Megabenthic invertebrate diversity in Mediterranean trawlable soft bottoms: a synthesis of current knowledge

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Abstract

Mediterranean bottom trawling is generally characterised by a highly diversified mixed catch, composed of fish, cephalopods, crustaceans, and other megabenthic invertebrates. Although management of Mediterranean trawling requires a multispecies approach on a community basis, this does not seem to be the case in the relevant literature. Herein, we present an extensive review of the existing knowledge on megabenthic invertebrate communities, focusing on the trawlable bottoms. A total of 207 publications from 1930 to the early 2021 was collected and classified into seven research areas. Research effort on soft bottom megabenthic invertebrates of trawlable grounds was higher for the Western Mediterranean and the depth zone of 50-200 m. Overall, 1,797 taxa were reported belonging to different taxonomic groups, the most diverse of which were Mollusca, Crustacea, Polychaeta and Porifera. Among the reported taxa, 43 species are alien to the Mediterranean Sea and 42 are included in the lists of threatened/ endangered and protected species under the Barcelona and Bern Conventions. The Western Mediterranean and the Aegean Sea, were the ecoregions with the highest number of megabenthic invertebrate species reported from trawlable grounds. All Mediterranean ecoregions were grouped according to their megabenthic fauna at a similarity level of 27%. The present work compiles the known scattered information, highlights knowledge gaps, and underlines the need for time series data on the megabenthic communities of the Mediterranean fishing grounds.

Keywords: benthos; faunal diversity; bottom trawl; threatened species.

Introduction

Marine ecosystems are complex and highly variable systems, which support a high degree of biodiversity (Costello *et al*., 2010) and play a key role in regulating the climate, having a great potential for a sustainable economy (Levin & Dayton, 2009). The Mediterranean Sea, regarded as the largest and deepest enclosed sea on Earth (Zenetos *et al*., 2002), is not an exception to this general fact. The high species richness coupled with a considerable proportion of endemic species makes the Mediterranean one of the world's biodiversity hotspots (Coll *et al*., 2010). Distribution of marine biodiversity in the Mediterranean Sea is rather heterogenous, with the flora and fauna being differently distributed among its various basins (UNEP-MAP-RAP/SPA, 2010a).

Although the high biological diversity of the Mediterranean Sea indicates a top conservation priority (Fraschetti *et al*., 2011), this rich and unique marine ecosystem is currently experiencing a deterioration of habitats related to various human-mediated activities (Lejeusne *et al*., 2010; Korpinen *et al*., 2019). The Mediterranean, like most enclosed seas, has been reported to have a highly threatened biodiversity at a global scale because of the cumulative impact of different variables (Costello *et al*., 2010). Although in the last decades scientists have raised awareness of environmental issues, when managers and stakeholders refer to natural capital protection major information gaps still exist, especially concerning the marine environment (Major *et al*., 2017).

Recent studies have identified a wide array of human activities that put the survival of Mediterranean benthic communities at risk, such as demersal fishing, pollution, construction of littoral infrastructures, and seafloor drilling, among others (Dailianis *et al*., 2018; Korpinen *et al*., 2019). During the past decades, a societal concern for the environmental consequences of trawling, particularly bottom trawling, has arisen (Muntadas *et al*., 2017). Benthic megafauna is probably the most vulnerable part of the benthic ecosystem, directly impacted by fishing gear

(Blanchard *et al*., 2004).

Bottom trawling as well as dredging, are the most widespread sources of anthropogenic disturbance on benthic habitats occurring over large surfaces of the continental shelf (Hiddink *et al*., 2017). The continental shelf habitats are among the most productive fishing grounds and have been trawled for centuries. Bottom trawling reduces biomass and diversity of benthic ecosystems, with most megabenthic taxa decreasing in abundance when trawling intensity increases (Buhl Mortensen *et al*., 2016) and this may lead to a decline of the complexity of benthic habitats (Kaiser *et al*., 2006) and seabed status (Pitcher *et al*., 2022).

The effects of bottom trawling can be seen in benthic diversity (Korpinen *et al*., 2019) and are found to be severe in deeper areas of the upper continental slope and in seamounts (Gage & Roberts, 2002; Ramirez-Llodra *et al*., 2011; Puig *et al*., 2012). The direct physical impact of bottom trawls can lead to chronic effects on ecosystem functions (Jennings *et al*., 2001), highly correlated with trawl gear penetration into the seabed (Hiddink *et al*., 2017). The recovery of benthic habitats depends on fisheries and environmental specific features. It can take median recovery times, from 2 to 6 years when 50% to 95% of the benthic biomass is unimpacted (Hiddink *et al*., 2017), to decades or centuries when referring to deeper areas that are more highly impacted. Trawling over the deep-sea corals damages the reef-like structures, which may be even thousands of years old with slow recovery rates and take decades or centuries to recover (Korpinen *et al*., 2019). This leads to the loss of larger sized vulnerable species such as corals and sponges, because their growth rate is too slow to recover between disturbance events. Moreover, animals like sponges and corals usually host a rich fauna of associated animals (Buhl-Mortensen & Buhl-Mortensen, 2004) acting as ecosystem engineers and when these species are severely impacted by bottom trawling, the whole ecosystem equilibrium is threatened.

Despite the recognition of the extensive negative effects of fishing on benthic habitats and the need for adequate reference areas, the European Red List of Habitats indicated that 49% of the Mediterranean benthic habitats are Data Deficient and that 83% of the remaining ones are of conservation concern (Near Threatened or Critically Endangered) (Gubbay *et al*., 2016). International conventions, such as the Convention of Biological Diversity (CBD,1972) and policies, such as the Marine Framework Strategy Directive (MSFD) (EU, 2008; EU, 2017) have tried to ensure that marine use is compatible with ecosystem conservation and maintenance of the good status of waters, habitats, and resources. Nevertheless, the implementation of these legislations is a crucial step toward the achievement of Good Environmental Status for Mediterranean marine ecosystems (Bevilacqua *et al*., 2020). However, without basic knowledge on seabed habitats and benthic communities it is not possible to accomplish successful implementation of this legislation (Terribile *et al*., 2016; Gerovasileiou *et al.*, 2019).

