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Sandy bottoms have limited species richness but substantially contribute to the regional coastal fish β-diversity: A case study of the Central Mediterranean Sea

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ABSTRACT

Global marine biodiversity loss impairs entire ecosystems and their stability. Robust biodiversity estimates are key to inform policies and management strategies, and need to consider the contribution of diverse habitats, including those for which estimates of biodiversity are scattered or totally absent. This study assessed the fish diversity associated with three main coastal habitats (rocky bottoms, *Posidonia oceanica* meadows, sandy bottoms), and their role in shaping the overall coastal fish diversity, also in relation to potential environmental and anthropogenic drivers affecting patterns of fish diversity in coastal areas. Using underwater visual census, we sampled 62 sites distributed on the three habitats, for a total of 496 replicates. We assessed the contribution of each habitat to β-diversity, divided into Local Contribution to β-diversity (LCBD), a comparative indicator of the contributions to β-diversity of each habitat, and Species Contribution to β-diversity (SCBD), which measures the relative importance of each species in affecting β-diversity. Finally, we modelled species diversity in relation to potential environmental and anthropogenic drivers. Overall, 72 species were recorded, with the highest species richness observed on rocky bottoms (56 species, 16 unique to this habitat), followed by *P. oceanica* (38 species, 0 unique) and sandy bottoms (32 species, 14 unique). Sandy bottom assemblages had a significantly higher contribution to LCBD than *P. oceanica* meadows and rocky bottoms, and two of the five species with the highest contribution to SCBD are exclusively associated with sandy bottoms. Finally, sea surface temperature, sea surface salinity, and habitat were highlighted as significant predictors of species richness. Our findings, aside from highlighting the environmental drivers of coastal fish diversity in the Mediterranean Sea, unravel the potential key role of sandy bottoms in contributing to overall coastal fish diversity and can inform conservation planning.

1. Introduction

Biodiversity is one of the key drivers of ecosystem functioning (Loreau et al. 2001; Hooper et al. 2005; Midgley 2012). Along with the onset of industrial uses of the seas and the rapid expansion of coastal populations, a steep increase in human-induced marine animal loss (also called "defaunation") has been recorded globally (McCauley et al. 2015). This process has led, in some cases, even to the loss of entire functional groups (Oliver et al. 2015; Corrales et al. 2018), hampering the ability of ecosystems to deliver Nature's Contributions to People (NCP, Díaz et al., 2018). Biodiversity also supports the productivity and stability of ecosystems (Cardinale et al. 2011), but different ecosystems

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and communities react in different ways and with different magnitudes to the changes in biodiversity that can be driven both by natural and anthropogenic stressors (Hooper et al. 2005). The challenges that marine natural systems are facing (Bellard et al. 2012; Hiddink et al. 2023) demand a deeper understanding of the attributes characterizing biodiversity, in order to better assess and manage the ecological processes occurring within those systems under constant change.

Marine fishes are among the many organisms facing a worldwide decline in abundance and diversity (Edgar et al. 2023). Fishes have been widely used as biodiversity indicators for a long time, as they hold several features making them suitable proxies to assess the biodiversity and health of marine ecosystems (Greenstreet et al. 2012; Dabuleviciene et al. 2023). In fact, fishes represent a highly diverse group, covering a wide range of ecological functions, and their taxonomic, biological, and ecological traits are relatively well known (Rice 2003; Stuart-Smith et al. 2013; Duffy et al. 2016; Pinna et al. 2023). Furthermore, the macroscopic nature of fishes allows the adoption of non-destructive approaches for their assessment, enabling the application of methods associated with reduced disturbance to species and ecosystems (MacNeil et al. 2008; Lowry et al. 2012), such as the Underwater Visual Census (UVC; De Girolamo and Mazzoldi, 2001; Lowry et al. 2012; Caldwell et al. 2016). Also at policy levels, fishes have been identified as key elements to assess marine biodiversity, as in the EU Marine Strategy Framework Directive (MSFD; European Commission, 2008), that suggests indicators for each taxon to monitor biodiversity at species, habitat, and ecosystem levels (European Commission 2010, 2017; Machado et al. 2020).

The habitat-based characterization of fish diversity can support the overall assessment of the biodiversity of an area because the differences found in biodiversity for each habitat can inform on the importance of understudied portions of complex ecosystems composed of more than just one habitat (Harper et al. 2022). This is particularly true in very heterogeneous and diverse ecosystems such as coastal ones. For example, despite the heterogeneity of the coastal areas of the Mediterranean Sea, there are few studies who analyzed multiple habitats simultaneously when it comes to fish diversity (e.g., Guidetti 2000; La Mesa et al. 2011; Giakoumi and Kokkoris 2013), and in some cases, this has been done on a restricted spatial scale (Guidetti 2000; La Mesa et al. 2011). Moreover, biodiversity assessments often lack an explicit quantification of the composition of assemblages across spatial scales, also in relation to the pressures, both anthropogenic and natural, they currently face (Mathon et al. 2023). Finally, while local diversity (α-diversity) generally calculated taking richness into account, provides a good summary of the structure of an ecological unit, β-diversity, intended as "the extent of change in community composition" among units (Whittaker 1960), provides useful information about the contribution of each habitat in shaping fish biodiversity, and highlights the differences between habitats.

