



Structure and Diversity of the Demersal Fish Assemblages off Psara Island (Central Aegean Sea) Caught by Experimental Bottom Trawling

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Abstract

Data with high spatial resolution on the structure and diversity of marine assemblages are valuable for fisheries management and conservation planning but are seldom available. This study provides fisheries-independent, baseline information on the structure and diversity of the demersal fish assemblages of the continental shelf and upper slope off the island of Psara (Central Aegean Sea). Experimental bottom trawl hauls were conducted during 2009–2010, using identically designed trawls. All the fish in the catches were identified onboard, enumerated, and weighted to the nearest g. Species abundance and biomass were transformed to CPUE. Forty-seven taxa were identified in the catches. For 18 of the species caught no other fisheries-independent information on their abundances and distributions is available for the wider area. Among the Elasmobranchii species collected, *Squalus acanthias*, *Dipturus oxyrinchus*, and *Raja clavata* are species of conservation concern. Species composition was generally more similar to that reported for assemblages of the Cretan Sea and the South Aegean Sea than for assemblages of the North Aegean. The assemblages were structured with depth, a pattern that may be driven in part by the differences in benthic habitat between depth zones. No trends by depth in total numerical abundance and species diversity were identified, whereas the bathymetric change in taxonomic diversity was attributed to the depth distributions of certain species-rich orders and families. The frequency distribution of the trophic level of the species followed the broad-scale pattern that applies in the Mediterranean Sea.

Keywords Community analysis · Bottom trawl fisheries · Bathymetric variability · Taxonomic diversity · Diversity curves

Introduction

Global marine biodiversity and provisioning of goods and services by marine ecosystems to the human societies are increasingly under threat due to cumulative anthropogenic impacts on the marine environment and biota (Halpern et al. 2019; Luybaert et al. 2020). Among the most important human impacts on the world's oceans are the adverse effects of unmanaged or ineffectively managed fisheries impacting fish populations and marine biodiversity (FAO 2018; Hilborn et al. 2020). The deleterious impacts of unsustainable fisheries have been especially evident in the Mediterranean (Colloca et al. 2017), a sea which has been exploited by humans since ancient times (Cortés-Sánchez et al. 2011). As an example, the multi-species and multi-gear fisheries

of the Aegean Sea (Stergiou et al. 2007), a sub-basin of the Eastern Mediterranean, have followed during the recent decades a course to unsustainability: After a period of expansion during the 1980s and early 1990s, in 1994 Greek fisheries entered a phase of contraction, with landings declining in parallel with decreasing fishing effort (Tsikliras et al. 2013). When assessed in 2010, the exploitation levels of biological resources in the Aegean Sea were found to be unsustainable, as a cumulative 87% of the stocks were characterized as either fully exploited (25%), overexploited (40%), or collapsed (22%) (Tsikliras et al. 2015). Based on our current awareness that the impacts of ineffectively managed fisheries may significantly harm marine biodiversity and impair ecosystem functioning, substantially improved management measures are required, pertaining to the Aegean Sea (e.g. Tsikliras et al. 2015), as well as many other seas of the global ocean (FAO 2018; Hilborn et al. 2020).

Time and area closures constitute widely used types of interventions in fisheries management and marine conservation (Jennings et al. 2001). Such fishing restrictions are typically implemented in marine protected areas, where fisheries management may be reconciled with the conservation of

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biodiversity (Rice et al. 2012; Weigel et al. 2014). Planning for the establishment of marine protected areas may require the collection of current data on the structure and diversity of fish assemblages in both nearshore and offshore waters, to take into account the ontogenetic migrations of many fish species (Grüss et al. 2011). Past investigations are also important, as they may assist in the assessment of temporal trends, the prediction of future changes (Bianchi et al. 2000; Christensen and Waters 2004), and nature conservation planning (Papworth et al. 2009; McClenachan et al. 2018). Additionally, community-level studies of fish assemblages in relation to their physical environment may produce information valuable to fisheries management that complements the assessments focusing on the status and dynamics of single species (Labropoulou and Papaconstantinou 2004). The collection of data on fish assemblages' distributions often requires fisheries-independent scientific surveys, as fisheries-dependent surveys can be biased in multiple ways by fishermen's targeting and behavior (Hilborn and Walters 1992). Nevertheless, data with sufficient spatial resolution on species distributions are generally seldom available to assist as baseline information in the planning of marine conservation actions and fisheries management (Osenberg et al. 2011). Indeed, fine-scale community analyses of the demersal megafauna are rather scarce in the Eastern Mediterranean (Peristeraki et al. 2017), as well as in the Greek Seas in particular (e.g. Tsimenidis et al. 1991; Kallianiotis et al. 2000; Madurell et al. 2004; Koulouri et al. 2016). Although a long-term collection of data on populations' distributions and demographic structure of demersal fauna is being compiled in the framework of the "International bottom trawl survey in the Mediterranean" (MEDITS), operating also in the Greek Seas since 1994, MEDITS focuses on broad-scale patterns (Bertrand et al. 2000).

This study aims to contribute to the description of the unstudied structure and diversity of demersal fish assemblages around the island of Psara (Central Aegean Sea, Greece). It is based on the samples that were collected by experimental bottom trawling surveys conducted during 2009–2010, with the objective to collect baseline data to inform the development of a preliminary management plan for the prospective establishment of a local network of marine protected areas. The results of this study may serve as a baseline for assessments of trends in the status of the local demersal fish assemblages and support marine conservation planning and fisheries management in the area.

Materials and Methods

Study Area

The study area is located in the east Central Aegean Sea (Fig. 1). It comprises a relatively steep continental shelf and

the upper continental slope around the Psara and Antipsara islands and extends eastwards to the north of Chios Island. Its deepest part (500 m deep) lies at the west of Psara Island, at the eastern margin of the 800 m deep Psara basin (Sakellariou et al. 2005). The local hydrography is dominated by the cyclonic circulation of the warm, saline waters originating from the Levantine Sea that enter the Aegean Sea through the eastern Cretan Straits and travel northwards, along the Eastern Aegean Sea (Zervakis et al. 2005).

