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Ecosystem changes in deep Eastern Mediterranean: a comparison between 1989 and 2023

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Major ecosystem changes have been observed in different oceanic regions and have also been reported in the deep sea as a result of complex physical and biological interactions. Here we investigated changes that have occurred in one of the world's most oligotrophic regions: the deep Eastern Mediterranean Sea. Across a wide area of the Ionian and Aegean Sea, at depths ranging from 500 to 2500 m, we compared historical data dated back to 1989 with new data collected in 2023 exactly at the same sites. Changes in environmental variables (including surface water processes), and sediment organic matter content were related to the benthic response in terms of prokaryotic abundance, and the meiofaunal abundance and composition. We report here that, over this time frame of ca 30 years, this region experienced a progressive increase in bottom water temperatures and of the primary production in the photic zone, which may have determined the accumulation of protein and carbohydrate concentrations in surface sediments. Such changes resulted in an increase of prokaryotic abundance, but contrary to our expectation, were associated with a shift in the meiofaunal community structure and a decrease in the number of higher taxa. This included a reduction in evenness and a major decrease in meiofaunal biomass linked to the major decline of juvenile polychaetes. These results may indicate the altered functioning of the deep-sea ecosystems, with a potential loss of ecosystem services and a simplification of the benthic food webs.

KEYWORDS

ecosystem changes, deep-sea ecosystems, benthic prokaryotes, meiofauna, Mediterranean Sea

1 Introduction

The deep ocean is experiencing changes in temperature, currents, oxygen concentrations, organic matter input, and cycling (Sweetman et al., 2017). Such changes are the result of the combination of multiple drivers, among which climate change, through its effects on primary production, and episodic events, such as dense shelf-water cascading and circulation perturbations, as in the case of the Eastern Mediterranean Transient (Canals et al., 2006; Roether et al., 1996; Pusceddu et al., 2010), play key roles. The functioning of deep-sea ecosystems is largely driven by food availability, which, in turn, primarily depends on organic carbon export from the photic zone (Corliss et al., 2009; Smith et al., 2009; Danovaro et al., 2017). However, the amount of organic matter reaching the deep seafloor is influenced by different environmental factors, such as production (including its temporal variability), temperature and thermocline, nutrient supply and mixed-layer depth (Brierley and Kingsford, 2009; Doney et al., 2012; Xiu et al., 2018; Lønborg et al., 2020; Yoon et al., 2022).

Long-term monitoring studies have indicated that deep-sea ecosystems are sensitive to climatic variability also through its influence on the quantity and quality of surface primary production (Rogers, 2015), but the dimension of such changes occurring in deep-sea ecosystems and their response to such long-term changes are still largely unknown due to the limited information on alterations happening over decadal timescales.

Recent studies suggest that in the deep-sea there may be an increase in POC fluxes at high latitudes along with changes in seasonality, with dramatic effects on the diversity and abundance of deep-sea communities. For instance, in the Northeast Pacific, changes have included increases in the faunal density but decreases in the diversity (Kuhnz et al., 2014). The changes in temperature, currents, oxygen concentrations and organic matter input are expected to have even a stronger impact in highly oligotrophic regions where deep-sea benthic ecosystems suffer an almost-permanent starvation (Danovaro et al., 2010). Changes in deep-water temperatures can have either direct and indirect effects on biodiversity (Yasuhara and Danovaro, 2016) and even minor temperature shifts, in the order of 0.1–0.4°C, can result in major changes in deep-sea biodiversity and community structure (Danovaro et al., 2004).

The Mediterranean Sea is a miniature ocean (ca 0.8% of the global ocean surface) with a bio-geographic position and a lower average depth (ca 1500 m vs 3750 m of the global ocean), which accelerate the effects of climate change (Parras-Berrocal et al., 2020; Schroeder et al., 2023). In the Western Mediterranean Sea, a warming trend has been observed since the decades 1960–1990, with a temperature increase of approximately 0.12°C at 1600-m depth (Bethoux et al., 1990). Such warming trend in deep waters accelerated over the last 30 years with a rise of bottom temperatures of ca 0.005°C y⁻¹ (Vargas-Yáñez et al., 2017; Kubin et al., 2023). Conversely, during the '80s - '90s, the Eastern Mediterranean basin showed a drop of deep-water temperatures (around 0.4°C), and an increase in salinity (Roether et al., 1996). This phenomenon, defined “Eastern Mediterranean Transient” (Theocharis et al., 2002), was

characterized also by the downwelling of surface waters, which caused a deep-water upwelling up to 100–150 m depth, promoting the primary productivity in the euphotic zone (Psarra et al., 2000). These changes had significant impacts on deep-sea biodiversity, and ecosystem functions in the '90s (Danovaro et al., 2001, 2004), including a significant decline in the meiofaunal functional diversity and evenness, coupled with changes in the community composition. These effects were particularly evident in nematodes and are thought to be linked to temperature changes. These examples make evident the highly dynamic response of deep-sea ecosystems to changes in the hydrodynamic and productivity features (Danovaro et al., 2001).