Fish biodiversity in Mediterranean coastal habitats can also be influenced by the interactions occurring between multiple habitats, especially if mobile organisms such as fish are considered (Carr et al. 2017; Staveley et al. 2019). In this perspective, different fish life stages can occur in different habitats: for example, seagrass meadows represent nursery areas (Madi Moussa et al. 2020), hosting a number of juveniles that will then disperse to other habitats (e.g., rocky, sand, corals) when they grow to adults. This is because seagrass meadows offer a sheltered, stable, and productive environment enhancing survival rate during one of the most vulnerable life stages (Dorenbosch et al. 2005; Nakamura et al. 2009). Therefore, when assessing fish biodiversity, marine habitats should not be considered as isolated compartments, but as components of a system (e.g., Coastal Ecosystem Mosaic, CEM: Sheaves 2009), accounting for their contribution to the overall diversity (Olds et al. 2016). Furthermore, there is a lack of information regarding the diversity of coastal fishes in soft bottoms, despite these habitats represent the majority of the coastal zone. Still, the limited evidence available suggested their non-negligible importance for coastal fish diversity, possibly hosting unique assemblages that support system's heterogeneity (Harper et al. 2022). Most of the information available about temperate coastal fish diversity is generally restricted to rocky bottoms (Bevilacqua et al. 2021) and seagrass meadows in marine protected areas and adjacent unprotected areas (see Giakoumi et al. 2017 and references therein). In this sense, the use of β-diversity could result in a useful tool to unveil the hidden diversity of such habitats, which is still largely neglected, clarifying their contribution to the diversity of the main Mediterranean coastal habitats, and their unique contribution to fish species composition. Finally, despite previous large-scale studies have highlighted the role of environmental and human drivers in shaping fish diversity patterns (Mouillot et al. 2011; Stuart-Smith et al. 2013; Guidetti et al. 2014; Duffy et al. 2016), scarce information is available about the role of putative drivers in structuring coastal fish diversity across different habitats.

In this context, the aim of this study is to assess patterns of coastal fish diversity in multiple habitats. To do so, we focused on the Mediterranean Sea, which represents a very heterogeneous system (Harmelin and Pergent 2006; Giakoumi and Kokkoris 2013), where a multitude of habitats can be found at a relatively small spatial scale, supporting high marine biodiversity (Bianchi and Morri 2000; Coll et al. 2010). In particular, we used as a case study the coastal waters of the Calabria Region, Southern Italy, covering three distinct habitats (rocky bottoms, sandy bottoms, and *Posidonia oceanica* meadows) to assess whether: 1) the three habitats sampled hold differences in the associated coastal fish assemblages (in terms of α-diversity, density, and biomass); 2) different habitats have similar contribution to the overall fish diversity of the coastal system investigated; and 3) fish diversity in the considered habitats can be influenced by the environmental and anthropogenic drivers considered.

2. Material and methods

2.1. Study area and sampling design

The sampling operations were carried out along the Calabrian coasts (Southern Italy, Central Mediterranean Sea, Fig. 1) between June and July 2022. The Calabria Region has a marked peninsular shape and coastlines extend for almost 800 km, covering a range of different marine habitats. The sampling design included five locations: three located in the Tyrrhenian Sea (Cetraro, Vibo Valentia, and Scilla; Fig. 1 b, c, d) and two in the Ionian Sea (Amendolara and Capo Rizzuto; Fig. 1f–e). For each location, a set of sites (62 in total) were selected from a wider array of possible ones to cover a large geographic range and capture the environmental variability of the area, and, therefore, to increase the range of values associated with the predictors (recorded at site scale; see section 2.2.) that could shape biodiversity patterns along the Calabrian coasts. Not all the locations hosted the three habitats considered (i.e. Amendolara hosted only rocky bottoms). Moreover, the sites were also selected based on the possibility to find high habitat heterogeneity within a reduced spatial scale. The original set of potential sites was compiled in QGIS software (version 3.24.2) using data from the European Nature Information System (EUNIS) database, a comprehensive system for habitat identification (http://eunis.eea.europa.eu/habitats.jsp, Montefalcone et al. 2021) and dividing the area into spatial units (i.e., cells). The spatial units have been designed using a grid with a resolution of ~4 km, corresponding to the spatial division of the Copernicus Marine Environment Monitoring Service (CMEMS, http://marine.copernicus.eu) environmental data. At the end of this process, each site was associated with a habitat type.

2.2. Data collection

We collected data about fish diversity using UVC. The transects' depth at which sampling operations were carried out ranged between 3 m and 28 m for operational reasons. Within each of the 62 sites, 8

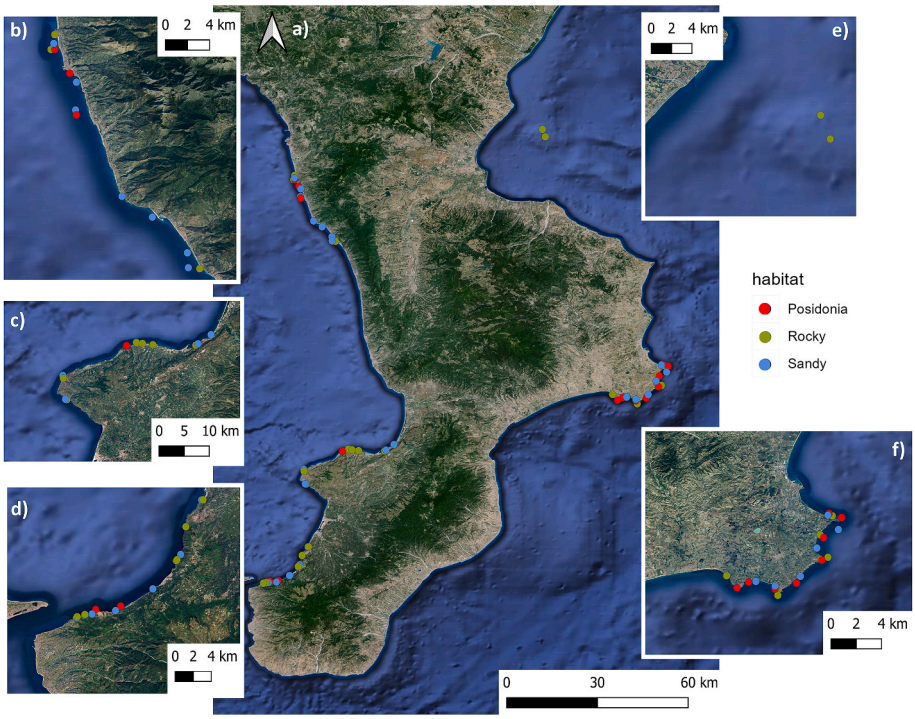

Fig. 1. a) Map of Calabria, study area. The dots represent the sampling sites (62 in total). The colors of the dots are used to differentiate the habitats (red = Posidonia meadows, green = rocky bottoms, blue = sandy bottoms). **b-f)** panels represent each location sampled (Cetraro, Vibo Valentia, Scilla, Amendolara, Capo Rizzuto, respectively).