Characterisation of soft bottom communities is important for the identification of potential Marine Protected Areas and fishing exclusion zones as a first step towards habitat protection, species conservation and sustainable use of marine resources (Marina *et al*., 2015). Therefore, it is highly necessary to undertake studies in order to identify components, assemblages, structure, and function of megabenthic communities in trawlable benthic ecosystems, and not only to investigate the occurrence of specific taxa. In this context, the availability of time series data on megabenthos distribution is essential for the implementation of the ecosystem-based approach to fisheries such as the EU's MSFD, the Common Fisheries Policy and other EU policies.

Acknowledging the need to evaluate and make easily accessible the existing knowledge on the status of Mediterranean megabenthic invertebrate communities on trawlable soft bottoms, we present an extensive literature review by combing all the available information from the beginning of the 20th century to date, either published or in grey literature, and describe the main spatial patterns of megabenthic invertebrate diversity in the basin.

Methodology

In order to gather the available information on the Mediterranean soft bottom megabenthic communities, an extensive literature review was conducted, mostly through Scopus, Google Scholar, as well as Google for literature in the form of theses, technical reports, etc. The key words "benthic biocenoses/assemblages", "megabenthic communities", "soft bottom biocenoses", "bottom trawl discards", "MEDITS", and "Mediterranean" as well as combinations of these key words were used, and all scientific works retrieved were examined for their text and references. Most literature sources dating from the beginning of the last century to 2021 were derived in the form of scientific papers, but grey literature was also considered.

We focused on original studies (only primary sources of data, review studies were not taken into account) and collected data on the megabenthic communities of soft substrata in circalittoral and bathyal zones, i.e., between 50 and 1000 m depth, which is the allowed depth range of bottom trawling in the Mediterranean Sea. Additionally, the taxonomic list of all taxa (TM list) of MEDITS available at the official website of the MEDITS program (International Bottom Trawl Survey in the Mediterranean [MEDITS], 2021) was taken into account for the ecoregions covered by the program (i.e., all Mediterranean ecoregions except the Tunisian Plateau). All species recorded in publications retrieved from the literature search were used to create a dataset of taxa with presence/absence data (Suppl. Table 2).

In order to evaluate scientific research effort, the literature collected was classified according to the year of publication, ecoregion, depth range of listed species, scientific approach and study method. With regards to scientific approach, publications were classified in the following categories: taxonomy (studies focused on the descriptions of new species), general community structure (studies describing community structure and func-

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tion), distribution (studies focusing on distributions of particular taxa), faunistic (faunal catalogues of specific taxa), discards (studies focusing on bottom trawls discards), disturbance (studies focusing on the effects of anthropogenic impact on benthic communities), and conservation/management(studies with a management perspective).

Our review is based on qualitative information on marine soft bottom megabenthic invertebrates. Herein, we consider as megabenthic invertebrates all invertebrates larger than 1 cm with an individual wet weight of more than 50 mg (Witbaard *et al*., 2013; Stratmann *et al*., 2020). Studies focusing exclusively on macrobenthic organisms were not considered. The taxa Porifera, Cnidaria, Mollusca, Polychaeta, Crustacea, Echinodermata, and Ascidiacea were examined separately while Brachiopoda, Bryozoa and Sipuncula, were grouped together as "Others", due to the limited available information.

Only species that were explicitly reported as either observed in Remotely Operated Vehicles (ROV) videos or collected by megabenthic sampling gear, i.e., bottom trawls and dredges were considered in this study. Otherwise, the species list of a publication was not taken into account in our taxa diversity analysis, but the paper was used in the research effort analysis. Although our focus is on megabenthic diversity, some macrofaunal species among Annelida, Brachiopoda, Bryozoa, Sipuncula, and micromolluscs that were caught by megabenthic sampling gears were also considered, as they form part of the community under study either as independent organisms or as symbiotics of other megabenthic organisms. Nomenclature and taxonomic classification are according to WoRMS (WoRMS Editorial Board, 2021).

To describe spatial patterns, we used published information by taxonomic group at an ecoregion scale (*sensu* Spalding *et al*., 2007) (Fig. 1) and by depth strata (50-200 m, 200-400 m, 400-600 m, 600-800 m and 800-1000 m). According to Spalding *et al.* (2007); ecoregions are "areas of relative homogeneous species composition, clearly distinct from adjacent systems….", which in ecological terms indicates strongly cohesive units, sufficiently large to encompass ecological or life history processes for most sedentary species. Based on this definition, an ecoregion was considered as the most representative spatial unit for the study of benthic communities, which mostly encompass sedentary organisms.

To avoid overestimation of species richness, taxonomic groups of the family or higher level taxon mentioned in the species lists were included in our estimates only in the case in which no species or genus representatives of these groups appeared in a certain examined area. Faunal similarities among the seven Mediterranean ecoregions were estimated using the Sorensen similarity index. Similarity matrices were constructed from the above-mentioned presence/ absence matrices and multivariate analyses, i.e. hierarchical clustering analysis (CLUSTER) and non-metric Multi-Dimensional Scaling (MDS), were performed. All the above analyses were performed using the PRIMER 6 Package.

Results

Research effort

A total of 207 publications, covering a time span of 91 years reporting on megabenthic invertebrates found in Mediterranean soft bottom trawlable grounds, was examined. The classification of publications according to their scientific approach (Table 1 and Suppl. Table 1) showed that most of them consisted of a combination of approaches, so that they were included in more than one research area.

