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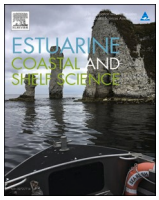

Re-discovering macerating *Posidonia oceanica* bottoms: Characterization of meiofaunal community inhabiting a peculiar Mediterranean habitat

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ABSTRACT

The highly efficient carbon storage capacity of beds formed by *Posidonia oceanica*, an endemic Mediterranean seagrass species, has been widely recognized. Recently, the supra-littoral deposits of leaf litter (i.e., *banquettes*) have been investigated in terms of their nutrients, biomass and associated community. Nevertheless, an overlooked fraction of the *P. oceanica* detritus never reaches the shore and sinks far away to deeper seafloor. Additionally, part of the supra-littoral deposit goes back to the sea during winter swells. This deep detrital compartment, mainly composed of sediment mixed with dead leaves and rhizomes coming from *P. oceanica* beds, has only been described once by Pères in 1953, who focused on the macrofaunal component. Here, we investigated for the first time the meiofaunal community inhabiting sediments characterized by *P. oceanica* detritus in a deposit located at 65–80 m depth off the Ischia Island (Gulf of Naples, Italy, Tyrrhenian Sea). Our results show that the meiofaunal community appears highly diversified and strongly dominated by nematodes (from 85% to 93%). Differences in meiobenthic assemblage structures were significant only when rare taxa were considered (i.e. taxa found in low abundances and characterized by a sporadic distribution in the study area). The nematode community revealed a very high biodiversity (number of families and genera: 31 and 104, respectively), with a clear prevalence of selective and non-selective deposit feeders that suggest the key role of this habitat in the benthic detrital food web. The richness of meiofauna and the taxonomic and functional diversity of the nematode assemblages account for a "good" to "moderate" ecological quality status. These findings support the high ecological value of the macerating seagrass bottoms, an overlooked component of the blue carbon cycle that deserves to be further investigated.

1. Introduction

Seagrass beds are among the most important and studied marine vegetated habitats worldwide (Boström et al., 2006; Rendina et al., 2022). *Posidonia oceanica* (L.) Delile is an endemic seagrass species of the Mediterranean Sea that forms wide and highly productive beds in shallow coastal waters (Pergent-Martini et al., 1994; Duarte and Chiscano, 1999). They can extend from 0.5 to 40 m water depth, although, in very oligotrophic water, they can occur up to 50 m (Duarte, 1991). They provide several ecosystem services, and particularly key regulation services, such as carbon sequestration/stock, water purification, sequestration of nutrients and contaminants, stabilization/consolidation of seabeds and coastal erosion protection (Boudouresque et al., 2016; Campagne et al., 2015). In addition, due to their high structural complexity and productivity, *P. oceanica* beds are spawning, settlement, nursery, and feeding habitats for many species at different trophic levels, ranging from primary producers, living on *P. oceanica* leaves, to top consumers, preying within the canopy (Appolloni et al., 2023; Capasso et al., 2024).

P. oceanica beds are protected and monitored at European level, by the Habitats (92/43/CEE), Water (2000/60/EC), and Marine Strategy Framework (2008/56/EC) Directives. Indeed, during the last decades,

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an alarming regression of *P. oceanica* beds along the Mediterranean coasts has been recorded (Blanco-Murillo et al., 2022). This phenomenon is mainly due to human activities, such as changes of alongshore currents by maritime works, trawling, anchoring, aquaculture, etc. (Marbà et al., 2014; Telesca et al., 2015).

Although anthropogenic pressure enhances leaf/rhizome undermining, leaf loss also occurs seasonally in *P. oceanica* due to its natural vegetative cycle (Bay, 1984). These leaves can be driven by currents both onshore, building up the supra-littoral deposits of leaf litter known as "banquettes", and offshore, depositing on the sea floor below the lower limit of *P. oceanica* beds (Cebrian and Duarte, 2001; Cresson et al., 2012). Banquettes provide ecosystem services, such as protecting beaches from coastal erosion by reducing the wave energy and contributing to the formation of dunes (Cantasano, 2021). These supra-littoral deposits also represent an important input of nitrogen and carbon to shoreline habitats (Rotini et al., 2020). Furthermore, they constitute a habitat hosting a diverse and abundant benthic community, mainly of detritivores and predators (Mateo et al., 2003; Boudouresque et al., 2016), yet most of the studies were focused on macrobenthos, without taking in account meiobenthos.

Meiofauna are the most abundant and ubiquitous component of the benthic environment, which could become a fundamental tool to answer several ecological questions (Balsamo et al., 2012; Schratzberger et al., 2013). Because of their worldwide distribution and abundance, small size, high turnover rates, meiofaunal assemblages rapidly respond to environmental changes in almost every habitat (Bongers and Ferris, 1999; Sahraeian et al., 2020). Meiofauna represent a highly diverse group of invertebrates with some exclusively benthic phyla. These invertebrates belong to different trophic groups and provide several ecosystem functions and services (Hentschel and Jumars, 1994; Giere, 2009). Energy flow studies on *P. oceanica* bed have shown that only a small portion of primary production is directly consumed by benthic organisms, while most of the plant material is processed in the detrital food chain (Holmer and Olsen, 2002). Meiofauna play a key role in the benthic food web, enhancing energy flow from the microbial community to the entire food web in sedimentary habitats by grazing on bacteria (Coull, 1999; Danovaro et al., 2007; Schratzberger and Ingels, 2018). Therefore, meiofaunal communities can also represent a useful tool to better understand ecosystem dynamics. Additionally, due to their biological characteristics, meiofauna represent a powerful bioindicator in pollution and restoration monitoring (Schratzberger, 2012; Boufahja and Semprucci, 2015; Semprucci et al., 2021).

Nematodes are the most successful, widespread, and abundant component of meiofauna, with several morpho-functional traits, which may be related to important ecological functions (Semprucci et al., 2018, 2022). One of morpho-functional traits is the trophic level that can be recognized by the buccal cavity morphology of each nematode (Wieser, 1953; Moens et al., 2013; Franzo et al., 2022; Grassi et al., 2022). Nematode community alone forms a complex food web driving energy flow from bacteria to fish communities (Schratzberger and Ingels, 2018; Cocozza di Montanara et al., 2022). This diversity in feeding strategy is also reflected in the species taxonomic diversity. Indeed, this phylum is likely the most diversified metazoan taxon on Earth with 10,873 marine species (Nemys eds., 2024), and it is not uncommon to find 50 or more species in a single sediment sample of 10 cm^2 surface (Giere, 2009).

