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# A train of marine heat waves affected benthic local beta but not alpha diversity

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ABSTRACT

Over the past decades, ocean temperatures have risen substantially, with far-reaching consequences for marine biodiversity and ecosystem functioning. Marine heat waves (MHWs), have increased in both duration and frequency, leading to shifts in species composition and ecosystem processes. We analysed the effects of repeated MHWs on recruitment of benthic communities in a Marine Protected Area (MPA) in Southern Sardinia. We used standardized sampling units, Autonomous Reef Monitoring Structures (ARMS), combined with high-throughput sequencing of mitochondrial cytochrome *c* oxidase subunit I. This allowed us to measure short-term variations in benthic biodiversity at two sites, Berni and Santa Caterina, which initially had different temperatures. We found 241 eukaryotic families belonging to 22 different phyla recruited on ARMS. Both before and after MHWs, Porifera were the most abundant phylum (21–37 %), followed by Bryozoa (27-16 %) and Cnidaria (15–18 %). Before MHWs, the two sites exhibited different taxa richness and taxonomic composition, with significantly higher alpha diversity in the warmer site. After the MHWs train, alpha diversity did not change significantly. However, the taxonomic composition of the two sites tended to homogenise, resulting in a significant decrease in beta diversity. In both sites, the variation in the benthic assemblage structure after the MHWs train was driven by the decreased abundance of slow-moving and less heat-tolerant taxa (e.g., Bryozoa, Nudibranchia, Rhodophyta). This decrease was counterbalanced by an increase in mobile and more heat-tolerant ones (e.g., Decapoda). The short-term outcome of repeated MHWs is a homogenization of the benthic recruits' community, without any significant change in the number of taxa. Because biodiversity and ecosystem functioning are generally positively linked, the short-term effects of MHWs may have limited impacts on ecosystem functioning. However, they could reshape the benthic community composition, altering the ratio of 'winners' to 'losers' taxa contributing to ecosystem functions.

## 1. Introduction

Climate change has become a major environmental threat, strongly affecting marine biodiversity and ecosystem functioning, and exacerbating consequences of other anthropogenic stressors. Besides gradual ocean warming, acidification, deoxygenation, and sea-level rise, the number of extreme climatic events, such as marine heat waves (MHWs), have increased all over the world (Frölicher et al., 2018; Perkins et al., 2012). Projections indicate that the future oceans will experience more frequent, more intense, longer lasting and anomalous interconnected events (Benedetti-Cecchi, 2021; Oliver et al., 2018).

MHWs are defined as periods of five or more days where sea surface temperatures (SSTs) are warmer than the 90th percentile for the location and period of the year, based on a 30-year fixed historical climatological baseline (Hobday et al., 2016).

The effects of MHWs on marine ecosystems and biodiversity have been reported in multiple regions especially within the Pacific, Atlantic and Indian Oceans (Wernberg et al., 2013, 2016; Smale et al., 2017, 2019). MHWs can alter marine species distribution (Azzurro and D'Amen, 2022; Olsen et al., 2022) and community composition (Ishida et al., 2023; Timmers et al., 2021) leading to complex biological responses (i.e., negative, positive, or neutral) from different taxa (e.g., plankton, algae, invertebrates, fishes, birds, and mammals) across multiple trophic levels (Ishida et al., 2023; Ruthrof et al., 2018; Sanford et al., 2019).

The Mediterranean Sea is considered an ideal model to assess the

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effects of climate change on marine biodiversity as it is currently experiencing faster warming rates than the global ocean (Lejeusne et al., 2010). In this basin, during the last decades, MHWs have triggered unprecedented climate driven mass mortality events and their occurrence is expected to increase in the upcoming decades (Garrabou et al., 2009, 2022; Stipcich et al., 2022).

Most of the studies carried out so far regarding the consequences of MHWs on marine ecosystems primarily focused on taxa that are charismatic and/or easy to document in the field (e.g., threatened species such as fish, corals, and sea turtles (Donaldson et al., 2017; Joyce et al., 2023; Rubio-Portillo et al., 2016; Troudet et al., 2017)). Nonetheless, the effects of MHWs on the recruitment and build-up of hard-bottom communities are poorly understood, still. A high proportion of hard-bottom fauna include small-sized animals also known as “cryptobenthos” (Carvalho et al., 2019; Pearman et al., 2020). These organisms inhabit concealed or interstitial spaces on hard-bottom substrata and encompass different lifestyles (e.g., sessile and mobile) and trophic functions (e.g. suspension feeders, detritivores, predators). They also interact within each other in a wide range of relationships including commensalisms, mutualisms and parasitism (Carvalho et al., 2019). Despite their ecological relevance, cryptobenthos are often overlooked during traditional benthic surveys due to the inherent difficulties in sampling and identification (Pearman et al., 2016, 2020). Therefore, there is an urgent need to understand how the recruitment of these communities could be impacted by MHWs.

During the last decade, many efforts have been made to standardize biodiversity data collection, allowing for studies at larger spatial and temporal scales (Obst et al., 2020). The study and monitoring of hard-bottom ecosystems is a challenge as they are three-dimensionally complex and difficult to access. A promising approach is based on the use of artificial substrates, passive samplers that can record the biodiversity and community composition in a standardized way, by taking advantage of their recruitment and establishment. Among them, Autonomous Reef Monitoring Structures (ARMS) have been used across the world’s oceans over the last few years for different research purposes (Timmers et al., 2021; Pearman et al., 2020; Obst et al., 2020). ARMS consist of stacked PVC plates, arranged in a three-dimensional structure, that provides suitable settlement surfaces for a variety of benthic species and can be deployed without causing a significant impact on the surrounding environment. With the alternating open and obstructed format in the gaps between plates, ARMS can mimic the structural complexity of hard-bottom substrata, allowing the colonization of a variety of organisms with different niche preferences. After ARMS retrieval (from weeks to years), recruited communities can be identified by the extraction and sequencing of environmental DNA (eDNA), which is an efficient approach allowing for the rapid assessment of species diversity (Leray and Knowlton, 2015; Ruppert et al., 2019).

In this study, we deployed ARMS and used high-throughput sequencing of mitochondrial cytochrome *c* oxidase I (COI) to study benthic recruitment at two sites differing in baseline temperature. This could allow us to understand how a train of summer MHWs may impact cryptobenthic biodiversity and influence taxonomic composition in two different sites.

