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The effect of two extreme climate events on coastal meiofaunal communities and ecosystem health

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ABSTRACT

Two consecutive extreme storms, "Daniel" (4–8 September 2023) and "Elias" (25–28 September 2023), struck the region of Thessaly resulting in flash floods, with Pagasitikos gulf being the main recipient. Eight sites were selected based on the degree of intensity of disturbance, with sample collection taking place immediately, 6 months and a year following the events. The first 2 cm of sediment were analyzed in terms of meiofauna, nematodes and sediment characteristics. Physical (temperature, salinity) and chemical (pH, dissolved oxygen, redox potential, nutrients) water quality parameters were, also, measured. Indicator species analysis (ISA) and nematode functional traits were used to assess the ecosystemic quality. The environmental parameters varied with time but not with disturbance intensity. The results indicated differences in meiofaunal diversity and abundance patterns between high and low intensities. Sediment redox was the most significant environmental factor affecting the meiofaunal and nematode communities. Nematode diversity and c-p scores were characteristic of recolonization, with higher diversities observed immediately after the events. Persisting genera in high intensity sites were initially absent. ISA indicated that almost all sites were associated with tolerant genera, however single groups of sites were also associated with sensitive ones, while the use of functional traits determined that after one year almost all sites attained moderate levels of ecosystemic quality. Ecosystemic restoration was delayed for high intensity sites. The rate of recolonization was related to intensity of disturbance, while the required time for meiofaunal community to reach stability was longer than expected, suggesting less tolerance than previously thought.

1. Introduction

Extreme weather events (EWEs) are characterized by abrupt environmental changes that disrupt ecosystemic processes (e.g. nutrient cycling), altering the physicochemical parameters of water and sediment (Fong et al., 2020; Piccolo, 2021). Recently, the National Academy of Sciences reported EWEs have been changing in terms of intensity, frequency and duration in the last few decades, while the impact of anthropogenic activities could magnify their severity in coastal ecosystems (Medicine et al., 2016; Pidcock and Mcsweeney, 2022).

EWEs affect all levels of biological organization, from changes in physiological processes of individuals to destabilization of communities (Armstrong McKay et al., 2022; Stroud et al., 2020). Regarding the coastal environment, sediment changes in the form of sediment translocation can have detrimental effects on benthic communities, resulting in local biodiversity loss (Corte et al., 2017; Mateo and Garcia-Rubies, 2012; Semprucci et al., 2017; Armynot du Châtelet et al., 2016). Meiofauna, another biotic component of coastal sandy sediments, has received less attention in terms of disturbance caused by EWEs, with most literature being limited to anthropogenic disturbances of various types (Schratzberger et al., 2023). Meiofaunal communities participate in key ecological processes like nutrient cycling (Giere, 2009). These organisms usually present high densities including representatives from most metazoan phyla and are thus considered suitable candidates for examining how environmental changes influence benthic invertebrates (Sarmento et al., 2017; Magni et al., 2022; Grassi et al., 2023). Existing literature on the responses of meiofauna to EWEs are limited to a tsunami and a cyclone, both concluding that recovery is facilitated within weeks (Altaff et al., 2005; Sugumaran et al., 2019). However, both studies focused on major taxa, while the fate of organisms at genus or species level remains unclear.

Nematodes are considered both the most diverse and abundant metazoan group in aquatic habitats, while their distribution ranges from unpolluted to heavily impacted habitats (Cocozza di Montanara et al., 2022). Their use as bioindicators is supported by a number of characteristics, such as providing more robust data sets than larger organisms, sampling-based advantages, functional diversity, etc. (for more details refer to Moreno et al., 2011 and references herein; Franzo et al., 2022; Sahraeian et al., 2020). Among these traits life-history strategy (c-p scores) and trophic groups are particularly informative (Wieser, 1953; Bongers, 1990). The c-p (colonizer–persister) scale categorizes nematodes from opportunistic, fast-reproducing colonizers (cp-1) to sensitive,

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K-selected taxa (cp-5), and is often used to indicate stages of ecological succession. Trophic guilds, based on buccal morphology, reflect the organisms' role in sediment food webs (e.g. deposit feeders, epistrate feeders, predators). To date there is no record of nematodes being used to assess the impacts of EWEs on ecosystemic health, with most of the existing research focusing on chemical stressors (reviewed in Ridall and Ingels, 2021).

The present study aims to connect the current knowledge regarding the regime of EWEs on coastal benthic biota, specifically the effect of the intensity of two extreme storms that resulted in severe flash floods, with the use of meiofaunal and nematode communities using field data. We hypothesize that intensity will have a negative impact on meiofaunal abundance and nematode diversity immediately after two EWEs, while communities will stabilize at a fast rate. Regarding the community composition of both meiofaunal taxa and nematodes, differences are expected to be associated with both level of intensity and time of sampling. The functional traits are also anticipated to be driven by the same factors, with the c-p scores exhibiting the most straightforward patterns, characteristic of the succession process following disturbance, in contrast to trophic groups, which are expected to show less distinct patterns (Moreno et al., 2011). Temporal changes in local abiotic conditions are expected to be reflected to variation in both meiofaunal and nematode community compositions.

2. Materials and methods

2.1. Study sites

Located in the north-western Aegean Sea (Greece), Pagasitikos gulf is a semi-enclosed basin, stretching over 31 km from North to South and 16 km from East to West. It is considered one of the most oligotrophic basins in the eastern Mediterranean Sea, while it is nitrogen limited, in contrast to most semi-enclosed gulfs being phosphate limited. Pagasitikos gulf is affected by several sources of anthropogenic activity such as industrial and agricultural sewage, while also hosting several types of biogenic habitats (Varkoulis and Vafidis, 2025). A detailed description regarding the oceanographic conditions of the gulf can be found in Petihakis et al. (2005), while the effect of its specific oceanographic patterns on meiofauna have also been documented (Voulgaris and Vafidis, 2025).

From 4 to 8 and between 25 and 28 of September, two extreme weather events (EWEs) occurred, namely "Daniel" and "Elias", resulting in increased precipitation (Argüeso et al., 2024), heavy damages related to infrastructure and changes in the landscape of several coastal localities, due to the erosion and deposition process. Due to increased water influxes, increased levels of water pollution are expected to also impact biodiversity (Diakakis et al., 2025).

To examine the effect of the two consecutive EWEs on the coastal ecosystem health, 8 sites were selected, based on the intensity of disturbance (Fig. 1). Low intensity sites were considered those that showed minimal topographic changes after the EWEs, while high intensity sites exhibited either severe changes in landscape, changes in granulometry due to sediment deposition, or both (Fig. s1, Text s1). Sample collection was carried out immediately after the EWEs and 6 months (mid-term) and a year (long-term) following the events, to determine changes in meiofaunal communities and assess the ecosystemic health of the localities. Despite meiofaunal organisms exhibiting rapid generation times, this sampling design was adopted instead of daily or weekly sampling intervals to adequately capture the effect of subsequent environmental changes on both meiofauna and nematodes. For meiofaunal samples 3 replicate corers (3.6 cm inner diameter) were collected from the first 2 cm of sediment, while an additional corer was collected for granulometric and organic content analyses (Grassi et al., 2023).

2.2. Water quality parameters

Temperature, salinity, pH, dissolved oxygen (DO) and redox potential (both in water and sediment) were measured at each station using multiprobe instruments. To determine ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), phosphate (PO_4^{3-}) and silicate (SiO_2) concentration, water samples were collected from the surface (0 m) and placed in 500 ml plastic vials. Mercury chloride (2 ml of $HgCl_2$ 0.1 M per 500 ml sample) was added to inhibit any biological activity and then, samples