Nowadays, the scientific research about meiofauna is growing faster than in the past, but the knowledge on biodiversity and community dynamics is imbalanced towards macrofauna, especially in seagrass ecosystems (Cocozza di Montanara and Sandulli, 2024). This is mainly due to the fact that macrofauna is easier to analyze and identify from a taxonomical point of view compared to meiofauna (Zeppilli and Leduc, 2018). However, macrofauna and meiofauna have different ecological roles in ecosystems, they may respond to natural and anthropogenic changes at different spatial and temporal scales (Baldrighi et al., 2021; Losi et al., 2021). Indeed, with its planktonic larval dispersal, macrofauna could be indicative of effects over larger spatial and longer temporal scales (Magni et al., 2022; Grassi et al., 2023). On the other hand, with direct benthic development, and generation times as short as one month, meiofauna may indicate effects over smaller spatial and shorter temporal scales (Semprucci et al., 2019; Sbrocca et al., 2021).

The ecological role of supra-littoral deposits of phanerogam leaves has been frequently addressed by the scientific community (Boudouresque et al., 2017), and some authors described the meiofaunal distribution in different seagrass habitats and adjacent sediment, including swallow macro-phytodetritus accumulations (above 20m w. d.) (see García-Gómez et al., 2022 for review). However, the destiny of the leaves transported to deep subtidal habitats and their possible functional role remains unknown, notwithstanding it might constitute a significant repository of benthic biomass. This type of deep detritic accumulation in the Mediterranean Sea was reported only once by Pères (1953) in a note from the dredging campaign carried out by the Marine Station of Endumè along the southern French coasts. In those samples, together with large amounts of *P. oceanica* fibers, Pères noticed the abundant presence of filter-feeding ascidians, ascribing this finding to the bacterial proliferation consequent to high quantity of organic matter (Pères, 1953).

In the present study, during a campaign to update the bionomic map around the Ischia Island (Gulf of Naples, Italy), a macerating *P. oceanica* site has been identified by using a Remotely Operated Vehicle (ROV). Here, the phanerogam fragments occurrence, soaked in a muddy-sandy substrate, increased the structural complexity of the homogeneous soft bottoms and the detrital component accumulation, represented a potentially unique habitat for many metazoans such as the taxa included in the meiofauna community (Hicks, 1986; Coull and Wells, 1983; Mascart et al., 2013). The aim of this pilot work is to characterize the meiofauna associated with a macerating seagrass deposit (dead leaves, rhizomes, and roots), giving the first insights into the meiofaunal community, especially nematode assemblages, inhabiting this overlooked habitat, analyzing both taxonomic and functional aspects.

2. Materials and methods

2.1. Study area and sampling routine

The study was carried out within zone D of Marine Protect Area "Regno di Nettuno". The study area was along a cross-shore gradient on a macerating *P. oceanica* bed (Fig. 1) located approximately 1 km away from the shore of the San Montano Bay, Ischia Island (Naples, Italy), where the presence of a lush *P. oceanica* bed is reported (Buia et al., 1992; Zupo et al., 2006). Seabed was explored with a ROV ("Perseus" of Ageotec) equipped with a high-definition video camera (DVS-3000), in order to detect the presence of deposits of macerating *P. oceanica* leaves and rhizomes (Fig. 2). In the spots characterized by the highest macro-phytodetritus cover, five stations with three replicates each were selected. Samples were collected in June 2020 at 65, 70 and 80 m water depth, by using a 25-L Van Veen grab and then subsampling the upper part of the material and sediment by syringes (26 mm Ø) to collect the top 10 cm. Samples were then stored at −20 °C until laboratory analysis.

2.2. Meiofaunal community analysis

Once in laboratory, each sample was sieved through a 500 μm mesh to remove the macrofaunal fraction, and then through a 31 μm sieve, the lowest size limit of meiofauna (Giere, 2009). Before sieving, samples were treated with ultrasound in order to detach organisms from the grain particles (Danovaro et al., 2004). Meiofauna were extracted from the sediment following the 'density gradient technique' using LUDOX® solution (d = 1.31 g/cm^3) and centrifuged three times to reach an extraction efficiency of >98% of meiofaunal organisms (Giere, 2009). Samples were stored in 70% EtOH and a few drops of diluted Rose Bengal (0.5 g l^{-1}; Heip et al., 1985) were added to stain organisms and