## 2. Materials and methods

### 2.1. Study area and sampling design

ARMS were deployed according to the methodology described below at two sites, namely, Berni (N39°05′108″, E009°25′722″) and Santa Caterina (N39°06′695″, E009°32′956″), within the Marine Protected Area (MPA) of Capo Carbonara (Western Mediterranean Sea; Fig. 1). The submarine landscape of the MPA Capo Carbonara is dominated by the outcropping of granite and associated magmatic rocks (Orrù et al., 2005). Berni site is an isolated almost surfacing granite relief located offshore the Simius Bay, in an axial position respect to the channel between Capo Carbonara and the Isle of Cavoli. The site hosts a *Posidonia oceanica* meadow and coralligenous platform reefs with red algae. Santa Caterina shoal is located on the other side of the Simius Bay respect to Berni and is also characterized by granite rocks with continuous coverage of macrofitobenthos.

In each site, four modified ARMS were installed by SCUBA divers on a horizontal rocky substrate at 9m depth on the 3rd of July 2022. Each ARMS was composed of five 22.5 × 22.5 cm PVC plates stacked on top of a 35 × 45 cm base plate with spacers separating the plates at a fixed distance of 1.27 cm. The construction of the ARMS followed the protocol

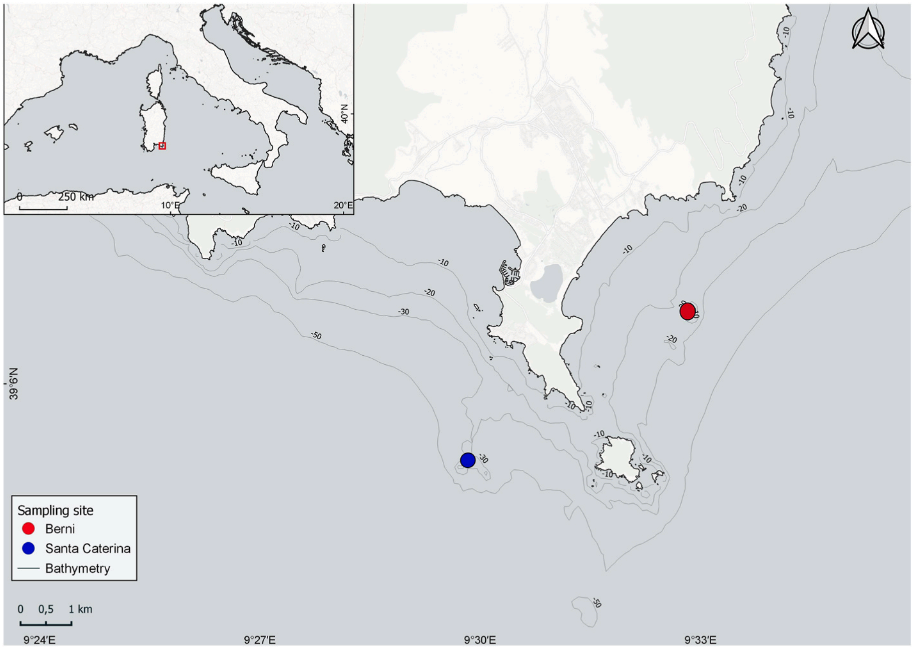

**Fig. 1.** Location of the two sampling sites, Santa Caterina (blue circle) and Berni (red circle), within the Marine Protected Area of Capo Carbonara (South Sardinia, Western Mediterranean Sea). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

available on the Smithsonian Institute website (https://naturalhistory.si.edu/research/global-arms-program/protocols).

In each site, two ARMS (R1, R2) were retrieved on the 3rd of July 2023 (hereafter $T_0$, assumed a priori to represent the period preceding summer MHWs), and the remaining two (R1 and R2) once the MHWs train ceased, on the 28th of September 2023 (hereafter $T_1$).

### 2.2. Environmental data collection

Water temperatures between the two sampling times were recorded at 3 min interval using two HOBO loggers (Onset Computer Corporation, Massachusetts, USA) deployed adjacent to the ARMS. The data obtained with the HOBO loggers, spanning from 3rd July to 28th September 2023 were compared with the concurrent Satellite-derived SST values produced by the NASA JPL (https://coastwatch.pfeg.noaa. gov/erddap/griddap/jplMURSST41. html) to assess the degree of penetration of any eventual MHW at the depth of ARMS deployment.

The NASA JPL temperature data for the 1982–2023 period were then used, using the Group for High Resolution Sea Surface Temperature (GHRSST), at a 1 km resolution (G1SST), for assessing the climatological means over the last 30 years and the occurrence of MHWs during the study period. Therefore, we used the "*rerdapp*" (Chamberlain et al., 2025) and the "*heatwaveR*" (Schlegel and Smit, 2018) packages to either calculate or display MHWs during the considered sampling period. MHWs were defined as periods in which daily mean temperatures (from satellite-derived SST data) exceeded the 90th percentile for at least 5 consecutive days relative to the 30-years climatological baseline (Hobday et al., 2016). Each identified MHW was then categorized according to (Hobday et al., 2018). The "*heatwaveR*" package allowed assessing the duration (days), maximum intensity ($i_{max}$: highest temperature anomaly value during the MHW) (°C) and mean intensity ($i_{mean}$: mean temperature anomaly during the MHW) (°C) of each MHW (Hobday et al., 2016).

### 2.3. ARMS retrieval and processing

At retrieval, each ARMS was placed in a large container filled with 100 μm filtered seawater, collected *in situ*, for the successive transport back to the laboratory. In the laboratory, the ARMS were disassembled within the filtered seawater. Each plate was scraped clear of the accumulated biomass that was immediately homogenized (using a blender) and preserved in 95 % ethanol for the successive steps (Leray and Knowlton, 2015).