To investigate the changes occurred on deep-sea ecosystems of the Mediterranean Sea from the '90s to the present (2023) we compared the results of a study carried out in 1989 (Danovaro et al., 1993, 1995) over a wide deep-sea region of the Eastern Mediterranean, by collecting samples in the same sites, using the same methodologies, to ensure a reliable comparison.

The aim of the present study is to gain insights into the biological response and to understand the sensitivity to environmental changes of a deep-sea ecosystem in the extremely oligotrophic Eastern Mediterranean Sea.

2 Materials and methods

2.1 Study area

The present study was carried out in the Eastern Mediterranean Sea (Figure 1), one of the most oligotrophic areas of the Mediterranean Sea (Tselepidis and Eleftheriou, 1992). In April 2023 sediment samples were collected onboard of the R/V *Aegaeo* in 11 stations at depths ranging from 500 to 2500 m (Supplementary Table 1) (Figure 1). The station location, sampling tools, procedures, protocols, and sample preservation and storage were the same as those used in September 1989. To ensure consistency with the sampling carried out in 1989, samples were collected using a USNEL-type box corer, ensuring the collection of undisturbed surface sediments with clear water on top of the sediment surface. For each station three replicates were collected. From each replicate deployment, one liner (corer) was used for meiofauna and one for the biochemical analyses thus ensuring the collection of independent replicates. For each replicate core used for biochemical analyses, a sediment sample was collected using a sterile spatula for prokaryotic analyses. Each core was sectioned in layers (0–1cm, 1–3cm, 3–5cm, 5–10cm, 10–15 cm) for a total of 330 samples preserved at -20°C until laboratory analyses.

2.2 Environmental variables

Monthly mean data on sub-surface (97-m depth) chlorophyll-a concentrations and potential bottom water temperature were obtained from datasets provided by EU Copernicus Marine Services (Escudier et al., 2020; European Union-Copernicus

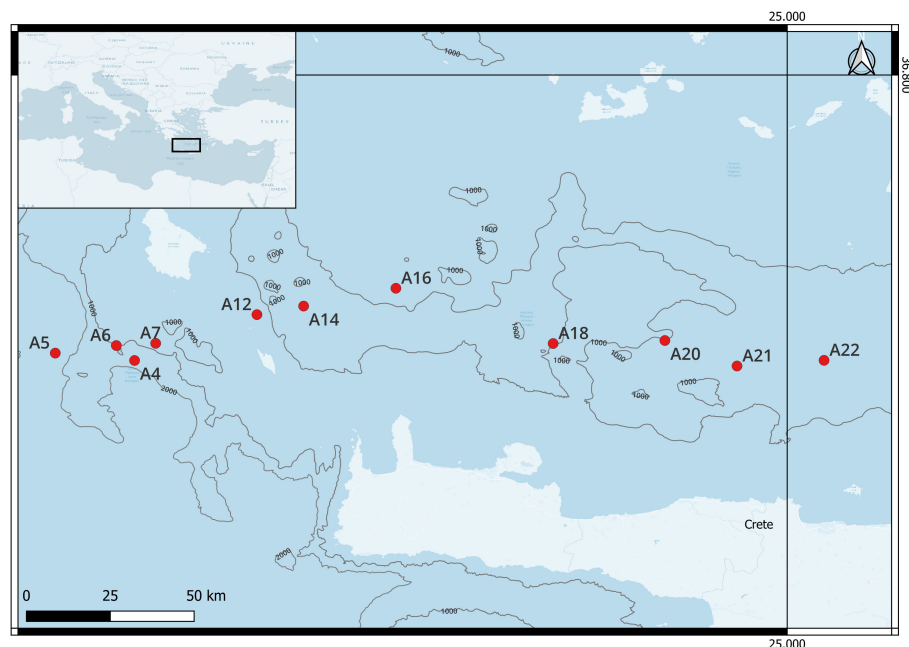


FIGURE 1

Map showing the sampling stations located off the northern coast of Crete, in the Eastern Mediterranean Sea.