The Central Aegean Sea lies between the oligotrophic South Aegean and the more productive waters of the North Aegean Sea (Tsiaras et al. 2012). Its eastern part, namely the waters around the islands of Lesbos, Chios, Samos and Ikaria, is important for the Aegean Sea fisheries: Catches in the area were 4958 metric t (31% of the total in the Central and South Aegean Sea), of which 1806 metric t were the catches of bottom otter trawls (35% of the total; HSA 2019). Following the general trend observed in Greek fisheries landings since the 1980s (Tsikliras et al. 2013), bottom trawl landings in the Eastern Aegean Sea islands have gradually decreased from a total of 2397 t in 1993 to 211 t in 2006 (HSA 2019). However, during recent years landings in the same area followed an increasing trend, reaching 2300 t in 2017 (HSA 2019).

To the west of Chios Island lie the smaller Psara and Antipsara islands. The local trawling fleet that fishes in the waters around the three islands consists of eight trawlers that target mainly the European hake (*Merluccius merluccius* (Linnaeus, 1758)), and fish in offshore waters (North Aegean Region, Regional Unit of Chios, Department of Fisheries, pers. comm.). Moreover, small-scale coastal fisheries is one of the main economic activities in the island of Psara, which had a population record of 458 inhabitants in the last resident population census in 2011 (HSA 2011). Thirty-four fishermen with active professional licenses are currently fishing in the area, using primarily nets and secondarily longlines (Port Authorities of Psara, pers. comm.).

Sampling Design

Five bottom trawl hauls (Fig. 1; Online Resource 1, Table S1) were planned to be conducted during daylight hours, at depths ranging from 30 to 500 m to capture potential variability with depth in assemblage structure. The scheduling of sampling was unfortunately hindered by restrictions in vessel availabilities, winter weather conditions, and fisheries regulations, which prohibit commercial bottom trawls from fishing above 50 m. Consequently, sampling was carried out in two stages, employing two vessels: Haul 1 was carried out by R/V *Philia* of the Hellenic Centre for Marine Research in November 2009, whereas hauls 2–5 were carried out by the commercial trawler *Venus II* in May 2010. However, the difference in sea temperature in the shallow waters between Psara and Antipsara between the two sampling periods was small, as

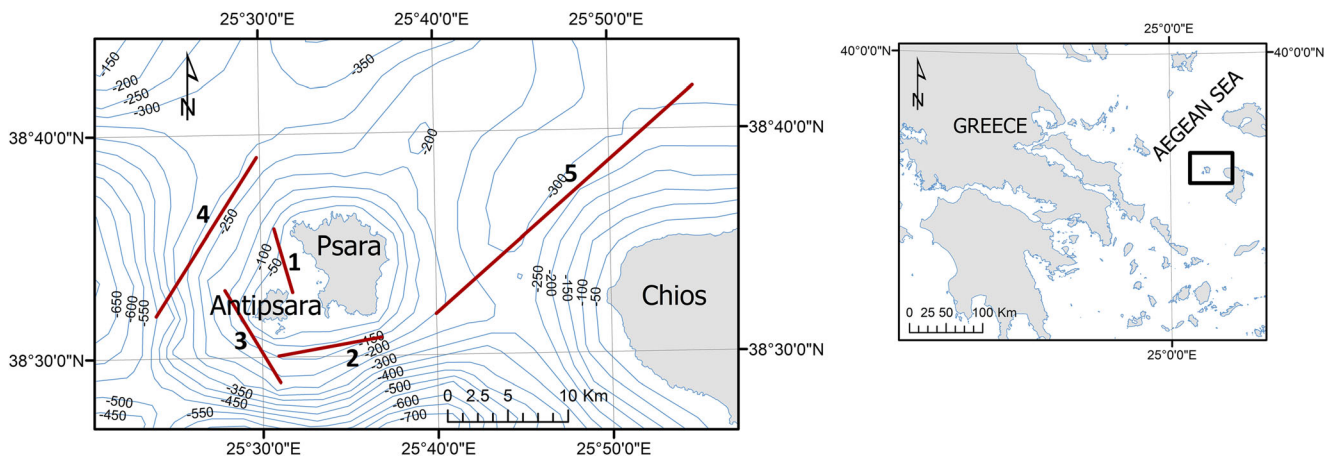


Fig. 1 Map of the study area, indicating the geographic locations of the hauls

SST was 18.9 °C in November and 19.1 °C in May, while the 2010 annual SST minimum that occurred in Feb was 16.3 °C. Furthermore, two identically designed trawls were used, with a horizontal net opening of 12 m and a cod end mesh size of 20 mm, while trawling speed was 3 knots for all hauls. All the fish in the catches were identified onboard to the lowest possible taxonomic level, enumerated and weighed to the nearest g. Species abundances and biomasses in the catches were standardized by transformation to CPUE by dividing catch size by the duration of the haul in h. The dominant families and species were defined for the data analyses as those that contributed >10% of the total abundance or biomass. Species names, authorities and taxonomy were checked using the World Register of Marine Species (WoRMS) online database (WoRMS Editorial Board 2019).

Data Analysis

Classifications of the samples (Q mode analysis; Legendre and Legendre 2012) and identification of species assemblages (R mode analysis) were carried out by means of hierarchical agglomerative cluster analysis with the CLUSTER routine of PRIMER 6.1.16 (Clarke and Warwick 2001b; Clarke and Gorley 2006) on square root transformed CPUE (individuals h^{-1}) data, using the average agglomeration method. The Bray-Curtis similarity index (Bray and Curtis 1957) was used as the resemblance measure for the Q mode analysis, while for the R mode analysis, resemblance was measured using the Whittaker's (1952) index of association. Testing of the homogeneity of the clusters, i.e. that they had no internal multivariate structure, was carried out with the SIMPROF (type I procedure for the Q mode analysis, type III for the R mode analysis) routine of PRIMER (Clarke et al. 2008; Somerfield and Clarke 2013).

Species diversity was calculated in units of “numbers equivalents”, using the formula ${}^qD = (\sum_{i=1}^S p_i^q)^{1/(1-q)}$, where

S is the number of species in the sample and q is the order of diversity (Jost 2006; Tuomisto 2010). Diversities of order $q = 0$ (i.e. species richness) and $q = 1$ (i.e. the exponential of the Shannon-Wiener entropy index; Shannon and Weaver 1949) were calculated. The advantage of diversity indices calculated in units of “numbers equivalents” over classic indices like the Shannon-Wiener or Simpson indices is that they measure diversity directly, and not a surrogate for diversity, thus enabling accurate comparisons of diversity between samples (Jost 2006; Maurer and McGill 2011). Evenness was measured as the ratio of the diversity of order $q = 2$ to the diversity of order $q = 1$ (Tuomisto 2012), with the formula $F_{2/1} = ({}^2D - 1)/({}^1D - 1)$ (Alatalo 1981). This index was chosen because evenness indices that are ratios of diversities have the advantage of being independent of species richness (Tuomisto 2012). The classic Shannon-Wiener entropy index H' (\log_e) and the evenness index of Pielou J' (Pielou 1969, 1975) were also calculated to enable comparisons with other studies. All the indices were computed with the vegetarian 1.2 R package (Charney and Record 2012), using R 3.6.1 (R Core Team 2019). Additionally, in order to take into account the sample sizes, which are well known to affect the observed species richness, we computed the diversity curves of the samples for diversity of order $q = 0$ with the iNEXT 2.0.19 R package (Hsieh et al. 2016). iNEXT computes diversity estimates for rarefied and extrapolated samples up to a user-specified size. We set the endpoint for the calculation of the curves to be equal to double the reference sample size (i.e. the observed sample size), because for species richness the extrapolation method is considered reliable up to that value (Hsieh et al. 2016).