### 2.4. DNA extraction, amplification, and sequencing

Environmental DNA was extracted (in a dedicated room for eDNA extraction and manipulation) from 10 g of the scraped and homogenized biomass using the DNeasy Powermax Soil kit (QIAGEN), as per the manufacturer's instructions with the exception of the bead-beating step, which was replaced by shaking incubations overnight at 56 °C with the addition of Proteinase K (0.4 mg $mL^{-1}$) (Leray and Knowlton, 2015). This commercial extraction kit can specifically remove humic substances that can inhibit PCR enzymes, thereby alleviating PCR biases. To avoid false positives, negative controls were included along the DNA extraction procedure to check for contaminations of the solutions and labware materials used. These negative controls were used as templates in subsequent PCR amplification reactions. Amplicons were generated via PCR in triplicate 20 μL reaction volumes for each sample targeting a 313-bp COI fragment using the specific primer set mlCOIintF (forward) and jgHC02198 (reverse) (Geller et al., 2013; Leray et al., 2013), following the protocol proposed by (Leray and Knowlton, 2015). PCR amplicons were prepared for Illumina MiSeq sequencing following (Pearman et al., 2020) and then sequenced by Macrogen Korea (Illumina MiSeq 2 × 300 bp PE).

### 2.5. Bioinformatic analyses

Adapter and primer sequences were removed from the raw data using Cutadapt (v3.2) (Martin, 2011). Additionally, forward and reverse reads were trimmed to 250 bp and 230 bp, respectively. The reads were subsequently processed using the DADA2 package (v1.18.0) (Callahan et al., 2016). Sequences with expected errors of 2 or more were excluded. Following error correction, the remaining paired-end reads were merged into Amplicon Sequence Variants (ASVs) with a minimum overlap of 10 bp and a maximum mismatch of 0bp. At this point, chimeric sequences were removed using the *removechimeradenovo* script within DADA2. During this process, subsampling was conducted based on the sample with the lowest read count among all samples to ensure comparability between them. Each ASV was aligned to the organism with the highest similarity in the corresponding Reference Database (NCBI_NT), using algorithms such as BLAST+(v2.9.0) with an e value threshold of 0.001. ASVs that were assigned to Bacteria were removed.

### 2.6. Statistical analyses

Alpha diversity metrics in each ARMS (as number of ASVs, Chao1 and Shannon's indices; Supplementary methods) were obtained and represented using the R software packages *phyloseq* (McMurdie and Holmes, 2013), *vegan* (Oksanen et al., 2009), and *ggplot2* (Wickham and Wickham, 2016). To assess differences in alpha diversity between sites ($n = 2$), time ($n = 2$) and their interaction we applied a multivariate distance-based permutational analysis of variance (PERMANOVA) based on Euclidean distance matrices of untransformed data and unrestricted permutations of the raw data.

The taxonomic composition in each site and in each date of sampling was determined at both the phylum and family level. Differences in the phyla composition between the two sites and the two sampling dates were assessed using PERMANOVA, based on Bray-Curtis similarity matrixes of fourth-root transformed data (with 999 permutations under a reduced model) of relative read abundance of the top nine abundant phyla (>3 %) and the top eight abundant families (>3 %) (Timmers et al., 2021). To visualize these differences, Canonical Analysis of Principal Coordinates (CAP) was prepared (Anderson and Willis, 2003). All the statistical analyses were carried out using the same sampling design, considering two factors as main sources of variance: site (fixed, two levels: Berni and Santa Caterina) and time (fixed, two levels: $T_0$ and $T_1$). Significant differences were investigated using posteriori pairwise tests. P values in both PERMANOVA and pairwise tests were obtained from Monte Carlo asymptotic distributions, because of the restricted number of unique permutations (Anderson and Robinson, 2003).

SIMPER analyses (based on ranked matrixes of Bray–Curtis similarities) were also carried out to assess the percentage of dissimilarity (Gray, 2000) in the assemblage composition between the sampling sites at each sampling date and between ARMS replicates at each site and sampling date, for either most abundant phyla or most abundant families and for identifying the taxa most responsible for the observed (significant) differences. All statistical analyses were carried out using the routines included in the software PRIMER 6+ (Clarke and Gorley, 2006).

Furthermore, we analysed the differences in read abundances of each taxon between sites and sampling times with a differential abundance testing method, using the R package *DESeq2* (Love et al., 2014). It uses a model based on negative binomial distribution, which is particularly suited for count data like those from sequencing experiments, identifying changes in taxa abundances related to different conditions. Significant differences were investigated using a posteriori pairwise test. P values in pairwise tests were obtained from Monte Carlo asymptotic distributions, because of the restricted number of unique permutations (Anderson and Robinson, 2003).

## 3. Results

### 3.1. Water temperature

The sea temperature recorded by the temperature loggers deployed near the ARMS at the two study sites, from the 3rd of July to the 28th of September 2023, intercepted the satellite-derived SST values from 28 July onwards. In the preceding weeks, the warming trend observed in SST did not correspond to a concurrent warming at 9 m depth (Fig. S1). During the 87 days of temperature measurements with the HOBO loggers, Berni site exhibited consistently higher temperatures (25.48 °C on average) than those at Santa Caterina (25.04 °C on average), corresponding to a relatively stable difference of ca. 0.44 °C. At both sites, temperature reached the highest value in August (27.48 °C and 27.36 °C, at Berni and Santa Caterina, respectively).

### 3.2. MHWs occurrence and characterization

At both sites, we detected the occurrence of a train of three consecutive moderate MHWs (i.e., events with a maximum intensity peaking between the seasonal climatologic threshold and the double of this threshold (Hobday et al., 2018)), each with site-specific intensity and duration (Fig. 2, Table 1). At Berni the first MHW occurred from the 14th to the 25th of July ($i_{max}$ 2.89 °C), the second from the 20th to the 28th of August ($i_{max}$ 2.14 °C) and the last one from the 18th to the 25th of September ($i_{max}$ 2.03 °C). At Santa Caterina the three MHWs occurred from the 12th to the 25th of July ($i_{max}$ 3.09 °C), from the 20th to the 28th of August ($i_{max}$ 2.15 °C), and from the 18th to the 25th of September ($i_{max}$ 1.94 °C). Differences in the MHW intensity between the two sites emerged, especially during the first MHW, with Santa Caterina experiencing a duration (14 days) and cumulative intensity (36.00 °C) much higher than that at Berni (12 days and 30.12 °C) (Table 1). At both sites, the rate of onset of the first MHW (0.15–0.16 °C d$^{-1}$) was the highest among the others (0.06–0.11 °C d$^{-1}$), whereas the highest rate decline occurred during the second MHW (0.29 and 0.36 °C d$^{-1}$ at Santa Caterina and Berni, respectively).