Marine Service, 2018, 2019, 2020; Feudale et al., 2023), by selecting the area of study (coordinates 36.132 N, 34.945 S, 22.893 W, 26.452 E). Chlorophyll-a data are available at a horizontal resolution of 0.25°, while the temperature data are at a resolution of 1/16° with 72 vertical levels. For both datasets, we used monthly means as provided, without applying further temporal or spatial aggregation. These datasets were selected for gathering information on temperature and primary productivity changes across the period 1989–2023.

2.3 Biochemical composition of organic matter

Protein, carbohydrate, and lipid contents of sediment samples were determined following the protocols described by Danovaro (2009), using a Shimadzu spectrophotometer (Model UV-1700). Proteins were extracted in a hot water bath and quantified using the Lowry method, with Reagent A (0.5 N NaOH), Reagent B (Folin–Ciocalteu reagent), and Reagent C (copper sulphate solution) (Supplementary Table 2), measuring absorbance at 650 nm. Carbohydrates were measured using the phenol–sulphuric acid method (absorbance at 485 and 600 nm) after drying and rehydration of the sediment. Lipids were extracted with a chloroform–methanol mixture, carbonized with sulfuric acid, and quantified at 375 nm. All samples were centrifuged at 800 × g between steps.

As determined in 1989, we also quantified the concentration of Labile organic matter (LOM) as the sum of all carbohydrate, protein and lipid concentrations, expressed in mg/g. The concentrations of carbohydrates, proteins and lipids were transformed into carbon

equivalents to determine the concentration of Biopolymeric C (BPC), using the coefficients 0.40, 0.49 and 0.75 $\mu\text{g C } \mu\text{g}^{-1}$ respectively (Fabiano et al., 1995).

2.4 Prokaryotic abundance

Prokaryotic abundance was analyzed following Danovaro (2009): surface sediment samples were collected manually with a sterile spatula and preserved in formaldehyde (2%). Samples were sonicated and subsamples were diluted 200 times. The subsamples were filtered on 0.22 Black Nucleopore filters and stained with SYBR Green I, afterwards they were incubated for 20 minutes and filtered again with pre-filtered seawater. Once ready, the filters were placed on a glass slide and examined under an epifluorescence microscope (Zeiss Universal microscope). Ten to twenty grids were randomly chosen and at least 200 cells were counted.

2.5 Meiofauna

Meiofauna extraction followed the protocol by Danovaro (2009). Samples were sonicated three times for one minute and sieved through a 500 and a 40 μm meshes, retaining the organisms within these size range, which were considered as the meiofaunal fraction (Danovaro, 2009). Remaining sediment was mixed with Ludox TM and centrifuged three times at 3000 rpm (800 × g). After each centrifugation, the supernatant was sieved again, and the collected material was fixed in 70% ethanol with Bengal Rose dye for staining. Identification and counting of meiofauna to the order level was performed using a Leica stereomicroscope (3.5X) on a

cuvette box with a grid of 200 cells. Individuals of each taxon were enumerated to determine the abundance (expressed as individuals per 10 cm²). The meiofaunal biomass was calculated by using the volumetric method, which consists in extrapolating organism dry weight from their biovolume. This can be obtained from body length (L) and width (W) of each individual, and specifically for nematodes using the equation proposed by Warwick and Price (1979). Meiofaunal specimens were first mounted on slides after formalin–ethanol–glycerol treatment to prevent dehydration (Danovaro, 2009), then measured following the same process as above but under an optical microscope (40x) and following the formula proposed by Andrassy (1956).

2.6 Statistical analyses

To test for differences in the biochemical composition of organic matter, meiofaunal abundance, biomass and composition, and prokaryotic abundance among stations and between 1989 and 2023, permutational analyses of variance (PERMANOVA) were performed. Additionally, to identify the potential drivers (primary productivity expressed as the concentration of chlorophyll-a, potential bottom temperature, organic matter components) of meiofaunal composition a Redundancy Analysis (RDA) was carried out (Supplementary Figure 1), based on Bray-Curtis similarity index calculated from meiofaunal abundance data (individuals per 10 cm²), after square-root transformation. All analyses were performed using PRIMER-e v.7 computer programme.