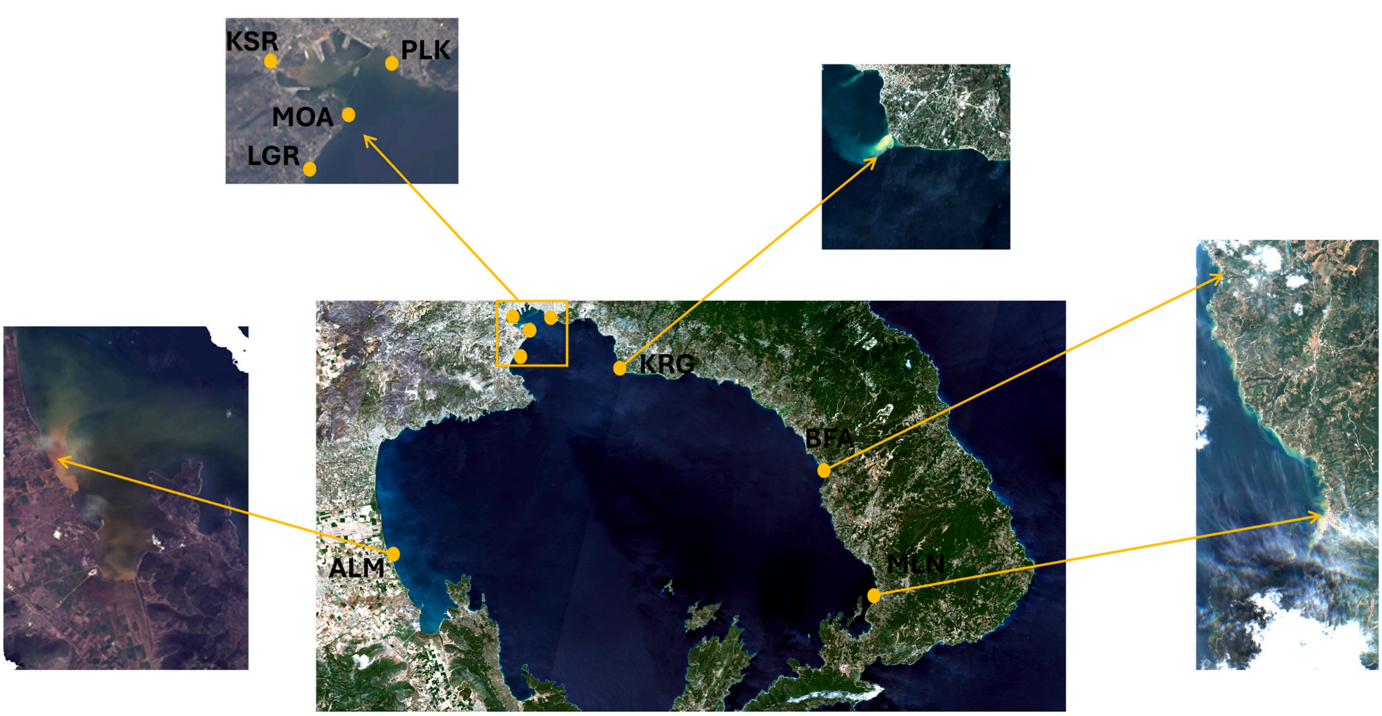

Fig. 1. Satellite images of Pagasitikos Gulf showing sampling sites (yellow) before and after the extreme storm "Daniel" (08/09/23). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

were stored at −20 °C until the analysis took place. Chemical analysis of NH_4^+, NO_2^-, NO_3^-, PO_4^{3-} and SiO_2 was based on the methodology developed by Eaton (1999), using a spectrophotometer (SHIMADZU UV-1800). The statistical procedures were performed using IMB SPSS Statistics version 29.0.

2.3. Granulometry and organic matter content

In the laboratory, samples were dried at 40–50 °C, pulverized using a porcelain mortar, and sieved through a 2 mm mesh for grain size analysis. The particle size distribution was determined using the Bouyoucos hydrometer method (Bouyoucos, 1962), which measures sedimentation rates of dispersed particles in a suspension to classify sand, silt, and clay fractions. For organic matter content determination, samples were further sieved through a 200 μm mesh to isolate finer organic fractions. Organic carbon (OC), total organic carbon (TOC), and organic matter (OM) content were analyzed using the wet oxidation method as described by Walkley and Black (1934), which involves chemical oxidation of organic carbon with potassium dichromate and sulfuric acid, followed by titration to determine carbon content. Despite being developed nearly a century ago, this method remains widely used and reliable for organic matter estimation (Avramidis et al., 2015).

2.4. Meiofaunal and nematode analyses

Meiofaunal organisms were first anesthetized using a 7 % $MgCl_2$ solution (Sbrocca et al., 2021). Samples were then fixed with 4 % buffered formaldehyde in filtered seawater (Baldrighi et al., 2019). In the laboratory, all meiofaunal samples were rinsed with a gentle jet of fresh water over a 0.5 mm sieve to exclude macrofauna, decanted over a 45 μm sieve ten times, centrifuged three times with Ludox HS40 (specific density 1.18), and stained with Rose Bengal (Heip et al., 1982). All meiofaunal organisms (except for protozoans for which only Ciliophora were considered) were counted and identified at the major taxon level, using a stereomicroscope, and density was recalculated as abundance 10 cm^{-2}.

The first 100 nematodes from each sample were picked out using a fine pin under a stereomicroscope (magnification × 40, Olympus SZX9), transferred from formalin to glycerol through a series of ethanol–glycerol solutions and mounted on slides in anhydrous glycerine (Heip et al., 1982). When a sample contained less than 100 individuals, all nematodes were used. Nematodes were identified at the genus level, using pictorial keys under a microscope (magnification x100, Zeiss Axio scope A1) (Bain et al., 2013; Platt and Warwick, 1983; Warwick et al., 1998; Nemys eds., 2025).

Nematodes were assigned to trophic groups based on Wieser (1953). These feeding groups consisted of selective (1 A) and non-selective (1 B) deposit feeders, epistrate feeders (2 A) and predators/omnivores (2 B). The Index of Trophic Diversity (ITD) was calculated for each station and sampling time based on the composition of nematode trophic guilds (1 A, 1 B, 2 A, and 2 B) (Heip et al., 1982). ITD was derived by summing the squared proportional abundances of these feeding groups at each station. The Maturity Index (Bongers, 1990; Bongers et al., 1991) for each replicate was calculated as the weighted average of the individual colonizer-persistent (c-p) values and was used to identify site- and time-specific disturbance. The contribution of each life-history group (c-p 1–5) to the total nematode community was then calculated and visualized and finally the ecological quality (EcoQ) of each site at each sampling time was assessed (for more details refer to Moreno et al., 2011).

2.5. Data analysis

All analyses were carried out in Rstudio (v. 4.2.3, R Core Team, 2020). Changes in environmental parameters were investigated using principal components analysis (PCA) on z-score transformed data ("FactoMineR" package). To examine the effect of intensity of disturbance caused by the events and time of sampling on total meiofauna, nematodes, copepods and polychaetes, as well as on richness of taxa, Pielou's evenness, Shannon's index and Simpson's inverse index, generalized linear models (GLMs) were used with either gaussian or Gamma error distribution, depending on the distribution of data (normal vs right-skewed) and the Akaike's criterion (AIC). Pairwise post-hoc tests were conducted using the function *emmeans* from the "emmeans" package, with p-values adjusted for multiple comparisons using the Bonferroni correction method (Lenth, 2024). For the examination of nematode diversity, sample-based rarefaction-extrapolation curves were constructed and the diversity metrics used were Hill's numbers, with q = 1 corresponding to genera richness (^{0}D), q = 2 is equal to Shannon diversity (^{1}D) and q = 3 is Simpson diversity (^{2}D). Bootstrapping was employed to construct 95 % confidence intervals (nboot = 200).

To examine changes, as well as similarities in meiofaunal and nematode community structure hierarchical clustering with Ward's criterion was used on the Bray-Curtis distance matrices, derived from the log (x+1) transformed meiofaunal and nematode data, pooled for site and sampling time. Non-metric multi-dimensional scaling (NMDS) was used to visualize the meiofaunal and community structure in different time intervals, while PERMANOVA with 9999 permutations was used to examine the statistical significance of these changes and distance from centroid for each group was tested using the betadisper function from "vegan" package. When p-values were significant ($p < 0.05$), pairwise permutational tests were conducted as post-hoc tests, also using 9999 permutations. To investigate potential effects of abiotic conditions on meiofaunal and nematode communities, a canonical correspondence analysis (CCA) and a distance-based redundancy analysis (db-RDA) were used, respectively. The selection of two different constrained ordinations was justified after preliminary analyses. It appeared that meiofaunal relationships to abiotic predictors were better described by a unimodal relationship, while a linear relationship was more effective for nematodes. Environmental variables were first tested for multicollinearity using the variance inflation factor (VIF) and the minimum number of predictors with highest explanatory power was determined by the stepwise forward selection process, using adjusted R^2 to prevent overfitting. The statistical significance of the resulting predictors was assessed using permutation-based significance tests using the *anova. cca* function from the "vegan" package.