replicates (from now on referred to as "transects"; see complete information about sites in Supporting Information Table S1) were performed, achieving a total of 496 transects. Among the total number of sites, 24 were rocky, 23 sandy, and 15 were *P. oceanica* (seagrass) meadows. At each site, the actual habitat sampled (Rocky, Sandy, *Posidonia*) was recorded, to visually confirm the EUNIS prediction via ground-truthing. Any discrepancy from the original habitat of the sampling design was recorded and each site was assigned to the verified habitat category to be used in the following analyses. Habitats, in the field, were classified based on the coverage of the dominant habitat at each site. Habitat coverage estimates were conducted visually for each replicate transect (see below) and averaged per site (see complete information about habitat coverage per site in Supporting Information Table S2). Given the inherent heterogeneous nature of Mediterranean coastal habitats at the scale of sampling, some sites (58 %) included more than one habitat, with the median coverage for the main habitat being 96.1 % and overall limited coverage of the other habitats.

Along each transect, sampling was carried out according to the protocol described by Harmelin-Vivien et al. (1985), largely adopted in the Mediterranean (e.g. Di Franco et al. 2009; Sala et al. 2012; Di Lorenzo et al. 2020). We used strip transects of 25 m × 5 m, with a total surface of 125 m^2. Along each transect, a trained diver operator using SCUBA equipment swam one way at a constant speed, covering each transect in approximately 6–8 min. The diver recorded all fish species, estimating the abundance and the size of all fishes encountered. The actual number of fishes encountered was recorded up to 10 individuals, whereas larger groups were recorded using categories of abundance (i.e., 11–30, 31–50, 51–200, 201–500, >500 ind.). Fish size (total length, TL) was recorded within 2 cm size classes for most of the species, and within 5 cm size classes for large-sized species (maximum size >50 cm) such as *Epinephelinae* (Bortone and Mille 1999; Edgar et al. 2004; Mallet and Pelletier 2014). Because of the cryptic nature of some benthic species in the Mediterranean assemblages (e.g., Blenniidae, Gobiidae, Scorpaenidae; Thiriet et al., 2016) during the way back to the starting point of each transect, the operator selectively looked for cryptic fish species (always identifying at the lowest possible taxonomic level) under rocks, in crevices and in other hidden portions of the sea bottom (e.g. under algal canopy or within the meadow), to ensure a complete and consistent census of all species. Some individuals could not be identified at species level, so a higher taxonomic level has been adopted (e.g., *Atherina* sp., *Pomatoschistus* sp., Mugilidae, *Sphyraena* sp., *Trachurus* sp.). For simplicity and given that the vast majority of fishes have been identified at species level (96.4 %), all taxa will be referred to as "species" from this point on. The diver also recorded the coverage of the habitat (in percentage, as previously described), starting and ending depths, then averaged to obtain a mean depth for each transect. The starting and ending depths of each transect have been kept within a limited range (approx. 4 m), to reduce within-replicate variability.

To maximize consistency in fish identification, UVCs were carried out at all sites by the same team of trained scientific divers.

Finally, values of 13 environmental variables (10 abiotic and 3 biotic; see complete table in Supporting Information, Table S.3) were retrieved from online databases, made available by Copernicus Marine Service (CMEMS). In addition, values of a compound index representing the human impact score on marine ecosystems in the Mediterranean Sea (Micheli et al. 2013), were also retrieved. All the variable values were associated with each site. Data with temporal variability were handled by averaging the monthly values of the year before the sampling.

2.3. Data analyses

From the raw data, species richness (i.e. total number of species) and fish density (i.e., number of fish individuals) was computed for each transect (using the *'vegan'* package in R; Oksanen et al. 2022). Fish biomass (i.e., wet weight, in g) per each individual recorded was estimated from size data using length–weight relationships from the available literature, selecting coefficients referring to Mediterranean samples whenever possible (Froese and Pauly 2023). Biomass per species and total biomass for each transect (i.e., community biomass, Cardinale et al. 2013) were then computed summing up the biomass of each individual

within each transect. Shannon-Wiener index (H'; Spellerberg and Fedor, 2003) and modified Simpson's index of diversity (1-D, where D represents Simpson's Index; Keylock, 2005) were also computed using the *'vegan'* R package (Oksanen et al. 2022). All the metrics above were calculated for each transect.

To assess the potential differences and uniqueness of the fish assemblages in the considered habitats, the "dominant habitat" for each fish species was identified. This value is intended as the habitat in which the abundance of a species was the highest and can inform about the habitat preference of a species and has been computed following Harper et al. (2022). We also compiled the information for the species that were found in just one habitat ("unique species" for a given habitat), and the percentage of them over the total number of species found in that habitat (Hall and Kingsford 2021; Harper et al. 2022). On the other hand, to assess potential similarity in the assemblages occupying different habitats, the species in common between two or all three habitats were identified. These two metrics have not been related to their abundance, but just to their occurrence in the specific habitat.

β-diversity was evaluated based on the approach proposed by Legendre and De Cáceres (2013). β-diversity estimates were computed using the function *'beta.div'* in the R package *'adespatial'* (Dray et al. 2012). The function calculates the two components of β-diversity: Local Contribution to Beta Diversity (LCBD), comparative indicators of the contributions to β-diversity of each habitat, and Species Contribution to Beta Diversity (SCBD), which measures the relative importance of each species in affecting β-diversity (Xia et al. 2022). The initial data were scaled using "Hellinger transformation" to avoid excessive effects related to very large values.

Potential variability in the univariate diversity metrics (species richness, mean density, mean biomass, Shannon-Wiener index, modified Simpson's index of Diversity, LCBD), between habitats and accounting for spatial variability (including locations and sites), were tested through analysis of variance (ANOVA, package *'nlme'* in R; Pinheiro et al. 2022), designed with a mixed-effects model, in which the 'site' (62 levels) was nested in the 'locations' (5 levels), being both random factors, and being nested in the 'habitat' (fixed; 3 levels: rocky, sandy, *Posidonia*). To assess whether the inclusion of the random factors improved the ANOVA based on the Akaike Information Criterion (AIC) results, models where each of the factors was removed were performed. For all the metrics, the full model was the best in fitting our data and was chosen over the reduced models. Once the model was run, model assumptions were verified by visually checking the absence of any pattern dealing with the residuals and their normality distribution (Zuur and Ieno 2016). Post-hoc tests on the main factor (habitat), whenever appropriate, were performed using pairwise comparisons among the groups (*'emmeans'* package in R; Lenth 2022).