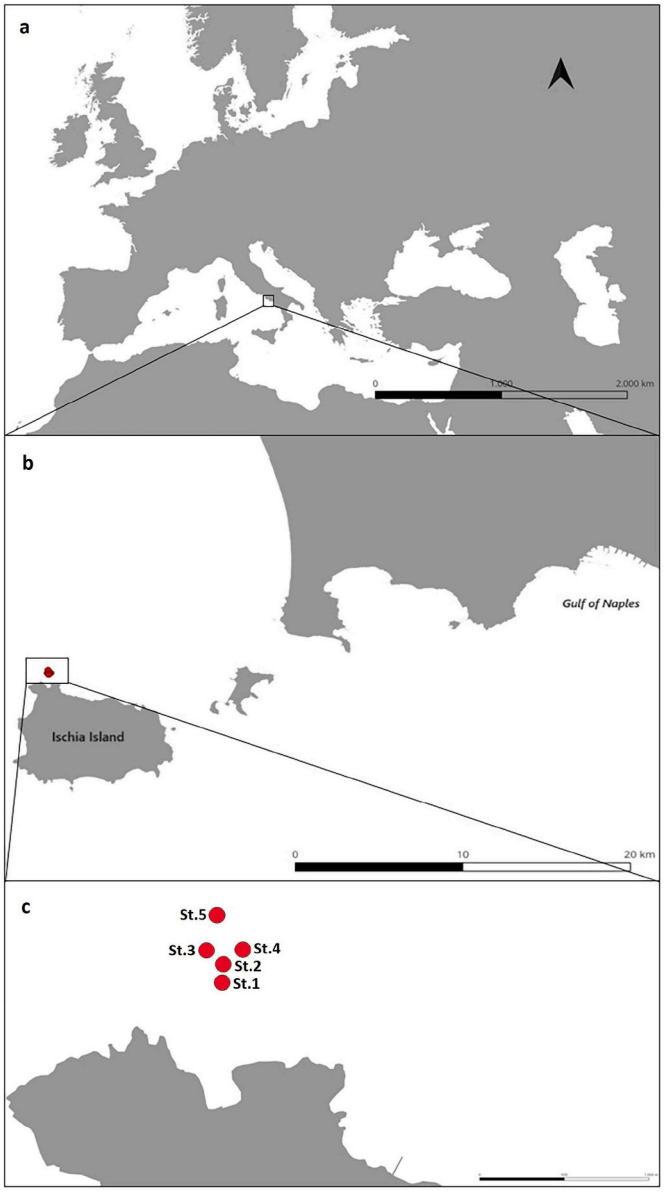

Fig. 1. – Map of the study area. **a.** Mediterranean Sea. **b.** Area off the Campania Coast (Italy; SW Tyrrhenian Sea). **c.** Northwest side of the Ischia Island where sampling stations are located, labeled from station-1 (St. 1) to station-5 (St. 5).

facilitate sorting under a Nikon® SMZ745T stereomicroscope (40x magnification). Using a Delfuss cuvette, each sample was sorted to the higher taxon level based on Higgins and Thiel (1988). The density of all the individuals found (both temporary and permanent meiobenthos) was standardized as abundance in 10 cm^{-2}. The meiobenthic taxa that represented <1% of the total meiofaunal abundance of all investigated samples were considered as rare taxa according to Pusceddu et al. (2011). The taxa diversity of the whole community was measured using the Shannon–Weaver index (H′) (log base e, Shannon and Weaver, 1949) and the evenness as the Pielou index (J) (Pielou, 1975).

2.3. Nematode community analysis

While counting, nematodes were randomly hand-picked for taxonomic identification (at genus level). About 100 nematodes were picked out from each replicate, then dehydrated at 60 °C for 48h in 5% glycerol solution (Seinhorst, 1959). Nematodes were mounted on permanent slides and identified under a light optical microscope (Nikon Optiphoto^{-2}) equipped with a 100 × oil immersion objective. The identification of nematodes at the genus level was carried out using the taxonomic guides of Platt and Warwick (1983, 1988), Warwick et al. (1998) as well as the original descriptions available on the Nemys website (Nemys, 2024). The synecological indices Index of Trophic Diversity (ITD), Maturity index (MI), Shannon–Weaver diversity index (H', log_e-transformed) and the evenness as Pielou index (J) were calculated to better describe nematode communities. In detail, each genus was assigned to a feeding strategy based on the morphology of nematode buccal cavity, according to Wieser (1953): selective (1A) and non-selective (1B) deposit feeders, epistrate feeders (2A) and predators/omnivores (2B). ITD was calculated according to Heip et al. (1985): $ITD = \Sigma\theta^2$, where θ is the percentage contribution of each feeding type. ITD values can range from 0.25 where each trophic group accounts for 25% of the whole nematode community, to 1.0 where one feeding type represents 100% of the community. To calculate MI, each genus was assigned to a value from 1 to 5 that indicates the life strategy of the genus (*i.e.* r-strategist/colonizers: c-p classes 1 and 2, intermediate colonizers: c-p value 3, and k-strategist/persisters: c-p 4 and 5; Bongers and Ferris, 1999; Bongers and Ferris, 1999). The MI represents the weighted average of the colonizer-persister (c-p) classes: $MI = \Sigma v\,(i)\,f\,(i)$, where v is the c-p class of genus i and f (i) is the frequency of that genus.

2.4. Statistical analysis

Biotic data of both meiofaunal and nematode communities were used to construct the taxa-by-replicate matrixes. As for multivariate analysis, an analysis of similarity (ANOSIM), based on Bray-Curtis (dis)similarity measures (replicate matrixes fourth-root and presence/absence transformed) was carried out to determine significant differences ($p < 0.05$) of the meiofaunal and nematode communities among stations. In order to visualize the possible differences of the community structures among the five stations, the non-metric multidimensional scaling (nMDS) ordination was performed on the average taxa abundances fourth-root and presence/absence transformed. The SIMPER (similarity percentage) routine was utilized to determine the contribution of each meiofaunal taxon or nematode genus to similarity/dissimilarity among stations. Furthermore, according to Pusceddu et al. (2011), given that the dominant meiobenthic groups (*e.g.* nematodes or copepods) might mask small community changes, in order to assess the possible differences of the community structure, meiofauna was analyzed using only rare taxa. Rare taxa were defined as the taxa that represented <1% of the total meiofaunal abundance of all investigated samples. The exclusion of dominant groups is often crucial because most of the rare taxa are usually more sensitive to environmental changes (*e.g.,* Bianchelli et al., 2016. An analysis of similarity (ANOSIM) was carried out to determine significant differences ($p < 0.05$) of the communities among stations and the SIMPER (similarity percentage) routine to determine the contribution of each taxon to similarity/dissimilarity among stations. Multivariate statistical analyses and the calculation of taxonomic diversity indices (*i.e.*, H′ and J) were performed with the PRIMER v7 + PERMANOVA (Anderson et al., 2008). Possible differences of the univariate parameters (*i.e.*, meiofaunal and nematode abundances, H′, J MI, ITD indices, trophic groups and c-p classes) among stations were evaluated using the Analysis of Variance (One-way ANOVA). Prior to statistical analysis, the logarithmic transformation log (1 + x) was performed to normalize the data. Tukey's multiple-comparison tests were used when significant differences ($p < 0.05$) were detected.