The majority (36.1%) of the studied publications were faunistic, focusing on specific taxa, followed by those studying community structure as a whole, and then those addressing the distribution of particular taxa, both with 23.8%. Fewer studies dealt with anthropogenic impacts

Fig. 1: The seven Mediterranean ecoregions considered in this work (modified from Spalding *et al*., 2007).

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Table 1. Number of studies on the Mediterranean megabenthos of trawlable soft bottoms per scientific approach and ecoregion. Note: some studies referred to more than one ecoregion and/or included more than one approach.

Scientific approach	Total	Alboran Sea	Western Mediterranean	Adriatic Sea	Ionian Sea	Aegean Sea	Levantine Sea	Tunisian Plateau
Taxonomy	5	2	1	0	0	2	0	0
General community structure	60	6	24	7	12	11	9	5
Distribution	60	16	25	17	20	23	1	0
Faunistic	91	9	29	16	24	28	7	4
Discards	9	0	3	0	1	5	0	1
Disturbance	24	1	13	4	2	2	1	1
Conservation/Management	3	1	2	0	0	0	0	0

on the ecosystem (9.5%) and with bottom trawl discards (3.6%). The rest remainder were taxonomic publications (2%) and conservation/management studies (1.2%) (Fig. 2).
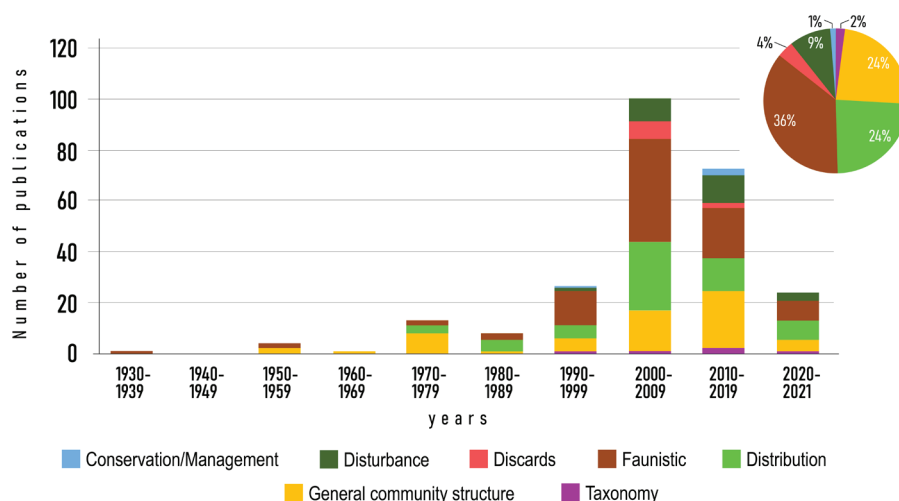
Research effort on soft bottom megabenthic invertebrates of trawlable grounds is not equally distributed over the Mediterranean (Fig. 3). Some ecoregions, such as the Western Mediterranean and the Aegean, have been intensively studied, resulting in considerable number of scientific publications over the years. The best-studied ecoregion, the Western Mediterranean Sea, accounted for 29.6% of all Mediterranean studies. Publications concerning the Western Mediterranean began in the 1950s but until 2000 only ten scientific papers appeared. Most papers in this area were published between 2000-2009 with 43 of the 84 Mediterranean studies of this decade carried out there. The Aegean Sea accounted for 21.9% of all Mediterranean studies. Research in this area started in 1954 and peaked in the 2000s. In the Ionian Sea, which has received a moderate amount of scientific attention (16.7%), one paper was published in the 1950s and after a 20-years research gap, the region started to be explored in the 1980s, reaching the peak of scientific publications in 2000. The Adriatic, Alboran, Levantine, and the Tunisian Plateau ecoregions seem to have received the least attention, accounting for 12.6%, 10.4%, 5.6% and 3.3% of publications, respectively.