To analyze the differences in the assemblage structure between the considered habitats, a PERMANOVA (Anderson 2001), based on Bray-Curtis dissimilarity, was carried out on square root-transformed data. A "dummy variable" (value 1) was added, to tackle the problems regarding the many zeros in the data matrix, which is a common issue in ecological data (Zuur et al. 2010). The same experimental design used for ANOVA was adopted (i.e., 'site' nested in the 'locations', being both random factors, and being nested in the fixed 'habitat' factor). PERMANOVA analyses were computed using PRIMER v7 & PERMANOVA + software (Anderson et al., 2008).

To graphically represent the multivariate information about the diversity in species composition in different habitats, a non-metric Multidimensional Scaling (nMDS) based on Bray-Curtis dissimilarity on square root-transformed data was carried out (using the 'metaMDS' function of the *'vegan'* package). Also in this case, a "dummy variable" was added to the original data.

To assess the potential drivers shaping patterns of coastal fish diversity we developed three models, a linear model, a Poisson Generalized Linear Model (GLM), and a Poisson Generalized Additive Model (GAM), (i.e., with the Poisson error distribution type), with species richness as response variable. The three models were tested based on AIC results and the graphic inspection of the residuals to select the best one. Before running the models, the 14 predictors were checked for multicollinearity (Zuur et al. 2010). The variance-inflation factor (VIF; Allison, 1999), a measure for the increase of the variance of the parameter estimates if an additional variable is added to the linear regression, was used for this purpose, and only the variables with a VIF value lower than 4 were retained for further analyses. We used a backward selection approach, useful to fit the regression models in which the choice of predictive variables was carried out manually. To this end, the stepwise model selection was performed by comparing the AIC of the full model and the ones of all the possible combinations of reduced models, to finally select the model with the lowest AIC value and the lowest number of variables.

Prior to all the analyses, we checked sample size adequacy (in our case the minimum number of UVC transects to be performed at each habitat) for properly discriminating habitats. Specifically, we implemented the package SSP (simulation-based sampling protocol) in R (Guerra-Castro et al. 2021), a suite of functions that uses the dissimilarity-based multivariate standard error (Anderson and Santana-Garcon, 2015) to evaluate the adequacy of different sampling efforts for testing hypotheses. SSP returns a range of sampling sizes for which sampling effort is considered 'suboptimal' and 'optimal'. In order to be as conservative as possible, we pooled all sites of a given habitat together, therefore not partitioning spatial variability. MultSE showed that a minimum of 6 (for Sandy) and 7 (for *Posidonia* and Rocky) transects were an 'optimal' sample size per habitat (Figs. S1–S3), numbers lower than the sample size we adopted at each site (and therefore much lower of the overall number of replicates performed at each habitat).

In order to assess the potential effect of the presence of secondary habitats in a site on the overall within-habitat dissimilarity, we calculated MultSE on subsets of the entire dataset for each habitat. Specifically, we calculated MultSE using only transects with $\leq$80% of coverage of the main habitats (for *Posidonia* and Rocky), transects with 80–90% coverage, and transects with coverage $\geq$90% for the main habitats. Results did not indicate substantial differences among the subsets within each habitat, and an absence of clear directionality (Figs. S1–S3), suggesting that no particular differences were associated to the transects with different coverage of the main habitats we sampled. Based on this evidence all the transects have been used for the analyses.

All the analyses were conducted using Rstudio 2022.07.2 (RStudio 2020) unless otherwise stated.

3. Results

In total, 72 species were recorded, belonging to 25 families (see complete table in Supporting Information, Table S.4). The most represented families were Labridae (13 species), Sparidae (13 species), Gobiidae (10 species), and Serranidae (7 species). Some of the species were regularly observed in a relevant number of replicates (e.g., *Coris julis*, 52.6 % of the transects), while others were observed on just a few occasions (e.g., the family Tripterygiidae, 3% of the transects). In a very limited number of cases, fish were identified at genus (e.g., *Trachurus*, *Sphyraena*) or family (e.g., Mugilidae) level due to the limitations of visual identification. A total of 56 (78%) species were found in rocky bottoms, 38 (53%) species in *Posidonia* meadows and 32 (44%) species in sandy bottoms.

Species richness (Fig. 2a) differed significantly between the habitats (df: 6, F: 360.2, $p < 0.05$, ANOVA, pairwise-tests all <0.001) with rocky bottoms showing the highest number of species per transect (10.22 $\pm$ 0.19 species/125 m^2, mean $\pm$ SE), followed by *Posidonia* meadows (6.96 $\pm$ 0.20 species/125 m^2) and sandy bottoms (1.26 $\pm$ 0.08 species/125 m^2).

Mean fish density (Fig. 2b) showed that sandy bottoms have significantly lower values than the other habitats, (df: 6, F: 29.7, $p < 0.05$, ANOVA, pairwise-tests all <0.001). Fish density resulted highest on