Taxonomic diversity indices like average taxonomic distinctness Δ^+ (Clarke and Warwick 1998) and variation of taxonomic distinctness Λ^+ (Clarke and Warwick 2001a) provide complementary information to that of species diversity indices. Δ^+ measures the average taxonomic breadth in the sample, whereas Λ^+ measures the degree of unevenness of the taxonomic tree of a sample, and both show a lack of

dependence on sampling effort (Clarke and Warwick 2001a). The taxonomic structure of the samples was assessed by the measurement of Δ^+ and Λ^+ with the TAXDTEST routine of PRIMER, using the species presence-absence matrix. The taxonomic diversity analysis may also reveal whether there is a significant departure of the Δ^+ or Λ^+ of a sample from expectation, i.e. the mean Δ^+ or Λ^+ of 999 subsets with the same species richness as the sample, randomly drawn from a “master list”, i.e. an appropriate broad spatial scale species inventory. We used as the “master list” of our analysis an inventory of the fish species of the Aegean Sea that we retrieved from the FishBase online database (Froese and Pauly 2019). The results of the analysis are presented by means of separate “funnel plots” for Δ^+ and Λ^+ , as well as an “ellipsis plot” for the bivariate approach (Clarke and Warwick 2001a). Identifying which species contributed the most to differences in taxonomic distinctness is considered helpful in the interpretation of Δ^+ patterns (Rogers et al. 1999). To this end, plots of the taxonomic trees of the species present in each bathymetric zone were produced with the visualization tool GraPhlAn (Asnicar et al. 2015) and Python 3.7 (Python Software Foundation 2019). These plots are presented as supplementary material in Online Resource 1, Fig. S3.

For the assessment of the bathymetric variability in the trophic levels frequency distribution (TL), we retrieved the trophic level values given for the species in FishBase (Online Resource 1, Table S2). The TL intervals for trophic groups were defined according to Stergiou and Karpouzi (2002), i.e. (a) pure herbivores ($TL = 2-2.1$), (b) omnivores with a preference for vegetable material ($2.1 < TL < 2.9$), (c) omnivores with a preference for animals ($2.9 < TL < 3.7$) and (d) carnivores with a preference for large decapods, cephalopods and fish ($3.7 < TL < 4.5$). Moreover we calculated the mean sample trophic level with the formula $mTL = \frac{\sum_{i=1}^n Y_i TL_i}{\sum_{i=1}^n Y_i}$, where mTL is the mean sample trophic level, Y_i is the biomass in the sample of species i , TL_i is the trophic level of species i and n is the total number of species in the sample (Pauly and Palomares 2005).

Results

Assemblage Structure

A total of 3782 fish individuals were collected in the hauls that were identified to a total of 47 taxa, representing 13 orders and 28 families of fish species (Table 1). Forty-three species in total were identified, not including the species of the Blenniidae, Gobiidae, Labridae and Triglidae families, which were incorporated in the analyses at the family level. Among the identified taxa, 37 species and 25 families belonged to Actinopterygii and 6 species and 3 families were

Elasmobranchii. The most species-rich families were the Sparidae (6 species), Carangidae (3), Serranidae (3) and Rajidae (3). Eighteen of the identified Actinopterygii taxa are not included among the MEDITS target species (MEDITS Working Group 2017) (Table 1).

Hierarchical cluster analysis based on the abundance data classified the samples (Q mode analysis) in three groups that corresponded to the upper shelf, the lower shelf and the upper slope (Fig. 2). The SIMPROF test (type I) showed that the three groups of samples indicated by the cluster analysis had significantly different multivariate structure (upper shelf & lower shelf samples: $\pi = 5.69$, $p < 0.05$; shelf & upper slope samples: $\pi = 7.02$, $p < 0.05$). On the contrary, multivariate structure was not significantly different between samples within the lower shelf or the upper slope.

Hierarchical cluster analysis based on the abundance data classified the species (R mode analysis) in three assemblages (Fig. 3). Based on the identities of the species exclusively present in a single depth stratum (Table 1), the three assemblages were designated to the upper shelf (11 taxa), the lower shelf (17 taxa) and the upper slope (19 taxa). The SIMPROF test (type III) showed that the three assemblages indicated by the cluster analysis had significantly different multivariate structure (upper shelf & lower shelf assemblages: $\pi = 0.05$, $p < 0.05$; shelf & upper slope assemblages: $\pi = 0.04$, $p < 0.05$).

We identified 18 taxa in the upper shelf, 24 taxa in the lower shelf and 24 taxa in the upper slope samples (Fig. 4). A large proportion of the identified taxa (33 taxa) were found to occur in the samples from a single depth stratum only. Four species occurred in both the upper and lower shelf, whereas the bathymetric ranges of another 4 species extended from the lower shelf down to the upper slope. Five species were found to occur in all depth strata.

The dominant families and species in terms of numerical abundance and biomass is presented in Table 2. Within depth strata, the numbers of families or species that were dominant in the catches were low in terms of either abundance (2–4 families and 2–4 species) or biomass (1–3 families and 2–3 species). The contribution of Elasmobranchii to the mean total abundance varied in the range of 5% (upper slope) to 10% (lower shelf), whereas their contribution to the mean total biomass ranged from 8% (upper shelf) to 28% (lower shelf). The most abundant elasmobranch species was *Scyliorhinus canicula* (Linnaeus, 1758), which comprised 20% of the biomass in the lower shelf catches. All the dominant species in the catches were target species and species of commercial value for the local bottom trawl fisheries (Tables 1 and 2).