3. Results

3.1. Meiofaunal community

A total of 13,900 individuals were counted belonging to 15 major meiobenthic taxa: Nematoda, Copepoda with their *nauplii*, Ostracoda, Tunicata, Gastrotricha, Turbellaria, Tardigrada, Kinorhyncha,

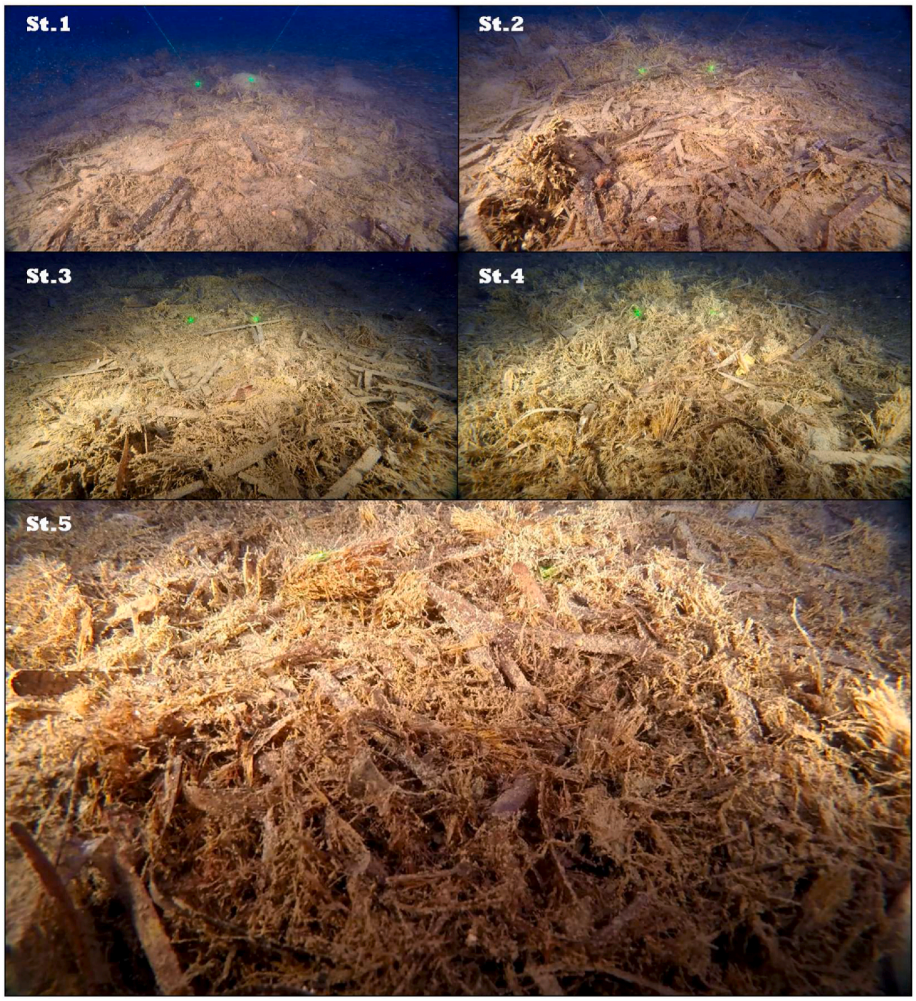

Fig. 2. ROV images of the macerating sediments of *P. oceanica* in the five sampling stations, labeled from station-1 (St. 1) to station-5 (St. 5).

Halacaridae, and some benthic taxa frequently belonging to temporary meiofauna such as Polychaeta, Oligochaeta, Sipuncula, Tanaidacea, Bivalvia and Isopoda (Fig. 3, Fig. S1). Abundance, richness (namely number of taxa), H' and J indices for both meiofauna and nematodes are summarized in Table 1. The number of taxa per station varied from a minimum of 8 at station-5, to a maximum of 13 at station-1. The highest abundance value was reported at station-3 (995 ± 145 ind. 10 cm^{-2}), followed by station-5 (961 ± 128 ind. 10 cm^{-2}); while the lowest one was reported at station-1 (857 ± 221 ind. 10 cm^{-2}). Nematoda was largely the dominant taxon, with a maximum value of 905 ± 144 ind. 10 cm^{-2} at station-3. Nematoda represented over 85% of the total meiofaunal community at all sampling stations, reaching 93% at station-5 (896 ± 151 ind. 10 cm^{-2}). The second dominant taxon was Copepoda with their *nauplii*, accounting together for 5% (station-5) to 13% (station-4) of the meiofaunal community, followed by Polychaeta, accounting for less than 2% of the community at all stations.

The same trend of H′ and J was observed, with the maximum values at station-1 (0.67 ± 0.25 and 0.28 ± 0.08, respectively) and the minimum values at station-5 (0.35 ± 0.06 and 0.17 ± 0.03, respectively). However, ANOVA did not detect any significant difference among stations neither in terms of the total meiofaunal abundance nor of the H' and J (One-way ANOVA test: $p > 0.05$).

To make discernible even minor changes of the meiofaunal structure, the most abundant taxa, *i.e.* Nematoda, Copepoda (adults and their *nauplii*) and Polychaeta, were excluded from the analyses, since their presence might mask the variations of the less abundant meiobenthic components, while rare taxa (*i.e.*, taxa accounting for less than 1%) were further analyzed (Fig. 4). The nMDS plot of rare taxa is displayed in Fig. 5 and it revealed a clear distinction of the stations, also confirmed by One-way ANOSIM test that showed the highest dissimilarities in terms of rare community structure (see Table 2). Furthermore, both ANOSIM and SIMPER routine highlighted that the main dissimilarity was mainly due to station-5, clearly distinguished from all the other stations and, in particular, from station-1 (Table S1). The primary taxa that contributed to the high dissimilarity of this station were Kinorhyncha and Isopoda, both more abundant at station-5.

3.2. Nematode community

Nematodes were the dominant taxon at all stations, ranging from 84% at station-4 to 93% at station-5. A total of 104 genera were identified, as listed in Table S2, while the number of genera, abundance and diversity index (H′ and J) are listed in Table 1. The H' index was minimum at station-4 and maximum at station-5 (2.80 and 2.98, respectively) while equitability (J) was minimum at station-4 and maximum at station-1 (0.84 and 0.89, respectively).

The most abundant life strategy classes were the c-p 2 (37%), followed by c-p 4 (34%), c-p 3 (29%) and c-p 1 (0.39%), while no k-strategist/persisters of class 5 were found in our samples (Fig. S2). MI values ranged from 2.62 ± 0.08 (station-5) to 2.75 ± 0.06 (station-4) (Fig. 6). Although significant differences were not revealed by ANOVA, discernible differences occurred between station-4, characterized by the highest MI, and station-5 and station-3 by the lowest values, while station-1 and 2 showed intermediate values.