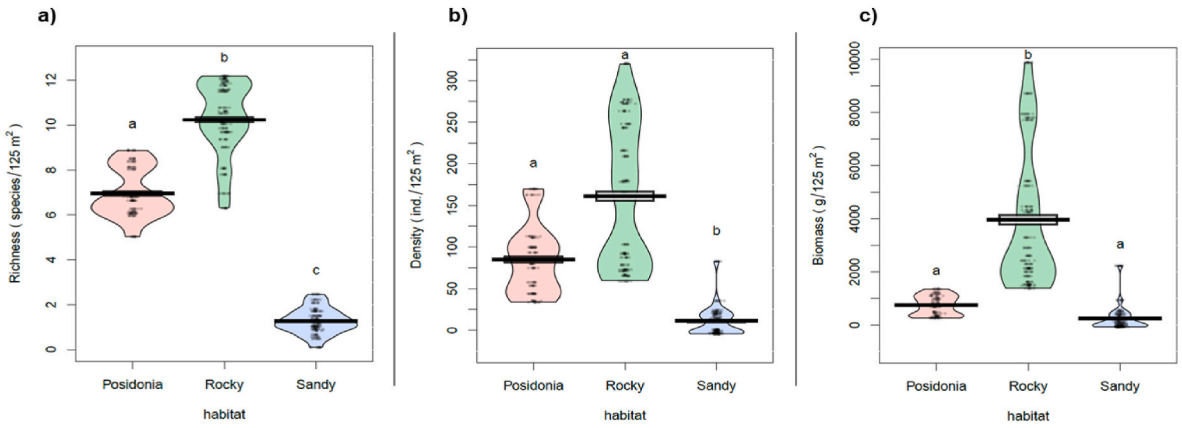

Fig. 2. Richness (a), density (b), and biomass (c) of fish species associated to each habitat. The plotted values are the ones predicted by selected models (see Methods section 2.3). The colored beans represent the density distribution of the data; the black bars show the standard error (SE) of the mean (black lines). The letters (a, b, c) over the beans represent the significant differences resulting from the ANOVA tests (i.e., same letter means that there are no significant differences between the habitats; see Results section 3.1).

rocky bottoms (161.22 ± 10.93 ind./125 m^2), followed by *Posidonia* meadows (84.81 ± 7.69 ind./125 m^2), and lastly by sandy bottoms (11.01 ± 4.21 ind./125 m^2).

Biomass values (Fig. 2c) were statistically higher for rocky bottoms compared to the other habitats (df: 6, F: 22.8, $p < 0.05$, ANOVA, pairwise-test <0.001), with a mean value of 3949.8 ± 344.2 g/125 m^2, followed by *Posidonia* meadows (738.7 ± 72.2 g/125 m^2) and sandy bottoms (244.3 ± 105.2 g/125 m^2). Further details about abundance, density, and biomass of single species are available in Supporting Information Figures S4, S.6, and S.7).

The Shannon index (H'), presented the highest value in rocky bottoms (1.43 ± 0.04), followed by *Posidonia* meadows (1.14 ± 0.04) and lastly by sandy bottoms (0.23 ± 0.03) (df: 6, F: 166.9, $p < 0.05$, ANOVA, pairwise-tests all <0.001; see Supporting Information figure S7).

The values for the modified Simpson's index of Diversity (1 – D) confirmed higher diversity of rocky bottoms, where this value was 0.62 (± 0.015), followed by *Posidonia* meadows with 0.5 (± 0.016), and lastly by sandy bottoms with at 0.37 (± 0.03). The differences between the groups were statistically significant (df: 6, F:11.6, $p < 0.05$, ANOVA, pairwise-test <0.001) for all group pairs except for rocky bottoms and *Posidonia* meadows.

In rocky bottoms, the number of unique species found was 16 (28.6% of the total number of rocky species), followed by 14 unique species in sandy bottoms (43.8% of the total number of sandy species). No unique species were recorded on *Posidonia*. On the other hand, the two habitats sharing more species were rocky and *Posidonia* (24 species), while sandy bottoms shared 4 species with only rocky bottoms (*Dasyatis Pastinaca, Gobius incognitus, Lithognathus mormyrus,* and *Pomatoschistus* sp.) and 2 with only *Posidonia* meadows (*Pagellus acarne* and *Pagrus*). Furthermore, 12 species are shared between all the three considered habitats (e.g., *Chromis*, *Sarpa salpa* and *Mullus surmuletus;* see Supporting Information figure S8).

Sandy bottoms were the ones with statistically highest LCBD values (0.0025 ± 7.45 × 10^{-5}), while no differences were recorded among *Posidonia* meadows and rocky bottoms, with respectively 0.0019 (± 3.54 × 10^{-5}) and 0.0016 (± 2 × 10^{-5}) (df: 6, F: 27.6, $p < 0.05$, pairwise-test <0.001). The most influential species, with a SCBD value of 0.18, is *Xyrichtys novacula*, inhabiting exclusively sandy bottoms, followed by *C. chromis* (0.12), *C. julis* (0.052), *Oblada melanura* (0.049), and *Bothus podas* (0.048) (Fig. 3b).

Within habitat multivariate variability was reduced in rocky bottoms, and in *Posidonia* meadows, with these two habitats overlapping in multivariate space (nMDS, Fig. 4). Sandy bottoms were instead completely separated from the other two clusters, and the differences in the rank-based distances between the sites were larger.

The PERMANOVA (Table 1) on the density data matrix revealed significant differences among the three habitats (df: 2, pseudo-F: 25.5, $p < 0.0001$. Both location (df: 10, pseudo-F: 2.4, $p < 0.001$) and site (df: 49, pseudo-F: 4.5, $p < 0.001$) factors were significant. The pairwise tests performed for the habitat factor confirmed that each habitat was significantly different from the others ($p < 0.001$).

The GAM-based model (see Methods section 2.3 and Table 2) assessed that all the factors were statistically significant ($p < 0.05$) apart from "chl" ($p = 0.0594$), that was still included because the model slightly improved. Among the three families of models tested, the one with the best fit (AIC results, Table S.5), was the GAM-based model. The backward selection of the variables optimized the previously selected model with a lower AIC (1915.221), and finally allowed the composition of the final model, that is a GAM model with a Poisson error distribution composed of:

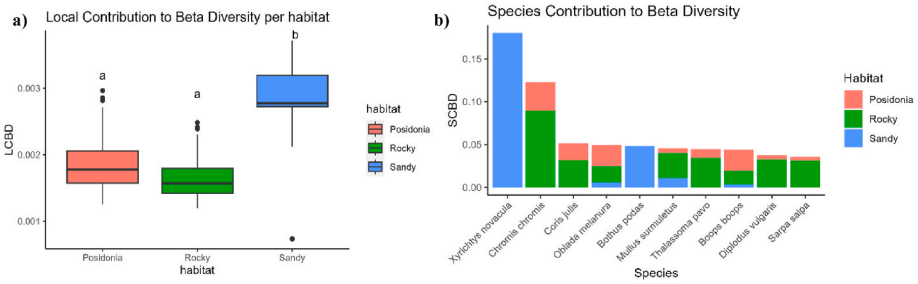

Fig. 3. Local Contribution to Beta Diversity (LCBD) per habitat (left panel, a), and Species Contribution to Beta Diversity (SCBD) (right panel, b). Each column for Fig. 3 (b) represents the contribution of the species to beta diversity, while the stacks within each column represent the relative abundances of that single species in each of the three habitats considered.