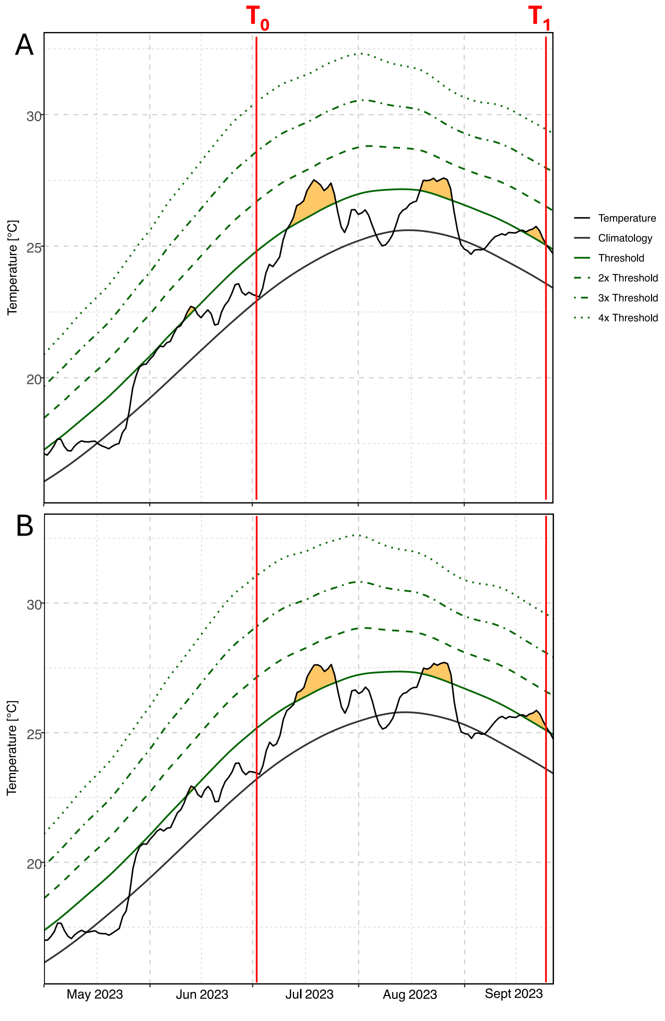

**Fig. 2.** MHWs occurrence, intensity and duration (estimated as in Hobday et al., 2018) at Berni (A) and Santa Caterina (B) during the study period, from the 3rd of July ($T_0$) to the 28th of September 2023 ($T_1$).

### 3.3. Biodiversity of benthos recruited on ARMS

The negative controls did not originate sequences. After quality checking and removal of chimeras, the resulting dataset contained 544039 raw reads, 45 % of which could be confidently assigned to eukaryotic organisms. A large proportion of reads (54 %) could not be assigned to any specific taxon, while 0.1 % of the total reads were assigned to prokaryotes (529 reads belonging to 47 ASVs). Among the 5194 ASVs retrieved, 1070 matched to Eukaryotic taxa, belonging to 241 families and 22 different phyla.

All the alpha diversity indices, except Shannon's, differed significantly between the two sites at both sampling times, but did not show any effect of the MHWs train, nor of the factors' interaction (Table 2). Alpha diversity indices in Berni were significantly higher (by 28–32 %) than those in Santa Caterina (Table S1; Fig. 3).

Either at $T_0$ or at $T_1$, Porifera were the most abundant phylum (21–37 %), followed by Bryozoa (27-16 %) and Cnidaria (15–18 %). Other phyla contributing >3 % to the community included Annelida, Mollusca, Echinodermata, Rhodophyta and Arthropoda. In both sampling sites, the abundance of Annelida, Echinodermata and Rhodophyta decreased while that of Arthropoda and Porifera increased (Fig. 4A).

Overall, Vesiculariidae (Bryozoa, 20 %) was the most abundant family, followed by an unassigned family of the order Poecilosclerida (Porifera, 14 %) and Sertulariidae (Cnidaria, 7 %). At Berni site the unassigned family of the order Poecilosclerida dominated the recruited assemblage both at $T_0$ and $T_1$, while, at Santa Caterina, Vesiculariidae dominated at $T_0$ and Sertulariidae at $T_1$ (Fig. 4B).

All phyla, except Entoprocta, Evosea, Haptophyta, and Nematoda (exclusive to Berni), occurred in both sites. In Berni, Haptophyta, Nematoda and Rotifera disappeared after the MHWs train, while Evosea occurred in very few reads (0.1 % of the total) only in late September. In Santa Caterina, Discosea and Rotifera occurred only at $T_0$, while Platyhelminthes occurred only after the MHWs train (2 %). The phyla composition of the recruited benthos varied significantly between sites, sampling times, and because of their interaction (Table 2). The composition of the recruited benthic phyla differed significantly between the two sites only before the MHWs train ($T_0$; Beta diversity = 16 % dissimilarity), while these differences were not significant and decreased after the MHWs train ($T_1$; Beta diversity = 10 %) (Fig. 5A, Table 3, Table S2). The variation between the two sampling sites before the MHWs train was mostly due to Bryozoa which contributed 22 % to the total differences, followed by unassigned Eukaryota (19 %) Porifera (17 %) and Annelida (13 %) (Table 3). The dissimilarity between sites after the MHWs train was mostly due to Mollusca (28 %), followed by Porifera (15 %), Echinodermata (14 %), Arthropoda (11 %) and Bryozoa (10 %) (Table 3). The dissimilarity in phyla composition between ARMS replicates increased after the MHWs train in both sites (from 8 to 11 % in Berni and from 6 to 9 % in Santa Caterina; Fig. 5B–Table 3).

