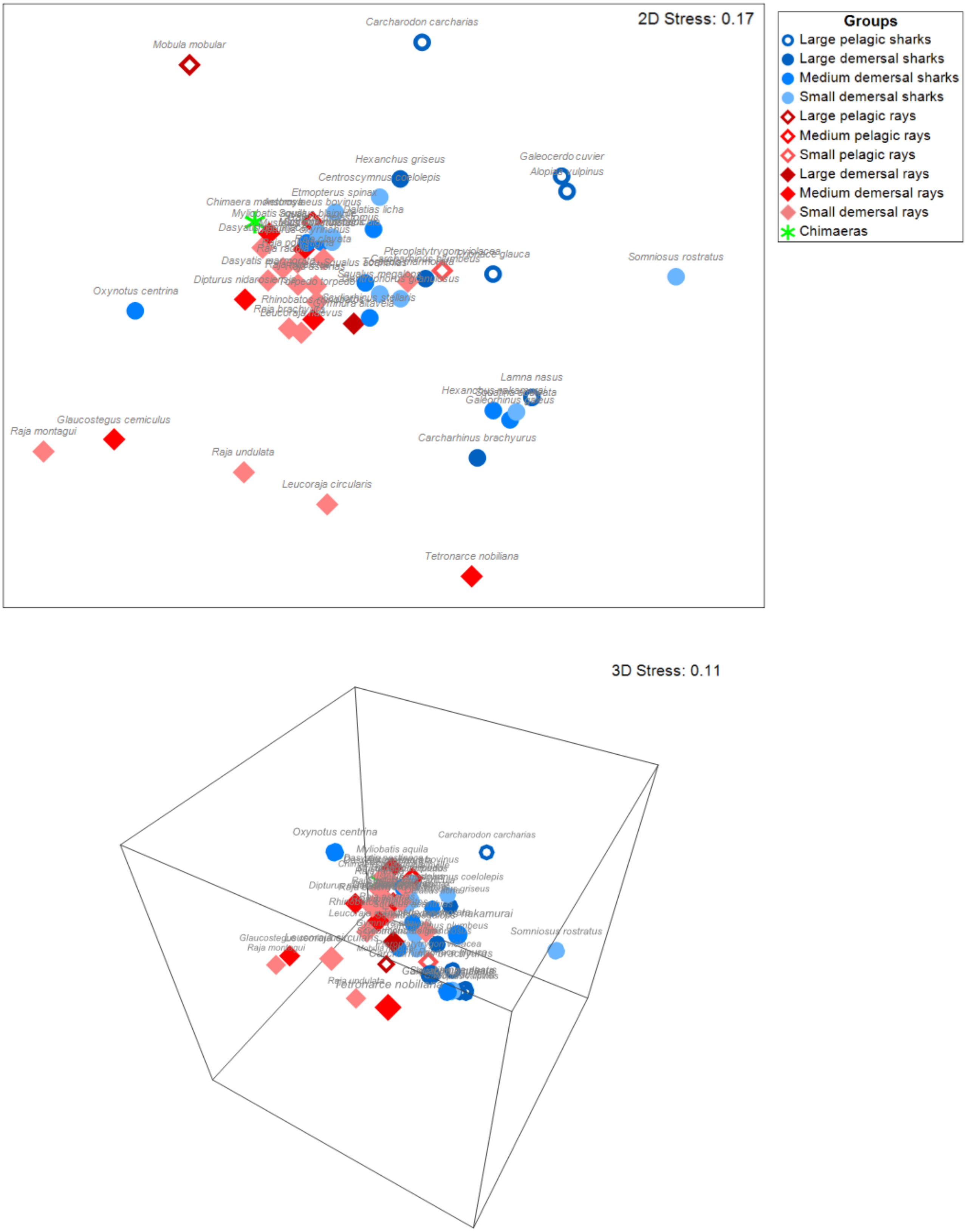
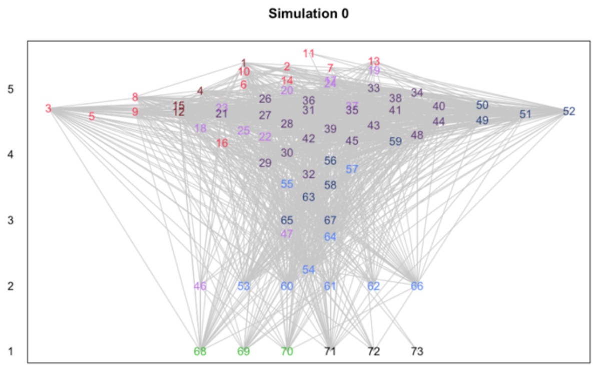
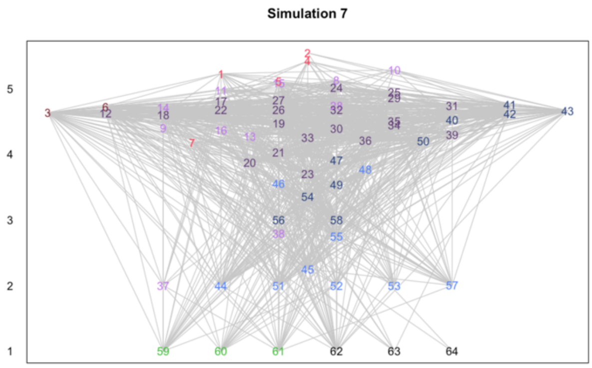