3 Results

3.1 Environmental parameters

Data from 1989 to 2023, showed an increasing trend in potential bottom temperatures in the entire investigated region. The results point out an overall average increase of ca 0.3°C over the past 30 years (from 14.16°C in 1989 to 14.49°C in 2023), as confirmed by linear regression analysis ($p < 0.001$) (Figures 2A, B). This warming trend cannot be explained by seasonal variability, as seasonal temperature changes within each year were limited to about 0.1°C in both 1989 and 2023.

We also explored the temporal patterns for sub-surface chlorophyll-a concentrations (data available only from 1993 to 2023). Although the data show a significant seasonal variability, we identified a tendency of chlorophyll-a concentration to increase over the past three decades ($p < 0.001$; Figure 2C).

3.2 Biochemical composition of organic matter

Overall, the organic matter in the sediments has increased when comparing the year 1989 with 2023. In particular, the labile organic

matter (LOM) and biopolymeric carbon (BPC) concentrations increased by 21% and 28% respectively (Figure 3A). Since they depend on the variables considered, it was observed that proteins increased significantly from $0.28 \text{ mg g}^{-1} \pm 0.02$ in 1989 to $0.67 \pm 0.04 \text{ mg g}^{-1}$ in 2023 (PERMANOVA $p < 0.001$), carbohydrates slightly increased from 1.71 ± 0.05 to $2.15 \pm 0.14 \text{ mg g}^{-1}$, while lipids showed a decrease from 0.33 ± 0.02 to $0.30 \pm 0.04 \text{ mg g}^{-1}$ (Figure 3B; Supplementary Table 2). In terms of organic matter composition, carbohydrates remained the dominant component although in lower percentage (63 vs. 60% in 1989 and 2023 respectively), while the contribution of proteins increased (12% in 1989 and 23% in 2023), and lipids decreased (24% in 1989 and 16% in 2023).

3.3 Prokaryotic abundance

Prokaryotic abundance overall increased significantly from 1989 ($0.72 \times 10^8 \text{ cells g}^{-1}$) to 2023 ($1.55 \times 10^8 \text{ cells g}^{-1}$) (Figure 4). In 1989, prokaryotic abundance ranged from 0.16 to $1.91 \times 10^8 \text{ cells g}^{-1}$. In 2023, prokaryotic abundance ranged from 1.26 to $2.00 \times 10^8 \text{ cells g}^{-1}$ (at station A16 and A5, respectively).

3.4 Meiofaunal assemblage composition

In 1989, overall, 11 meiofaunal higher taxa, from the level of order to phylum were observed: nematodes, polychaetes, harpacticoid copepods, turbellarians, oligochaetes, tardigrades, ostracods, tanaidaceans, kinorhynch, molluscs and halacaridae. In 2023, the total number of higher taxa was 10, which not only reduced but also changed, with the lack of oligochaetes, ostracods and molluscs that were present in 1989 and the presence of cumaceans and priapulids larvae that were instead missing in 1989. In addition, we observed a clear shift in the assemblage structure, with a reduction of rare taxa, defined here as those that were either absent or contributing <1% to the total abundance (Pusceddu et al., 2011), (represented as “others”), and a marked increase in the dominance of nematodes (Figure 5).

3.5 Meiofaunal abundance and biomass

The average abundance of meiofauna did not change significantly between 1989 and 2023 (Figure 6A). In 1989, at Station A20 an unusual peak in turbellarian abundance (196 ind. 10 cm⁻²) was observed. Such value was not confirmed in 2023. Other stations showed some differences in terms of total abundance (mostly due to nematodes) or rare taxa. Nematodes were always the most abundant taxon but increased their numerical dominance from 1989 (68% of total meiofaunal abundance) to 2023 (93%).

In terms of biomass, a significant decrease from 1989 to 2023 was observed (Figure 6B). The highest biomass value was observed in 1989 at station A20 ($585.1 \text{ } \mu\text{g C}/10 \text{ cm}^2$), compared to the highest value of $13.7 \text{ } \mu\text{g C}/10 \text{ cm}^2$ at station A12 in 2023. Station A4 was the