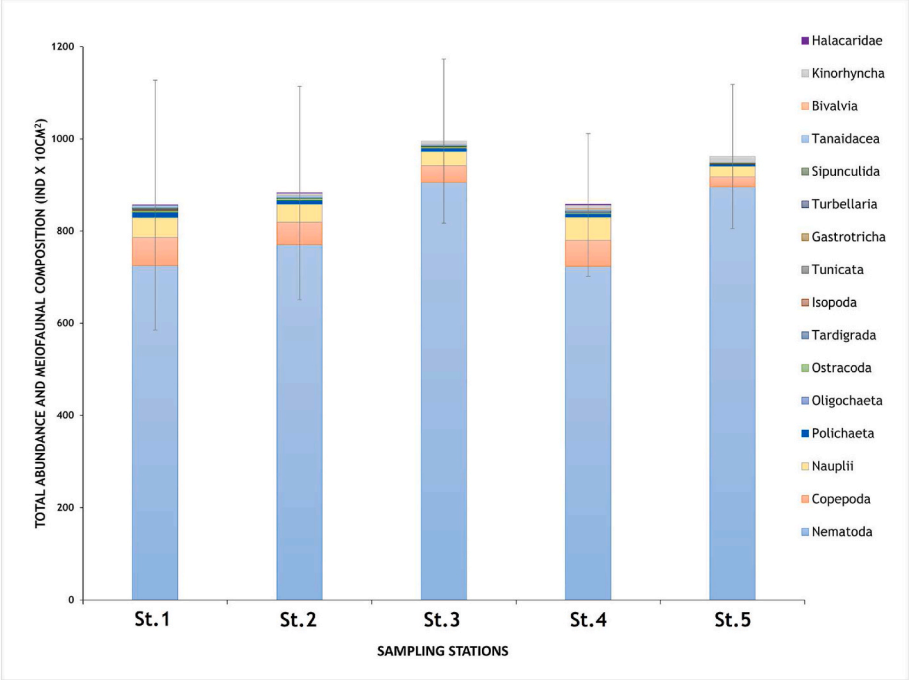

Fig. 3. Abundance and composition of the whole meiofaunal community found in the study area at the five sampling stations. Error bars represent standard deviation of the whole community.

Table 1
Meiofaunal and Nematoda univariate parameters (i.e., number of taxa, abundance, Pielou-J index, Shannon-H' index) obtained from the analyzed samples.

	Station	St. 1	St. 2	St. 3	St. 4	St. 5
	Depth (m)	65	65	70	70	80
Meiofauna	**N° taxa**	13	9	11	11	8
	Abundance	857 ± 271.1	883 ± 231.5	995 ± 177.8	858.3 ± 154.7	961.3 ± 156.2
	J index	0.28 ± 0.08	0.25 ± 0.06	0.18 ± 0.03	0.27 ± 0.08	0.17 ± 0.03
	H' index	0.66 ± 0.25	0.54 ± 0.18	0.42 ± 0.10	0.62 ± 0.20	0.34 ± 0.05
Nematoda	**N° genera**	36	38	40	41	42
	Abundance	725.08 ± 281.8	770.62 ± 210.9	905.28 ± 144.4	723.44 ± 119.2	896.11 ± 151
	J index	0.89 ± 0.005	0.87 ± 0.003	0.87 ± 0.05	0.84 ± 0.01	0.87 ± 0.01
	H' index	2.90 ± 0.04	2.95 ± 0.08	2.85 ± 0.29	2.80 ± 0.09	2.98 ± 0.05

The trophic group composition of the stations is reported in Fig. 7. It is possible to notice that deposit feeders (both selective and non-selective, 1A and 1B, respectively) account together for more than 60% of the total nematode abundance at all stations, while epistrate feeders (2A) ranged from 18% at station-5 to 31% at station-1. Finally, predators (2B) accounted for less than 10%. ITD showed the highest values at station-4 (0.38 ± 0.02) and lowest at station-1 and station-5 (0.30 ± 0.01 and 0.30 ± 0.03, respectively) (Fig. S3).

However, the five sampling stations did not show any significant difference both in the taxonomical (*i.e.*, H', J) and functional variables (*i.e.*, MI, ITD, c-p classes and trophic groups) (One-way ANOVA: $p >$ 0.05).

ANOSIM performed on nematodes showed significant differences in terms of community structure (Table 2) with the station-5 that revealed the most marked differences from the other stations, followed by station-1 (Fig. 8). In detail, *Astomonema*, Chromadorida sp. 2, *Molgolaimus*, *Cheironchus*, *Cervonema*, *Campylaimus*, *Linhystera*, *Pseudochromadora* and *Tricoma* were the taxa that mainly contributed to distinguish station-5, while *Ptycholaimellus*, *Dichromadora*, Sphaerolaimidae sp. 1, *Gomphionchus*, *Desmodora*, *Setosabatiera*, *Quadricoma* characterized station-1 (SIMPER routine) (Table S3).

4. Discussion

Detrital habitat of macerating *P. oceanica* represents a sink of exported carbon, which hosts animal assemblages consuming and processing seagrass carbon even if they are far away from the donor seagrass bed. Most of the time, phytodetritus and organic matter exported from the seagrass beds has been investigated focusing on the on-shore banquettes, or on shallow deposits (above 20m depth) near the seagrass bed, analyzing the macrofauna component (Covazzi et al., 2006; Gallmetzer et al., 2005; Remy, 2016; Remy et al., 2021), while necromass transported and accumulated to deepest seabeds (below 50m depth) and the associated meiofaunal component have been overlooked so far. This pilot study allowed us to set a baseline on the meiofauna inhabiting this peculiar habitat forgotten for 70 years.

Information about meiofauna inhabiting Mediterranean soft bottoms at comparable depths is scarce, since 60–80 m of depth is a poorly investigated bathymetric range. However, from one of the very few available studies, it is possible to notice that the macerating *P. oceanica* substrata of the Ischia Island showed much higher meiofaunal abundances (857−995 ind. 10 cm^{-2}) than those from soft sediments at similar bathymetry (170−558 ind.10 cm^{-2}: De Leonardis et al., 2008). The occurrence of phytodetritus accumulations can, in fact, enhance secondary production and support development of well-structured meiofaunal communities (Vetter, 1996; Mateo and Romero, 1997;