3. Results

To detect which nematode genera are associated with combinations of intensity level and time of sampling an indicator species analysis (ISA) was conducted, based on the framework suggested by De Cáceres et al. (2010) using the "indicspecies" package (De Caceres and Legendre 2009). Genera associated with multiple groups were also considered. This analysis uses three key metrics, namely specificity (A), fidelity (B) and coverage. A value of 1 for specificity for a genus would indicate that this genus is found on only for a particular site or group of sites, while a value of 1 for fidelity means that this genus is always found in this site or group of sites (De Cáceres and Legendre 2009).coverage shows the proportion of sites of a given site group where indicator genera are found and suggests how well a group of sites is represented by the associated indicator genera (De Cáceres et al., 2012). This analysis was used in combination to the functional traits of nematodes to assess the ecosystemic health. Results

3.1. Environmental parameters

PCA revealed distinct patterns in environmental factors under varying intensity and flood conditions, with the two main principal components accounting for 53.2 % of the total variance (Fig. 2). The highest positive contributors to PC1 were SiO_2, PO_4^{3-}, NO_2^- and Clay %

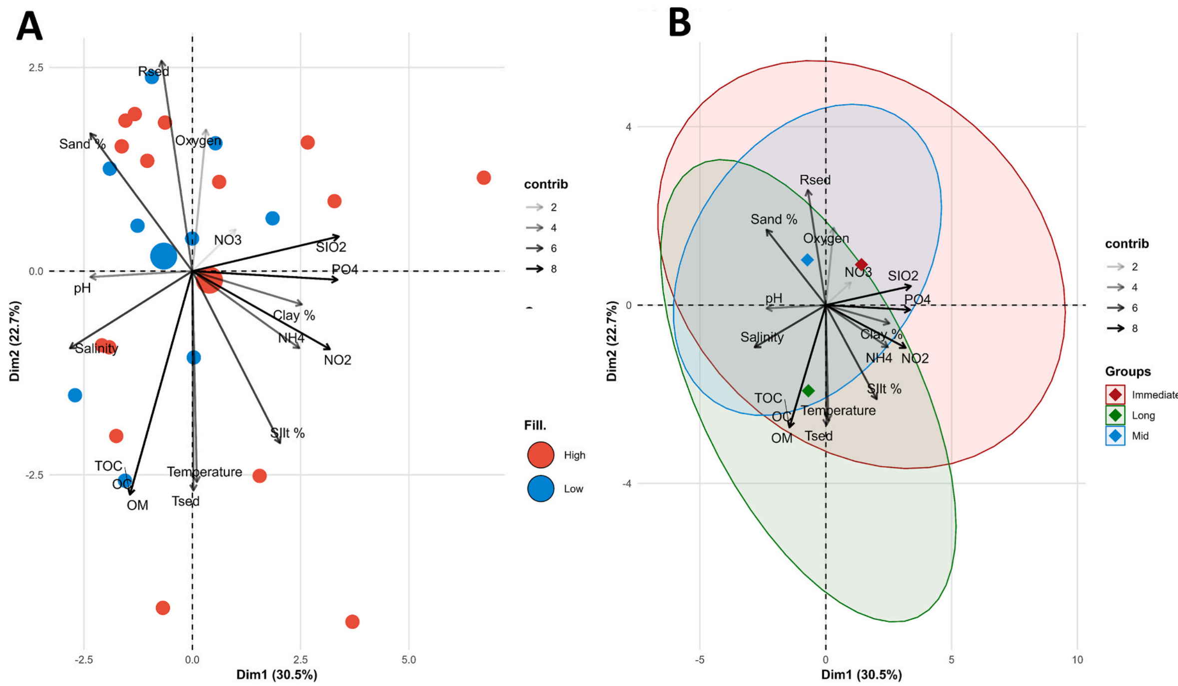

Fig. 2. Principal components analysis (PCA) of the environmental variables for A. the intensity of the extreme storm event and B. the different time intervals. Contribution of the variables is represented from high (black arrows) to low contribution (grey arrows). Larger circles indicate the centroids of each group.

while salinity, sand %, and pH exhibited negative loadings. PC2 was primarily positively influenced by redox of sediment, oxygen and sand. Negative loadings for PC2 were observed for water and sediment temperature, silt %, organic carbon, total organic carbon, and organic matter. Despite some overlapping in the intensity PCA, high and low intensity conditions were differentiated primarily along the nutrient concentrations (NO_3^-, NO_2^-, PO_4^{3-}) and sediment properties (sand %, clay %). A clear separation was observed with sampling time, particularly for the long-term flood group, which diverged from immediate and mid-term responses. This differentiation was driven by sediment characteristics (TOC, OM, silt %, -clay %), salinity and water temperature (Fig. 2 B).

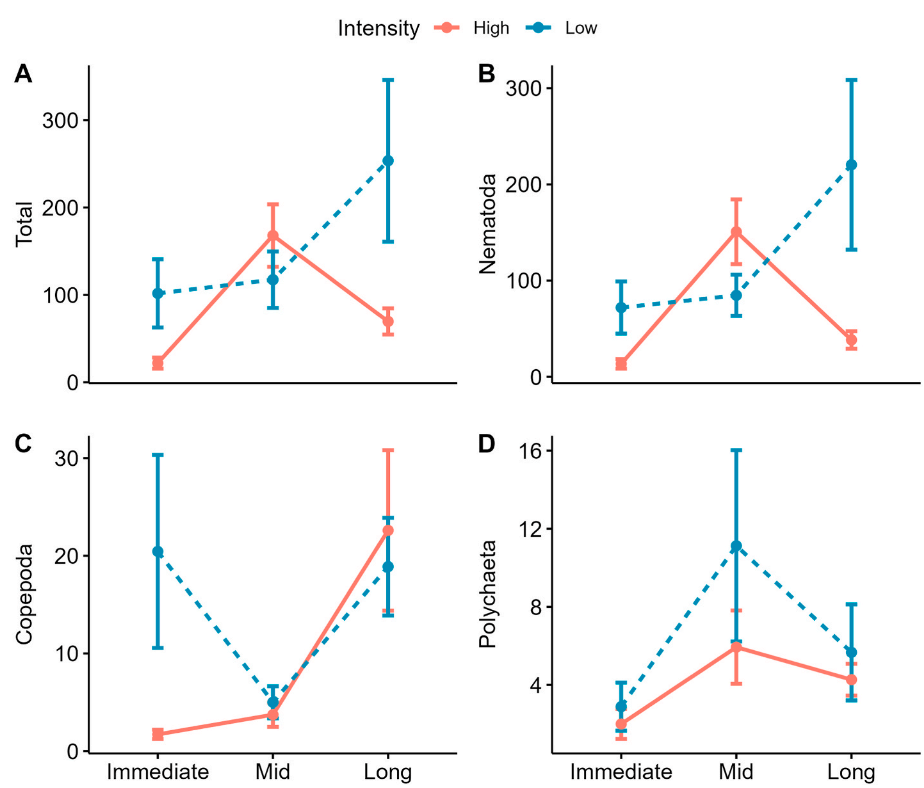

Fig. 3. Temporal changes in A. total meiofaunal, B. nematode, C. copepod and D. polychaete densities (ind/10cm2) for the two intensity levels. Error bars indicate + - 2nd. Dev.

3.2. Meiofaunal taxa

3.2.1. Abundance

Total meiofaunal abundance showed significant differences between the high and low intensity sites, immediately and after one year following the events, as suggested by the GLMs ($p = 0.004$ and $p = 0.008$, respectively). Within the high intensity group, differences were observed between all sampling times, while for the low intensity sites no statistical variation was reported. Abundance of nematodes was significantly different between levels of intensity only in the long-term sampling time ($p < 0.001$). Nematode densities were significantly different between the mid-term and the other two sampling periods regarding the high intensity sites, while for the low intensity group only the immediate and long – term sampling intervals differed. Differences in copepod densities between intensity levels were only observed immediately after the two EWEs ($p = 0.026$), while significant differences were also reported for the high intensity group, between the 1- year interval and the other two sampling times. The abundance of polychaetes did not vary between intensity levels for any of the sampling periods, while significant differences were only observed between the immediate and mid-term sampling intervals for the low intensity sites (Fig. 3; Table s1; Table s2).

3.2.2. Diversity

Overall, 17 taxa were found, comprised of nematodes, copepods (adults and *nauplii*), polychaetes, turbellaria, oligochaetes, ciliates, gastrotrichs, kinorhynchs, gnathostomulids, tardigrades, rotifers, nemerteans, halacarids, cnidarians, sipunculids, loriciferans and enteropneusts. The relative abundances of the most important taxa pooled for time of sample collection and replicate are given in Fig. 5.

GLMs indicated that taxon richness was significantly different between intensity levels only immediately after the two EWEs ($p = 0.007$), while no differences were observed within intensity level and among sampling times. Pielou's evenness varied between high and low sites immediately after and one year after the events ($p = 0.017$ and $p < 0.001$, respectively). For the high intensity sites, differences between the mid-term sampling time with the other two sampling times were observed, whereas for the low intensity group only the immediate and one - year sampling periods exhibited significant differences. Shannon's index and Simpson's inverse index presented identical trends, with differences between intensity levels only for the long-term sampling time ($p = 0.024$ and $p = 0.04$, respectively). Both indices did not significantly vary between the immediate and long-term groups for the high intensity sites. Regarding the low intensity group, Shannon's index showed significant differences only between the immediate and long-term sampling, intervals while for Simpson's index differences were observed between the immediate and the other two groups (Fig. 4, Table s1; Table s2).

3.2.3. Community structure

Hierarchical clustering resulted in three clusters, grouping the high intensity sites immediately after the EWEs in one cluster, the mid- and long-term sampling times in another group and all sampling intervals from a low intensity site in a separate cluster (Fig. 5). Combining the NMDs with PERMANOVA ($F_{perm} = 6.47$, $p_{perm} = 0.0001$) and pairwise permutation results, it is evident that the three time - intervals exhibit significantly different meiofaunal communities ($P_{perm} < 0.001$ for all pairwise tests; Fig. 6A).

Relationship between environmental parameters and community structure.