The bulk of research effort in the Mediterranean Sea has focused on the depth zone 50-200 m (Fig. 4) in most ecoregions while most of the studies carried out on shelf areas deeper than 400 m were conducted in the Western Mediterranean, the Aegean and the Ionian Sea.
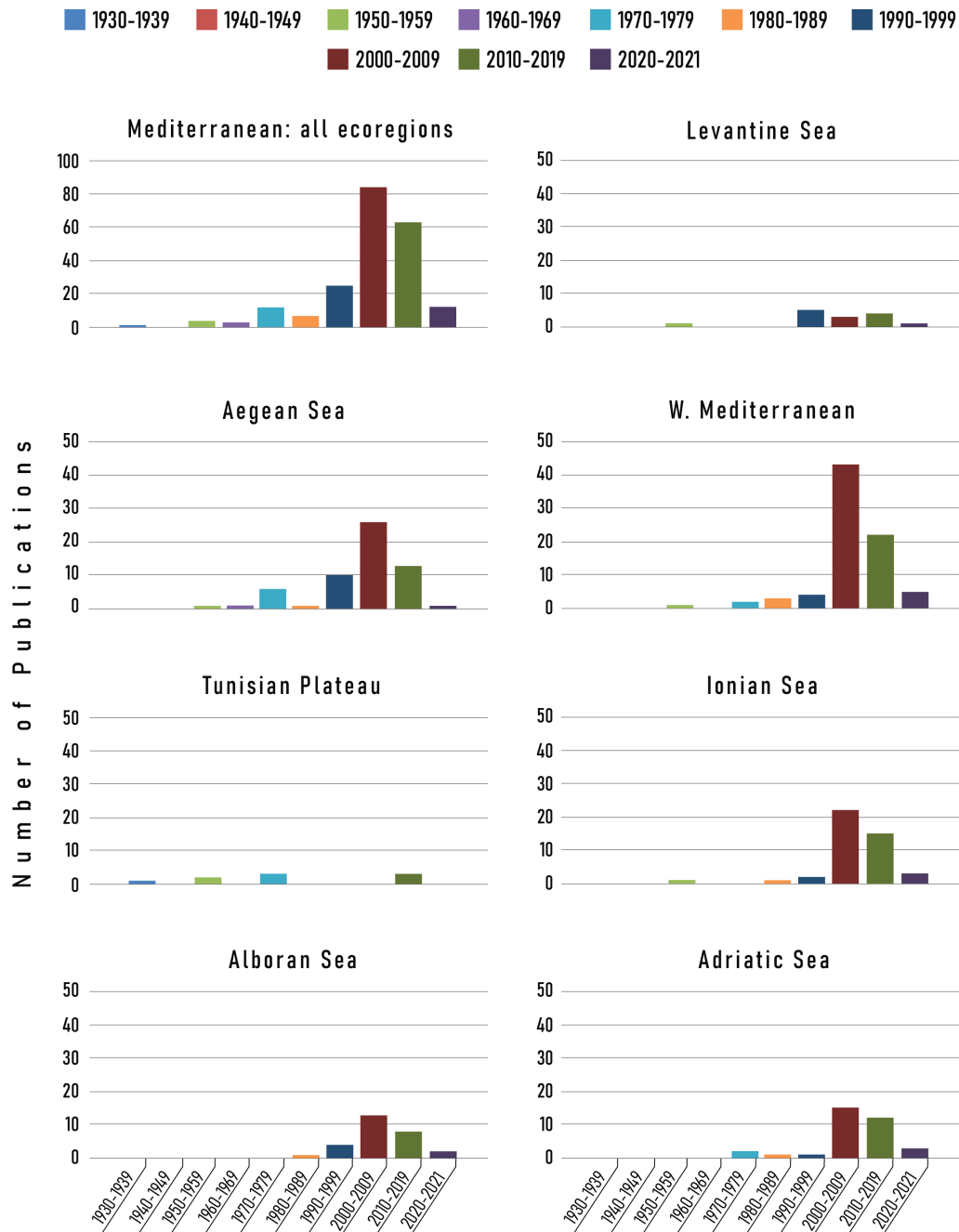
Megabenthic taxa diversity

Totally 1,797 taxa of megabenthic organisms have been reported from the Mediterranean soft bottom trawlable grounds (Fig. 5 and Suppl. Table 2). The following invertebrate groups were found in order of decreasing diversity: Mollusca with 430 taxa covering 23.9% of the recorded taxa, Crustacea (19.5%), Polychaeta (16.4%), Porifera (14.4%), Cnidaria (7.3%), Echinodermata (6.4%) and Ascidiacea (6%). "Others", comprising various small groups, represented 6.2% of the total megabenthic diversity.

The number of soft bottom megabenthic invertebrate species among the Mediterranean ecoregions showed a statistically significant positive correlation with research effort (Spearman Rank Correlation = 0.714). An exception to this general trend was observed in the case of the Alboran and Levantine ecoregions, which had smaller number of publications but higher numbers of recorded species than the Adriatic and Ionian seas. The Tunisian

Fig. 2: Number of publications on megabenthic invertebrates of trawlable soft bottoms in the Mediterranean per decade, scientific approach (bar graphs), and overall percentage of publications per scientific approach (pie chart).

Fig. 3: Number of publications on megabenthic invertebrates of trawlable soft bottoms per decade in the Mediterranean and in each ecoregion separately.
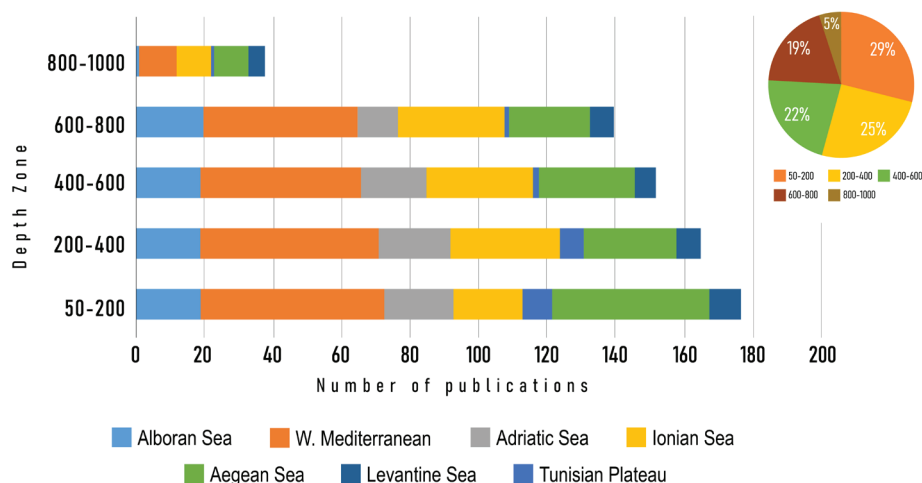
Plateau had the smallest number of both publications and species number (Fig. 6).