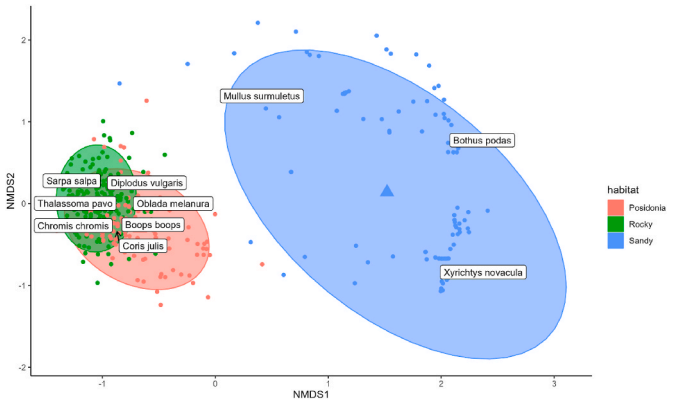

Fig. 4. Nonmetric Multidimensional Scaling (nMDS) for the sites (points) per habitat type (colors). The groupwise centroids (triangles) have been calculated to allow the clusterization and highlight the distinctions between the habitats. The species displayed in the labels (10) are the ones with the highest contribution to β-diversity. Stress: 0.17.

Table 1
PERMANOVA output on the square root transformed data of the fish density.

Source	df	SS	Pseudo-F	p (perm)
habitat	2	5.17 x 10^5	25.504	<0.0001
location(habitat)	10	1.14 x 10^5	2.4339	<0.0001
site(location(habitat))	49	2.31 x 10^5	4.4813	<0.0001
Residuals	434	4.56 x 10^5		
Total	495	1.42 x 10^6		

Table 2
Test on the terms of the selected GAM model for species richness. The df values noted with "*" are referred to "expected" degrees of freedom.

Factor	df	Chi squared	p-value
habitat	2	882.610	<2 x 10^{-16}
chl	1	3.553	0.0594
s(SST)	1.609*	7.452	0.00396
s(SSS)	5.587*	62.163	<2 x 10^{-16}

$$\text{Richness} \sim f(\text{habitat}) + s(\text{SST}) + s(\text{SSS}) + \text{chl}$$

Where "habitat" is the main factor related to richness, "Sea Surface Temperature" (SST) and "Sea Surface Salinity" (SSS), are included in a smoothing term with a shrinked cubic regression spline, and "chlorophyll-a" (chl) is linearly correlated to the response variable. The number of knots has been chosen in accordance to Wood (2017).

The model results showed that habitat (Fig. 5a) appears highly significant in shaping richness values, in accordance with results presented earlier on. In regard to the environmental variables, fish richness was negatively correlated with SST (Fig. 5b), and the predicted trend shows a change in the steepness after around 21 °C. Similarly, as SSS increases, species richness decreases, showing an almost linear trend for this variable (Fig. 5c). As for the chlorophyll-a concentration (Fig. 5d), this variable causes similar responses to SST and SSS, so its increase leads to a linear reduction of species richness.

4. Discussion

The present study uncovered the underestimated contribution of sandy habitats to fish biodiversity, in particular in terms of contribution to β-diversity. Rocky bottoms and *P. oceanica* meadows showed a tendency to share several species. Conversely, sandy bottoms, which were the least diverse among the three according to assemblage metrics, held marked differences regarding the specific composition. In fact, sandy bottoms shared a limited number of species with the other habitat types, and they presented a high number of unique species, and the highest proportion of unique species over the total number of species recorded in a habitat. So, even if sandy bottoms were less diverse in terms of species richness, our results highlighted the unique importance of them in hosting unique species that contribute to the overall coastal fish diversity patterns.

Fish richness we recorded is consistent with, or higher than, other studies performed in the Mediterranean Sea using the same methodologies (UVC) and considering a similar spectrum of habitat-types (Guidetti 2000; La Mesa et al. 2011; Giakoumi and Kokkoris 2013). Those studies represent important evidence of the effect of habitat type on fish assemblages' composition. In the present study, assemblage descriptors (richness, density, biomass, and diversity indices) generally showed significant variability between the habitats considered, with the highest values associated to rocky bottoms, followed by *P. oceanica* meadows, and lastly, by sandy bottoms. This evidence was also supported by our analyses, which account for a large set of variables (environmental and related to anthropogenic pressure), that have been included in past studies as potential drivers of change in species composition (Anderson and Millar 2004; Mesa et al. 2006; Giakoumi and Kokkoris 2013; Henseler et al. 2019). In our case, mean biomass was not significantly different between *P. oceanica* meadows and sandy bottoms also in accordance with other studies (e.g., Giakoumi and Kokkoris 2013). Further, mean density did not significantly differ between rocky bottoms and *P. oceanica* meadows. This information, along with higher values of biomass in rocky bottoms, could be supportive of the nursery role of *P. oceanica* meadows (Guidetti 2000; Díaz-Gil et al. 2017), with a relatively high number of generally small-sized individuals (and so accounting for a limited biomass), characterizing juvenile fishes (Francour 1997). Sandy bottoms were instead associated with lower density and biomass values, as expected from previous studies (Guidetti 2000; Giakoumi and Kokkoris 2013). It must be clarified that other factors, such as the level of protection (Sala et al. 2012; Guidetti et al. 2014; Di Franco et al. 2021) or the biotic and abiotic complexity (García-Charton et al. 2004; Di Franco et al. 2021), could be influencing biomass to a larger extent than the habitat type recorded at such a small resolution, but were not directly analyzed in this context.

