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Functional diversity and metabolic response in benthic communities along an ocean acidification gradient[☆]

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ABSTRACT

Altered ocean chemistry caused by ocean acidification (OA) is expected to have negative repercussions at different levels of the ecological hierarchy, starting from the individual and scaling up to the community and ultimately to the ecosystem level. Understanding the effects of OA on benthic organisms is of primary importance given their relevant ecological role in maintaining marine ecosystem functioning. The use of functional traits represents an effective technique to investigate how species adapt to altered environmental conditions and can be used to predict changes in the resilience of communities faced with stresses associated with climate change. Artificial supports were deployed for 1-y along a natural pH gradient in the shallow hydrothermal systems of the Bottaro crater near Panarea (Aeolian Archipelago, southern Tyrrhenian Sea), to explore changes in functional traits and metabolic rates of benthic communities and the repercussions in terms of functional diversity. Changes in community composition due to OA were accompanied by modifications in functional diversity. Altered conditions led to higher oxygen consumption in the acidified site and the selection of species with the functional traits needed to withstand OA. Calcification rate and reproduction were found to be the traits most affected by pH variations. A reduction in a community's functional evenness could potentially reduce its resilience to further environmental or anthropogenic stressors. These findings highlight the ability of the ecosystem to respond to climate change and provide insights into the modifications that can be expected given the predicted future pCO_2 scenarios. Understanding the impact of climate change on functional diversity and thus on community functioning and stability is crucial if we are to predict changes in ecosystem vulnerability, especially in a context where OA occurs in combination with other environmental changes and anthropogenic stressors.

1. Introduction

Ocean acidification (OA), caused by increasing anthropogenic CO_2 levels in the atmosphere and the subsequent uptake by the oceans is resulting in pH lowering and alteration to the carbonate chemistry, and has the potential to cause large scale changes to the structure of ecosystems. Higher pCO_2 concentrations in the marine environment may have negative effects on calcifying species, but positive effects on marine producers that may benefit from altered CO_2 concentrations (Riebesell et al., 2017; Zunino et al., 2017; Hancock et al., 2020; Martínez-Crego et al., 2020; Figuerola et al., 2021).

Changes in ocean chemistry are expected to cause significant and

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lasting damage to marine ecosystems, especially among benthic invertebrates (Kroeker et al., 2011). Benthic organisms play a pivotal role in maintaining marine ecosystems stability through bioturbation (reworking sediments and organic matter) (Aller and Cochran, 2019) and through the exchange of inorganic nutrients with the water column (Griffiths et al., 2017). Moreover, benthic invertebrates often represent a key nutritional component within many organisms' diets, including for many juvenile fish species of commercial importance (Hüssy et al., 1997). Benthic organisms represent the memory of most aquatic systems, because of their tight links with the substrates, playing a crucial role in increasing biodiversity and ecosystem functioning (Lathlean and McQuaid, 2017). Given the central role of benthic organisms, it is crucial to increase our understanding of the effects of OA, not only at the individual level, but through the entire ecological hierarchy. This enhanced knowledge, particularly at the community level, will allow us to predict how possible biodiversity loss may impact ecosystem functioning.

Ecologists are increasingly focusing their studies on traits – rather than species names and numbers *per se* – to measure the health of ecosystems, starting the so called "biodiversity revolution" (Cernansky, 2017). Organisms are considered according to attributes of their biology and ecology rather than phylogeny. This allows for easier mechanistic links between impacts and traits, as opposed to impacts and species, providing a more accurate analysis of the sensitivity of marine taxa to OA (Gray et al., 2022). The analysis of functional traits represents an essential step in assessing the impact of stressors on organisms, populations, and ecosystems. Functional traits are behavioral, physiological, and morphological characteristics (Schoener, 1986; Cadotte et al., 2011), most of which coincide to optimize individual growth and reproduction (Arnold, 1983), in response to changing environmental conditions (Violle et al., 2007). In particular, metabolic traits integrate various typical indicators of energy acquisition and allocation in animals, including body size, diet, mobility, life history, and habitat utilization (Enquist et al., 2015). This integration results in a reduced set of continuous variables that can be accurately measured for individuals using standardized methods. Furthermore, these traits are universally applicable to all animals, irrespective of their body structure, habitat, or taxonomic categorization (Brandl et al., 2023). Functional traits are crucial because, according to current ecological theory, they reflect changes in the environment, and thus can be used to predict variations in individual trait performance (Arnold, 1983; Lavorel and Garnier, 2002; Suding et al., 2008). Measuring functional traits of an organism allows us to gather information about the direct impact of anthropogenic-driven environmental changes on the fitness of the individual (Violle et al., 2007; Enquist et al., 2015). Expression of specific traits associated with given environmental conditions can be a determinant of an organism's survival capacity and, when functional traits of an entire population are impacted or loss of particular traits occurs, the expected result is an alteration to the ecological equilibrium, thereby undermining ecosystem functioning (Violle et al., 2007; Harley et al., 2017; Connell et al., 2018). Functional diversity is therefore another side of the coin in biodiversity and is defined by "functional traits differences between organisms present in a community or an ecosystem" (sensu de Bello et al., 2021). Measuring functional diversity is important as it may have a strong impact on community dynamics and stability as well as ecosystem processes (de Bello et al., 2021). Many studies to date have focused on the use of a trait-based approach to estimate communities' ecological sensitivity to global environmental changes induced by climate change (Foden et al., 2013; Hare et al., 2016), yet only a few have considered OA as the main stressor (Teixidó et al., 2018, 2024; Esposito et al., 2022).

Considering all the above, here we describe the effects of environmental changes on benthic communities' functional diversity and metabolic response associated with different acidified conditions measured along a natural OA gradient generated by CO_2 degassing activity of hydrothermal origin. Together with analyses on community composition and functional diversity, we also use the communities' respirometric oxygen consumption rates as a proxy for the metabolic machinery functioning.

The results of the present work improve our understanding of how benthic communities respond to elevated pCO_2 conditions, providing important insights as to how environmental changes caused by OA can affect functional diversity. Improved understanding of community functioning will help predict any potential detrimental effects on the stability of the ecosystem, that could ultimately lead to the loss of associated ecosystem services.