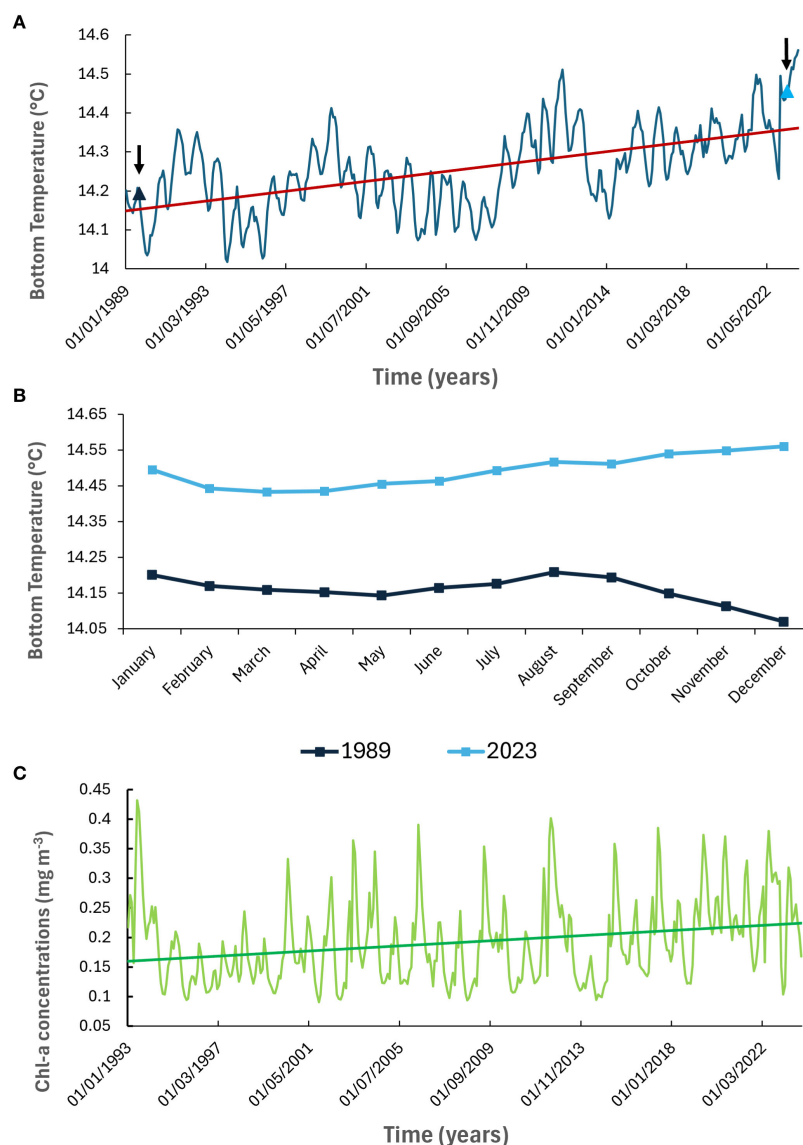


FIGURE 2

Temporal pattern in potential bottom water temperatures from 01/01/1989 to 01/12/2023 in the Southern Aegean Sea (coordinates 36.132 N, 34.945 S, 22.893 W, 26.452 E), the dark blue triangle represents the temperature at the sampling time (September) in 1989, the light blue triangle represents the temperature at the sampling time (April) in 2023 (A). Average monthly temperatures in 1989 and in 2023 (B). Temporal patterns of sub-surface chlorophyll-a concentrations from 1993 to 2023 (C).

only one that did not experience a notable change in biomass values ($2.8 \mu\text{g C}/10 \text{ cm}^2$ in 1989 and $2.90 \mu\text{g C}/10 \text{ cm}^2$ in 2023) (Supplementary Table 3). The average among stations in 1989 was $246.5 \mu\text{g C}/10 \text{ cm}^2$, which decreased to $4.7 \mu\text{g C}/10 \text{ cm}^2$ in 2023. The results from the PERMANOVA test confirmed statistically these results with $p < 0.001$. This drastic shift can be attributed to changes in the taxonomic composition. In 1989, polychaetes were the dominant taxon contributing to biomass values (ca 72%), followed by nematodes (14%) and copepods (12%). However, in 2023, nematodes were the primary contributors to biomass (57%), followed by copepods (27%) and polychaetes (13%) (Supplementary Figure 2).

4 Discussion

The Mediterranean basin is characterized by a clear gradient of decreasing productivity moving eastwards (Danovaro et al., 2010), which is due to the limited continental (river) inputs in the Eastern basin and the increasing distance from the nutrient rich and productive Atlantic waters. The ultra-oligotrophic Cretan Sea in the Eastern Mediterranean has become a paradigmatic example to comprehend the biotic response to such extreme trophic conditions and the Mediterranean gradient is a model to investigate the response of deep-sea ecosystems to a progressive food limitation due to climate change (Danovaro et al., 2001, -2008).