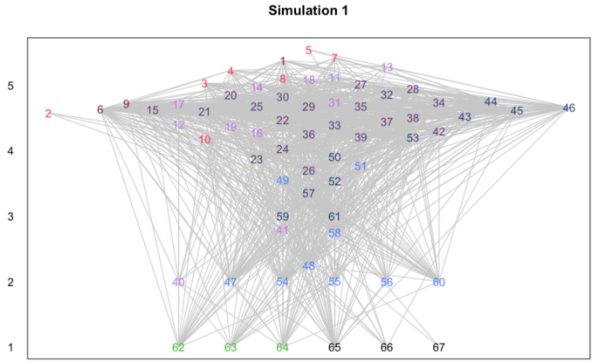
Figure 2A. NMDS plots of 50 chondrichthyan species grouped according to size, habitat and taxonomic group. The plots were generated using Bray-Curtis similarity (2D-stress = 0.17, 3D-stress = 0.11).



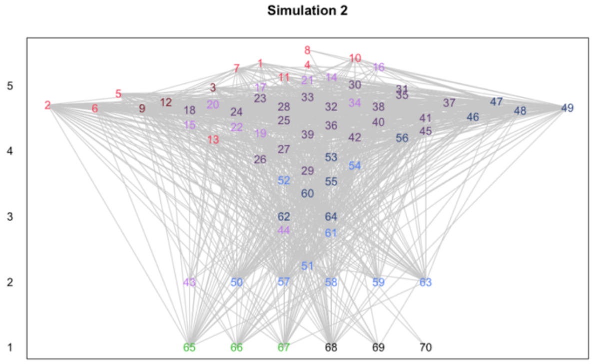
No extinction



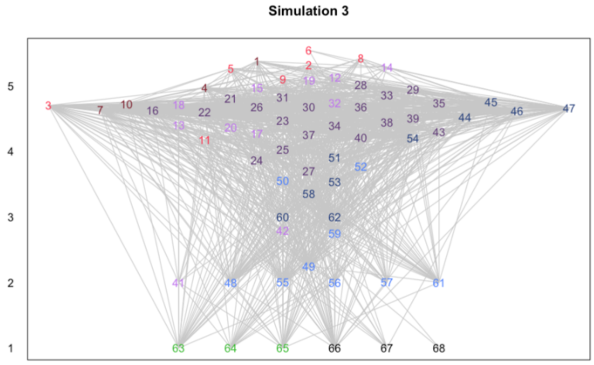
Extinction of all threatened chondrichthyan species