2. Materials and methods

2.1. Study area and sampling activities

Sampling was carried out in one of the shallow hydrothermal systems of Panarea island (Aeolian Archipelago, Southern Tyrrenian Sea, Italy), the Bottaro islet, 3.3 km east of Panarea island, Aeolian Archipelago, (38°38′13.58″ N; 15°6′33.95''E). The study area is characterized by the presence of a crater formed during the massive gas eruption which occurred in November 2002 (Esposito et al., 2006). Today, the crater is represented by a depression (about 14 m wide, 20 m long and 11 m deep) where the degassing activity is mainly concentrated. The cold CO_2-rich emissions generate an acidification gradient with pH values ranging from 6.0 to 7.8, inside the depression, and reaching 8.1 at 30–35 m at the rim of the crater (Goffredo et al., 2014; Esposito et al., 2022). Along the OA gradient generated, 3 stations at a depth of 8–10 m were defined: station Bottaro 3 (B3), located at the rim of the crater characterized by the presence of the macroalgae *Cystoseira brachycarpa* and most affected by OA (7.8 pH), station Bottaro 2 (B2) at 7 m distance (7.9 pH) with both *Cystoseira brachycarpa*. and patches of the seagrass *Posidonia oceanica*, and station Bottaro 1 (B1) 35 m from B3 in a control area, without bubbling and ambient pH values, with *Posidonia* meadow settled on rocks and interspersed *Cystoseira* patches (Goffredo et al., 2014; Esposito et al., 2022). In September 2019, artificial structures (nylon scouring pads) were placed at each station to be colonized by organisms living in the study area. These supports consisted of nylon scouring pads (8 cm in diameter and 2.5 cm thickness) which have been shown to be excellent at capturing both larval and adult stages of benthic organisms from surrounding biotopes, and already used in other vent systems (Ischia vents, Cigliano et al., 2010, Ricevuto et al., 2012, 2014; Barruffo et al., 2021). The pads were placed in moorings (2 solid bricks of 6 kg) in four replicates per station (N = 12) with two groups of pads per mooring (N = 36). The pads were placed in two ways: bottom (i.e., 2 pads horizontally placed in direct contact with the mooring) and floating (i.e., represented by four single pads piled vertically) (Fig. 1). This arrangement was chosen to imitate the spatial heterogeneity of the surrounding environment (especially the dominant macroalgae) allowing for better colonization success.

Retrieval of the artificial support took place in early October 2020, via scientific SCUBA diving. Following a year of exposure, it was not possible to find and recover all the moorings and scouring pads, as they were probably lost due to adverse sea conditions. The total number of groups of pads recovered was 25 (B1: n = 7, B2: n = 6, B3: n = 12). Each group of pads was detached from the mooring and placed directly in single labeled containers underwater and transported to the OGS Panarea ECCSEL NatLab, Italy, to conduct respirometric measurements on the associated communities. At each station, water samples were collected with Niskin bottles, to be used in the laboratory during respirometric and for pH measurement. Temperature was also measured in the sampling sites using HOBO Pendant® loggers (mod. MX2201, ±0.5 °C accuracy) throughout the entire underwater operation. pH determination was performed using a double wavelength spectrophotometer (Cary 60 Scan UV–visible) by mean ± SD of n: 3 water sample for each station: B1: 8.03 ± 0.03; B2: 8.02 ± 0.01; B3: 7.99 ± 0.01. For more information about physico-chemical variables in the study area

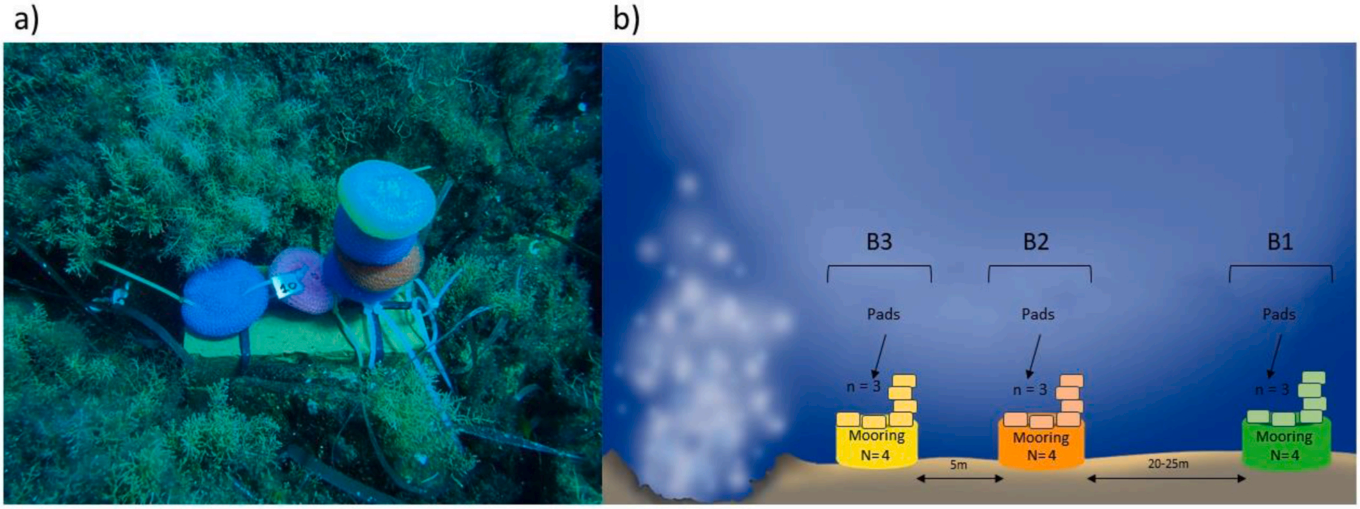

Fig. 1. a) Picture of a single mooring set-up showing positioning of the two groups of scouring pads, bottom (left part) and floating (pile on the right), at the moment of deployment (September 2019) before colonization (Photo by Gamby M.C.), b) graphical representation of the sampling design (B3:station Bottaro 3, B2: station Bottaro 2, B1: station Bottaro 1).

please refer to Esposito et al. (2022).

2.2. Laboratory analysis

Each group of pads (bottom and floating) and their living communities were placed in closed glass respirometric chambers (3000 ml). These chambers where filled with air-saturated and filtered (Whatman GF/C 0.45 μm) seawater (salinity of 38 psμ) collected from each respective station. Respirometric analyses were carried out at 25 °C, i.e., at the same seawater temperature recorded during the sampling and on average representative of the season. Temperatures were kept stable by means of a thermal bath and monitored throughout the recording period. To ensure the constant mixing of the water, each chamber was equipped with a magnetic bar and an individual stirring device (Giomi et al., 2016; Marchessaux et al., 2022). The concentration of dissolved oxygen (ppm or mg/L) was measured continuously for 1 h by means of 3 optical oxygen meters (Pyro Science Firesting O_2) using specific software (Pyro Science) (Montalto et al., 2017; Marchessaux et al., 2022). At the end of the experiments, each group of scouring pads was cut open to extract the associated communities and record wet weight, then the organisms were fixed in 70% alcohol for subsequent analysis. Samples were sorted into main taxonomic groups and then identified to the lowest possible level (family, genus, and species). After identification of the benthic species, organisms were subdivided by main taxonomic groups (e.g., molluscs, polychaetes, amphipods etc.), and dried at 105 °C for 24 h and reweighed to determine Dry Weight (DW, g). Respiration rates were reported as oxygen consumption per unit mass and expressed as mg O_2 L^{-1} h^{-1} g^{-1}dry tissue.