Our results show a decrease in species number according to depth both for the total recorded megabenthos and for each invertebrate group separately (Fig. 7 and Suppl. Table 2). Mollusca, Polychaeta, and Porifera were the most diverse groups in the depth zone of 50-200 m, while in deeper trawlable grounds (> 400 m), Polychaeta and Porifera were replaced by Crustacea, which, with Mollusca, were the dominant taxa.
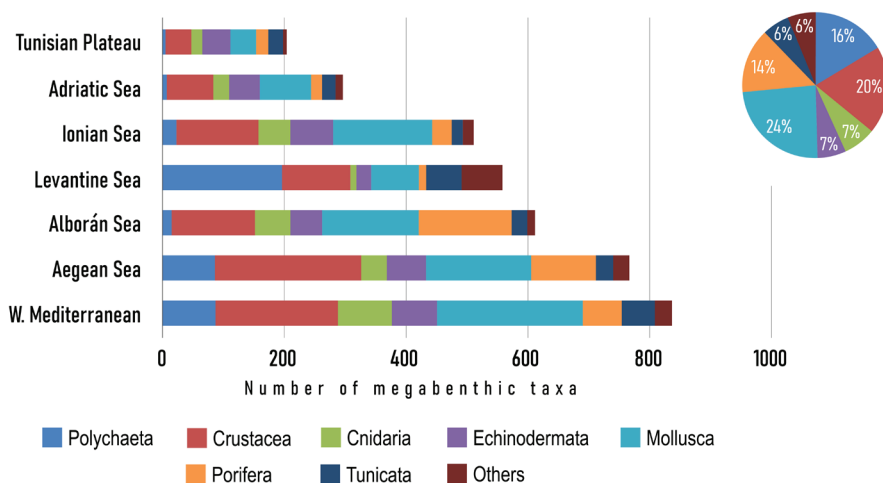
From the 1,797 taxa, only 2.84% (51 taxa) were present in all seven ecoregions. The number of species recorded exclusively in one ecoregion varies. Levantine Sea occupies the first place, with 47.2% of its total pres-

ent taxa appearing exclusively in this ecoregion. Aegean Sea came second with 30.5% of its taxa being exclusively present there, while Western Mediterranean and Alboran Sea showed 26.1% and 25.9% taxa uniqueness each. Ionian Sea reaches 16.1% and Tunisian Plateau with Adriatic Sea showed lower percentages of 6.4% and 4.7% in taxa uniqueness.

Similarity analysis (based on presence/absence data) of the soft bottom megabenthic communities in the trawlable grounds at the seven Mediterranean ecoregions (Fig. 8a, b) shows that all ecoregions were grouped together at a similarity level of 35%, except for the southeastern Levantine Sea. Furthermore, two distinct groups were formed at a similarity level near 50%; Western

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Fig. 4: Number of studies on soft bottom megabenthic invertebrates in trawlable soft bottoms per ecoregion and depth zone (bar graphs) and overall publications per ecoregion (pie chart).

Fig. 5: Number of megabenthic taxa in the trawlable soft bottoms of the Mediterranean ecoregions (bar graphs) and overall percentage of taxa in each faunal group (pie chart).

Mediterranean grouped with Alboran Sea at a similarity level of 56% and the Adriatic with the Ionian seas with 49% similarity level. The Aegean Sea and the Tunisian Plateau, although inside the 35% similarity group, stood separately from the two above-mentioned groups and from each other.
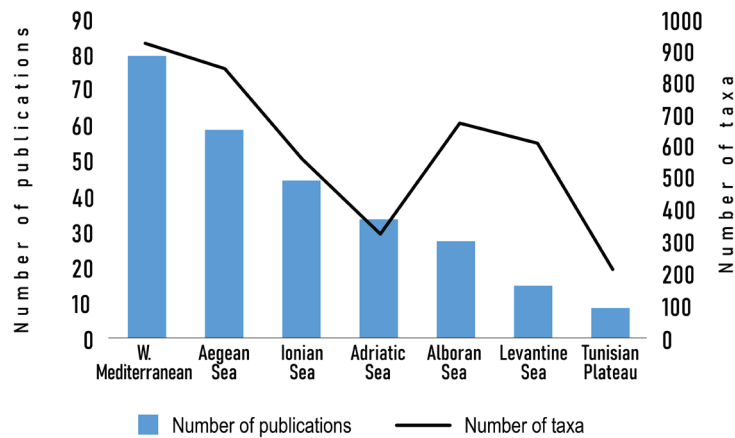
Discussion

Research effort

Marine research in the Mediterranean basin proliferated in approximately the mid-1900s (Costello *et al*., 2010) when research resources, i.e., experts, institutes and vessels became available. From the very beginning (1930s), research relevant to megabenthic invertebrates in trawlable grounds focused on the biology and population characteristics of specific species (Fig. 2), while publications on community structure appeared in the 1950s and increased progressively over the years. It was not before 1990 that the first studies dealing with anthropogenic disturbance on benthic communities were pub-
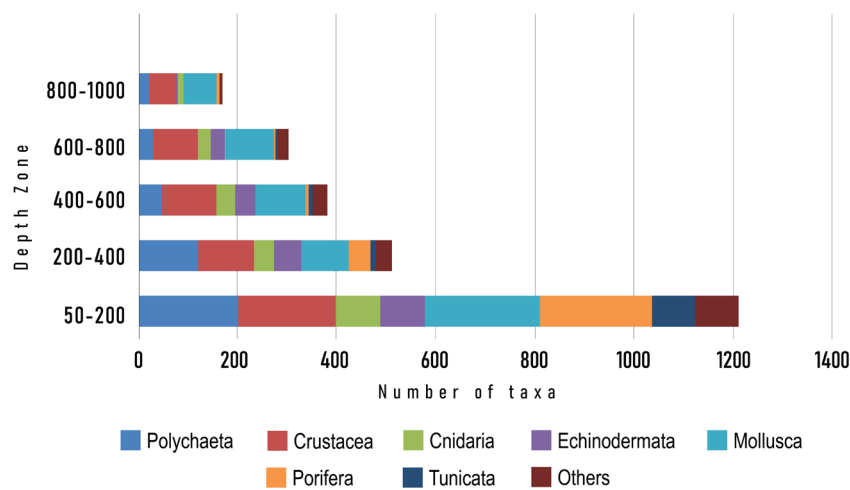
lished (Smith *et al*., 1997) and it took ten more years to begin investigating megabenthic invertebrates as part of the discards in the bottom trawl fisheries (Smith *et al*., 2000; Machias *et al*., 2001; Bozzano & Sardà, 2002; Sánchez *et al*., 2004; Fryganiotis, 2006; Sartor *et al*., 2006; Damianidis *et al*., 2007; Voultsiadou *et al*., 2011; Consoli *et al*., 2017). Concerning conservation and management of soft bottom megabenthic communities, only two publications were found (Galil, 2004; Robles, 2010).