Diversity

No particular pattern was identified in the variability of total abundance with depth, whereas total biomass was higher at

Table 1 List of the species caught in the surveys, indicating species taxonomy and occurrences in the samples. Species that are not targeted by MEDITS surveys are distinguished by an asterisk. Species commercial value ranking levels for the local bottom-trawling fisheries are given in the last column as follows: 1; main target species, 2; target species caught

less often, 3; non-target species of commercial value that are caught less often or caught in small quantities, 4; species of no commercial value that are discarded. The ranking of the species' commercial value was based on expert judgement by the authors

Class	Order	Family	Species	1	2	3	4	5	Value	
Actinopterygii	Anguilliformes	Muraenidae	* <i>Muraena helena</i> Linnaeus, 1758	+					4	
		Clupeiformes	Clupeidae	<i>Sardina pilchardus</i> (Walbaum, 1792)		+				3
	Gadiformes	Gadidae	<i>Micromesistius poutassou</i> (Risso, 1827)				+		1	
			Merlucciidae	<i>Merluccius merluccius</i> (Linnaeus, 1758)				+	+	1
	Gadiformes	Phycidae	<i>Phycis blennoides</i> (Brünnich, 1768)				+	+	3	
	Lophiiformes	Lophiidae	<i>Lophius budegassa</i> Spinola, 1807				+		4	
			<i>Lophius piscatorius</i> Linnaeus, 1758					+	4	
	Perciformes	Blenniidae	*Blenniidae spp.		+					3
		Caproidae	* <i>Capros aper</i> (Linnaeus, 1758)					+		1
	Carangidae	Carangidae	<i>Trachurus mediterraneus</i> (Steindachner, 1868)				+		+	4
			* <i>Trachurus picturatus</i> (Bowdich, 1825)				+	+		2
	Centranchidae	Centranchidae	<i>Trachurus trachurus</i> (Linnaeus, 1758)			+	+			3
			<i>Spicara maena</i> (Linnaeus, 1758)			+	+			2
	Gobiidae	Gobiidae	<i>Spicara smaris</i> (Linnaeus, 1758)			+	+			3
			* <i>Gobius</i> sp.		+					2
	Labridae	Labridae	* <i>Coris julis</i> (Linnaeus, 1758)		+	+				2
			*Labridae spp.		+					3
	Mullidae	Mullidae	<i>Mullus barbatus</i> Linnaeus, 1758			+		+	+	3
			<i>Mullus surmuletus</i> Linnaeus, 1758		+	+	+	+	+	3
	Scombridae	Scombridae	<i>Scomber scombrus</i> Linnaeus, 1758				+			3
			* <i>Serranus cabrilla</i> (Linnaeus, 1758)		+	+	+			2
	Serranidae	Serranidae	* <i>Serranus hepatus</i> (Linnaeus, 1758)		+		+			3
			* <i>Serranus scriba</i> (Linnaeus, 1758)		+					2
	Sparidae	Sparidae	<i>Boops boops</i> (Linnaeus, 1758)				+			3
			* <i>Dentex maroccanus</i> Valenciennes, 1830		+					2
	Diplodus	Diplodus	<i>Diplodus annularis</i> (Linnaeus, 1758)			+				4
			<i>Pagellus bogaraveo</i> (Brünnich, 1768)				+	+	+	3
	Pagellus	Pagellus	<i>Pagellus erythrinus</i> (Linnaeus, 1758)		+	+	+			3
			<i>Pagrus pagrus</i> (Linnaeus, 1758)			+	+			2
	Trachinidae	Trachinidae	* <i>Trachinus araneus</i> Cuvier, 1829			+	+			4
			* <i>Trachinus draco</i> Linnaeus, 1758		+					3
	Trichiuridae	Trichiuridae	* <i>Trichiurus lepturus</i> Linnaeus, 1758					+		2
<i>Citharus linguatula</i> (Linnaeus, 1758)							+		2	
Pleuronectiformes	Citharidae	<i>Lepidorhombus boscii</i> (Risso, 1810)		+		+	+		3	
		* <i>Scorpaena porcus</i> Linnaeus, 1758					+		3	
Scorpaeniformes	Scorpaenidae	* <i>Scorpaena scrofa</i> Linnaeus, 1758		+		+	+	+	3	
		<i>Helicolenus dactylopterus</i> (Delaroche, 1809)				+	+		2	
Sebastidae	Triglidae	* <i>Chelidonichthys cuculus</i> (Linnaeus, 1758)			+	+			1	
		Triglidae spp.		+		+	+		2	
Syngnathiformes	Centriscidae	* <i>Macroramphosus scolopax</i> (Linnaeus, 1758)				+			3	
		<i>Zeus faber</i> Linnaeus, 1758		+	+	+	+		3	
Zeiformes	Zeidae	<i>Galeus melastomus</i> Rafinesque, 1810					+		3	
		<i>Scyliorhinus canicula</i> (Linnaeus, 1758)		+	+	+	+		2	
Elasmobranchii	Carcharhiniformes	Rajidae	<i>Dipturus oxyrinchus</i> (Linnaeus, 1758)					+	4	
		<i>Raja clavata</i> Linnaeus, 1758			+	+	+	+	2	
Squaliformes	Squalidae	<i>Raja miraletus</i> Linnaeus, 1758		+					1	
		<i>Squalus acanthias</i> Linnaeus, 1758				+	+		3	

the upper shelf samples (Online Resource 1, Fig. S1). Species richness varied between 15 and 20 between samples, and the Shannon-Wiener index was close to 2 in all samples. No particular patterns were identified in the variability of species diversity indices with depth (Online Resource 1, Fig. S1), even when the sample sizes were taken into account by the computation of the diversity curves of the samples for species richness (Online Resource 1, Fig. S2).