Despite the composition of the recruited benthic families did not vary significantly between sites nor between sampling times, the results of the DESeq2 tool revealed significant variations in the number of reads of several families after the MHWs train for the two factors' (site and time) interaction (Table S3). Among them and considering the families that exhibited the same variation pattern in both sites, after the MHWs train,

**Table 1**

Occurrence dates (start, peak, end), duration, intensity (average, maximum and cumulative), onset and decline rates, and category (according to Hobday et al., 2018) of the three MHWs at the two sampling sites.

| Sampling Site | Start date | Peak date | End date | Duration (days) | Average intensity (C°) | Maximum intensity (C°) | Cumulative intensity (C°) | Onset rate $^{\circ}C\ d^{-1}$ | Decline rate $^{\circ}C\ d^{-1}$ | MHW category |
|---|---|---|---|---|---|---|---|---|---|---|
| Berni | 14/07 | 19/07 | 25/07 | 12 | 2.51 | 2.89 | 30.12 | 0.15 | 0.17 | I Moderate |
| | 20/08 | 26/08 | 28/08 | 9 | 1.93 | 2.14 | 17.38 | 0.08 | 0.36 | I Moderate |
| | 18/09 | 22/09 | 25/09 | 8 | 1.76 | 2.03 | 14.11 | 0.11 | 0.14 | I Moderate |
| Santa Caterina | 12/07 | 19/07 | 25/07 | 14 | 2.57 | 3.09 | 36.00 | 0.16 | 0.20 | I Moderate |
| | 20/08 | 26/08 | 28/08 | 9 | 2.00 | 2.15 | 18.02 | 0.06 | 0.29 | I Moderate |
| | 18/09 | 22/09 | 25/09 | 8 | 1.67 | 1.94 | 13.37 | 0.10 | 0.14 | I Moderate |

**Table 2**

Results of the PERMANOVA carried out to assess differences in observed ASVs, Chao1 index, Shannon index and taxonomic composition (multivariate) at the phylum level, between the two sites and sampling times (df = degrees of freedom; MS = mean square; Pseudo-F = statistic F; P(MC) = probability levels obtained from Monte Carlo asymptotic distributions; * = P < 0.05; ns = not significant).

| Variable | Source | df | MS | Pseudo-F | P (MC) |
|---|---|---|---|---|---|
| **Observed ASVs** | Time | 1 | 450 | 0.47 | ns |
| | Site | 1 | 14112 | 14.60 | * |
| | Time × Site | 1 | 512 | 0.53 | ns |
| | Residual | 4 | 966.5 | | |
| **Chao1 index** | Time | 1 | 544.83 | 0.57 | ns |
| | Site | 1 | 14904 | 15.47 | * |
| | Time × Site | 1 | 506.26 | 0.53 | ns |
| | Residual | 4 | 963.58 | | |
| **Shannon index** | Time | 1 | 0.02 | 0.06 | ns |
| | Site | 1 | 1.08 | 4.22 | ns |
| | Time × Site | 1 | 0.26 | 1.01 | ns |
| | Residual | 4 | 0.26 | | |
| **Taxonomic composition at phylum level** | Time | 1 | 185.38 | 4.73 | * |
| | Site | 1 | 150.28 | 3.83 | * |
| | Time × Site | 1 | 136.24 | 3.48 | * |
| | Residual | 4 | 39.20 | | |
| | Total | 7 | | | |

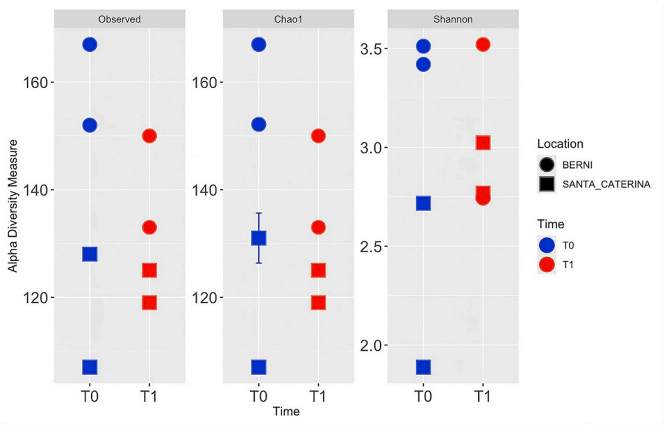

**Fig. 3.** Observed ASVs, Chao1 index, and Shannon index values at the two sites under scrutiny at the beginning of July 2023 ($T_0$, blue) and in late September 2023 ($T_1$, red). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

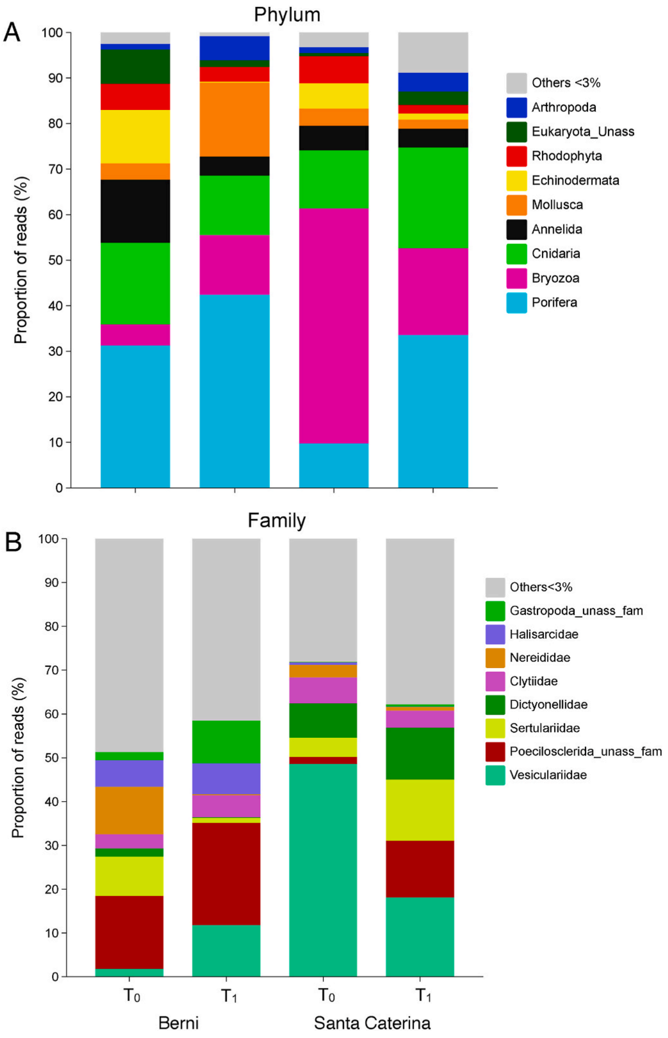

**Fig. 4.** Taxonomic percentage composition of the recruited benthic phyla (A) and families (B) at the two sampling sites before ($T_0$) and after ($T_1$) the MHWs train.