To measure the functional diversity (FD) of the communities associated with the artificial supports along the pH gradient, we focused on finding the main functional traits of each species. We therefore selected a total of five functional trait categories (i.e., calcification, feeding mode, longevity, motility and living habits and reproduction) extracted from the literature (Esposito et al., 2022). These traits are useful for calculating the main functional diversity indexes. Calcification rate of the organisms was chosen to identify those species particularly sensitive to pH variations (i.e., highly, weakly, or not calcified species), while motility and living habits were recorded to identify those organisms able to move between the stations or those settling in a specific one guided by the environmental conditions (i.e., borrower, crawler, crawler/climber, domicolous, domicolous/algal dweller, sessile and swimmer). Longevity of the organisms was included to obtain information concerning the maximum life span of the species colonizing the artificial support (i.e., 1, 1–3, 3 and 10 years). We also recorded main reproductive and developmental mode dividing them by "direct", species incubating the broods with juveniles directly hatching from the eggs; "indirect planktic", with external fertilization, free spawning, and development of larva with a short or long life in the plankton or near the bottom; and "indirect benthic", where development includes a larval stage with some pelagic life periods, but eggs are deposited in the benthic environment. Lastly, we selected a total of seven feeding modes (i.e., deposit feeder, filter feeder, grazer, parasite, predator, scavenger, and suspension feeder) to identify differences in trophic organization of the communities. Information concerning all the functional traits selected were gathered through a literature search using the main benthic traits databases available (MarLIN, 2006; Polytraits, 2013; Bolam et al., 2014; Beauchard et al., 2017; Parr et al., 2014; Esposito et al., 2022; ICES, 2022; Palomares and Pauly, 2023). The list of the taxa found their functional traits attributes and data source references are listed in Table S1.

2.3. Data elaboration and statistical analysis

The differences in oxygen consumption among communities were analyzed using a Type II ANOVA, with station as grouping variable and pads' position as blocking factor. The validation of variance and normality assumptions was demonstrated through tests for homogeneity of variance and normal distribution of residuals. Specifically, Levene's test was used to assess variance assumptions, while Shapiro-Wilk test was employed for testing normality assumptions. Pairwise comparisons were tested using Tukey's HSD (Honestly Significant Difference) test. The analysis of variance and the post-hoc test were conducted using the rstatix package (Kassambra, 2023).

Differences in community composition between sampling stations and pads' position were assessed by performing a multivariate Permutational Analysis of Variance (PERMANOVA) with station as grouping variable and pads' position as blocking factor. "Pairwise.adonis" function of the R packages "vegan" (Jari Oksanen et al., 2022) was used to perform post-hoc multilevel comparison of the significant group. We conducted a PERMDISP analysis to examine the presence of dispersion homogeneity, considering its potential impact on PERMANOVA results (Anderson et al., 2017). The analysis was based on a distance matrix of relative abundances transformed using Hellinger transformation (Legendre and Gallagher, 2001). Principal component analysis (PCA) was then used to analyze composition of the community in the three stations along the OA gradient and the contribution of the most important species.

Community weighted means (CMW), corresponding to the average trait value in a community weighted as a function of the species' relative abundance, were calculated to analyze traits distribution, and to identify which were the most represented traits in the community. We tested differences in CWM for the five functional categories selected (i.e., calcification, motility and living habits, longevity, reproduction and feeding mode) between stations using a PERMANOVA including pads' position as blocking factor. "Pairwise.adonis" function of the R packages "vegan" (Jari Oksanen et al., 2022) was used to perform post-hoc multilevel comparison of the significant group. We visualized the functional composition of the community across OA gradient using CWM in a PCA analysis. Subsequently, we analyzed the three primary components of functional diversity i.e., functional richness, evenness, and divergence (Carmona et al., 2016) calculating the principal functional diversity' indexes (i.e., functional richness, evenness, dispersion, divergence, and Rao) using the function "dbFD" of the R package "FD" (Laliberté et al., 2014). Differences in functional diversity indexes between stations were analyzed using a Type II ANOVA, with station as the grouping variable and pads' position as the blocking factor. Beforehand, the assumptions of normality and variance homogeneity were assessed using Shapiro-Wilk and Levene's tests, respectively. Pairwise comparisons were then conducted using Tukey's HSD (Honestly Significant Difference) test (Kassambra, 2023). Furthermore, we partitioned functional diversity measuring within-community (α) and among-communities (β) components, using the Rao quadratic entropy index, applying Jost correction (Jost, 2007) to avoid underestimation of beta diversity (de Bello et al., 2010).

Principal Components analysis for community composition, both in terms of taxonomic and functional diversity, and for functional diversity indexes were calculated using the R packages "vegan" (Jari Oksanen et al., 2022) and "stats" (R Core, 2021). Evaluation of importance of ordination axes in PCA were checked looking at eigen values (i.e., principal components to be retained with eigen values > 1) for each axis and graphically through the broken stick model (MacArthur, 1957; Frontier, 1976). All statistical analyses were conducted within R (R Core T, 2023) environment "R version 4.3.2 (2023-10-31)"

3. Results

3.1. Taxonomic composition of the community

Taxonomical identification resulted in a total of 113 taxa. Of these, 70 taxa were identified at the species level while 43 were identified at the lowest possible level (phylum, family, genus) (see Table S1). The two most represented species groups were crustaceans (44 taxa) and polychaetes (37 taxa) accounting for 38.9% and 32.7% of the total community respectively; followed by mollusks (23 taxa, 20.3%). Only 3 taxa (2.6%) belonged to the echinoderms and 6 to a mixed group composed of different taxa (i.e., Sipunculida, Ascidiacea, Bryozoa and Hydrozoa, which are mainly sessile) accounting for only 5.3% of the community. Most of the motile taxa found are typical mesograzers associated with shallow vegetated systems.

Statistical analysis on the community composition revealed a significant difference between the three sampling stations ($F_{(2,21)} = 1.64$, $p = 0.024$) with a significant difference between the most acidified station (B3) and the control station (B1) ($p = 0.009$). Position of pad (bottom *vs* floating) was not significant, leading to the exclusion of this possible confounding factor (Table 1). Results of PERMDISP analysis did not reveal the presence of heterogeneity across groups (Table S2).

Table 1
PERMANOVA table with results of the analysis on community composition between the three sampling stations. DF = degree of freedom, SS = sum of squares, MS = mean squares. Significant results are highlighted in bold.