Average taxonomic distinctness Δ^+ was higher and variation in taxonomic distinctness Λ^+ was lower in the samples from the upper slope in comparison to the samples from the shelf (Fig. 5). The funnel plots depicted all samples as having Δ^+ values that did not depart significantly from expectation, whereas they showed the samples from the shelf as being on the verge of having significantly higher Λ^+ values from expectation. The ellipsis plot showed the samples from the lower

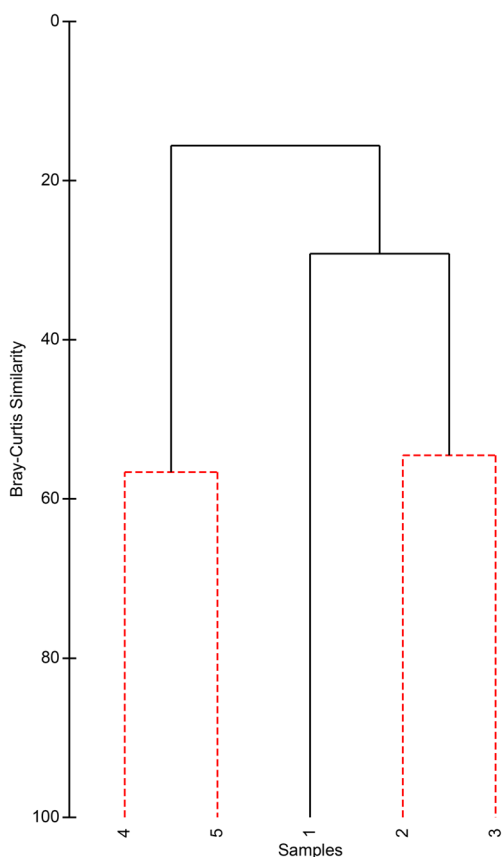


Fig. 2 Dendrogram produced by the CLUSTER analysis of the samples (Q mode analysis), based on the abundance data. Dashed lines in the dendrogram branches join samples that form valid clusters with no significant internal multivariate structure, according to the results of the SIMPROF (type I) test

shelf as being significantly different from expectation. Plots of the taxonomic trees of the species present in each bathymetric zone are given as supplementary material in Online Resource, Fig. S3.

Trophic Levels

The trophic levels (TL) of the species caught in the hauls ranged from 2 to 4.5 (Online Resource 1, Fig. S4). Blenniidae spp. were the only taxon of pure herbivores ($TL = 2-2.1$) that was found in the samples and were present only in the upper shelf sample. Omnivores with a preference for plant material ($2.1 < TL < 2.9$) were not found in any sample. Omnivores with a preference for animals ($2.9 < TL < 3.7$) were the modal class in all samples. Carnivores with a preference for large decapods, cephalopods and fish ($3.7 < TL < 4.5$) were also found in all samples, but their relative frequencies were higher in the upper slope samples. The high-level carnivores ($TL = 4.4-4.5$) *Lophius budegassa* Spinola, 1807, *Lophius piscatorius* Linnaeus, 1758, *M. merluccius*, *Trichiurus lepturus* Linnaeus, 1758, and *Zeus faber* Linnaeus, 1758 were found only in the upper slope samples,

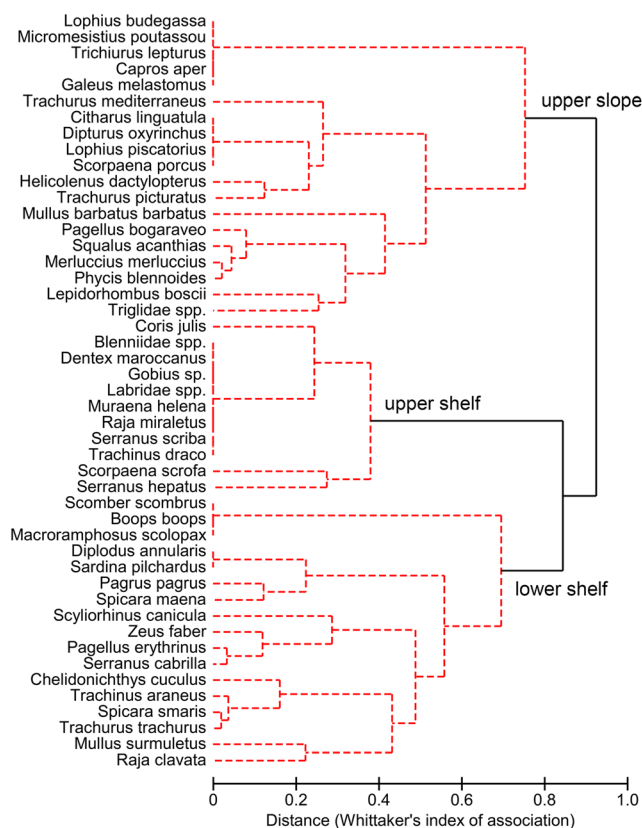


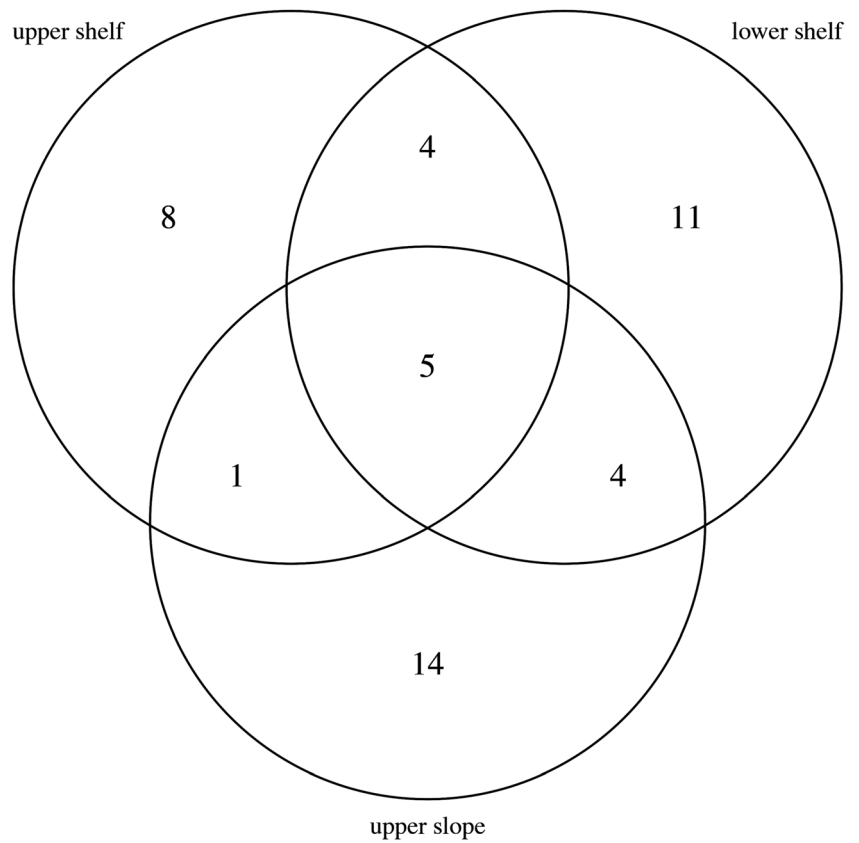
Fig. 3 Dendrogram produced by the CLUSTER analysis of the species (R mode analysis), based on the abundance data. Dashed lines in the dendrogram branches join species that form valid associations with no significant internal multivariate structure, according to the results of the SIMPROF (type III) test

with the exception of the latter species, which was also found in the shelf samples. mTL ranged from 3.46 to 4.15, with a mean value of $3.75 (\pm 0.12 \text{ SE})$. It was lower in the shelf samples (sample 1: 3.71, 2: 3.60, 3: 3.46) than in the upper slope samples (4: 4.15, 5: 3.8).