the number of reads of Diogenidae and Plumnidae (Arthropoda, Malacostraca, Decapoda) significantly increased in Santa Caterina and that of Terebellidae (Annelida, Polychaeta, Terebellida) significantly increased in Berni (Fig. 6); conversely, Champiaceae (Rhodophyta, Florideophyceae, Rhodymeniales) and Pinnulariaceae (Heterokontophyta, Bacillariophyceae, Naviculales) significantly decreased in Santa Caterina, while Microporidae (Bryozoa, Gymnolaemata, Cheilostomatida) and Facelinidae (Mollusca, Gasteropoda, Nudibranchia) disappeared in both sites (Fig. 6).

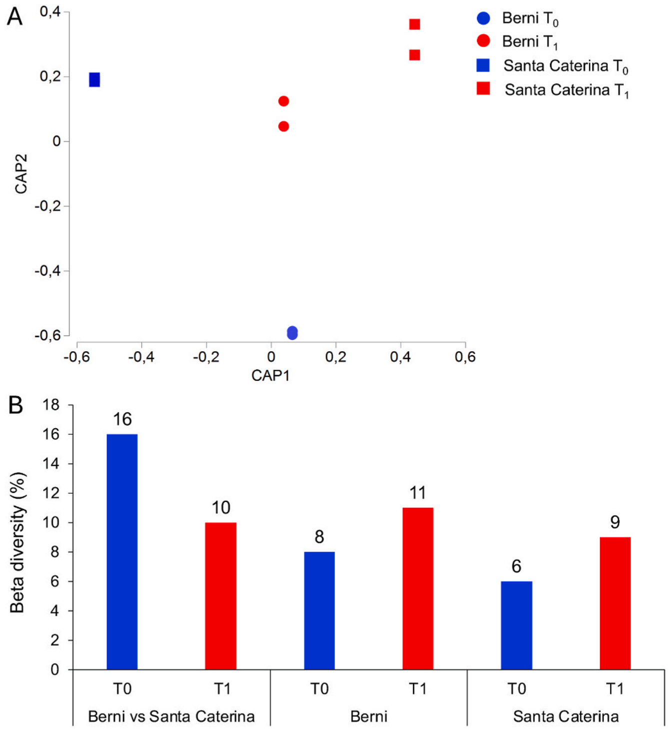

**Fig. 5.** (A) Output of Canonical Analysis of Principal coordinates (CAP) using Bray-Curtis similarity matrix on forth-root transformed data illustrating the differences in the phyla composition of benthic communities in the two investigated sampling sites at $T_0$ and $T_1$. (B) Beta diversity (% of dissimilarity calculated on the taxonomic composition of benthic taxa by using SIMPER analyses) between the two sites at both $T_0$ and $T_1$, and between the two ARMS replicates at each sampling site and time.

**Table 3**

Results of the SIMPER analysis assessing beta diversity (% dissimilarity) in the phyla composition between the two sites at the two sampling times, separately and between ARMS replicates (R1, R2) from the same site at each sampling time. Reported are also the phyla significantly explaining the observed differences, and the percentage of explained difference.

| Time/Site | Contrast | Percentage of variation explained |
|---|---|---|
| $T_0$ | Berni vs Santa Caterina | Bryozoa (22 %), Unassigned Eukaryota (19 %), Porifera (17 %), Annelida (13 %) |
| $T_1$ | Berni vs Santa Caterina | Mollusca (28 %), Porifera (15 %), Echinodermata (14 %), Arthropoda (11 %), Bryozoa (10 %) |
| Berni $T_0$ | R1 vs R2 | Porifera (16 %), Cnidaria (15 %), Annelida (14 %), Unassigned Eukaryota (12 %), Rhodophyta (11 %), Bryozoa (10 %) |
| Berni $T_1$ | R1 vs R2 | Porifera (17 %), Mollusca (14 %), Bryozoa (14 %), Cnidaria (14 %), Annelida (11 %) |
| Santa Caterina $T_0$ | R1 vs R2 | Bryozoa (18 %), Cnidaria (13 %), Porifera (12 %), Rhodophyta (12 %), Echinodermata (11 %), Mollusca (10 %) |
| Santa Caterina $T_1$ | R1 vs R2 | Porifera (16 %), Cnidaria (14 %) Bryozoa (14 %), Annelida (11 %), Arthropoda (10 %), Unassigned Eukaryota (10 %) |

## 4. Discussion

### *4.1. Variation of the recruited benthic community after MHWs train*

MHWs can affect the composition of benthic communities causing shifts in species abundance, and, in some cases, leading to the complete disappearance of taxa, ultimately altering species richness (Pansch et al., 2018). This is due to the fact that different species have different biological traits, behaviour and tolerances to temperature changes (Joyce et al., 2023). Nonetheless, we show here that the train of moderate MHWs that hit the southern coasts of Sardinia during summer 2023 did not alter phyla richness but significantly changed the taxonomic composition of the recruited benthic assemblages.