Factor	DF	SS	MS	F-value	p - value
station	2	0.525	0.126	1.640	**0.024**
pad	1	0.264	0.063	1.647	0.064
Residuals	21	4.155	0.742		

The cumulative variance explained by the first two axes of the PCA on community matrix was 32.31%. Variance explained by the first axis PC1 was 19%, while PC2 explained only 13.31% of the variance. The graphical visualization of the PCA biplot highlighted a vertical pattern of distribution of the three assemblages, which appeared to reflect the OA gradient of the study area, with B3 and B1 diametrically opposite in the graph and B2 in an intermediate position. The analysis also allowed identification of the species that have the greatest contribution within the communities and that influence the distribution of the data. In particular, the highest correlation with PC1 axes was measured for the ophiuroid *Amphipholis squamata* (0.52), the isopod crustacean family Janiridae (0.34), the Harpacticoida copepods (0.31) and the mussel *Musculus costulatus* (0.25). Results for the PC2 axis confirmed a high correlation of Janiridae (0.53) and Harpacticoida (0.41), which are the most important species together with Leptochaelidae (0.37) and the echinoderm *A. squamata* (0.24) (Fig. 2).

3.2. Community respirometric oxygen consumption rates

Respirometric analysis of the communities attached to the artificial supports revealed a statistically significant difference in the oxygen consumption rate between the different sampling stations ($F_{(2,20)} = 4.462$, $p = 0.025$). Communities colonizing the scouring pads exposed to the lowest pH level exhibited a higher oxygen consumption rate (expressed as mg O_2 L^{-1} h^{-1} g^{-1}dry tissue) (M = −0.015, SD = 0.009). Mean rate for the intermediate level station (B2) were −0.014, (SD = 0.006), while communities thriving in the control station (B1) showed the lowest consumption rate (M = −0.005, SD = 0.002). Post-hoc analyses showed that oxygen consumption rate was statistically significant ($p = 0.025$) for B3 and B1 stations, while no significant difference was found between intermediate (B2) and the most acidified station (B3) (Fig. 3).

3.3. Community weighted mean (CWM) and functional traits analysis

Community weighted mean measurements were applied to the five selected functional traits' categories to highlight the contribution of the functional traits in influencing the distribution of the data. Results of PERMANOVA analysis revealed no statistical differences in community weighted means for the functional trait category selected between stations (Table 2). Results of PERMDISP analysis did not reveal the presence of heterogeneity across groups (Table S3). However, a PCA biplot showed different spatial distributions of the functional traits along the pH gradient. The first axis alone explained 49.92% of the total variance of the data having "calcifier_highly" as the most correlated variable (0.51) with the higher contribution to this axis (27%). On the opposite side, species sharing the trait "calcifier_weak" and "calcifier_not", moves toward the acidified site of B3 with the higher contribution (23% and 18%) to PC2 axis which explains 26.18% of the total variance. Contribution to the first axis is also explained by the two reproductive modes "indirect/planktic" (13%) and "direct/brooding" (11%) with a correlation with the PC1 of 0.35 and 0.34 respectively, moving in the opposite direction with the former related to the position of the intermediate station of B2 and the latter to the most acidified B3. Then, 10% of the contribution to PC1 was also explained by species having a life span of 3–10 years (0.31). While species with a shorter life span showed a positive correlation with the PC2 axis, having a contribution of 20% for species living 1–3 years and 17% for those having a 1-year life span (Fig. 4).

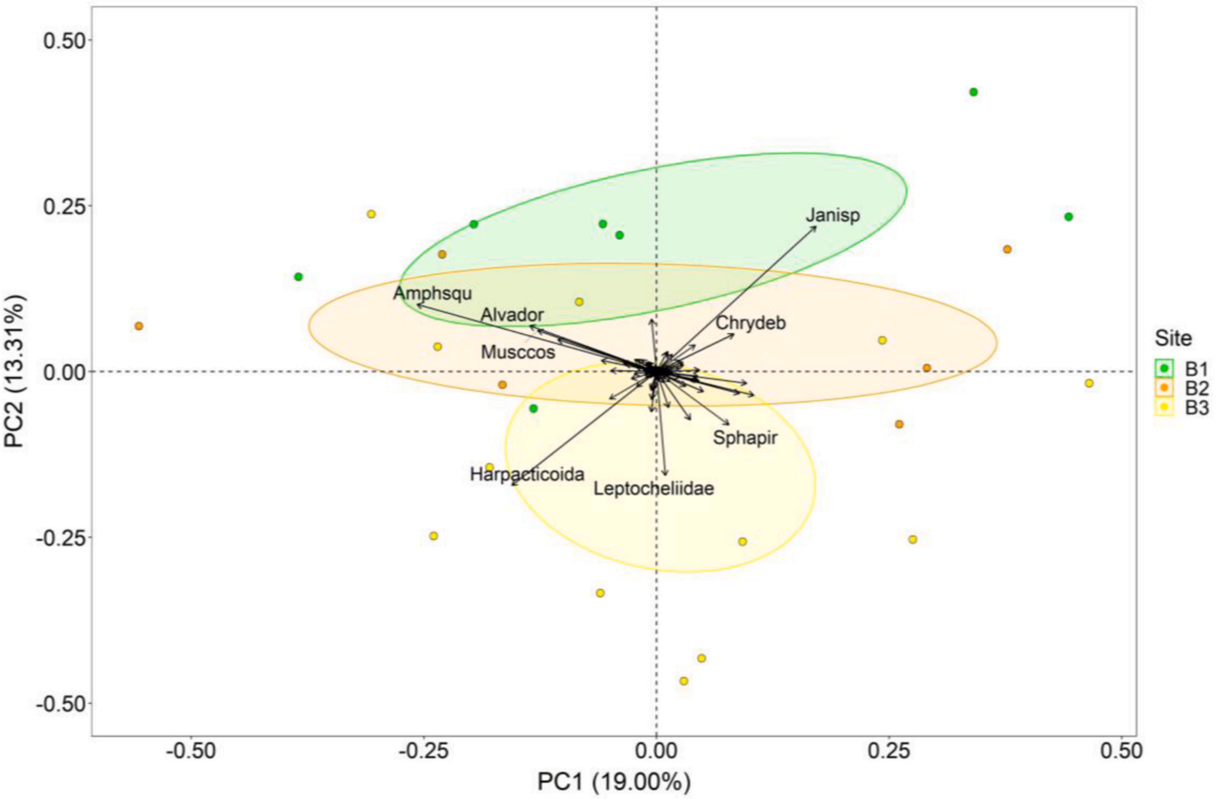

Fig. 2. PCA biplot of species composition within the communities colonizing the scouring pads placed in the three sampling stations. Ellipses indicate mean point of the groups and confidence interval. B3:station Bottaro 3, B2: station Bottaro 2, B1: station Bottaro 1.