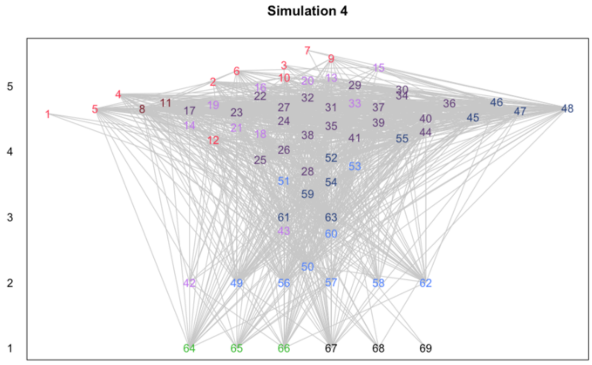
Extinction of threatened demersal chondrichthyans



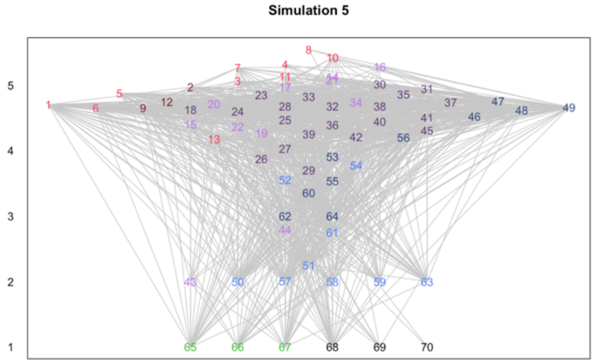
Extinction of threatened pelagic chondrichthyans



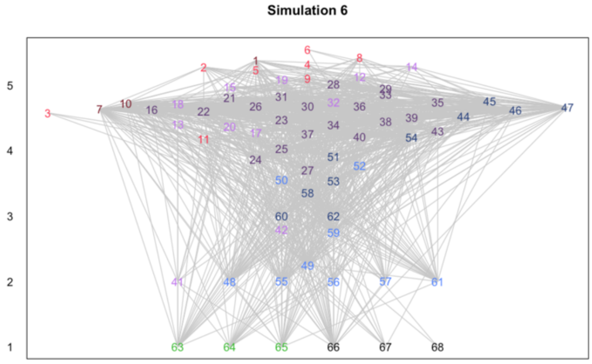
Extinction of threatened rays



Extinction of threatened sharks



Extinction of threatened large chondrichthyans



Extinction of threatened small and medium chondrichthyans

Figure 3A: Meta-web topology resulted from the different simulations of chondrichthyans extinction.

Table 1A: Mediterranean chondrichthyan species conservation status and population trends according to the IUCN global and Mediterranean (Med.) assessments. CR: Critically Endangered, EN: Endangered, VU: Vulnerable, NT: Near Threatened, LC: Least Concern, DD: Data Deficient, NA: Not Assessed, ↓: Decreasing, ↑: Increasing. Source: IUCN (2021). The predicted status by Walls and Dulvy (2020) for DD species is shown (Pred).