In this study we focused on cryptobenthos which encompasses different taxa, some of which particularly vulnerable to MHWs, while others more resistant (Arias-Ortiz et al., 2018; Caputi et al., 2019). First, the MHWs train caused the loss or significant decrease of some sessile or warming sensitive families, like Facelinidae (Nudibranchia), Microporidae (Bryozoa), Champiaceae (Rhodophyta) and Pinnulariaceae (Heterokontophyta). Among these, nudibranchs are a species-rich and plastic lineage that includes several eurythermal members able to cope with wide and frequent temperature fluctuations (Wägele et al., 2014). Nevertheless, conversely to other Gastropoda, they lose their shells after the larval stage and lack a water-impermeable cuticle in the adult phase. Although nudibranchs typically have high thermal tolerance, they show limited resilience to heating (i.e., plasticity or ability to reversibly adjust heat tolerance to cope with temperature rise) (Angilletta, 2009; Verberk et al., 2018). Accordingly, in our study, the nudibranch Facelinidae family disappeared in both sampling sites, supporting the view that nudibranchs are particularly vulnerable to MHWs trains (Armstrong et al., 2019). Suspension-feeding invertebrates, such as Bryozoa, are an essential link between pelagic and benthic food webs and are highly susceptible to environmental stressors due to the limitations in food acquisition and reproduction imposed by their sessile behaviour (Gili and Coma, 1998). Bryozoa mostly feed on smaller phytoplankton and exhibit a limited capacity to switch to alternative food sources in the event of phytoplankton shortage (Michaud et al., 2022). MHWs can impair phytoplankton production, thus indirectly affecting the abundance and taxonomic composition of sessile suspension-feeders, including Bryozoa (Michaud et al., 2022; Reed et al., 2016). Our study confirms such patterns because, besides Cnidaria (corals in particular), Bryozoa resulted one of the taxa mostly affected by the MHWs train (Garrabou et al., 2022; Smale and Wernberg, 2013). We also observed a significant decrease of Pinnulariaceae (Heterokontophyta; Diatoms), that are known to be particularly sensitive to warming (Morin et al., 2015; Remy et al., 2017). Diatoms, indeed, could completely vanish from communities exposed to MHWs due to both the direct impacts of heating on them and the compensatory growth of competing organisms like small flagellates (Remy et al., 2017).

At the same time, the results of our study show that some other taxa can survive to and successfully recruit after the MHWs train. In our study, the read abundance of Porifera increased after the MHWs train in both sites. This is not completely unexpected since sponges are generally less affected by temperature rise than other benthic sessile organisms as corals and macroalgae, due to the high thermal tolerance of their larval stage (Bell et al., 2018). Sponge larvae, indeed, do not show any adverse effect nor alterations in gene expression and associated microbiota until the temperature of 36 °C (far above the temperatures we recorded at the two sampling sites) (Webster et al., 2011, 2013). Other taxa can activate recovery processes and/or develop stress resistance mechanisms to survive (Brown et al., 2023; Minuti et al., 2021). In our study, for instance, the read abundance of some Decapod families (e.g., Diogenidae, Pilumnidae) increased after the MHWs train in both sites. Marine crabs (in particular the common crab species *Carcinus maenas*) can compensate the decrease of venous dissolved $O_2$ concentrations due to acute warming through the exploitation of the hemocyanin-bound

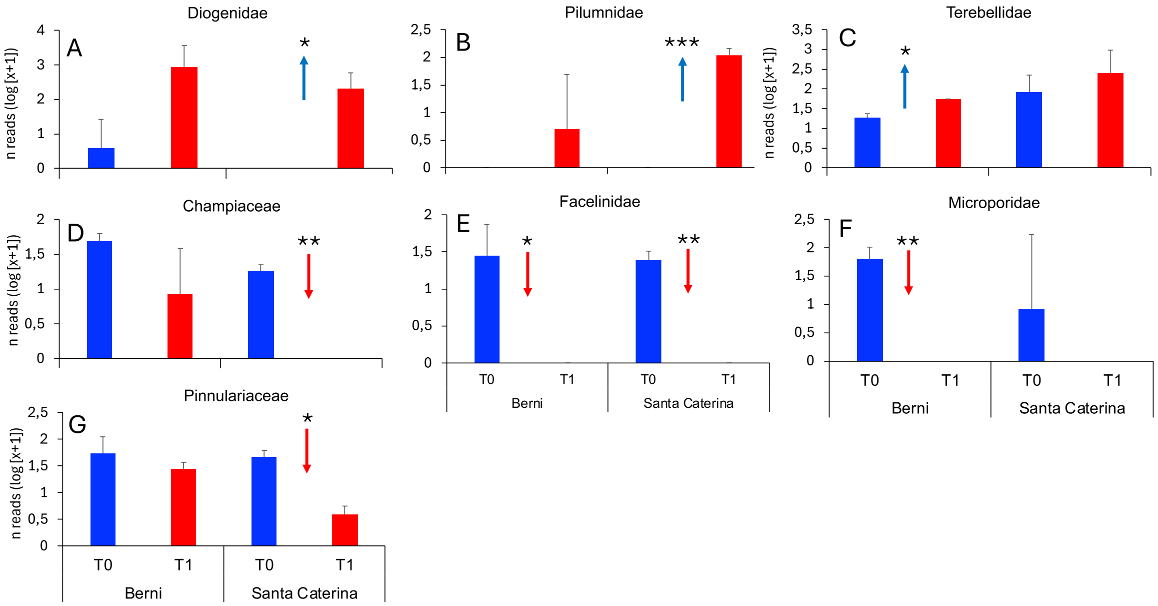

**Fig. 6.** Abundance of families (log x+1 transformed number of reads) at the two sites in each sampling time. Illustrated are only families that exhibited the same variation pattern in both sites between the two sampling times and whose abundances significantly increased (A–C) or decreased (D–H) from $T_0$ to $T_1$ (DESeq2, $p < 0.05$).

oxygen reserve (Giomi and Poertner, 2013). More in detail, with warming, hemocyanin progressively unloads oxygen which can thus compensate the crab rising oxygen demand, sustaining aerobic metabolism while reducing the energetic cost of circulation. The exploitation of hemocyanin oxygen transport can thereby widen crab thermal tolerance range, making crabs less vulnerable to MHWs than other benthic organisms (Giomi and Poertner, 2013).

The variation in the taxonomic composition of the recruited cryptobenthos observed after the MHWs train might be also the result of modified biological interactions among taxa, also known as "post interactive" effects (Woodin et al., 2013). MHWs, indeed, can stimulate a peculiar behaviour of some organisms, which may, in turn, enhance their impact on others, as in the case of grazers on macrophytes (Ito et al., 2024). Accordingly, our data show that the read abundances of mesograzers like the Gastropoda *Bittium* sp. and *Ocinebrina* sp. increased significantly after the MHWs train. Although we did not investigate the abundance of grazers other than that of the recruited benthic ones, the observed decrease of Rhodophyta after the MHWs train suggests an increased grazing pressure. This hypothesis, though needing further studies and confirmation, is aligned with reported effects of MHWs on various levels of the ecological hierarchy in temperate benthic ecosystems, from individual physiology, trophic groups' biomass and ecosystem carbon fluxes (Ito et al., 2024).