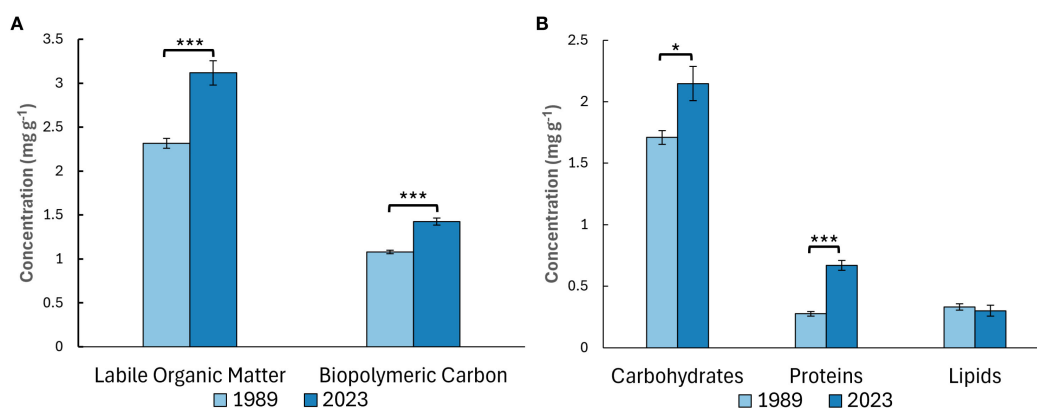


FIGURE 3

Carbohydrate, protein, lipid, biopolymeric carbon and labile organic matter contents in the sediments of the studied area in 1989 and 2023. The plots show the biopolymeric carbon (BPC) and labile organic matter (LOM) (A) and the carbohydrates, proteins, and lipid (B) contents in the two sampling years (1989 vs 2023) within the area of study. Error bars represent standard errors. Significant differences are reported as: *p < 0.05, ***p < 0.001.

During the last 30 years several changes have occurred in the Mediterranean Sea at regional level. From 1990 to 1995, the so-called “Eastern Mediterranean transient” determined an increase in primary production (Psarra et al., 2000). After 1995, the eastern Mediterranean water masses returned to the pre-transient conditions, but according to the chlorophyll-a data reported here (Copernicus data base) the increasing trend of primary productivity continued also in the following decades, until a few years ago, also as a result of a novel upwelling of nutrient-rich deep waters observed in 2017–2019 (Potiris et al., 2024).

The comparison between two sampling periods (1989 vs 2023, i.e., ca 30 years apart and without taking into account the presence of a seasonal variability), cannot reflect the full succession of ecological and environmental changes that occurred in the deep sea, the results from two snapshots were useful to understand how deep-sea ecosystem changed during this time

frame. In addition, the analysis covered a wide area (extending for ca. 5000 km) and across a considerable bathymetric range (500–2500 m depth) and was based on the use of the same sampling devices, methodologies (including sieves size, cores’ length) and protocols used for the analyses carried out in 1989, ensuring a robust and consistent comparison.

Generally, an increase in the ocean productivity, as the one observed in the Eastern Mediterranean from 1993 onward, is associated with an increase in the export of organic matter to the deep seafloor (Tamelander et al., 2013). The results reported here for a wide sector of the Eastern Mediterranean confirmed that the increase of primary production observed from satellite data resulted in a significant increase of the concentrations of labile organic matter on surface deep-sea sediments, particularly in terms of proteins and carbohydrates, which led to an overall increase in the food availability to the deep-sea biota.

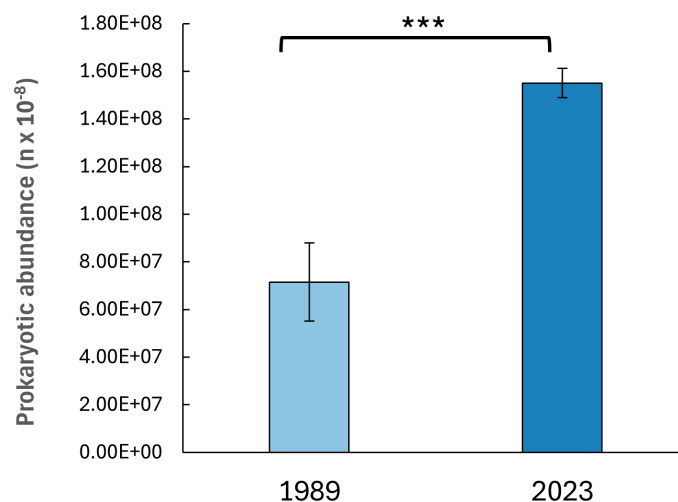


FIGURE 4

Prokaryotic abundances in 1989 and in 2023. Error bars represent standard errors. Significant differences are reported as: ***p < 0.001.