Except for one publication in 1930 (Held, 1930) on the trawlable areas of the Tunisian Plateau, the study of Mediterranean benthic communities actually began in 1954 with the cruises of *Calypso*. The first exploration of this vessel/mission was along the east coast of Tunis and the Sicilian-Tunisian continental shelf (Pérès & Picard, 1958). In the next three decades, few studies were published whereas an increasing number of surveys on megabenthic communities appeared from 1991 to the last decade (Fig. 2). However, several old publications not available in digital form or written in languages other than English may have escaped our attention.
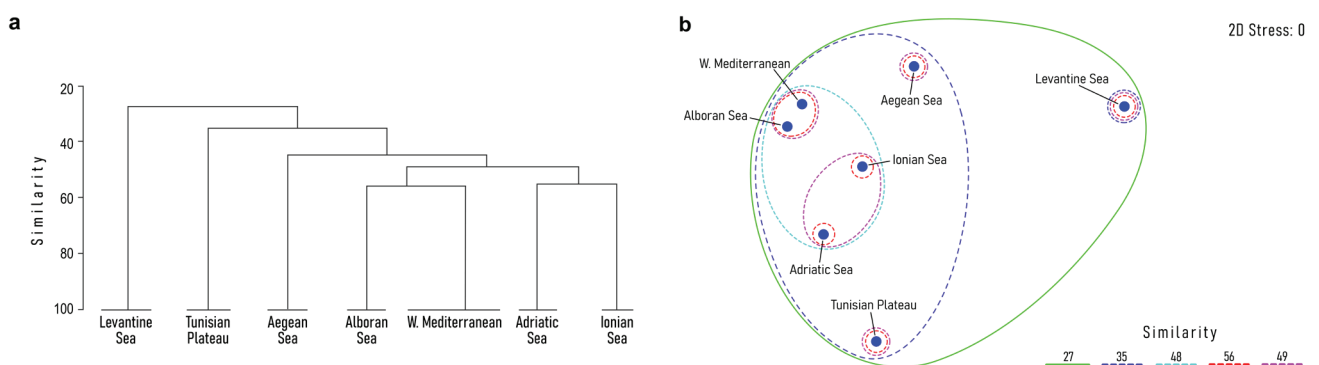
During our research, the majority of publications on soft bottom megabenthos were found to be faunistic, fo-

Fig. 6: Research effort compared with megabenthic invertebrate species richness in trawlable soft bottoms of the Mediterranean ecoregions.

Fig. 7: Bathymetric patterns of megabenthic species number in the trawlable soft bottoms of the Mediterranean Sea.

Fig. 8: Similarity of megabenthic assemblages in the trawlable soft bottoms of the Mediterranean ecoregions derived from hierarchical clustering analysis (a) and non-metric MDS plots (b).

cusing on the investigation of diversity and distribution of specific taxa in different ecoregions. However, Mediterranean bottoms in their majority are complex habitats with a wide variety of organisms filling different ecological niches (UNEP-MAP-RAC/SPA, 2010b). In spite of this, only 23.8% of the publications examined herein addressed megabenthic organisms in a community context and attempted to record and understand community structure and function. Moreover, only 3.6% of the publications we examined dealt with bottom trawl discards, one of the priority issues in the Mediterranean environment (EEA, 2006).

Since 1994, the Mediterranean International Trawl Survey (MEDITS) has been sampling the demersal community of fish, cephalopods, elasmobranchs, and crustaceans on Mediterranean soft bottoms. MEDITS represents a unique large-scale and long-term source of spatial data on megabenthic species and communities of the Mediterranean. Of the 54 published papers that have addressed the benthos of the Mediterranean trawlable areas, based on MEDITS data, 37 (68.5%) focused on biological and population characteristics of particular taxa; 14 (25.9%) focused on benthic communities in a holistic perspective; and the remaining 5.6% addressed disturbance and conservation aspects (Suppl. Table 1).

The limited number of publications addressing benthic communities as a whole, based on MEDITS data, is probably due to the fact that in the MEDITS protocol, the number of individuals for non-commercial invertebrate species (codes E and D of MEDITS taxonomic categories), is not mandatory. As a result, these organisms are not a research priority onboard and they are often not even recorded at species level. Given that fact, scientific groups have focused on the biology and population characteristics of specific crustacean and cephalopod taxa, which belong to the GI and G2 priority lists of the MEDITS protocol (these lists include species for which total number of individuals, total weight, individual length (G2), and some biological parameters including sex, maturity, and individual weight and age (G1) should be recorded onboard). This practice has led to the loss of valuable quantitative information on the presence and distribution of other components of megabenthic communities for almost 25 years. Over the years, megabenthos in trawl surveys has gained more attention as a primary tool for providing data useful per se for the assessment of fish communities and ecosystems (Cotter *et al.*, 2009). Subsequently, the survey scope has broadened from demersal species populations to their communities and more recently to the sensitivity of species and communities to trawling impact (González-Irustra *et al.*, 2018; Rijnsdorp *et al.*, 2018; Jac *et al.*, 2020a, b, 2021; Labrune *et al.*, 2021). And, despite the fact that since 2012 benthos has been introduced in the MEDITS protocol, this was only on a voluntary basis, thus resulting to the collection of fragmentary information based on the degree of specialisation of each scientific team.