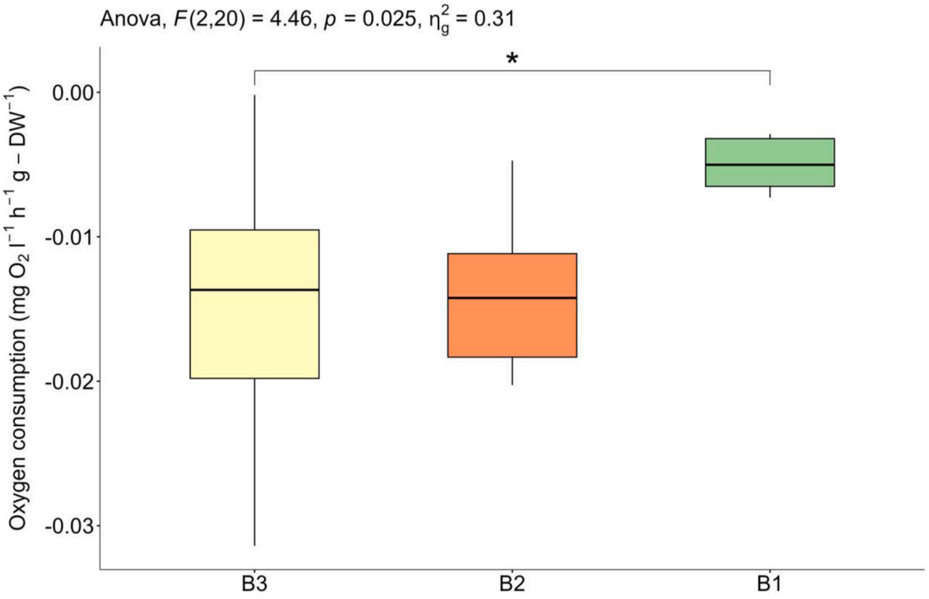

Fig. 3. Oxygen consumption rates of the communities colonizing the scouring pads deployed in the three sampling stations. B3:station Bottaro 3, B2: station Bottaro 2, B1: station Bottaro.

3.4. *Measures of functional diversity*

The analysis on the functional diversity between the three stations did not reveal any statistically significant result irrespective of the functional index considered (Table 3), with the only exception of functional evenness which showed significant results between stations ($F_{(2,19)}$, $p = 0.034$). In particular, the most acidified station (B3) showed the lowest functional evenness value (M = 0.74, SD = 0.04), while the highest was measured for the control station (B1) (M = 0.80, SD = 0.04); evenness' value for the intermediate station (B2) was M = 0.78, SD = 0.04 (Fig. 5). As evidence, post-hoc least squares means analysis revealed a statistically significant difference between B3 and B1 station ($p = 0.034$).

Results for the principal component analysis reflected what we

Table 2
PERMANOVA table with results of the analysis performed on community weighted mean (CWM) for the five functional traits categories between the three sampling stations. DF = degree of freedom, SS = sum of squares, MS = mean squares.

Source	Factor	DF	SS	MS	F value	*p* - value
Calcification	station	2	4.30	2.150	0.768	0.536
	pad	1	8.91	8.909	3.182	0.056
Feeding mode	station	2	9.449	4.724	0.647	0.779
	pad	1	5.400	5.400	0.740	0.601
Longevity	station	2	12.203	6.101	1.712	0.152
	pad	1	8.974	8.974	2.518	0.089
Motility and living habits	station	2	17.164	8.582	1.118	0.337
	pad	1	13.711	13.711	1.787	0.093
Reproduction	station	2	11.547	5.773	2.162	0.101
	pad	1	4.383	4.382	1.641	0.192

obtained with the ANOVA model. The first two principal component axes explained together 83.93% of the variance. Functional dispersion (FDis) and Rao were the most correlated variables with PC1, which explained almost 49% of the variance, a correlation value of 0.52 and a contribution of 28% to the variance explained by the first axis. However, the most important pattern visualized in the PCA biplot seems to be explained by the second PC axis, that explained 35.04% of variance. Functional evenness (FEve) was the most correlated variable to PC2 (0.55), with a 32% contribution to the total variance, followed by number of species (0.48), showing a lower percentage of contribution to the PC variance (27%). The latter variables point in the opposite direction inside the biplot, driving the distribution of the ellipses (i.e., sampling station) with a major overlapping of intermediate (B2) and control (B1) and the acidified site (B3) far from the higher values of FEve (Fig. 6).

Measures of the partitioning of taxonomic and functional diversity revealed that, despite the great turnover in species composition (beta TD = 83.62%), the functional turnover between the communities in our sampling stations was very low (beta FD = 14.17%). Most dissimilarity in traits between species was found within station and not across station, despite the environmental changes due to the acidification and changes in species composition (high beta TD) (Fig. 7).

4. Discussion

Our findings emphasize how OA can affect community composition, altering species distribution and functional diversity in OA-affected environments. From a taxonomic point of view, the biodiversity recorded (113 taxa), was lower than previously observed in natural communities in the same area found in association with *Cystoseira brachycarpa* (184 taxa, Esposito et al., 2022). However, 50.8% of the taxa collected in the scouring pads, mainly crustaceans and polychaetes (representing more than 75% of the whole abundance), match the list of benthic species occurring in the natural vegetated substrate. This confirms that the communities associated with the scouring pads are quite similar to the natural assemblages living in association with the dominant and habitat-former algal species of this biotope and is consistent to what was observed in the Ischia CO_2 vents (Cigliano et al., 2010; Ricevuto et al., 2012, 2014). The prevalence of some species over others, observed along the OA gradient, seems to be related to the functional traits selected. This allows us to relate species adaptation to OA, as some species are thriving in conditions that are potentially averse to other species. Principal component analyses carried out on the community weighted means (CWM) of the selected traits, illustrates how OA represents a filtering driver for traits selection which has shaped the differences between the three sampling stations. Our results were consistent with what is reported in the current literature (Kroeker et al.,