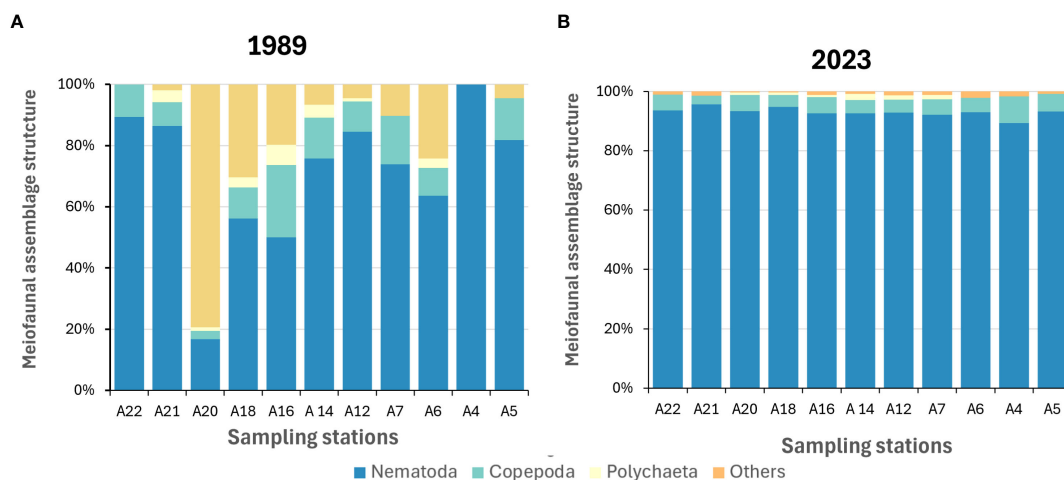


FIGURE 5
Meiofaunal assemblage structure in terms of main taxa in 1989 (A) and in 2023 (B).

These results confirm the tight link between processes occurring in the water column and the benthic response, and were reflected by a ca 20% increase in concentrations of the bulk of labile organic matter in 2023 when compared to 1989. The linkage between primary productivity (increase in sub-surface chlorophyll-*a* concentrations, used as a proxy of primary productivity) and sedimentary organic matter composition was evident for the two biochemical classes of organic matter (proteins and carbohydrates) that dominate the biochemical composition of phytoplankton.

Changes in food availability, especially in ultra-oligotrophic deep-sea sediments, typically determine a significant benthic response (Danovaro et al., 2000; Nomaki et al., 2021). Prokaryotes displayed the most significant response to the increase in food supply, doubling their abundance in 2023 when compared to 1989. This result is somewhat expected as it is known that the microbial components can react promptly to changes in environmental conditions and food availability (Danovaro et al., 2000). Conversely, the results for the multicellular components (metazoan meiofauna) were far more complex than expected, as meiofaunal abundance did not change

significantly from 1989 to 2023, but nematodes increased notably their contribution to the total meiofaunal abundance. This result was associated with a shift in the meiofaunal community structure and, even more importantly, with a decrease of the relative abundance of meiofaunal taxa. In particular, in 2023, we reported the lack of oligochaetes, molluscs and ostracods that were present in 1989 and the appearance of cumaceans and priapulids larvae that were missing in 1989. We cannot exclude that some of these taxa might be subjected to seasonal or recruitment-related changes over time, yet the observed turnover in higher taxa and their complete absence in the whole deep-sea region, leads to hypothesise that the observed changes are significant and evident at high taxonomic levels (i.e., class level).