Canonical correspondence analysis (CCA) and permutational tests suggested sediment temperature and redox as the factors best explaining differences in meiofaunal communities. These factors explained 15.26 % of the total variance, separating the communities of the 1 – year interval from those of the other two sampling periods. Both factors showed a stronger correlation with CCA2, with sediment temperature exhibiting a positive relationship (0.8), whereas for sediment redox a negative correlation was observed (−0.9). The 1 – year interval seems to be different

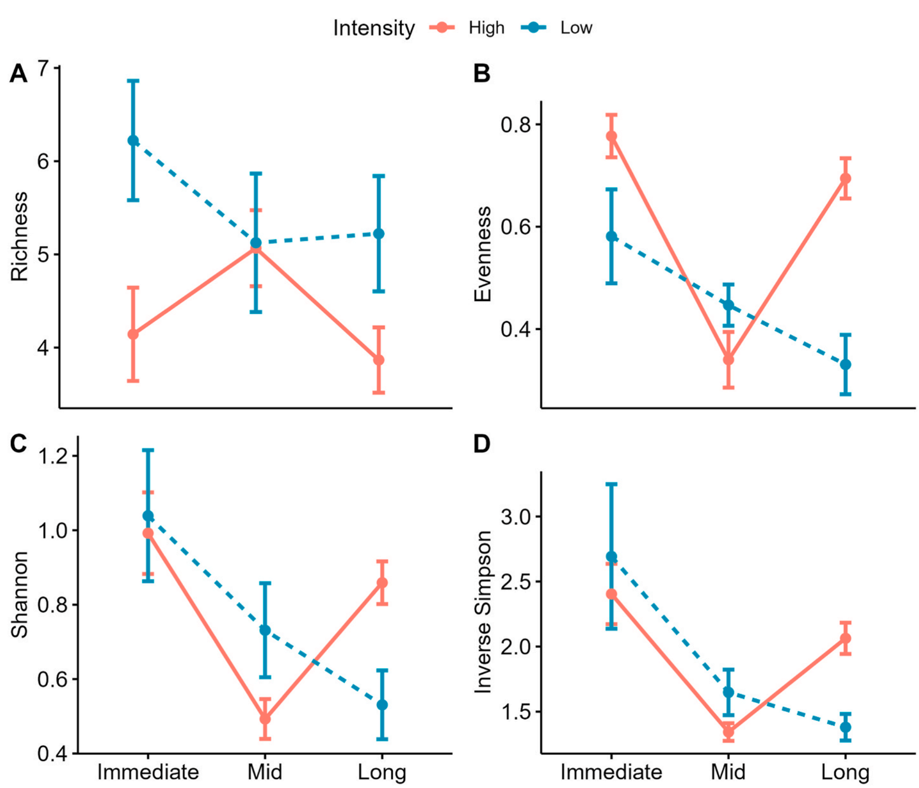

Fig. 4. Temporal changes in A. taxa richness, B. Pielou's evenness, C' Shannon's diversity and D. inverse Simpson's index for the two intensity levels. Errorbars indicate + -2 st. dev.

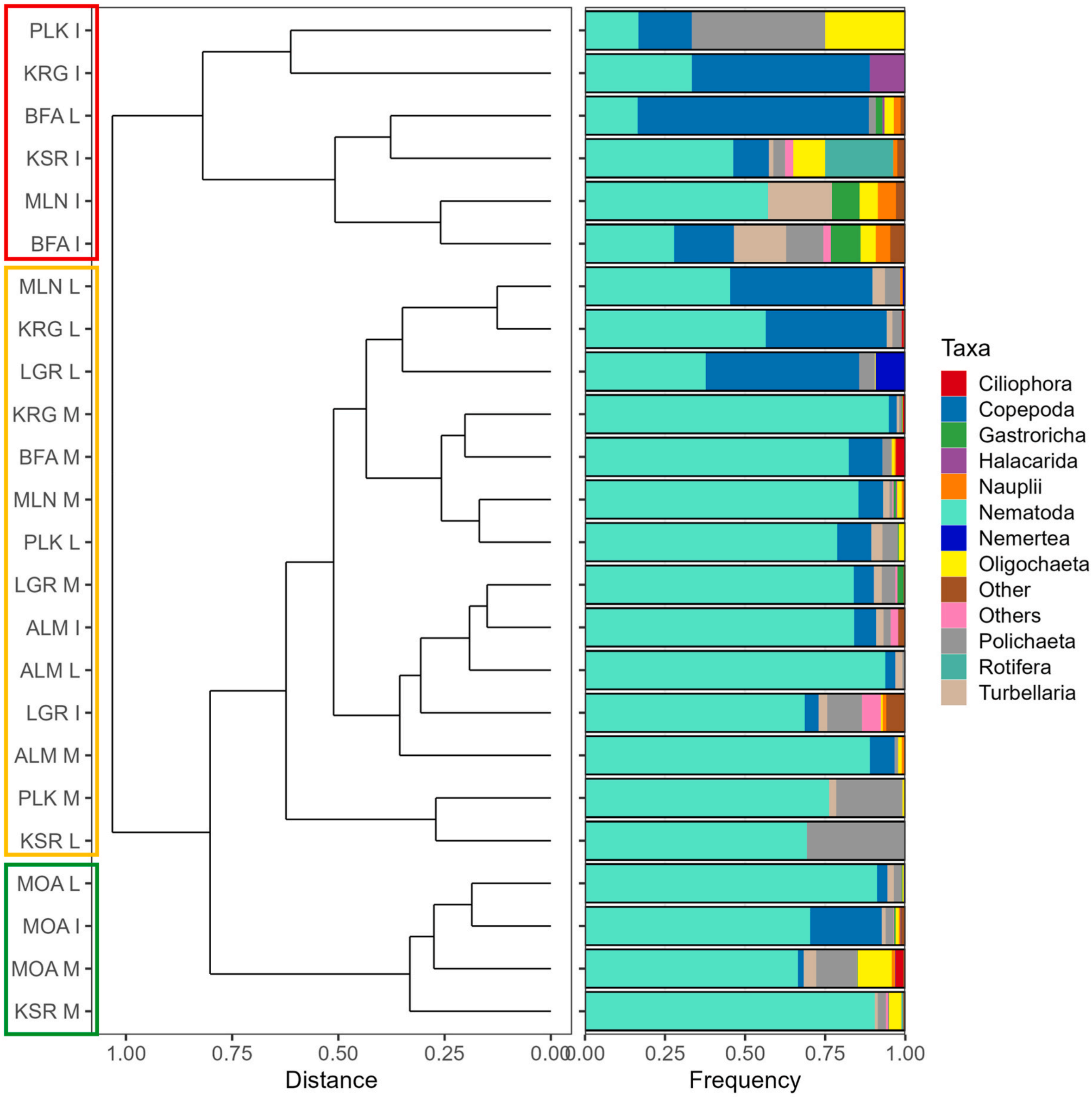

Fig. 5. Visualization of hierarchical clustering on meiofaunal communities using Ward's method, combined with the relative frequencies of the most important taxa (>2 %). Replicate samples were pooled together for sampling time and site and the log (x+1) transformed data were used to construct the Bray-Curtis distance matrix. Raw data were used for relative frequencies. Different colors indicate sites belonging to the same cluster. I- Immediately after the EWEs, M-mid-term, L-long-term. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

compared to the other two sampling times mainly along the CCA2 (Fig. 7A).

3.3. Nematodes

3.3.1. Diversity

Overall, 69 genera were reported, belonging to 23 families, 9 orders and 2 classes. Among those highest relative abundances were reported for *Viscosia* (35.8 %) and *Daptonema* (21.06 %), (Table s4).

Using Hill's numbers, no differences were observed between intensity levels for genera richness, in contrast to sampling interval, where the long-term interval exhibited lower values compared to the other two sampling intervals, indicated by the confidence intervals. Effective number of common species was significantly lower for the low intensity sites compared to the high intensity ones and for the long-term interval compared to the immediate and mid-term interval. The same trend was observed for the number of dominant species, but with significant differences being reported also between mid-term interval and immediate sampling period (Fig. 8).

3.3.2. Community structure

Hierarchical clustering resulted in 3 clusters with the nematode communities of the high intensity sites immediately after the EWEs grouped together, while the other two clusters contained the mid- and long-term intervals and all sampling times of one low intensity site, respectively (Fig. 9). PERMANOVA ($F_{perm} = 3.94$, $p_{perm} = 0.001$) and permutational pairwise post – hoc tests indicate that the time intervals following the EWEs had significantly different nematode communities, while NMDS suggests that communities immediately after the events being more distinct compared to the other two ones (Fig. 6B).

Relationship between environmental parameters and community structure.