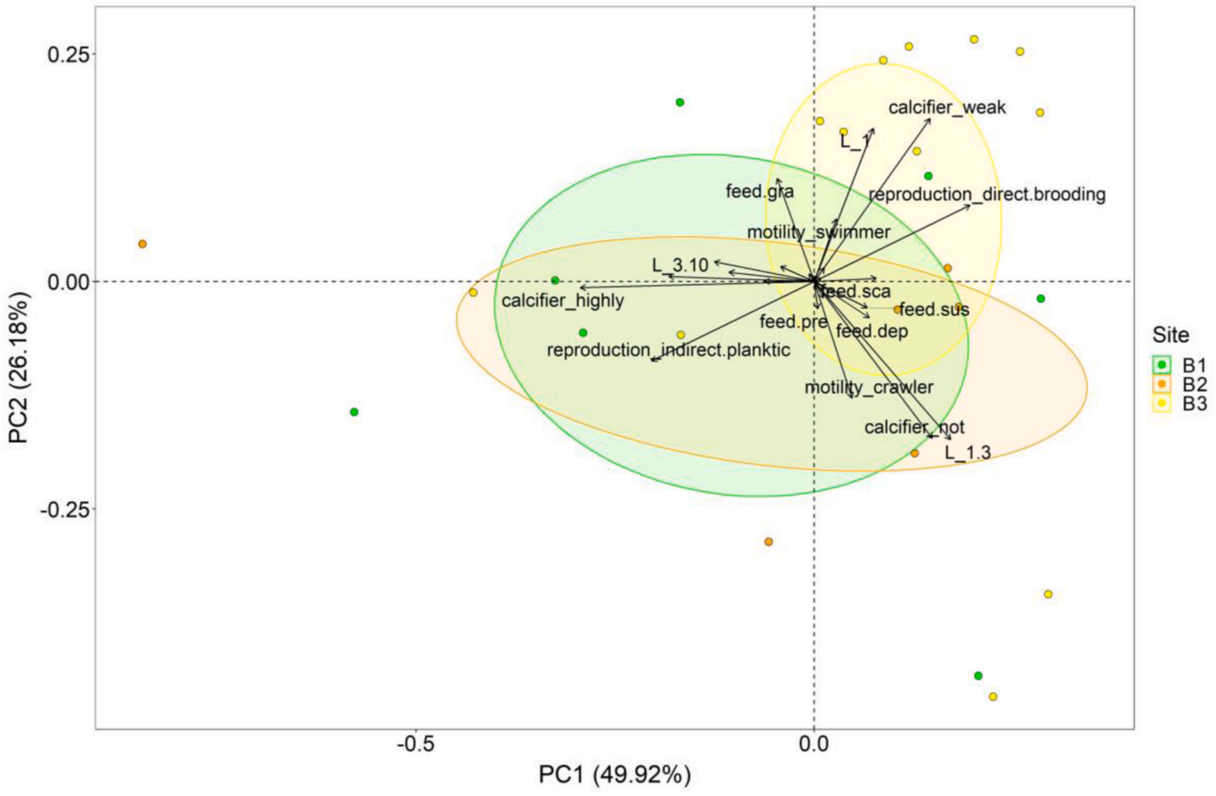

Fig. 4. PCA analysis showing Community Weighted Means (CWM) on the functional traits measured for the species of the communities associated with scouring pads in the three stations identified along the pH gradient of the Bottaro crater vent system, from the most acidified (B3) to the control (B1). Mean point of the groups with confidence interval indicated by respective ellipses. B3:station Bottaro 3, B2: station Bottaro 2, B1: station Bottaro 1.

Table 3
ANOVA table with results of the analysis on functional diversity between the three sampling stations. DF = degree of freedom, SS = sum of squares, MS = mean squares. Significant results are highlighted in bold.

Source	Factor	DF	SS	MS	F value	*p* - value
Number of species	station	2	83.8	41.9	1.414	0.266
	pad	1	96.7	96.69	3.264	0.086
Functional Richness	station	2	0.024	0.012	0.471	0.631
	pad	1	0.004	0.004	0.175	0.680
Eveness	station	2	0.009	0.004	4.149	**0.032**
	pad	1	0.003	0.003	2.735	0.115
Functional Divergence	station	2	<0.001	<0.001	0.168	0.847
	pad	1	<0.001	<0.001	0.094	0.763
Functional Dispersion	station	2	<0.001	<0.001	0.120	0.888
	pad	1	<0.001	0.002	1.221	0.282
Rao	station	2	<0.001	<0.001	0.132	0.877
	pad	1	<0.001	0.001	1.621	0.217

2011; Cattano et al., 2018; Teixidó et al., 2018; Harvey et al., 2021), showing a weak correlation of "heavy calcifiers" organisms with the more acidified stations and suggesting a higher distribution towards those with lower levels of OA. pH lowering is known to have negative effects on calcifying organisms, due to its impact on the ability to produce carbonate structures (Riebesell et al., 2017; Zunino et al., 2017). As calcification rates in water decreases with elevated pCO_2, calcifying organisms may exhibit a reduction in exoskeleton size up to a 50% as demonstrated in some serpulid polychaetes (Díaz-Castañeda et al., 2019). Exposition to elevated CO_2 concentrations, comparable to those predicted in future climate change scenarios (IPCC, 2018), may lead to severe exoskeleton deformation of some chitinous (Long et al., 2019) and calcareous taxa (Byrne and Fitzer, 2019). The result is that the impairment of growth and development of these organisms may impact feeding, reproduction, movement, and mechanical protection, which is likely to increase relative sensitivity to OA and have indirect impacts on fitness (Gray et al., 2022).

Our results provide salient evidence supporting the idea that marine species survival when faced with OA can be related to life history characteristics and reproductive strategies. Species with a short lifespan (i.e., 1-year) were correlated with the most acidified station (B3). Selection of species with short lifespans could represent a relevant trait for the stability of the whole community. Life history characteristics relate to the capacity to withstand and cope with disturbance; species with higher intrinsic rates of increase (r), and therefore higher recovery rates, are expected to display smaller decreases in abundance in response to a given rate of mortality (Duplisea et al., 2002). Opportunistic species (r-strategist) possess a high recovery rate as they mature early and produce many offspring compared to K-strategists leading to slower recover from disturbance (Rijnsdorp et al., 2020). Due to compensatory adaptations in their life history, r-strategists species tend to achieve maturity earlier, have a higher annual reproductive output and a higher natural mortality (Hoenig, 1983; Charnov, 1993). The inherent characteristic of having high population growth rates is often associated with higher metabolic rates (Brown et al., 2004; Savage et al., 2004). The higher oxygen consumption measured in the communities colonizing the scouring pads placed in the most acidified station supports higher presence of opportunistic r strategic species that, thanks to their life history traits, can survive in the presence of the disturbance generated by the CO_2 venting and OA conditions in the Bottaro crater. Moreover, our findings align with a similar study on early successional coral reef communities, where rates of respiration increased by 20% along with changes in community across a pH gradient at shallow-water volcanic CO_2 seeps (Noonan et al., 2018).

Our findings confirm the correlation between a direct brooding reproduction strategy and acidified conditions, aligning with