### 4.2. Impacts of MHWs on beta diversity

The MHWs train registered in the two sites caused also an overall homogenization of the recruited cryptobenthic communities, with beta diversity (dissimilarity) between the two sites decreasing from 16 % to 10 %. Taxonomic homogenization, defined as an increase in similarity of species composition among assemblages over time (McKinney and Lockwood, 1999), has been documented worldwide following a variety of disturbances (Ito et al., 2024; McKinney and Lockwood, 1999; Aulus-Giacosa et al., 2024; Olden et al., 2011; Simões et al., 2020). Generally, impacts due to anthropogenic activities or climate change may induce the widespread replacement of "losers" (i.e., habitat-specific ecological specialists) by "winners" (i.e., broadly-adapted ecological generalists and opportunists) (McKinney and Lockwood, 1999; Baskin, 1998). However, the ultimate outcome of homogenization will critically depend on the ecological roles of these organisms. In a previous study focusing on the impact of MHWs on a temperate benthic community, it has been demonstrated that after three subsequent MHWs, the trophic trait "suspension feeding" became less common than before, with potential consequences for the functioning of the entire benthic ecosystem (Pansch et al., 2018). Cryptobenthos encompasses a wide variety of taxonomic groups with different ecologically important roles, including suspension feeders, predators, herbivores, detritivores. In this study we reported the disappearance of Haptophyta, Nematoda and Rotifera in Berni and of Discosea and Rotifera in Santa Caterina, while Evosea and Platyhelminthes were recruited only after the MHWs train. While the ecological role of some phyla (such as Rhodophyta) is robust regardless of taxonomic classification, the same does not apply to others, like nematodes. Nematodes, in fact, include species, even within the same family, belonging to different trophic guilds and with diversified ecological functions (Daché et al., 2025). Thus, to properly understand the consequences of MHWs on benthic ecosystems it is crucial to increase taxonomic, functional, and sequencing efforts on lesser-known taxa, identifying species that dominate under disturbing conditions and understanding their ecological role.

Beta diversity, a descriptor of spatial variation in community structure, quantifies how species composition differs among "spatial units" within the landscape, and can vary with the spatial scale of assessment (Whittaker, 1972). The complex interplay between environmental factors and biological processes may influence the spatial distribution of species and taxonomic composition, thereby significantly contributing to the generation of different beta diversity patterns at different spatial scales (Soininen et al., 2007).

In our study, after the MHWs train, in addition to the observed decrease in beta diversity (i.e., reduced dissimilarity) between the two sites, we also found an increase in the percentage of dissimilarity between the ARMS replicates within the same sampling site. At larger spatial scales (i.e. sites hundreds of meters apart), currents can enhance connectivity influencing community composition and, ultimately, reducing the dissimilarity between neighbouring sampling sites (Bevilacqua et al., 2023). On the contrary, at smaller spatial scale (i.e., ARMS replicates few meters apart), other factors, such as larval dispersal potential, adult movement, and local resource availability and energy flux, can influence recruitment and species interactions, contributing to enhance beta diversity (Mouquet and Loreau, 2002).

Of course, we cannot exclude that a small percentage portion of the variations observed may reflect also the natural seasonality. Seasonality, indeed, can influence benthic communities through fluctuations in temperature, organic matter input, oxygen availability, and changing biological interactions (Rousi et al., 2013; Frattini et al., 2025). Currents, also, can affect cryptobenthos recruitment, influencing larval dispersal, displacing organisms and altering habitat structure (Villalobos et al., 2022). Despite these potential covariates, considering the small distance (a few hundreds of meters) between the two sampling sites, our results suggests that the MHWs train might have played a companion role in shaping cryptobenthic biodiversity. Nevertheless, numerous studies on species and community responses to climate change have emphasized the need for long-term data series and high-frequency sampling (Rousi et al., 2013) to disentangle interactions between seasonal, interannual or even decadal and random fluctuations in population dynamics from those due to extreme climatic events. In fact, monitoring the effects of climate change on communities requires at least thirty years of observations to significantly discriminate seasonal or random fluctuations in taxonomic composition from changes due to climate change (Hobday et al., 2018). Thus, we acknowledge that further efforts should be devoted to look at the cryptobenthic biodiversity variations over multiple temporal scales (e.g. seasonal to interannual) to gain clearer views of how communities change on seasonal base and to disentangle the effects of seasonality from that of extreme climatic events, like marine heatwaves.

## 5. Conclusions

Our findings highlighted that short-term effects of MHWs may not reduce richness but can cause shifts in taxonomic composition and homogenization of cryptobenthic communities, ultimately altering ecosystem processes in the longer term. Such effect was driven by the variation in abundance of some of the most abundant benthic phyla, like Bryozoa, Porifera, Rhodophyta, Arthropoda. Our analyses suggested also that sessile and slow-moving taxa, i.e. nudibranchs, bryozoans, red algae, diatoms, were generally more negatively impacted by MHWs than mobile ones, i.e. decapods, likely due to differences in morphology, behaviour, thermal tolerance, stress resistance, and larval traits. Additionally, beta diversity between the two sampling sites decreased after the MHWs train, leading to an overall homogenization of the recruited benthic communities. The ultimate consequences of taxonomic variation and homogenization will critically depend on the ecological functions that “winners” and “losers” play within the ecosystem, which is not fully understood yet for many taxonomic groups belonging to the cryptobenthos. To provide robust predictions about the consequences of MHWs trains on marine benthic ecosystems, future efforts should thus be devoted to deepening our knowledge on life history traits, functional role, and responses (positive, negative, neutral) to MHWs of cryptobenthic communities. We also believe that a more extensive sampling design in terms of both spatial and temporal scales and a multi-gene approach would give a more comprehensive view of the effects of MHWs on cryptobenthic alpha and beta diversity.

## CRediT authorship contribution statement

**Laura Carugati:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis, Data curation. **Davide Moccia:** Writing – review & editing, Visualization, Investigation. **Alessandro Cau:** Writing – review & editing, Investigation. **Vincenzo Donnarumma:** Writing – review & editing, Formal analysis, Data curation. **Antonio Pusceddu:** Writing – review & editing, Supervision, Resources, 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.2025.107705.

## Data availability

Data will be made available on request.

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