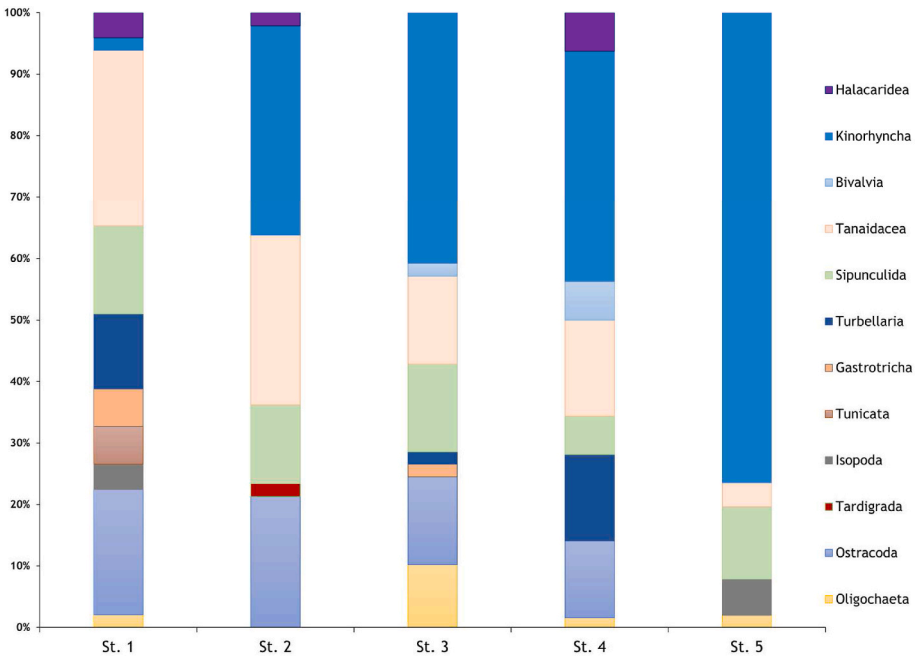

Fig. 4. Composition of rare meiofaunal taxa (i.e., taxa <1% of the total community) found in the study area at the five sampling stations.

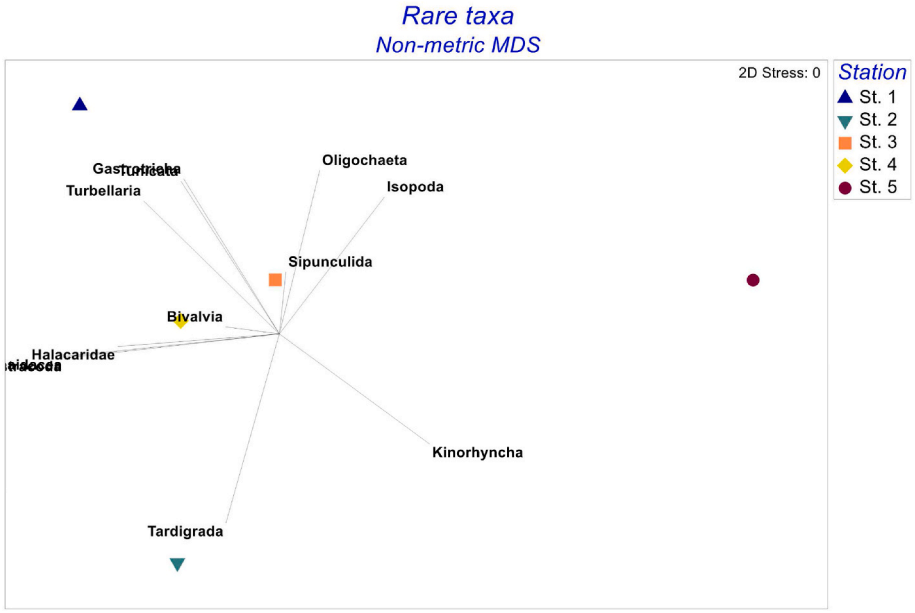

Fig. 5. Non-metric multidimensional scaling (nMDS) ordination, derived by Bray-Curtis (dis) similarity measures carried out on rare meiofaunal taxa. Different symbols represent the five sampling stations.

Lepoint and Hyndes, 2022). Our data revealed abundances consistent with values detected in shallow unvegetated substrates adjacent to Mediterranean seagrass meadows. Indeed, meiofaunal community associated to seagrass meadows from Mediterranean beds showed abundance ranges from 969 to 2800 ind. 10 cm^{-2} inside the seagrass meadows, and from 400 to 1214 ind. 10 cm^{-2} in the adjacent unvegetated substrates (Novak, 1982; Mirto et al., 2010, 2014; Mascart et al., 2013, 2015; Pusceddu et al., 2016; Carugati et al., 2018; Polese et al., 2018; Da Ros et al., 2021). However, in contrast to literature (Muthumbi et al., 2004; De Leonardis et al., 2008; Balsamo et al., 2010; Frontalini et al., 2011; Semprucci et al., 2010; Wang Wang et al., 2019) no significant change of meiofaunal density was observed with increasing water depth.

The studied macerating *P. oceanica* bottoms showed a well-structured meiofaunal community, with a slightly lower number of taxa (8–13) compared to other shallow Mediterranean areas (10–21) (Polese et al., 2018; Semprucci et al., 2018). In addition, our results showed higher values of taxa than those reported in shallow seagrass systems (7–10 taxa, Pusceddu et al., 2016; Carugati et al., 2018; Da Ros et al., 2021). The number of meiofaunal taxa can be useful to assess the ecological quality of marine sediments and, according to the classification proposed by Danovaro et al. (2004 and modified in agreement with the WFD classification), Ischia sediments can be classified as "moderate" (8–11 taxa) to "good" (12–16) EcoQ status with an overall decrease of the EcoQ with the depth.

As suggested by Bianchelli et al. (2010), the general dominance of

Table 2
Results of the One-way ANOSIM on the meiofaunal and nematode community structure data obtained from the analyzed samples (data were fourth root and presence/absence transformed).