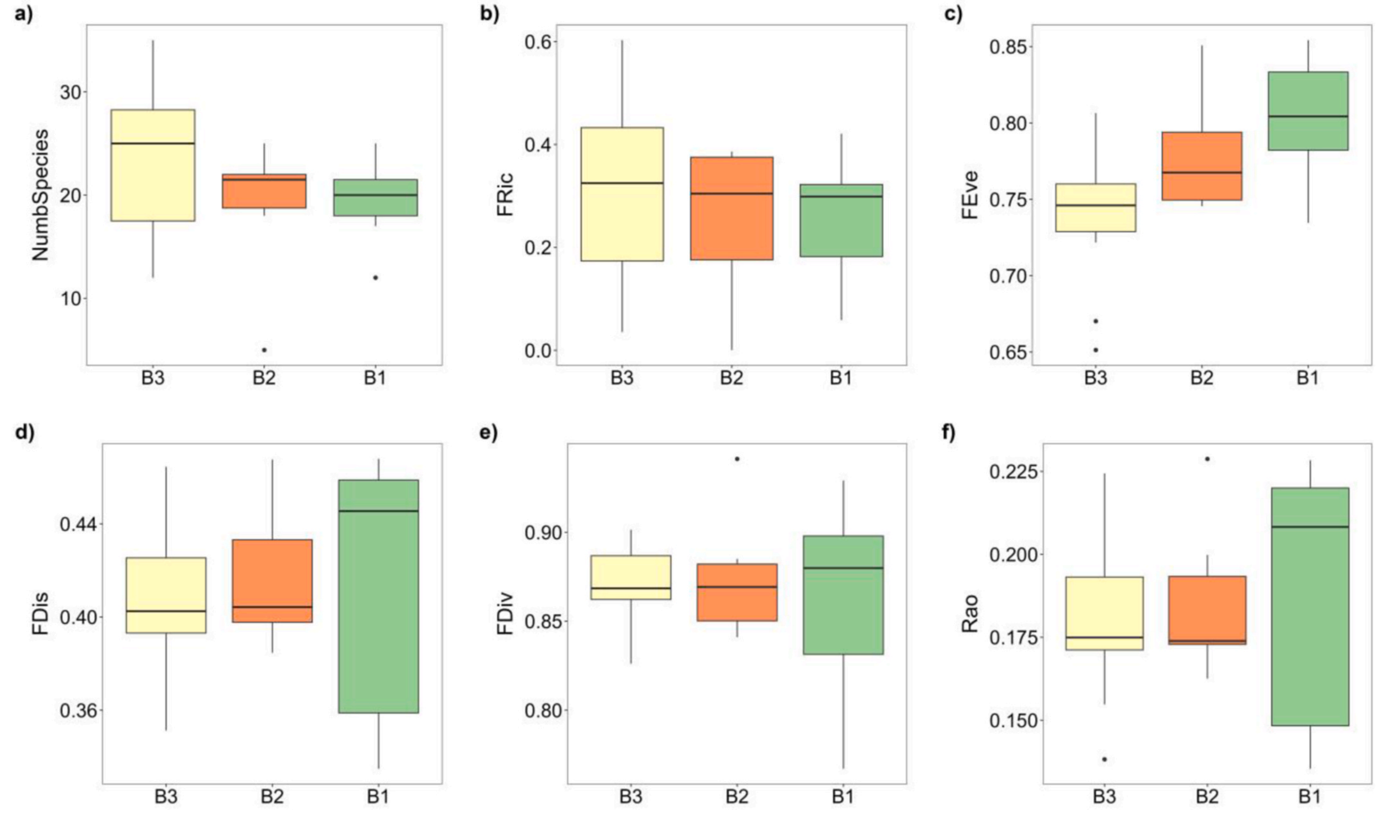

Fig. 5. Trends of the functional indexes: a) number of species, b) functional richness (FRic), c) functional evenness (FEve), d) functional dispersion (FDis), e) functional divergence (FDiv) and f) Rao, calculated for the three stations along the pH gradient of the Bottaro crater vent (B3 most acidified; B1 control). B3:station Bottaro 3, B2: station Bottaro 2, B1: station Bottaro 1.

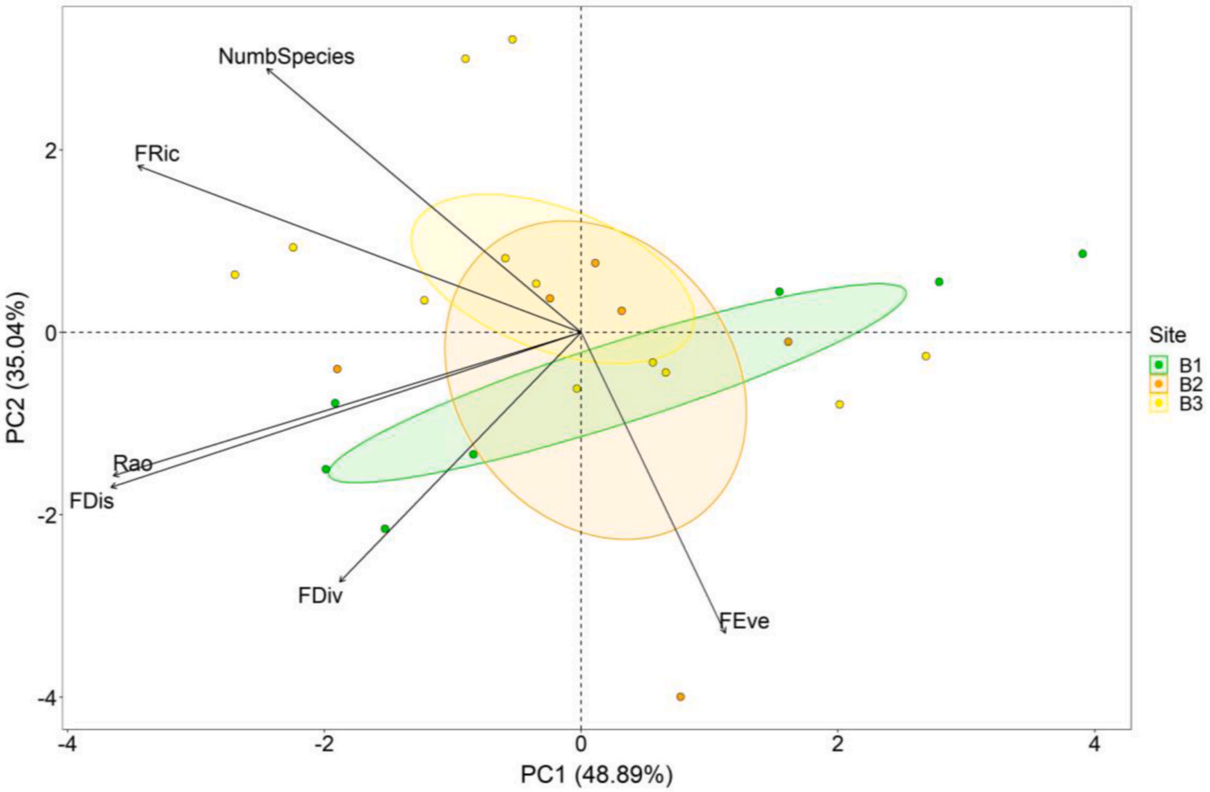

Fig. 6. PCA biplot of the functional diversity indexes (i.e. number of species, Fric: functional richness, FEve: functional evenness, FDis: functional dispersion, FDiv: functional divergence and Rao) measured for the communities associated with scouring pads of the three sampling stations along the pH gradient of the Bottaro crater vent system, from the most acidified B3 to the control B1. Mean point of the groups with confidence interval indicated by respective ellipses. B3:station Bottaro 3, B2: station Bottaro 2, B1: station Bottaro 1.