Discussion

This study is a contribution to the characterization of the structure and diversity of the demersal fish assemblages off Psara Island (Central Aegean Sea). To this end, it presents the results of a fisheries-independent, baseline community analysis of demersal fish assemblages of the continental shelf and upper slope off the island of Psara. Eighteen of the identified taxa are not included among the MEDITS target species (MEDITS Working Group 2017), and thus there is no other fisheries-independent information in the literature regarding the distributions of their populations in the wider area. Our results regarding a suite of structural aspects of the assemblages showed significant similarities, as well as important differences, with the findings of other similar studies that were

Fig. 4 Venn diagram showing the numbers of exclusive and shared species between depth zones



carried out in different parts of the Aegean Sea and elsewhere in the Mediterranean. Furthermore, our use of taxonomic and contemporary species diversity indices in a study of demersal fish assemblages is, to our knowledge, novel for the Greek seas, and sets baselines for more robust trends assessments in the area.

The numerically abundant species are the ones most likely to be observed in samples, even when sample size is small (Gotelli and Colwell 2011). Accordingly, given the comparatively small total sample size in the present study, we contrasted species composition with other regional case studies by focusing on dominant species. Species composition was

Table 2 The dominant families and species in the bathymetric zones, in terms of abundance and biomass

		Upper shelf	Lower shelf	Upper slope
families	abundance	Sparidae (44%) Serranidae (32%)	Centracanthidae (46%) Sparidae (14%)	Sparidae (21%) Sebastidae (15%) Trichiuridae (14%) Merluccidae (13%)
	biomass	Sparidae (61%)	Sparidae (30%) Centracanthidae (23%) Scyliorhinidae (20%)	Trichiuridae (19%) Merluccidae (18%)
species	abundance	<i>Dentex maroccanus</i> (28%) <i>Serranus cabrilla</i> (24%) <i>Pagellus erythrinus</i> (16%)	<i>Spicara smaris</i> (44%) <i>Macroramphosus scolopax</i> (13%)	<i>Pagellus bogaraveo</i> (21%) <i>Helicolenus dactylopterus</i> (18%) <i>Merluccius merluccius</i> (13%) <i>Trichiurus lepturus</i> (11%)
	biomass	<i>Pagellus erythrinus</i> (31%) <i>Dentex maroccanus</i> (30%)	<i>Spicara smaris</i> (20%) <i>Scyliorhinus canicula</i> (20%) <i>Macroramphosus scolopax</i> (17%)	<i>Merluccius merluccius</i> (17%) <i>Trichiurus lepturus</i> (16%) <i>Helicolenus dactylopterus</i> (11%)

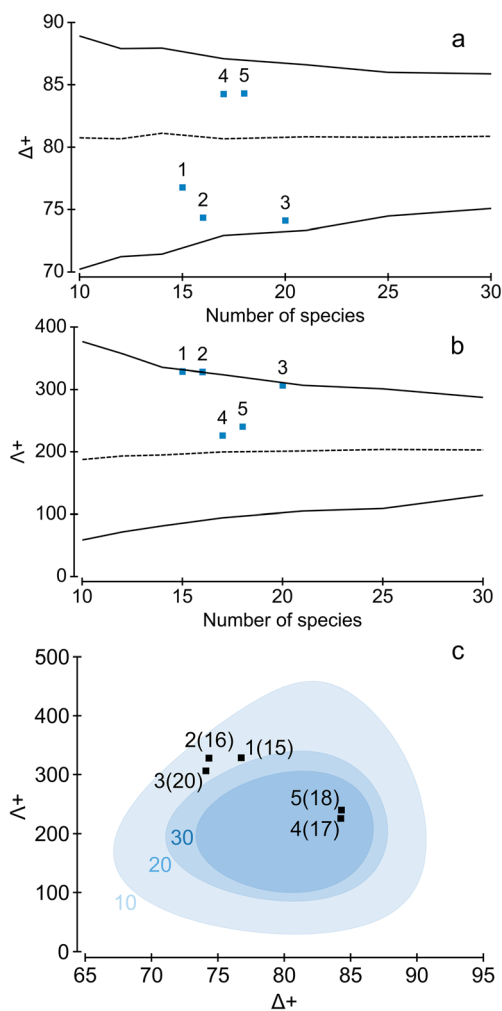


Fig. 5 Funnel plots for (a) average taxonomic distinctness ($\Delta+$) and (b) variation of average taxonomic distinctness ($\Lambda+$) and (c) ellipsis plot for both $\Delta+$ and $\Lambda+$. In the funnel plots, the $\Delta+$ and $\Lambda+$ of the master list and the 95% confidence intervals are plotted as a function of sample size. In the ellipsis plot, 95% probability contours are given for sample sizes of 10, 20 and 30 species. The observed species richness of the samples is given in parentheses

generally more similar to that reported for assemblages of the Cretan Sea and the South Aegean Sea than assemblages of the North Aegean, or the Thracian Sea: *Spicara smaris* (Linnaeus 1758), *Macroramphosus scolopax* (Linnaeus, 1758), *Pagellus erythrinus* (Linnaeus, 1758), and *Serranus cabrilla* (Linnaeus, 1758) were numerically dominant species in both the study area and the Cretan Sea (Kallianiotis et al. 2000), and the latter two species were also reported to be dominant in the South Aegean continental shelf (Tserpes et al. 1999). Apart from *M. scolopax*, different species were found to be numerically dominant in Saronikos Gulf and the Cyclades (South Aegean Sea) by Vassilopoulou et al. (1998). Except for *Merluccius merluccius*, the dominant species in the demersal fish assemblages of the North Aegean and the Thracian Seas (Labropoulou and Papaconstantinou 2004) were distinct from those dominant in the study area. Three of the demersal

species assemblages defined by Kallianiotis et al. (2004) in the North and Central Aegean Sea were associated with sampling stations in the vicinity of the area of the present study. Although several of the characteristic species of the assemblages were recorded in the present study too (*Phycis blenoides* (Brünnich, 1768), *Lepidorhombus boscii* (Risso, 1810), *Chelidonichthys cuculus* (Linnaeus, 1758), *Capros aper* (Linnaeus 1758)), among the most abundant species only *Pagellus bogaraveo* (Brünnich, 1768) was present in our samples. The species that were reported as dominating the demersal fish assemblages in the aforementioned studies were either less numerous (e.g. *Mullus barbatus* Linnaeus, 1758, *Micromesistius poutassou* (Risso 1827), *C. aper*), or altogether absent from the study area (e.g. *Argentina sphyraena* Linnaeus, 1758, *Gadiculus argenteus* Guichenot, 1850).