Community structure variables	Data transformation	
	Fourth root	Presence/absence
Whole meiofaunal community structure	Global R = 0.36; p = 0.008	Global R = 0.34; p = 0.007
Rare meiofaunal taxa structure	Global R = 0.40; p = 0.001	Global R = 0.34; p = 0.007
Nematode community structure	Global R = 0.60; p = 0.001	Global R = 0.55; p = 0.001

the most abundant taxa masks the relative contribution variations of the minor meiobenthic groups. In fact, the highest dissimilarity along the depth gradient was found analyzing rare taxa, while overall lower dissimilarity scores were detected both when fourth root and presence/absence transformations were applied to the whole meiofaunal community data. This suggests that the differences in the meiofaunal community composition between stations were mainly due to communities having a different pool of rare taxa, rather than to the exclusive occurrence of specific meiobenthic groups. This study further supports the idea that rare taxa might be regarded as proxies of environmental variations and that habitat-specific topographic features play a significant role in their distribution (Bianchelli et al., 2010; Gambi et al., 2010; Baldrighi et al., 2021). Within the rare taxa found in the present study, there were members of both temporary (*i.e.,* belong to the meiofaunal size category only as newly settled larvae that later grow to become macrofauna) and truly permanent meiofaunal taxa (*i.e.,* fully benthic

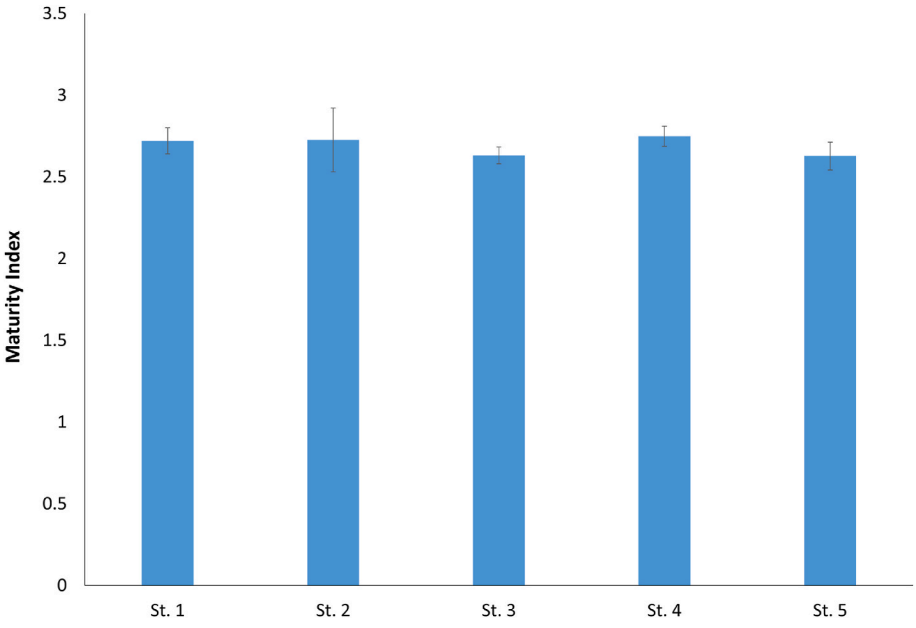

Fig. 6. Maturity Index (MI) values detected in the study area and calculated on the base of the nematode life strategies (i.e., c-p classes).

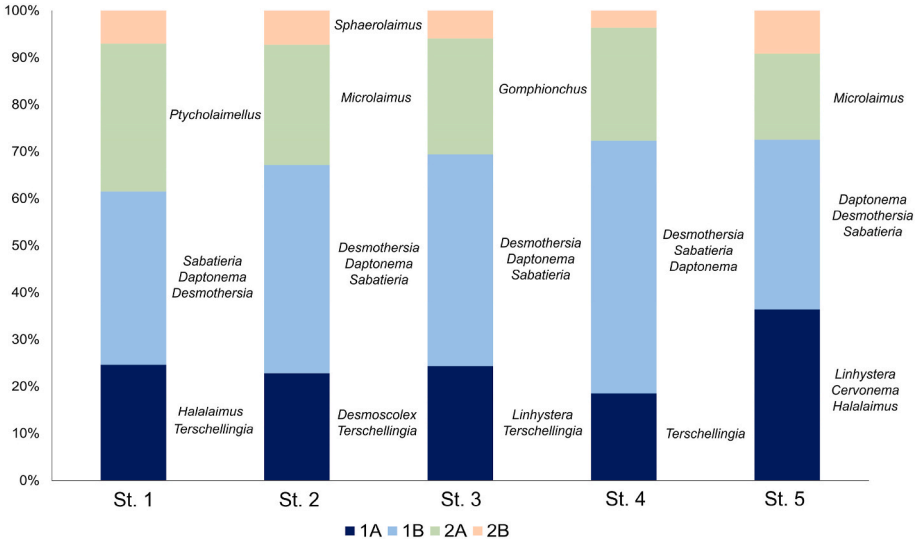

Fig. 7. Percentages of the trophic groups (i.e., 1A: selective deposit feeders, 1B: non-selective deposit feeders, 2A: epistrate feeders and 2B: predators/omnivores according to Wieser, 1953) found in the study area. Only taxa found in each station with percentages higher than 5% of the whole community were reported in the graph.

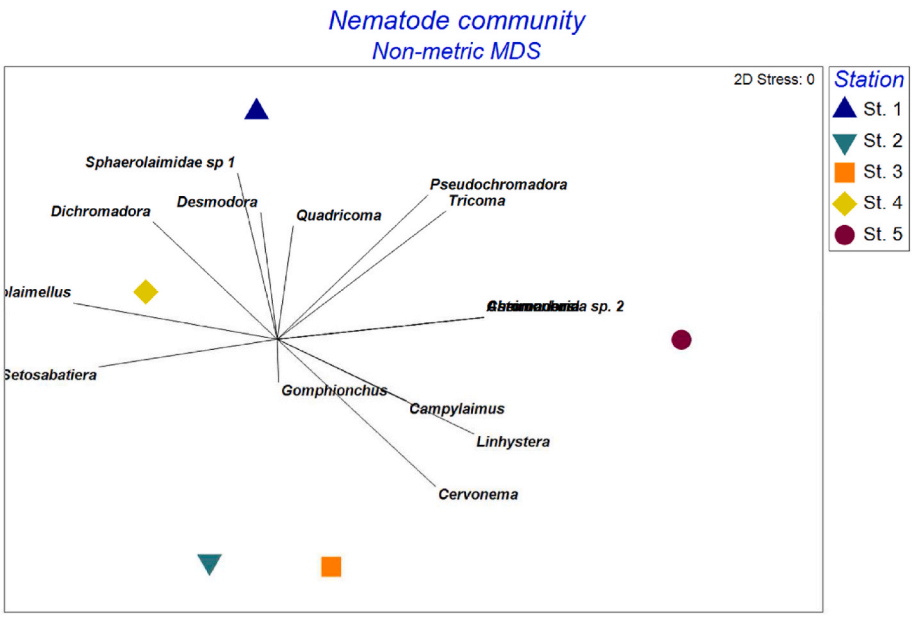

Fig. 8. Non-metric multidimensional scaling (nMDS) ordination, derived by Bray-Curtis (dis) similarity measures carried out on the nematode community. Different symbols represent the five sampling stations.