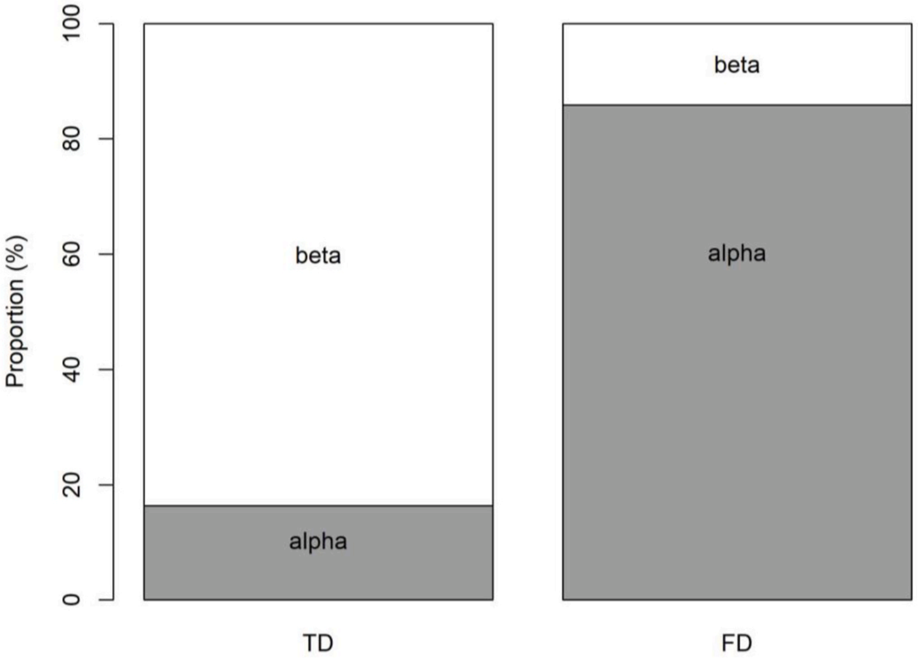

Fig. 7. Proportion of alpha (grey colour) and beta (white colour) diversity for taxonomic diversity (TD) and functional diversity (FD).

observation of Esposito et al. (2022) regarding the prevalence of brooding habits in benthic communities associated with *Cystoseira brachycarpa* along a pH gradient in the Bottaro crater and other vent systems (Gambi et al., 2016; Teixidó et al., 2018). Different life history and physiological reasons can underpin the higher tolerance to OA of brooding species. For example, organisms that withstand high pCO_2 during early development stages exhibit greater tolerance to OA later in life Gray et al. (2022); Indeed, Lucey et al., 2015 highlighted how brooding species of polychaete worms inhabiting naturally acidic seawater vent systems, gain a competitive advantage over non-brooding species in environments with elevated pCO_2 levels thanks to their ability to adapt during larval development (Lucey et al., 2015). Brooding bivalves embryos and larvae can experience respiration-driven hypercapnia when female close off their brood chamber (Chaparro et al., 2009; Noisette et al., 2014). As demonstrated in flat oysters *Ostrea angasi* respiratory waste products undergo significant fluctuations within internal brood chambers, where parental-stress-induced isolation can lower chamber pH, reaching as low as 7.46 (Cole et al., 2016). Given that brooding bivalves are able to tolerate higher levels of pCO_2 during periods of hyperapnia could make brooding bivalves' larvae more tolerant to OA in later life stages compared to larvae of broadcast spawning bivalves which are not exposed to periods of hypercapnia in the same way (Cole et al., 2016).Furthermore, even if not so strongly correlated, PCA suggested that species capable of active swimming (e.g. Harpacticoida and Ostracoda) and grazers (e.g. *Ampithoe ramondi* and *Elasmopus rapax*) showed a higher incidence in the acidified conditions. Grazers can indirectly benefit from OA thanks to the reduction of phenolic substances in the tissue of algae and other vegetal organisms (Arnold et al., 2012; Mannino and Micheli 2020; Vinuganesh et al., 2022) and from increased organic matter quality (higher N content, Ricevuto et al., 2015). Organisms with higher motility are subjected to more anaerobic respiration than slow-moving or sessile taxa (Melzner et al., 2009). Regular anaerobic respiration gives these organisms the capacity to buffer increased pCO_2 preventing acidosis which allows for a more efficient removal of excess internal CO_2 (Melzner et al., 2009). Therefore, this could represent an important trait for improving resistance to rapid increases in oceanic pCO_2 and to cope with future altered ocean conditions (Gray et al., 2022).

The analysis of functional diversity indices demonstrates how OA can affect the distribution of traits within a community leading to the selection of specific traits that allow for species survival in the altered environmental conditions. While we observed high taxonomic beta diversity due to species composition turnover, functional diversity is primarily explained by alpha diversity, which may be linked to the decreased functional evenness observed in the lower pH station (B3). Unevenness of species affiliation to different functional groups led to the presence of some functional groups with very little redundancy and therefore increases the risk of losing ecosystem function with species loss (Galland et al., 2020). Functional redundancy should reflect how stable a community's functional structure is to the potential loss of species, and then low functional redundancy translates in higher vulnerability by the loss of one or more species. Low functional redundancy should thus imply lower buffering capacities of communities towards potential environmental changes (Laliberte et al., 2010; Ricotta et al., 2016).

5. Conclusion

Ocean acidification has an overall impact on the composition of a benthic community as further corroborated by the results presented here. The gradient generated by OA due to the CO_2 degassing activity in the Bottaro crater resulted in a pattern of disturbance that was sufficient to re-arrange the composition of the ecological communities that colonized the deployed artificial structures. Changes in community composition are accompanied by modifications to its functional diversity. The altered conditions of the ecosystem act like a filter that selects those species with the most suitable functional traits needed to survive OA. When the artificial structures were recovered, one year after the exposure to elevated pCO_2, communities that had settled under low pH conditions displayed an array of pre-adapted functional traits that allow them to live under acidified conditions. However, the filter operated by ocean acidification selected an uneven distribution of functional traits, potentially reducing the stability of the benthic communities to further environmental or anthropogenic stressors, increasing their vulnerability. These findings support the idea that ecosystems can respond to OAthrough biodiversity modifications and provides insight into the potential effects of future rises in pCO_2 levels on our oceans' benthic ecological communities. We have illustrated that the effects of increased pCO_2, predicted over the next decades, on biodiversity can be better understood through the lens of functional traits. Accordingly, understanding the impacts of climate change on functional diversity - and therefore on community functioning and stability - is of great importance in predicting changes in ecosystem vulnerability and its ability to adapt to environmental change, not only in the context of increasing OA but also in a context of multiple anthropogenic stressors that are driving environmental change.

CRediT authorship contribution statement

M. Berlino: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **M.C. Mangano:** Conceptualization. **G. Di Bona:** Methodology, Formal analysis. **M. Lucchese:** Methodology. **S.M.C. Terzo:** Methodology. **C. De Vittor:** Conceptualization. **M. D'Alessandro:** Methodology, Investigation. **V. Esposito:** Investigation, Data curation, Conceptualization. **M.C. Gambi:** Methodology, Conceptualization. **P. Del Negro:** Conceptualization. **G. Sarà:** Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2024.106520.

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