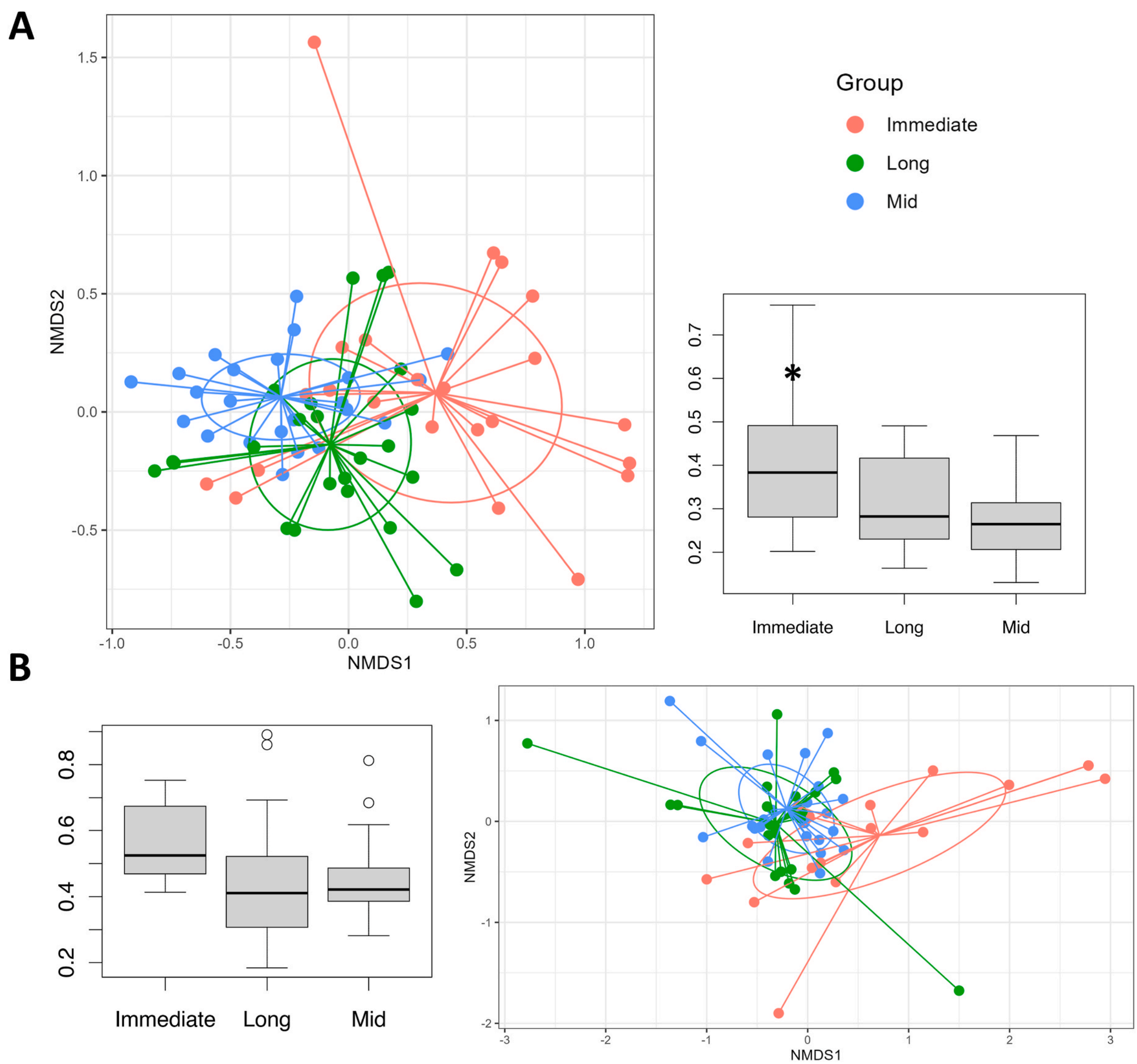

Fig. 6. Non-metric Multidimensional Scaling (NMDS) for A. meiofaunal (stress = 0.17) and B. nematode (stress = 0.10) communities grouped by time after the EWEs. Box-plots show distance from centroid for each group. Asterisk indicates statistical significance.

The results of the db – RDA and permutational tests for constrained ordination indicated the redox of sediment and NH_4^+ concentration as the factors best explaining variation in nematode communities. The overall explained variation from both RDAs resulted to 23.2 %, with redox of sediment showing negative correlation to both RDAs (−0.71 for both RDAs), while NH_4^+ concentration showed a negative relationship to RDA1 (−0.5) and positive relationship to RDA2 (0.85). The long-term sampling period appears to be distinguished from the immediate and mid-term intervals, primarily along the RDA1 (Fig. 7B).

3.4. Ecosystemic quality assessment

3.4.1. Indicator species analysis

The Indicator Species Analysis (ISA) identified 13 genera significantly associated with different groups of sites, out of a total of 68 genera analyzed. Seven genera were associated with a single group, two genera with two groups, two genera with three groups, and two genera were found across five groups.

Among the groups, *Prochromadorella* was significantly associated with the High - Immediate group. The High - Mid group included *Neochromadora* and *Paracanthonchus*. The Low - Long group was characterized by *Paracyatholaimus* and *Aponema*, while the Low - Mid group included *Ptycholaimellus* and *Chromadorina* (Table s3).

Certain genera were associated with multiple groups. *Dorylaimopsis* was linked to Low - Immediate and Low - Long, whereas *Theristus* was found in both Low - Immediate and Low - Mid. *Sabatieria* and *Terschellingia* were associated with Low - Immediate, Low - Long, and Low - Mid. The most widely distributed genus were *Viscosia* and *Daptonema*, which were associated with five groups: High - Long, High - Mid, Low - Immediate, Low - Long, and Low – Mid (Table s3). Coverage for single groups of sites indicates that, the High – Mid, Low – Mid and Low – Long groups are best described by their associated genera (Fig. 10).

3.4.2. Nematodes functional traits

It appears that the relative frequency of c-p scores and trophic groups, as well as maturity index and trophic diversity values were generally site – specific. Regarding the high intensity sites, KRG showed a dominance of the 2 A group in the first two sampling periods, LGR exhibited higher frequency for 1 B in the first sampling time and equally high frequencies of 1 B and 2 B in the second sampling interval, MLN presented higher frequency of 2 A in the first and of 1 B in the second sampling intervals and in PLK only the 2 A group was present in the first sampling time, whereas in the second sampling period 2 B exhibited the highest frequency. All high intensity sites showed a clear dominance of

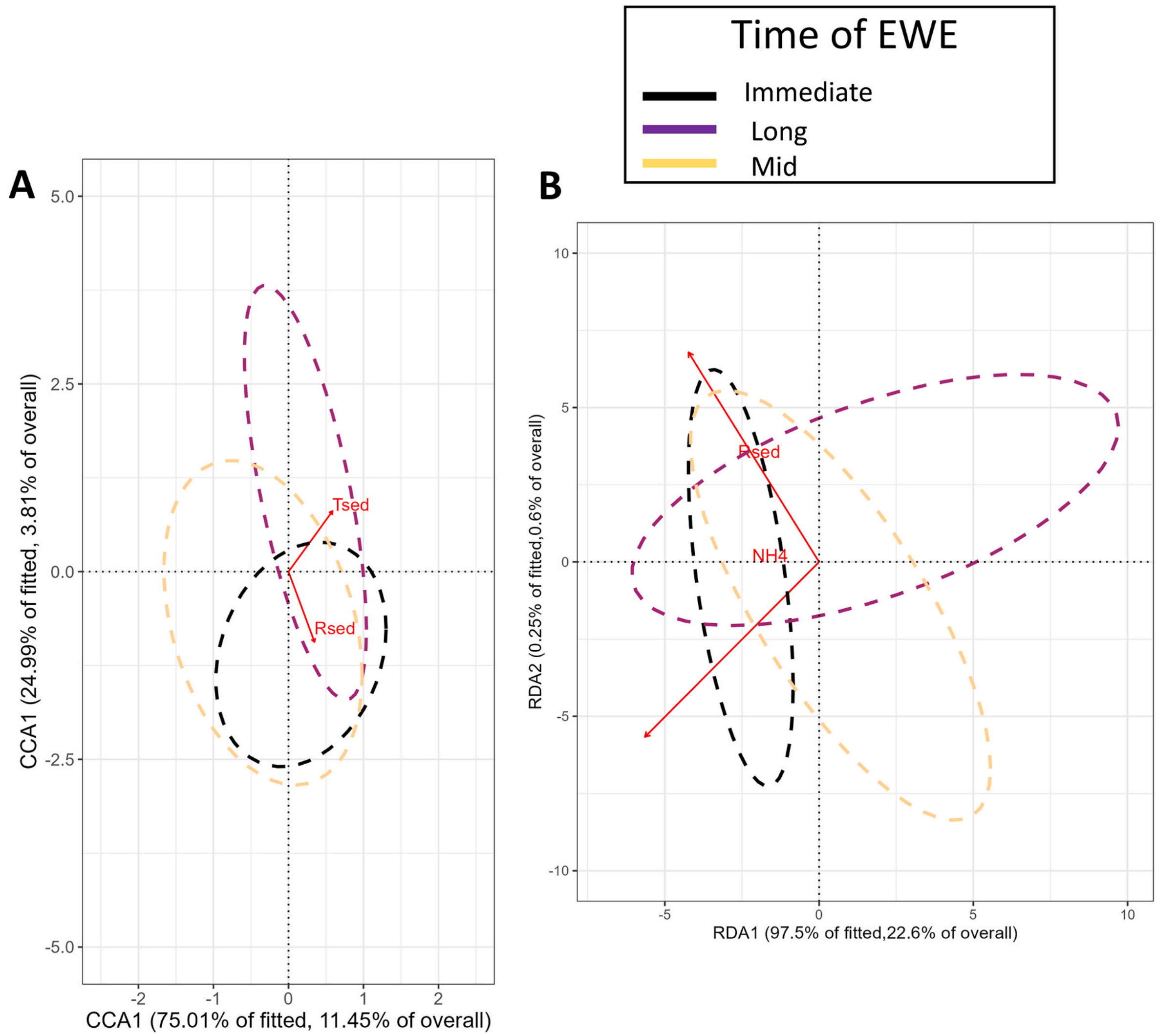

Fig. 7. A. Canonical Correspondence Analysis (CCA) on meiofaunal communities and B. distance-based Redundancy Analysis (db-RDA) on nematode communities with time after EWEs. Ellipses correspond to 95 % confidence interval (distance from centroid) for each group. Red arrows show the statistically significant environmental predictors, with arrow length being indicative of relative importance of predictors. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