Species diversity

In our study of megabenthos in trawlable grounds, Mollusca and Crustacea prevailed contributing 23.9 and 19.5%, respectively, of the total taxa recorded (Table 2 and Suppl. Table 2). The dominance of these two groups was also recorded by Coll *et al.* (2010) for the total Mediterranean invertebrate species (Table 2). Furthermore, the dominance of relatively small and fast-growing species, such as Crustacea and Mollusca, has been observed to be a general community response to trawling (Hiddink *et al.*, 2006). The contribution of all taxa (excluding "Others") to the megabenthos of trawlable grounds was higher than the percentage of the overall Mediterranean invertebrate species recorded by Coll *et al.* (2010). As expected, Porifera contributed with a higher percentage to the megafauna compared to the total Mediterranean invertebrate species (14.4% vs. 6.2%), since they include numerus conspicuous megabenthic species. On the contrary, taxa included in the category "Others" like Brachiopoda, Bryozoa, and Sipuncula were underrepresented since they rarely appear in megabenthos. Nonetheless, such estimates should be treated with caution as only data from trawlable grounds were used herein and the absence of data on particular taxa in certain ecoregions (see below), may well reflect a lack of study effort and/or of experts than an actual absence of species. Moreover, this incompatibility may be due to the specificity of the field of study itself, since some taxa, such as annelids or molluscs, are more likely to be found on soft substrata. Further investigation is needed while the ecological importance of habitat-forming megabenthos, such as sponges, and their vulnerability to trawling is acknowledged.

The Western Mediterranean with more than 800 taxa and the Aegean Sea with more than 700 taxa were the ecoregions with the highest taxa diversity; the Alboran Sea, the Levantine Sea, and the Ionian Sea were next (with ca. 500-600 taxa), followed by the Adriatic Sea and the Tunisian Plateau (ca. 200-300 taxa). This appears to be consistent with the general pattern of regional benthic diversity in the Mediterranean: the Western Mediterranean has been reported to host much higher species numbers in comparison with the central Mediterranean, the Adriatic, and the Aegean seas (Coll *et al.*, 2010). However, Costello *et al.* (2010) highlighted that the relative number of

Table 2. Contribution of invertebrate groups to the megabenthos of Mediterranean trawlable soft bottoms (%) as compared to the contribution of the same groups to the total Mediterranean fauna (Coll *et al.*, 2010). The group "Others" includes Brachiopoda, Bryozoa and Sipuncula.

Taxa	Mediterranean trawlable grounds	Mediterranean Sea
Mollusca	23.9	19.4
Crustacea	19.5	20.5
Annelida	16.4	10.7
Porifera	14.4	6.2
Cnidaria	7.3	6.9
Echinodermata	6.4	1.4
Tunicata	6.0	2.1
Others	6.2	32.5

recorded species in a given area is significantly positively correlated with the number of studies undertaken there. In fact, our study on megabenthic invertebrates showed a clear positive correlation between richness and number of studies except for those of the Alboran Sea and the Levantine Sea ecoregions (Fig. 6). The geographic position of these two ecoregions in the Mediterranean basin (close to Gibraltar and to the Suez Canal, respectively) might explain this increase in species number (range expansion of species from the Atlantic Ocean and/or introduction of species from the Red Sea). This, with the 47.2% of the Levantine taxa exclusively, indicating the uniqueness of this area, show that further study is needed to investigate species richness in these ecoregions.

Moreover, the small number of soft bottom invertebrate taxa reported in a given ecoregion does not necessarily suggest poorer benthic diversity; it rather reflects a lack of specialists, which results in the identification of fewer species in certain groups. Herein, we observed only few cases of taxa which were poorly presented (fewer than ten species) in certain ecoregions; for example, in the Adriatic Sea there were only seven representatives of Annelida, five records of Annelida in the Tunisian Plateau, and six taxa of the "Others" group. In the case of Annelida, one explanation could be the design of the present study: we considered publications exclusively on megabenthos, excluding those using macrobenthic samplers such as grabs. Hence, annelids and other macrobenthic species considered in this work are only those that remained in the megabenthic collectors, such as trawls and dredges, or those macroscopically identified by divers and ROV images. On the other hand, the poor representation of large-sized taxa in our results may suggest the absence of specialists in certain Mediterranean ecoregions or even the fact that research results are not regularly published. Consequently, the usage of grey literature (i.e., unpublished scientific reports or data) seems to be valuable in identifying diversity patterns across the Mediterranean ecoregions.

Vulnerable and Endangered Species

At present, 42 megabenthic invertebrates inhabiting the Mediterranean basin (Suppl. Table 2) are included in the lists of endangered and threatened species (Annex II) (UNEP/MAP-SPA/RAC, 2018) and species whose exploitation is regulated (Annex III) (UNEP/MAP-SPA/RAC, 2012) under the Barcelona convention and/or in the strictly protected fauna species (Annex II) and protected fauna species (Annex III) of the Bern Convention (1979).

It is worth mentioning that all 13 protected fauna species and ten of the 28 strictly protected species listed in Annexes II and III of the Bern Convention for the Mediterranean basin are present in the Mediterranean trawlable grounds based on the present study. Also, 12 of species listed in Annex II of endangered and threatened species with 28 species whose exploitation is regulated (Annex III) of the Barcelona Convention were also included in the current study with representatives of these

species being recorded in all ecoregions (Suppl. Table 2).