Class	Group	Order	Family	Scientific name	Common name	IUCN Med (Pred)	Med. Trend	IUCN Global	Global trend	Habitat
Holocephali		Chimaerifomes	Chimaeridae	*Chimaera monstrosa*	Rabbit fish	NT	Unknown	VU	↓	demersal
Elasmobranchii	Batoidea	Myliobatiformes	Dasyatidae	*Dasyatis marmorata*	Marbled stingray	DD	Unknown	DD	Unknown	demersal
				D. pastinaca	Common stingray	VU	↓	DD	Unknown	demersal
				Himantura uarnak	Honeycomb stingray	DD	NA	VU	↓	demersal
				Pteroplatytrygon violacea	Pelagic stingray	LC	Unknown	LC	Unknown	pelagic
				Taeniura grabata	Round fantail stingray	DD (VU)	Unknown	DD	Unknown	demersal
			Gymnuridae	*Gymnura altavela*	Spiny butterfly ray	CR	↓	VU	↓	demersal
			Myliobatidae	*Aetomylaeus bovinus*	Bull ray	CR	↓	DD	Unknown	pelagic
				Myliobatis aquila	Common eagle ray	VU	↓	DD	Unknown	demersal
		Rajiformes	Mobulidae	*Mobula mobular*	Devil fish	EN	NA	EN	↓	pelagic
			Pristidae	*Pristis pectinata*	Smalltooth sawfish	CR	↓	CR	↓	demersal
				P. pristis	Common sawfish	CR	↓	CR	↓	demersal
			Rajidae	*Dipturus batis*	Blue skate	CR	↓	CR	↓	demersal
				D. nidarosiensis	Norwegian skate	NA	NA	NT	↓	demersal
				D. oxyrinchus	Longnosed skate	NT	↓	NT	↓	demersal
				Leucoraja circularis	Sandy ray	CR	↓	EN	↓	demersal
				L. fullonica	Shagreen ray	CR	↓	VU	↓	demersal
				L. melitensis	Maltese ray	CR	↓	CR	↓	demersal
				L. naevus	Cuckoo ray	NT	↓	LC	Unknown	demersal
				Raja asterias	Mediterranean starry ray	NT	↓	NT	↓	demersal
				R. brachyura	Blonde ray	NT	↓	NT	↓	demersal
				R. clavata	Thornback ray	NT	↓	NT	↓	demersal

Table 1A (continued).

			R. miraletus	Brown ray	LC	Stable	LC	↑	demersal
			R. montagui	Spotted ray	LC	Stable	LC	Stable	demersal
			R. polystigma	Speckled ray	LC	Unknown	LC	Unknown	demersal
			R. radula	Rough ray	EN	↓	EN	↓	demersal
			R. undulata	Undulate ray	NT	↓	EN	↓	demersal
			Rostroraja alba	White skate	EN	↓	EN	↓	demersal
		Rhinobatidae	*Glaucostegus cemiculus*	Blackchin guitarfish	EN	NA	CR	↓	demersal
			Rhinobatos rhinobatos	Common guitarfish	EN	↓	EN	↓	demersal
			Rhinoptera marginata	Lusitanian cownose ray	DD (EN)	↓	NT	Unknown	demersal
	Torpediniformes	Tospedinidae	*Tetronarce nobiliana*	Electric ray	LC	Stable	DD	Unknown	demersal
			Torpedo marmorata	Marbled electric ray	LC	Stable	DD	Unknown	demersal
			T. torpedo	Common torpedo	LC	↓	DD	Stable	demersal
Selachimorpha	Carcharhiniformes	Carcharhinidae	*Carcharhinus altimus*	Bignose shark	DD (CR)	Unknown	NT	↓	demersal
			C. brachyurus	Copper shark	DD (CR)	Unknown	VU	↓	demersal
			C. brevipinna	Spinner shark	DD	NA	VU	↓	demersal
			C. falciformis	Silky shark	NA	NA	VU	↓	demersal
			C. limbatus	Blacktip shark	DD (EN)	Unknown	NT	Unknown	demersal
			C. obscurus	Dusky shark	DD (CR)	Unknown	EN	↓	demersal
			C. plumbeus	Sandbar shark	EN	↓	VU	↓	demersal
			Galeocerdo cuvier	Tiger shark	NA	NA	NT	↓	pelagic
			Prionace glauca	Blue shark	CR	↓	NT	↓	pelagic
			Rhizoprionodon acutus	Milk shark	NA	NA	VU	↓	demersal
		Scyliorhinidae	*Galeus atlanticus*	Atlantic sawtail cat shark	NT	↓	NT	Unknown	demersal
			G. melastomus	Blackmouth catshark	LC	Stable	LC	Stable	demersal
			Scyliorhinus canicula	Lesser spotted dogfish	LC	Increasing	LC	Stable	demersal
			S. stellaris	Nursehound	NT	↓	NT	Unknown	demersal

Table 1A (continued).