Most elasmobranchs have a high trophic level (Stevens et al. 2000). At the same time, the elasmobranchs constitute globally important marine biological resources resources that are especially vulnerable to overfishing due to their life-history traits (Bonfil 1994). As a result, elasmobranch populations are in decline worldwide, and the conservation status of many species in the Mediterranean is alarming (IUCN 2016). In Greece, most of the Elasmobranchii species are bycatch, and a large portion is usually discarded (Damalas and Vassilopoulou 2011). Nevertheless, 577 metric tons of catsharks and rays were landed in 2018, a mere 0.3% of the total fish production (HSA 2019). Elasmobranchs were present at all depth zones in the study area, although they were more species-rich at the upper slope (5 species) than at the upper (2) or lower shelf (2). Elasmobranchii species found around Psara were also recorded in the Cretan Sea by Kallianiotis et al. (2000), except *Dipturus oxyrinchus* (Linnaeus, 1758) and *Squalus acanthias* Linnaeus, 1758. *S. acanthias* was reported by Tserpes et al. (1999) to be an abundant species of the continental slope of the South Aegean Sea. *D. oxyrinchus*, *S. acanthias* and *Raja miraletus* Linnaeus, 1758 were not recorded from Saronikos Gulf or Cyclades by Vassilopoulou et al. (1998). Concerning the conservation status according to the IUCN Red List of Threatened Species (IUCN 2019) of the Elasmobranchii species found in the study area, *D. oxyrinchus* is considered as a near-threatened species globally, in Europe, and in the Mediterranean, with a decreasing population trend (Ellis et al. 2015), *S. acanthias* is vulnerable globally and endangered in Europe and in the Mediterranean, also with a decreasing population trend (Fordham et al. 2016), and *Raja clavata* is considered as a near-threatened species globally, in Europe and in the Mediterranean, with a decreasing population trend (Ellis 2016). The rest of the Elasmobranchii species in the samples are of least-concern conservation status.

There are no published historical data on the number of species of Elasmobranchii in the study area to compare with the number of species recorded in the present study. Thirty-

three Elasmobranchii species were recorded by Peristeraki et al. (2017) in samples of the demersal megafauna assemblages of the South Aegean Sea from the 2000s and early 2010s, and thirty chondrichthyan species were encountered in the by-catch of the demersal trawl fisheries in Cyclades during 1995–2006 by Damalas and Vassilopoulou (2011). Moreover, a total of 27 demersal sharks, rays and skates were included in the food web model of the North Aegean Sea ecosystem for 2003–2006 by Tsagarakis et al. (2010). However, all the aforementioned studies had a much larger spatial scale, temporal frame and sampling effort than the present study. Kallianiotis et al. (2000) found 15 species of Elasmobranchii in a study of similar spatial scale to the present study, carried out off Heraklion, Crete, in 1994–1995, but that study was based on seasonal samplings and a much higher sampling effort. On the other hand, Vassilopoulou et al. (1998) reported just three chondrichthyan species in their study for the area of Cyclades during 1995–1996, despite the considerable sampling effort employed. Pertaining to the information available on the biomass densities of Elasmobranchii in the Eastern Aegean Sea, unfortunately the gaps in the existing MEDITS data from the 2010s on the targeted species would not permit a reliable assessment of their temporal trends.

As found in other studies in the Aegean Sea and elsewhere, the structure of the demersal fish assemblages showed a pattern with depth: Three different assemblages were distinguished, corresponding to the upper shelf, the lower shelf and the upper slope, respectively. Species turnover between the assemblages was considerable, as most of the species were recorded in a single depth stratum. There are several reports in the literature of distinct assemblages occupying different bathymetric zones of the continental shelf (e.g. Vassilopoulou et al. 1998; Tserpes et al. 1999; Colloca et al. 2003; Labropoulou and Papaconstantinou 2004; Massutí and Reñones 2005), although studies exist that reported only a single shelf assemblage (e.g. Kallianiotis et al. 2000). Our results followed the general trend of structural dissimilarity being greater between shelf and slope assemblages than between lower and upper shelf assemblages, consistent with a species break that corresponds with the shelf edge, as found previously (e.g. Labropoulou and Papaconstantinou 2004; Massutí and Reñones 2005). The depth gradient in the sea is correlated with a number of environmental parameters, including hydrostatic pressure, light intensity, temperature, salinity, and dissolved oxygen, and all these variables may potentially affect the distributions of fishes (Moyle and Cech Jr 1996). Moreover, the three bathymetric zones sampled in the present study also had somewhat differing benthic habitats or substrate types: The upper shelf sample was collected over soft bottom substrate with rhodoliths, in close proximity of an extensive *Posidonia oceanica* (Linnaeus) Delile, 1813 meadow, the lower shelf hauls were carried out over rhodolith beds and

muddy substrate, whereas the upper slope samples were collected over muddy substrate. Substrate type has been regarded as an important driver structuring demersal fish assemblages (e.g. Colloca et al. 2003), and we assume that assemblage structuring with depth in the study area may be driven in part by the differences in substrate type between the depth zones.