The calculation of β-diversity, dividing it into a contribution of each habitat (LCBD) and contribution of the species (SCBD), made it possible to specifically detect which were the habitats and species most contributing to β-diversity. Sandy bottoms had the highest LCBD values. To our best knowledge, there is no other evidence of the application of LCBD and SCBD to fish fauna in Mediterranean marine coastal habitats, but the result is in accordance with a recent study carried out in a tropical ecosystem by Harper et al. (2022), that followed a similar approach. In our study, *X. novacula* and *B. podas* were ranked among the top five contributors to β-diversity (SCBD). It is already known that both species are commonly inhabiting sandy and muddy bottoms (Castriota et al. 2005; Esposito et al. 2010), and in our case these two species were uniquely associated with this habitat. The other three species among the top five contributors of β-diversity were *C. chromis*, *O. melanura*, and *C. julis*. These species are defined as generalist species, inhabiting most of the coastal habitats of the Mediterranean Sea, but with a marked preference for hard and vegetated substrates (Fasulo et al. 2010; Gkafas et al. 2013; Pinnegar 2018). In fact, we found high abundances of individuals belonging to these species in both rocky bottoms and *P. oceanica* meadows, while observations on sandy bottoms were sporadic. First, the mentioned high densities and density distribution are partly explanatory of their contribution as species to β-diversity. Second, this result could be interpreted as an added proof of the similarity in species composition of the two mentioned habitats, which had quite similar LCBD values, probably due to the similar capability of the two habitats to support a similar set of species (e.g., by providing refuges and protection from predators, food items, etc.). In general terms, when considering the species present in rocky bottoms and *Posidonia* meadows and comparing them to the ones on sandy bottoms, it is possible to

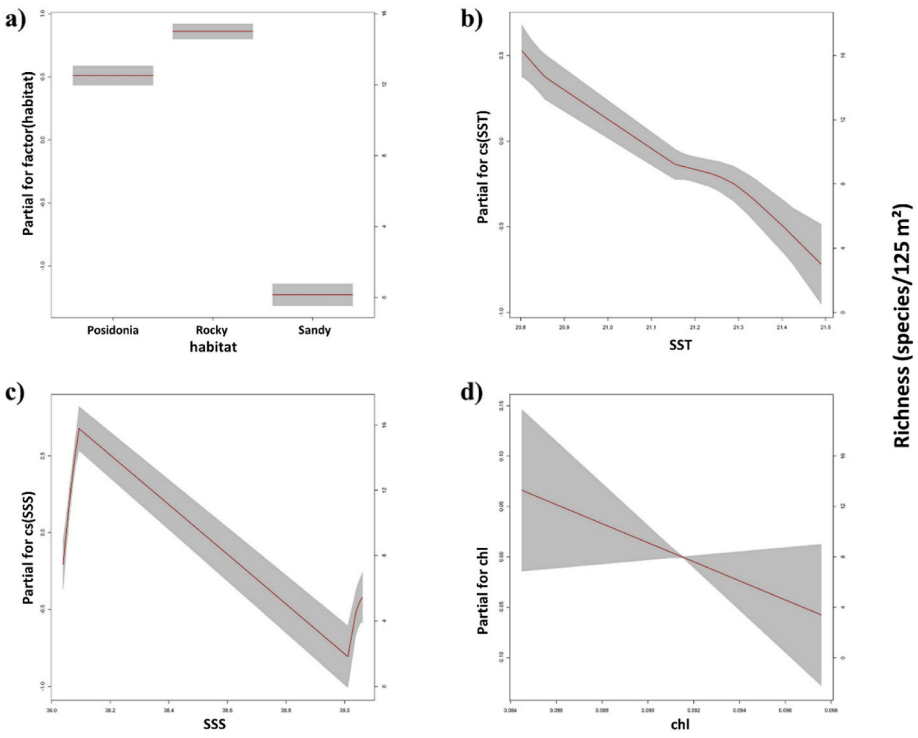

Fig. 5. Results of the GAM model for the specific richness regarding each individual variable. (a) Habitat, (b) Sea Surface Temperature (SST), (c) Sea Surface Salinity (SSS), and (d) Chlorophyll-a (chl). Dual y-axes indicate partial effect (on the left) and Species richness (species/125 m^2) for each of the four plots.

explain a consistent part of the marked differences in fish assemblages' composition found both for the LCBD and the nMDS. The rank-based positions of the species confirmed that *X. novacula* and *B. podas* were the most "distant" species from rocky bottoms and *P. oceanica* meadows and were probably responsible for the disproportionate contribution of sandy bottoms to LCBD. Moreover, the results regarding the species composition of the fish assemblages in the three habitats considered are consistent with previous evidence comparing similar habitats in the Mediterranean Sea (Guidetti 2000; Giakoumi and Kokkoris 2013).

From a methodological point of view, the division of β-diversity in SCBD and LCBD has been recently applied in tropical (Harper et al. 2022) and inland ecosystems (Heino and Grönroos 2017), but very few times in the Mediterranean Sea (Bevilacqua et al. 2023), and never on fish assemblages. Despite the lack of a robust set of evidence on similar systems, those components of β-diversity could be important from a basic ecological and conservation point of view. LCBD indicates the ecological uniqueness of a site (or habitat in our case; Legendre and De Cáceres 2013), being a very useful approach to characterize habitats, possibly at different spatial scales. SCBD could be a useful indicator of species that need a special focus, being the most contributing to β-diversity, but are neglected by conservation initiatives at the moment due to their association with less-considered habitats. To mention, a possible limitation of this approach is that values of LCBD could be negatively correlated to the species richness of each site (Harper et al. 2022) or abundance (in the case of abundance-based data; Heino and Grönroos 2017), so this value could be inflated by these correlations for species-poor sites. Nonetheless, in our case, all the other results confirm that sandy sites are able to create heterogeneity and generate β-diversity across the seascape. For the same reason, the high abundances of some of the mentioned species could have had an influence on the calculation of their SCBD values (Carlucci et al. 2018). Another aspect to consider is that among the species uniquely found in sandy bottoms (and so contributing to LCBD for this habitat and to the overall pool of species), three species (*Deltentosteus quadrimaculatus, Hippocampus hippocampus, and Parablennius tentacularis*) were sampled in sites where a limited coverage of *Cymodocea* was present, and they could well be associated more with this seagrass species than strictly sandy bottoms. However, heterogeneity in coastal habitats is the rule, and identifying a large number of "pure habitat" sites at multiple locations could prove unrealistic, and it is often the case that secondary minor habitats are included in sampled sites (see e.g., Di Franco et al. 2009; Guidetti et al. 2014). In addition, our analyses of dissimilarity-based multivariate standard error (see methods section) revealed that transects and sites with limited coverage of secondary habitats did not considerably increase overall within-habitat variability.