	Sphymidae	*Sphyrna lewini*	Scalloped hammerhead	NA	NA	CR	↓	pelagic
		S. mokarran	Great hammerhead	NA	NA	CR	↓	pelagic
		S. zygaena	Smooth hammerhead	CR	↓	VU	↓	pelagic
	Triakidae	*Galeorhinus galeus*	Tope shark	VU	↓	CR	↓	demersal
		Mustelus asterias	Starry smooth-hound	VU	↓	LC	Unknown	demersal
		M. mustelus	Smooth-hound	VU	↓	VU	↓	demersal
		M. punctulatus	Blackspotted smooth-hound	VU	↓	DD	Unknown	demersal
Hexanchiformes	Hexanchidae	*Heptranchias perlo*	Sharpnose sevengill shark	DD (NT)	Unknown	NT	↓	demersal
		Hexanchus griseus	Bluntnose sixgill shark	LC	Stable	NT	↓	demersal
		H. nakamurai	Bigeyed sixgill shark	DD (EN)	Unknown	NT	↓	demersal
Lamniformes	Alopiidae	*Alopias superciliosus*	Bigeye thresher	EN	↓	VU	↓	pelagic
		A. vulpinus	Thresher	EN	↓	VU	↓	pelagic
	Cetorhinidae	*Cetorhinus maximus*	Basking shark	EN	↓	EN	↓	pelagic
	Lamnidae	*Carcharodon carcharias*	Great white shark	CR	↓	VU	↓	pelagic
		Isurus oxyrinchus	Shortfin mako	CR	↓	EN	↓	pelagic
		I. paucus	Longfin mako	DD (CR)	Unknown	EN	↓	pelagic
		Lamna nasus	Porbeagle	CR	↓	VU	↓	pelagic
	Odontaspididae	*Carcharias taurus*	Sand tiger shark	CR	↓	VU	Unknown	demersal
		Odontaspis ferox	Smalltooth sand tiger	CR	↓	VU	↓	demersal
Squaliformes	Centrophoridae	*Centrophorus granulosus*	Gulper shark	CR	↓	EN	↓	demersal
		Centrophorus uyato	Little gulper shark	NA	NA	EN	↓	demersal
	Dalatiidae	*Dalatias licha*	Kitefin shark	VU	↓	VU	↓	demersal
	Echinorhinidae	*Echinorhinus brucus*	Bramble shark	EN	↓	EN	↓	demersal
	Etmopteridae	*Etmopterus spinax*	Velvet belly	LC	Stable	LC	Unknown	demersal
	Oxynotidae	*Oxynotus centrina*	Angular roughshark	CR	↓	VU	Unknown	demersal

Table 1A (continued).

	Somniosidae	*Centroscymnus coelolepis*	Portuguese dogfish	LC	Stable	NT	↓	demersal
		Somniosus rostratus	Little sleeper shark	DD (NT)	Unknown	LC	Stable	demersal
	Squalidae	*Squalus acanthias*	Picked dogfish	EN	↓	VU	↓	demersal
		S. blainville	Longnose spurdog	DD	Unknown	DD	Unknown	demersal
		S. megalops	Shortnose spurdog	DD (NT)	NA	LC	↑	demersal
Squatiniformes	Squatinidae	*Squatina aculeata*	Sawback angelshark	CR	↓	CR	↓	demersal
		S. oculata	Smoothback angelshark	CR	↓	CR	↓	demersal
		S. squatina	Angelshark	CR	↓	CR	↓	demersal

ANNEX B: Meta-web data

A list of the species included in each functional group together with a list of the references included in the trophic ecology and meta-web analyses are provided at:
https://www.dropbox.com/sh/oaep0f2q2k46xgv/AADWU90btLpLvov9-AH_As1-a?dl=0