The numerical abundance of demersal fish was found in several areas of the Aegean Sea to be lower on the continental slope than on the continental shelf (e.g. Vassilopoulou et al. 1998; Labropoulou and Papaconstantinou 2004; Kallianiotis et al. 2000). Yet, our results show no significant effect of depth on the total numerical abundance of the demersal fish, whereas total biomass was found to be higher at the upper shelf samples, mainly due to the large catches from that depth zone of *Dentex maroccanus* Valenciennes, 1830 and *P. erythrinus*. Depth is also considered to be among the most important environmental predictors of variation in species richness of demersal fish assemblages, but the pattern of change in species richness may vary, depending on a number of parameters: geographic location, the bathymetric range examined, the taxonomic scope, and the scale of observation (e.g. Colloca et al. 2003; Labropoulou and Papaconstantinou 2004; Massutí and Reñones 2005; Leathwick et al. 2006; Zintzen et al. 2012; Peristeraki et al. 2017). We identified no significant effect of depth on species richness, even when the effect of sample size was considered. Our findings that showed no change in abundance and species richness or diversity were unexpected: The main types of benthic habitats in the area of the upper shelf sampling station consisted of a *P. oceanica* meadow, reefs and rhodolith beds, which are well known to support a high diversity and abundance of fish species due to their structural complexity and high diversity and abundance of food resources (Guidetti 2000; Kamenos et al. 2004; Riosmena-Rodriguez and Medina-López 2010). However, our results may be attributed, at least partly, to the fact that they are not based on a complete cycle of seasonal samplings: It is well-established that seasonal variability of demersal assemblages structure is often important in shelf and even in the deeper waters, slope assemblages (e.g. Madurell et al. 2004; Panayotova and Todorova 2015). Other plausible causes could be inadequate sample sizes, as indicated by the computed diversity curves for the shelf samples, and more intense fishing impacts on the demersal assemblages of the shallower depth zones.

Taxonomic distinctness Δ^+ and variation in taxonomic distinctness Λ^+ provide information on the structure of the taxonomic tree of the samples that is independent and complementary to that offered by the more widely used species diversity indices (Clarke and Warwick 2001a, 2001b). They have been utilized in various contexts, including biodiversity assessments (Leonard et al. 2006), and assessments of the effects of fisheries on fish diversity (e.g. Hall and Greenstreet 1998; Rogers et al. 1999; Campbell et al. 2011), but, to our

knowledge, not as yet in studies of the fish assemblages of the Greek seas. Taxonomic distinctness in fish assemblages is considered to be driven by natural processes, such as the range of niches offered by the natural variability of the marine environment, and human impacts, such as the pressure from fisheries (Rogers et al. 1999). We found that the samples from the slope had a higher average taxonomic breadth, i.e. lower species relatedness, and a more even taxonomic tree than the shelf samples. Furthermore, although taxonomic distinctness did not significantly differ from expectation in any of the samples, the shelf samples were on the verge of having a significantly less even taxonomic tree than expected. It is likely that this is not a fisheries pressure-related pattern, but a natural one, attributable to the higher family-level diversity within the order Perciformes and species-level diversity within the families Serranidae and Sparidae in the shelf samples (Online Resource 1, Fig. S1a, b). We do not consider this an unexpected finding, since Perciformes is an extremely diverse order living in the shallower waters of the ocean (Moyle and Cech Jr 1996). Nevertheless, we consider the estimation of taxonomic diversity indices to set baselines for more robust diversity trends assessments for the demersal fish assemblages in the area, complementing the information offered by the estimation of species diversity.

Our results pertaining to the relative frequencies of the trophic groups follow the broad-scale pattern given by Stergiou and Karpouzi (2002) for the Mediterranean Sea: Omnivores with a preference for animal material was the best represented group, followed by the carnivores with a preference for large decapods, cephalopods and fish, whereas the other two groups were either very rare or absent. The high-level carnivores (TL > 4.4) *M. merluccius*, *Lophius budegassa*, *Lophius piscatorius*, *Trichiurus lepturus*, and *Zeus faber* were found predominantly in the upper slope samples, with the exception of the latter species, which was also found in the shelf samples. Most of these high-level carnivorous species are considered bathydemersal and their absence from the shelf samples may thus be explained by their natural depth distributions.

Trophic level-based indicators like mTL have been widely used to assess the impacts of fisheries on fish assemblages and marine ecosystems (Pauly et al. 1998; Essington et al. 2006; Shannon et al. 2014). Fisheries exploitation level in the study area, as this can be assessed with the mTL indicator, was not found to be higher than average in the Aegean Sea: The mean mTL of the samples (3.75) was in fact above the range 3.4–3.7 given by Peristeraki et al. (2019) for the whole of GSA 23 (Aegean Sea) for the MEDITS survey catches during 1994–2014. However, the mean mTL of the samples was lower than the value 3.89 (± 0.021 SE) reported by Adamidou and Kallianiotis (2010) for bottom trawls catches recorded by on-board sampling in the Thracian Sea in 2004.

All the dominant species in the catches were target species and species of commercial value for the local bottom trawl

fisheries (Tables 1 and 2): *M. merluccius*, a main target species for trawlers in the broader study area, was dominant in the samples from the upper slope. Target species for trawlers that are however typically caught less often were dominant in the upper shelf samples (*D. maroccanus*), the lower shelf samples (*Scyliorhinus canicula*) and the upper slope samples (*T. lepturus*, *Helicolenus dactylopterus* (Delaroche, 1809)). Furthermore, with respect to the variation of species body size with depth, most of the species with the smallest body sizes, i.e. *Coris julis* (Linnaeus, 1758), *Sardina pilchardus* (Walbaum, 1792), *Spicara maena* (Linnaeus, 1758), *Serranus hepatus* (Linnaeus, 1758), *Diplodus annularis* (Linnaeus, 1758), *M. scolopax* and *S. smaris*, were exclusively present in the shelf samples. On the contrary, most of the species with the largest body sizes, i.e. *T. lepturus*, *L. piscatorius*, *S. acanthias*, *D. oxyrinchus*, *M. merluccius*, *P. blennoides* and *L. budegassa*, were exclusively present in the slope samples. As the minimum depth of occurrence in FishBase (Froese and Pauly 2019) for all these species is above 200 m, their absence in the shelf samples may be an indication of present or past fishing impacts. However, other studies have shown a contrasting pattern regarding the bathymetric distributions of the commercial values and body sizes of the demersal fishes: For example, Labropoulou and Papaconstantinou (2004) found that the species predominant in the shelf samples were large-bodied species and of commercial importance, whereas the samples from the upper slope were dominated by small-bodied species that are not commercially important.

Sample replication and the temporal frame of the study were restricted due to funding constraints. Further experimental surveys, with a better replication and conducted on a seasonal and multiannual basis, would be appropriate in order to gain a more accurate and comprehensive knowledge of the trends of the local demersal fish assemblages in the area of Psara. Still, this baseline study represents the best available fisheries-independent knowledge of the state of the structure and diversity of the demersal fish assemblages in the study area.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

Ethics Approval Not applicable.

Consent to Participate Not applicable.

Consent for Publication Not applicable.

Code Availability Not applicable

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