the 2 B group in the last sampling time, except for KSR. In contrast KSR, initially showed relatively similar frequencies for all four trophic groups with a slight increase of 2 A, while in the second sampling interval higher frequencies were observed for 1 B and 2 B, however in the last sampling period there was a clear dominance of 1 A.

For the low intensity sites, ALM showed a dominance of 1 B, which was replaced by 2 B in the final sampling interval, whereas in BFA the first sampling time showed equal frequencies for 1 A, 1 B and 2 B, the second sampling period a dominance of 2 B and the last sampling time higher frequencies for 2 A. In MOA frequencies remained stable, with a slight increase of 2 B in the intermediate and final sampling periods.

In KRG, MLN and PLK c-p 2 and c-p 3 scores were observed initially in varying frequencies but in the long-term all sites exhibited a dominance of c-p 3. LGR, also a high intensity site, showed the same pattern, however in the mid-term interval the presence of c-p 4 was also reported. KSR, although also a high intensity site, showed a unique pattern, in that c-p 2 and c-p 3 had initially similar frequencies, with c-p 3 being replaced by c-p 4 in the mid-term interval, whereas in the long-term interval a clear dominance of c-p 1 was observed. For the low intensity sites, ALM and BFA showed a gradual increase in c-p 3 frequencies with time, while c-p scores in MOA remained relatively similar, with a slight decrease of c-p 3 frequencies towards the long-term sampling period (Fig. 11).

The ITD values for KRG, LGR and MLN fluctuated in the mid-term interval but remained similar between the ending of the events and the long-term interval. However, in KSR an increase was observed from the mid-term towards the long-term interval, while for PLK the highest value was reported immediately after the EWEs and the lowest at the mid-term interval. Regarding the low intensity sites, ALM showed an initial decrease in ITD, however it reached the highest values in the long-term interval, while BFA exhibited a gradual increase, also peaking one year after the events. The ITD values for MOA remained stable (Fig. 11 A).

KRG, MLN and PLK showed a gradual increase in MI, while for LGR the lowest value was observed immediately after the EWEs and highest 6 – months after. KSR showed the lowest MI values out of all sites in all time intervals, 1 -year following the events. ALM and BFA showed a gradual increase in MI, while for MOA a slight decrease was observed (Fig. 11B).

3.4.3. *Ecosystemic health assessment*

The EcoQ of all sites at all time intervals is given in Table 1. Bad ecosystemic quality was observed only for the high intensity sites, immediately after the EWEs, except for KSR, where bad ecosystemic

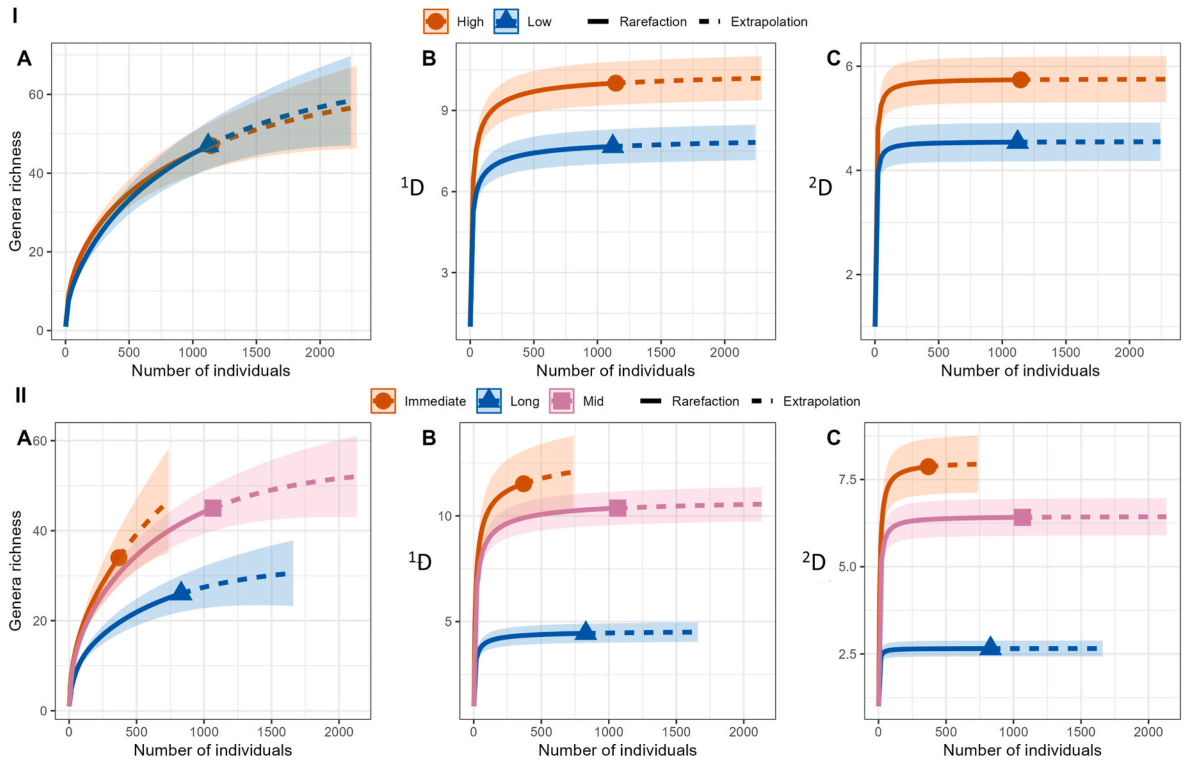

Fig. 8. Rarefaction-interpolation curves for Hill's numbers for nematode genera for I. different levels of intensities and II. different times from the EWEs. A. genera richness, B. ^{1}D corresponds to Shannon diversity and C. ^{2}D corresponds to Simpson diversity. Shaded areas indicate bootstrapped confidence intervals (95 %, 200 iterations).

quality was reported one year after the events. All other sites exhibited a moderate level of quality one year following the EWEs, however, the low intensity sites maintained their ecological status throughout the one – year interval except for ALM, which initially presented poor ecological quality (Table 1).

4. Discussion

The intensity and extent of disturbance have been repeatedly recognized as important drivers of changes in biological communities (e. g. Čada et al., 2016; Thakur et al., 2014; Vaselli et al., 2008). This relationship extends to swifts in the abundance of organisms, as well as changes in diversity patterns, both being related to the regime of disturbance (Cox et al., 2016; Wilby et al., 2015). Most meiofaunal studies have examined the short – term effects of natural disasters on meiofaunal communities and have reported a rapid recovery regarding meiofaunal densities (Altaff et al., 2005; Grzelak et al., 2009, 2014; Sugumaran et al., 2019). Although no data prior to the two EWEs were available for the examined sites, it is evident that the high intensity sites did not recover, as the meiofaunal densities one year following the events are comparable to those immediately after. The effect of varying levels of disturbance appear to be taxon specific, highlighted by the gradual increase of copepods in the high intensity sites and the similar densities of polychaetes between high and low intensity sites are indicative of their sensitive and tolerant natures, respectively (Altaff et al., 2005). Although other reasons might be responsible for the substantial changes in densities and diversity metrics regarding the mid- and long-term intervals for the high intensity sites (e.g. food limitations), such a hypothesis seems improbable as a similar pattern was observed for most sites, although they are significantly different in geographic location and topography.

The clusters that resulted from hierarchical clustering clearly show that meiofaunal communities were similar for the high intensity sites, whereas community structure was similar for most sites six months and a year following the EWEs. The fact that all sampling intervals of one site, that belonged to the low intensity group, comprised a separate group enhances the hypothesis that intensity played the primarily role in shaping meiofaunal communities. Other studies have shown that meiofaunal communities return to their pre – disturbance structure within days or weeks, however some of the meiofaunal communities examined here did not stabilize even after a 6-month interval (e.g. Grzelak et al., 2014; Kotwicki and Szczucirhski, 2006; 2015Mohan and Dhivya).