Among the species listed, is one of the most emblematic and famous anthozoan of the basin, the red coral *Corallium rubrum* (Linnaeus, 1758). The red coral has been harvested since ancient times, mainly for jewellery, but in several ecoregions today, it is considered "ecologically extinct" (Tsounis *et al*., 2010). Additionally, four cold water corals, *Dendrophyllia cornigera* (Lamarck, 1816), *D. ramea* (Linnaeus, 1758), *Desmpolhyllum dianthus* (Esper, 1794), and *Madrepora oculata* Linnaeus, 1758 are included in our list. The negative effects of bottom trawling on cold water coral communities have been documented, especially since deep sea trawling become important in the Mediterranean since 1930's, with the red shrimps *Aristeus antennatus* (Risso, 1816) and *Aristaeomorpha foliacea* (Risso, 1827 in) being the main targets (Sarda *et al*., 2004). The critically endangered "bamboo coral", *Isidella elongata* (Esper, 1788), is a Mediterranean near-endemic and, protected species included in our taxa data list (Suppl. Table 2). The role of *I. elongata* facies as essential fish habitats for various species of commercial value, such as red shrimps and the blackmouth catshark *Galeus melastomus* Rafinesque, 1810 has being highlighted by Cartes *et al*. (2013), Mastrototaro *et al*. (2017), Gerovasileiou *et al*. (2019), and Carbonara *et al.* (2020). Moreover, Maynou & Cartes (2012) demonstrated that even low trawling activity over *I. elongata* facies can cause the disappearance of the facies and of some related species.

These outcomes can be very helpful in a management perspective for the implementation of appropriate measures in order to prevent possible habitat and trophic webs alteration.

Alien species

Among the reported taxa, 43 species (Suppl. Table 2) are alien to the Mediterranean Sea (Zenetos *et al*., 2022). They belong to Crustacea (17), Mollusca (10), Tunicata (9), Annelida (7) and Echinodermata (1). The nomenclature of some species erroneously reported in the literature has been revised following recent updates. *Penaeus pulchricaudatus* Stebbing, 1914 reported as *P. japonicus* Spence Bate, 1888; *Portunus (Portunus) segnis* (Forskål, 1775) reported as *P. pelagicus* (Linnaeus, 1758); *Anadara kagoshimensis* (Tokunaga, 1906) reported as *Anadara inaequivalvis* (Bruguière, 1789); *Magallana gigas* (Thunberg, 1793) reported as *Crassostrea gigas* (Thunberg, 1793); and *Trachysalambria palaestinensis* (Steinitz, 1932) reported as *T. curvirostris* (Stimpson, 1860).

The vast majority of non-indigenous species (NIS) (36 species) has been reported from the 50-100 m zone in the Levantine basin. They are mostly Lessepsian species (unaided introductions via the Suez Canal) but also species introduced with vessels, all well established in the Levantine Sea. Their finding in the trawl hauls highlights the importance of fishing as a vector for alien species transportation (fishing gear). It is noteworthy that not only is megafauna transferred with such vectors but also

microfauna living on/in muddy substrata such as the micromolluscs *Pseudominolia nedyma* (Melvill, 1897) and *Rhinoclavis kochi* (Philippi, 1848).

The true number of NIS among soft bottom megabenthos is suspected to be higher as many species identified up to the genus level have representatives among aliens e.g., *Batophora* sp. possibly *Batophora occidentalis* var. *largoensis* (J.S. Prince & S. Baker) S. Berger & Kaever ex M.J. Wynne.; *Chaetozone* spp. possibly *Chaetozone corona* Berkeley & Berkeley, 1941; *Cylichna* sp. possibly *Cylichna villersii* Audouin, 1826; and *Didemnum* spp. possibly *Didemnum ahu* Monniot C. & Monniot F., 1987 or *Didemnum vexillum* Kott, 2002.

Faunal community structure

The patterns of similarity among the Mediterranean ecoregions according to their megabenthic communities of trawlable soft bottoms was not surprising, since neighbouring areas of the Western and Central Mediterranean were grouped together at the highest observed similarity level. The fact that the Aegean Sea was the most similar ecoregion to the former group was also expected since its faunistic similarity with the northwestern Mediterranean subareas was previously demonstrated by the fauna of certain invertebrate groups and was attributed to environmental variables such as latitude, salinity, temperature, and water circulation, besides the distance of Gibraltar which is usually considered (Voultsiadou, 2009). Moreover, Company *et al*. (2004) focused on decapods and indicated that individual species might structure their populations according to similar basic patterns, regardless of differences in local environmental features; so, it is possible for a particular taxon to occur in different Mediterranean geographical areas, given that the basic parameters (i.e., depth or bottom type) are fulfilled. On the other hand, the scientific community has, since the last decade, pointed out that an expected result of the warming trend is the homogenisation of the Mediterranean biota, disrupting present biogeographical entities (UNEP-MAP-RAC/SPA, 2010a); this homogenisation is also suggested by the expansion of the Atlantic biota in the Mediterranean via the Gibraltar Strait (Bianchi, 2007), the expansion of south Mediterranean species to the north (Bianchi *et al*., 2018), and the introduction of alien species via the Suez Canal (Katsanevakis *et al*., 2014). However, the low similarity of the Tunisian Plateau and the Levantine Basin with the other ecoregions, could be due to a combination of their southern and warmer characters with the limited research effort invested in the megabenthos of their trawlable bottoms.

Despite the fact that ca. 500 marine institutes are operating in the Mediterranean basin, the trawlable grounds in the Mediterranean ecoregions are not well studied for their megabenthic fauna, and time series data on the distribution of megabenthos is scarce. MEDITS trawl surveys provide an important opportunity to build such a time series, despite some difficulties that need to be addressed, beginning with the registration of benthic organisms as a mandatory route in the MEDITS protocol and not as a voluntary procedure. Such initiatives could provide a baseline on the status of the Mediterranean trawlable bottoms and contribute to management policies and practices.

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Supplementary Data

The following supplementary information is available online for the article:

Table S1. List of references used for our analysis. Citations organized by year of publication, ecoregion, scientific approach and study method.

Table S2. Taxa checklist ($n = 1,797$ taxa). Taxa organized alphabetically by phylum and species. Superscripted letters are as follows: a) alien species; b) Endangered and threatened species; c) Species whose exploitation is regulated; d) Strictly protected fauna species; e) Protected species.