species that remain in the meiofaunal size-range during their whole lifespan, Giere, 2009; Worsaae et al., 2023). Kinorhynchs were more abundant at station-5. This phylum is one of the less studied meiobenthic groups and it was detected at all the investigated stations (a total of 100 specimens were found). It is worth noting that, among kinorhynchs, two new species of the genus *Echinoderes,* still under description, were found. This benthic group is usually associated with fine-grained sediments, and it seems to have a crucial role in the benthic food web, feeding on bacteria and promoting the flow of energy and the transfer of organic matter to higher trophic levels (Dal et al., 2016). As proposed by Mirto et al. (2012) and Dal et al. (2016), since their sensitivity to sulfidic compounds deriving from high level of organic enrichment, kinorhynchs could be considered, in the future, useful tools for the assessment of anthropogenic organic impact in marine environments by using the nematodes/kinorhynchs ratio (Ne/Ki).

Nematode community inhabiting seagrass beds has captured the interest of several researchers, especially focusing on biodiversity and trophic structure. The composition of the nematode community revealed that the study area was inhabited by a much higher number of families and genera, compared to soft bottoms at similar bathymetries in Mediterranean Sea (104 genera in the present study *versus* 49–54 in De Leonardis et al., 2008, and 88 in Sandulli et al., 2002; 31 families in the present study *versus* 26 in Gambi et al., 2019). Comesomatidae and Xyalidae were the dominant families (19% and 18%, respectively), followed by Richtersiidae and Chromadoridae (12% and 9%), which are all documented in subtidal substrata worldwide (Heip et al., 1985; Wieser, 1956; De Leonardis et al., 2008; Semprucci et al., 2013, 2014). *Sabatieria, Desmothersia* and *Daptonema* (Comesomatidae, Richtersiidae and Xyalidae, respectively) were, in particular, the most frequent and abundant genera.

The multivariate analysis carried out on nematode community structure underlined a marked difference with the depth as rare meiofaunal taxa revealed (from lower to higher depths, station-1 to station-5, respectively; Fig. 8). Among the genera that mainly distinguished the deeper stations, there were *Astomonema* and *Molgolaimus.* The high abundance of *Astomonema*, which is characterized by an obligate symbiosis with sulfur-oxidizing bacteria (Dando et al., 1991; Austen et al., 1993; Giere, 2009), can suggest the presence of anoxic conditions especially at station-5. This genus was also documented by De Leonardis et al. (2008) in the Adriatic and Ionian subtidal habitats. *Molgolaimus* also seems well suited to stressful conditions, being found as abundant genus in 'extreme' environments, such as hydrothermal vents, low-oxygen zones or in areas under human impact (Muthumbi and Vincx, 1996; Vanreusel et al., 2010; Losi et al., 2021; García-Cobo et al., 2024). Furthermore, it is argued that the species belonging to *Molgolaimus* display biological and physical characteristics allowing them to exploit a high variety of environmental conditions and generally increase their abundance and diversity in habitats that are limiting for many meiobenthic groups (Grassle and Maciolek, 1992; Lambshead, 1993; Fonseca et al., 2007; Semprucci et al., 2013). The other nematode genera at station-5 (*Cheironchus*, *Cervonema*, *Campylaimus*, *Linhystera*, *Pseudochromadora* and *Tricoma*) were all sediment-dwelling taxa, typical of very fine sediments in the deep-sea habitats or organically enriched sediments (Heip et al., 1985; Vanreusel et al., 2010; Semprucci et al., 2014). The nematode fauna of the shallower site (station-1: *Ptycholaimellus*, *Dichromadora*, Sphaerolaimidae sp. 1, *Gomphionchus*, *Desmodora*, *Setosabatiera*, *Quadricoma*) are typical of fine sand with large amounts of detritus (Heip et al., 1985; Semprucci et al., 2013, 2014; Losi et al., 2021).

The accumulation of *P. oceanica* fragments in this peculiar habitat triggers the proliferation of bacteria involved in the decomposition of the phytodetritus. Thus, given the trophic composition of the described nematode assemblage, the high abundance of bacteria on plant detritus led to a nematode community mainly dominated by selective and non-selective deposit feeders (1A and 1B, respectively) (Vetter, 1995; Mateo and Romero, 1997; Lepoint and Hyndes, 2022), which accounted together for more than 60% of the total abundance. However, the guild of epistrate feeders, with a buccal cavity armed by small denticles and teeth (2A) is also well represented as previously reported in several studies carried out in seagrass bottoms (Danovaro and Gambi, 2002; Fonseca et al., 2011; Losi et al., 2012). These findings highlight the fundamental role in the blue carbon cycle of the neglected offshore *P. oceanica* maceration sites, that constitute an important carbon stock and a source for detrital food webs.

No significant variation or evident pattern was observable in nematode diversity or functional indices. Despite the dominance of c-p 2 (tolerant taxa) in the investigated sediments, MI resulted overall high, thanks to the valuable contribution of c-p 4, mainly represented by Selachinematidae and Desmoscolecidae. According to Moreno et al. (2011), the ecological status of the study area falls, on the base of

nematodes, in the "good" EcoQ class when considering MI, and in the "moderate" one when considering H'. This result is in line with the whole meiofaunal community and supports the high naturalistic value of these types of habitats that should be considered a repository of a high benthic biodiversity hosting rare and undiscovered species.

5. Conclusions

Deep *P. oceanica* detrital beds are valuable habitats with good environmental quality as highlighted by taxonomic and functional features of both whole meiofauna and nematode communities, despite the lack of knowledge of this peculiar environment. It is important to promptly deepen the characteristics of this undiscovered habitat, strictly connected to the much better-known living seagrass beds, and to shed light on the role of the overlooked deep detrital component of the blue carbon cycle.

Understanding how changes in community composition and taxa contribution influence the transfer of matter and energy through the trophic levels may be fundamental to predict natural or anthropic changes in marine environments.

CRediT authorship contribution statement

Adele Cocozza di Montanara: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Federica Semprucci:** Writing – review & editing, Writing – original draft, Validation, Supervision. **Francesco Rendina:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Giovanni Fulvio Russo:** Writing – review & editing, Supervision, Resources, Project administration. **Roberto Sandulli:** Writing – review & editing, Validation, Supervision.

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 request.

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Appendix A. Supplementary data

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