To our knowledge there are no studies that statistically examine the effect of abiotic factors on meiofaunal communities after the occurrence of natural disasters. Previous research investigated the effects of periodic events (i.e. monsoons) on meiofaunal and nematode communities showing significant variation related to physical disturbance (Semprucci et al., 2010). However, such climatological patterns are both expected and usually have a time span of at least a few months, thus are inherently different from EWEs. Generally, meiofauna in coastal systems are affected by food availability or granulometry. However, none of these parameters effectively explained variation in meiofaunal community structure. An absence of influence of granulometry and organic content on meiofaunal communities has rarely been documented in meiofaunal studies (Schratzberger et al., 2023 and references herein). However, other properties of organic carbon, such as the C/N ratio was shown to affect meiofauna, although in deeper waters (Tachibana et al., 2023). Changes in other environmental factors such as sediment redox and temperature can also significantly affect meiofaunal communities, as shown in the present study. Nonetheless, the causes of these fluctuations can many times be complex, but in this case they probably result from gradual changes of fresh water influxes and a varying degree of pollution due to wastewater discharges (Giere, 2009).

Natural disasters were shown to initiate recolonization processes at community level, as shown for macrofaunal communities following a tsunami, with an initial dominance of filter feeders, which were then replaced by predators (Lomovasky et al., 2011). The present study

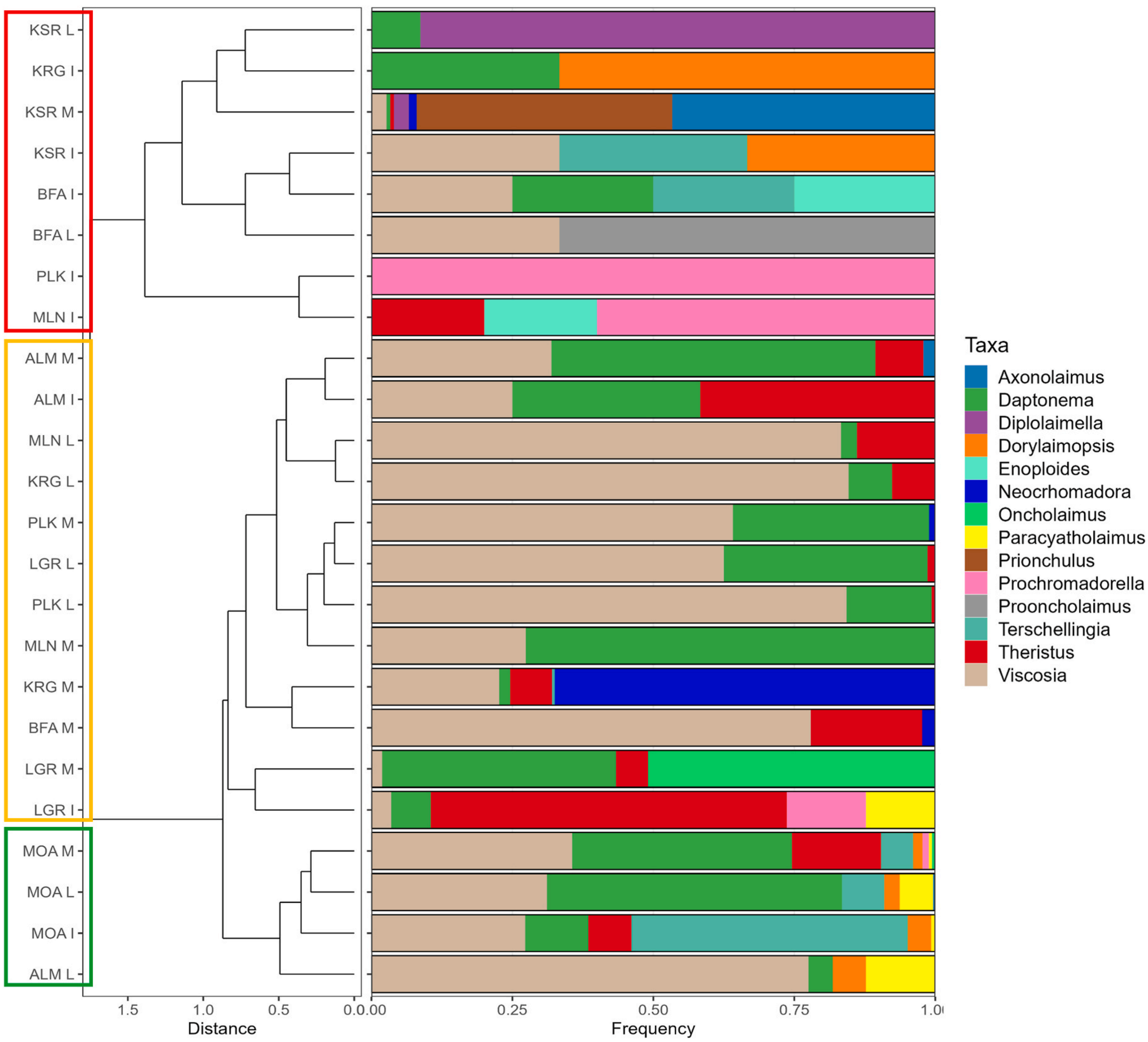

Fig. 9. Visualization of hierarchical clustering on nematode communities using Ward's method, combined with the relative frequencies of the most important taxa (>2 %). Replicate samples were pooled together for sampling time and site and the log (x+1) transformed data were used to construct the Bray-Curtis distance matrix. Raw data were used for relative frequencies. Different colors indicate sites belonging to the same cluster. I- Immediately after the EWEs, M-mid-term, L-long-term. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

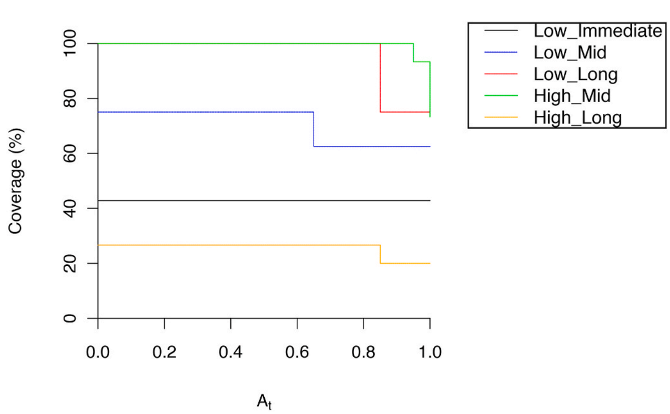

Fig. 10. Coverage plot indicating how well groups of sites are represented by their respective indicator genera. The high intensity group immediately after the EWEs was not shown due to high discrepancies among sites.

suggests that these mechanisms are influenced by the intensity of the event on a local scale. Although previous studies reported a rapid recovery of nematode densities following a natural disaster, our results suggest that higher taxonomic resolution is required in order to acquire a realistic conclusion regarding the state of nematode communities (Altaff et al., 2005; Grzelak et al., 2009, 2014; Sugumaran et al., 2019). Diversity metrics varied with both intensity level and time after the events, with dominance being indicative of stability in community structure, as low intensity and longer time intervals yielded greater dominance of fewer genera. Specifically, we propose that at the initial stage following disturbance most genera are removed, while in the mid-term interval colonizers rapidly occupy the ecological space, but are later replaced by the superior competitors. This hypothesis is in accordance with the theoretical framework of rationalized disturbance theory, most probably being an example of competition in a changing environment (Pulsford et al., 2016).

This does not necessarily contradict previous research suggesting that increased physical disturbance results in decreased nematode diversity, since in many sites (e.g. PLK) the initial genera richness was extremely low (Schratzberger et al., 2009). Using multivariate analyses, we confirmed the trend that was observed for the major taxa, with the high intensity sites being clustered together immediately after the EWEs,