It has to be noted that the species richness recorded in each habitat/site could have been affected also by the tridimensional habitat complexity, with high complexity-habitats/sites that could have challenged the possibility to record some species, especially the cryptic ones. This could be the case of particularly complex rocky sites (both in terms of abiotic and biotic components, see Di Franco et al. 2021), or site with highly dense *Posidonia* meadows, with individuals that could live in crevices or under the algal canopy or within the seagrass meadow (see Thiriet et al. 2016). To prevent or limit this potential bias, great care was taken by the observers to look for cryptic fish and small individuals in crevices, under algal canopy or within the meadow, to ensure a complete and consistent census of all species.

The significant contribution of sandy bottoms to β-diversity and to the overall species richness also help to explain why these "poor" and "underestimated" habitats are worth considering in biodiversity conservation practice. Most Mediterranean Marine Protected Areas (MPAs) have been designated to protect rocky bottoms that host species of high commercial value or *Posidonia oceanica* beds that are a priority conservation habitat according to the EU Habitats Directive (92/43/EEC). Conversely, shallow sandy bottoms have rarely been considered habitats worthy of protection in the Mediterranean Sea. However, according to systematic conservation planning, a rigorous framework for designing protected areas (Margules and Pressey 2000), networks of MPAs should adequately encompass the diversity of habitats that are present in a region and all the species they host while also sustaining a high density of individuals (Di Lorenzo et al. 2016). Therefore, future conservation plans should target the protection of sandy bottoms as well (see

Giakoumi et al. 2011) to ensure that marine biodiversity is conserved at larger scales, especially in light of the need to move towards the accomplishment of the 30 × 30 conservation target, i.e., to effectively protect 30% of the ocean by 2030 (Hermoso et al. 2022).

Our predictive model highlighted that the habitat-type is the main predictor of species richness, but also that sea surface temperature (SST) and salinity (SSS) significantly influenced species richness, and more specifically, we highlighted a negative correlation of species richness with SST and SSS. This result can hold an informative value for incoming scenarios of warming/tropicalization of the Mediterranean basin and be useful added evidence to correctly address future guidelines for conservation purposes. In addition, a decrease in fish species richness has also been observed along a latitudinal and longitudinal gradient in region-wide studies at the Mediterranean basin scale (e.g., Guidetti et al. 2014; Giakoumi et al. 2019). In these studies, species richness was found to be higher in the northwestern than in the southeastern Mediterranean Sea, where the average sea temperature is higher, and the waters are characterized as oligotrophic. Our results regarding the contribution of Sea Surface Temperature support this trend, even if restricted to a reduced spatial scale. Moreover, while non-indigenous species have been recorded over the sampling operations, the drivers of species richness could still be favoring some native range-expanding species (e.g., *S. cretense;* Azzurro 2008) to spread more than others, knowing that temperature and salinity are among the major drivers of fish species re-distribution and northward shift in the Mediterranean Sea (Chaikin et al. 2022; D'Amen et al. 2023). These drivers are widely used in the characterization of climate change (Bethoux and Gentili 1999; Beaugrand 2014), thus evidence on their effects on fish richness is important in increasing the predictive capacity regarding fish assemblages' distribution. Moreover, increasing values of SST and SSS could favor the appearance of non-indigenous species, with relevant effects on the dynamics of entire ecosystems (Bax et al. 2003; Azzurro et al. 2022). Despite the range of SST (approx. 0.7 °C) and SSS (approx. 1 psμ) considered in our study could appear limited, this variation could determine non-negligible effects on the investigated assemblages. In fact, the variation in SST covered by our study equates to the raise in SST that occurred globally in the last 6-7 decades (see Venegas et al. 2023) and more specifically to approximately 50% of the change in SST predicted in the Mediterranean Sea (one of the area of the global ocean heating fastest) between 1961–80 and 2040–59 (Albouy et al. 2013) with these changes in SST that have been associated to major changes in species distribution and abundance.

It is worth mentioning that in this study we did not detect any effect of human impact on fish assemblages, using the human impact score developed by Micheli et al. (2013) as a proxy. Nonetheless, the presence of anthropogenic impacts on the Mediterranean Sea biodiversity is widely known (Coll et al. 2012), so the absence of significant effect in our study could be due to a different number of reasons, including the possibility that the impact score considered could not describe effectively the human impact at the spatial resolution considered in our study.

A further development of our study could be related to its scalability to a larger spatial domain, such as the entire Western Mediterranean, in order to be able to capture a wider range of variability in potential drivers of species richness, and account for a larger pool of species (Blowes et al. 2020), also by sampling over different seasons, given the possible normal variability of coastal fish assemblages throughout the year.

The present study is one of the few integrated works about fish biodiversity covering different habitats of the Mediterranean Sea, providing a useful reference from an ecological, conservation, and methodological point of view to stimulate further investigation on the plethora of habitats of which this basin is composed and complement the information on fish diversity of the coastal habitats and on their relative importance in a holistic form.

CRediT authorship contribution statement

Enrico Cecapolli: Writing – original draft, Investigation, Formal analysis, Data curation. **Antonio Calò:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Sylvaine Giakoumi:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Conceptualization. **Manfredi Di Lorenzo:** Writing – review & editing, Methodology, Conceptualization. **Silvestro Greco:** Writing – review & editing. **Emanuela Fanelli:** Writing – review & editing. **Giacomo Milisenda:** Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Antonio Di Franco:** Writing – original draft, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on reasonable request.

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Appendix B. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106701.

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