Such changes were substantiated by a significant drop in meiofaunal biomass from 1989 to 2023. In particular, polychaetes decreased in both abundance and contribution to total biomass by approximately 60% or more. This was accompanied by a dramatic decline in turbellarians, with losses exceeding 90%. While differences in sampling months may account for the presence of larval forms, the substantial decline in both temporary and

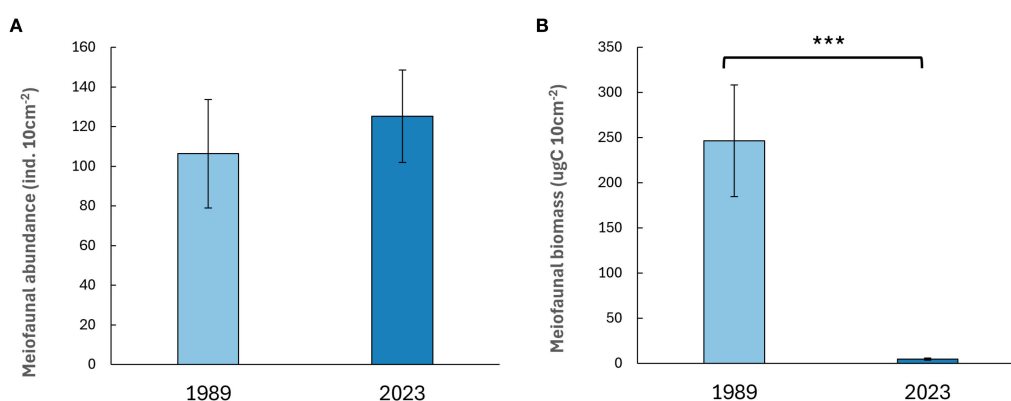


FIGURE 6
Meiofaunal abundance (A) and biomass (B) in 1989 and in 2023. Error bars represent standard errors. Significant differences are reported as: ****p* < 0.001.

permanent meiofaunal taxa (i.e., polychaetes and turbellarians, respectively) indicates the presence of significant ecological changes that extend beyond seasonal variability.

These changes were corroborated by macrofaunal analyses conducted at the same stations and sampling times, which showed a marked decrease in abundance (from >100 to 16.8 individuals m⁻²), as well as in their contribution to the macrofaunal assemblage—from 60–72% in 1989 to 5–10% in 2023 (Marcucci, 2024).

The shift toward smaller and more opportunistic taxa may be a consequence of these changes, potentially leading to a substantial alteration in ecological functions, as the most affected taxa, polychaetes and turbellarians, represent a significant fraction of deep-sea predators. These predatory taxa were largely replaced by deposit feeders and bacterivorous taxa (dominant among deep-sea nematodes), which reflect an increase in organic detritus and in the abundance of benthic prokaryotes.

The overwhelming dominance of nematodes in 2023 coupled with the disappearance of some higher taxa and the drop in the overall meiofaunal biomass over ca 30 years, suggest that major environmental changes and ecological changes occurred, and that these changes had a clear impact on deep-sea biota leading to an overall simplification of the benthic food webs.

The comparison between the two sampling periods also indicates that, despite the increase in primary productivity, the deep-sea ecosystems of the Eastern Mediterranean showed the increase of the dominance of the microbial biomass and the decrease in animal biomass, a process that could be defined as “miniaturization” of the key biological components accounting for the whole biomass. Such changes were coupled with a lower ability to channel the larger inputs of primary organic matter, observed in 2023, into biomass, which indicate the global impoverishment of the deep-sea ecosystem functions and thus a lower capacity to support the transfer of energy (biomass) to higher trophic levels.

Our results provide new insights into the functioning of the extremely oligotrophic deep-sea ecosystems, such as the Eastern Mediterranean Sea, and suggest that food availability alone is not sufficient to predict the complex multitrophic interactions occurring in the deep sea. In addition, the results obtained comparing the same deep-sea region from 1989 and 2023 indicate a drop in ecosystem services (here expressed in terms of biomass) and a simplification of the benthic food webs.

The results of the present study from the deep-Mediterranean Sea and the presence of ecosystem shifts in other marine ecosystems worldwide, suggest the need of a more systematic and long-term time-series monitoring and as well as the collection of ecological data to better assess the ecological implications of such changes over the largest ecosystems of the biosphere.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AK: Writing – original draft, Data curation, Investigation, Visualization, Writing – review & editing, Formal Analysis. CG: Validation, Methodology, Data curation, Writing – review & editing. ML: Methodology, Data curation, Validation, Writing – review & editing. CC: Visualization, Funding acquisition, Conceptualization, Writing – review & editing. AD: Writing – review & editing, Funding acquisition, Resources, Visualization. MT: Resources, Validation, Funding acquisition, Writing – review & editing. RD: Supervision, Funding acquisition, Conceptualization, Writing – original draft, Resources, Project administration.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2025.1612914/full#supplementary-material>

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