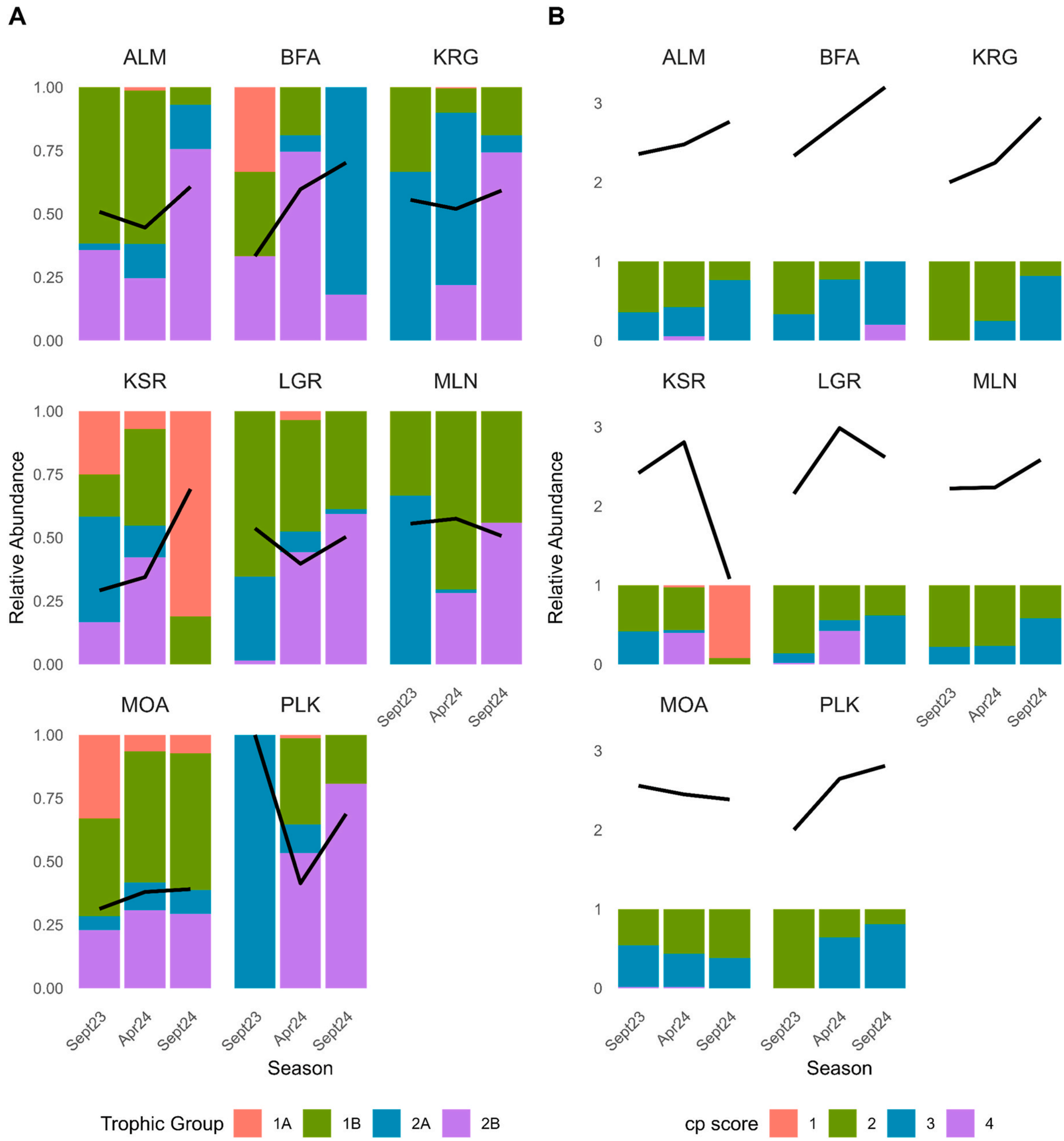

Fig. 11. A. Relative frequency of A. trophic groups and B. c-p scores for all sites at each time interval following the EWEs. Black lines show the A. trophic diversity index (ITD) and B. maturity index (MI), respectively.

most of the mid- and long – term sampling intervals grouped in a different cluster and the site that was least affected by the events belonging in a separate group.

The environmental parameters that best explained variation in nematode communities were the sediment redox and the NH_4^+ concentration. Similarly to the major taxa granulometry and organic carbon did not appear to influence nematodes' structure, which is unexpected since different levels of sediment deposition occurred in most of the study sites. However, the two environmental factors hint at the influence of agricultural discharges in some sites (Yan et al., 2019). This could indicate that when studying the effect of EWEs, the degree of anthropogenic pressure should also be taken into account.

Combining ISA and the functional traits of nematodes, the ecosystemic health of the examined sites was assessed. The recolonization hypothesis is enhanced by the differences in trends in c-p scores between high and low intensity. Although both groups showed a gradual increase in c-p 3 genera, sites belonging to the low intensity group exhibited faster replacement rates of c-p 2 with c-p 3 genera. Initial increased disturbance due to higher intensities was also reflected in MI and ITD, with low intensity sites generally showing higher MI and lower ITD values, respectively. Changes in the functional traits of nematodes are mainly linked to heavy metal contamination and organic matter pollution, due to anthropogenic activities (Bianchelli et al., 2018; Hua et al., 2021; Ingels et al., 2011; Losi et al., 2021). However, the relationship between ITD and physical disturbance was found to be inconsistent, which is confirmed by our study, since trophic diversity showed large variations and discrepancies compared to the other indices (Schratzberger et al., 2009). The inconsistency of ITD was also evident for other types of disturbances, such as in different levels of pollution (Moreno et al., 2011). Interestingly, MI exhibited patterns that could potentially be characteristic of different successional stages, with a gradual increase observed for most sites. This contradicts previous

Table 1
Environmental quality assessment based on the maturity index (MI), relative frequency of c-p 2 and c-p 4 and trophic diversity (ITD) for the examined sites and sampling times. The ecological quality of each site at each time of sampling is indicated with different colors: red-bad, yellow-poor, white-modeterate, blue-good.

Intensity	Site	Time	MI	c-p 2 %	c-p 4%	ITD	Ecological Quality
High	KRG	Immediate	2	100	0	0.56	Bad
		Mid	2.2	75.3	0	0.52	Poor
		Long	2.8	18.1	0	0.6	Moderate
	MLN	Immediate	2.2	77.8	0	0.56	Poor
		Mid	2.2	76.5	0	0.58	Poor
		Long	2.6	41.7	0	0.51	Moderate
	LGR	Immediate	2.2	86.4	1.9	0.54	Poor
		Mid	3	44	42.5	0.4	Good
		Long	2.6	38.3	0	0.5	Moderate
	KSR	Immediate	2.4	58.3	0	0.3	Moderate
		Mid	2.8	53.8	39.9	0.34	Good
		Long	1.1	7.9	0	0.7	Bad
	PLK	Immediate	2	100	0	1	Bad
		Mid	2.6	35.5	0	0.41	Moderate
		Long	2.8	19.2	0	0.67	Moderate
Low	ALM	Immediate	2.4	64.3	0	0.51	Poor
		Mid	2.5	57.9	5.7	0.46	Moderate
		Long	2.8	23.5	0	0.61	Moderate
	BFA	Immediate	2.3	66.7	0	0.33	Moderate
		Mid	2.8	23	0	0.6	Moderate
		Long	3.2	0	20	0.7	Moderate/Good
	MOA	Immediate	2.6	45.6	1.3	0.31	Moderate
		Mid	2.4	56.6	1.3	0.38	Moderate
		Long	2.4	61.6	0	0.39	Moderate

research related to a tsunami, where MI was a poor indicator of succession, probably due to the absence of data in the first successional stages (Semprucci et al., 2016).

Adequate representation of single groups of sites was possible only for three groups, however *Sabatiera* and *Terschellingia* exhibited high specificity for the sites belonging to low intensity group at all sampling intervals, while *Daptonema* and *Viscosia* showed high specificity and fidelity for all sites except for the high intensity ones immediately after the EWEs. Notably, these species are commonly found in sites characterized by various stressors, mainly due to anthropogenic activity (e.g. Losi et al., 2021, 2013; Moreno et al., 2008). On the other hand, *Prochromadorella* is considered resistant to hydrodynamic pressure, which is probably why this genus was associated with the high-immediate group (Semprucci et al., 2010). The results of the present study are indicative of the complex interaction of EWEs and anthropogenic activities on nematode taxonomy, resulting from an initial disturbance that led to successional processes. Ultimately, the nematode community will be shaped by competition-colonization trade-offs. These trade-offs are additionally constrained by specific abiotic stresses resulting from human activities such as increased agricultural or industrial influxes due to the flash-floods. In such cases the use of functional traits rather than taxonomy might be more suitable, as shown here by the use of a limited number of nematode features (Semprucci et al., 2022).

5. Conclusion

EWEs are increasing in both frequency and intensity, with their influence becoming exceedingly severe on coastal ecosystem. In the present study, the differences in trends regarding the recolonization process between intensities of disturbance suggest that the required time for meiofaunal communities to reach stability, as well as for ecosystemic restoration is directly related to the intensity of the events. This finding will be of great benefit for the conservation and restoration of biodiversity, especially in areas where anthropogenic activities are already present, as was the case for Pagasitikos gulf. Future meiofaunal studies should contribute to increasing our understanding regarding the tolerance levels of additional nematode genera, as sensitive genera might be more important than tolerant ones, when assessing the ecosystemic health status. Besides intensity other potential characteristics such as frequency of EWEs should be considered as potential drivers of influence on meiofauna. In this context, the combined use of the taxonomic and functional aspects of nematodes appears to be a robust tool, as showcased in the present study.

CRediT authorship contribution statement

Anastasions Varkoulis: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Konstantinos Voulgaris:** Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Androniki Dimoudi:** Methodology. **Konstantinos Georgiou:** Methodology. **Konstantinos Skordas:** Methodology. **Nikos Neofitou:** Methodology. **Dimitris Vafidis:** Writing – review & editing, Writing – original draft, Validation, Supervision, Project administration, Conceptualization.

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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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2025.107289.

Data availability

Data will be made available on request.

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