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Fish assemblages cope with ocean acidification in a shallow volcanic CO_2 vent benefiting from an adjacent recovery area

Alice Mirasole [a,b,*], Geraldina Signa [c], Paola Gianguzza [a], Chiara Bonaviri [a], Antonio Mazzola [a,c], Salvatrice Vizzini [a,c]

[a] University of Palermo, Department of Earth and Marine Sciences, via Archirafi 18, 90123, Palermo, Italy
[b] Stazione Zoologica Anton Dohrn, Department of Integrative Marine Ecology, Villa Dohrn-Benthic Ecology Center, Punta San Pietro s/n, 80077, Ischia, Napoli, Italy
[c] CoNISMa, National Inter-University Consortium for Marine Science, Piazzale Flaminio 9, 00196, Roma, Italy

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ABSTRACT

Shallow CO_2 vents are used to test ecological hypotheses about the effects of ocean acidification (OA). Here, we studied fish assemblages associated with *Cymodocea nodosa* meadows exposed to high pCO_2/low pH conditions at a natural CO_2 vent in the Mediterranean Sea. Using underwater visual census, we assessed fish community structure and biodiversity in a low pH site (close to the CO_2 vent), a close control site and a far control site, hypothesising a decline in biodiversity and a homogenization of fish assemblages under OA conditions. Our findings revealed that fish diversity did not show a unique spatial pattern, or even significant relationships with pH, but correlated with seagrass leaf canopy. Among-site similarity was found in the abundance of juveniles, contrary to the expected impacts of OA on early life stages. However, pH seems an important driver in structuring fish assemblage in the low pH site, despite its high similarity with the close control site. This unexpected pattern may represent a combined response of fish mobility, enhanced food resources in the acidified site, and a 'recovery area' effect of the adjacent control site.

1. Introduction

The uptake of anthropogenic CO_2 by the ocean is causing complex changes in the carbon chemistry balance, including a reduction in seawater pH, through a process known as ocean acidification (OA). This process may have direct and indirect effects on marine ecosystems and biodiversity (e.g. Barry et al., 2011; Cheung et al., 2009; Fabricius et al., 2011; Foo et al., 2018; Gattuso et al., 2015; Nagelkerken and Connell, 2015). OA can exert negative direct effects on marine organisms, especially calcifying species (i.e. algae, corals, mollusks and echinoderms) impairing calcification, growth, development and reproduction (Kroeker et al., 2013). More difficult to disentangle are the indirect effects of OA, which may be as important as direct effects to forecast the overall ecosystem responses (Riebesell and Gattuso, 2015). For example, OA may indirectly affect marine organisms by reducing habitat complexity through the decline in habitat-forming species that support high biodiversity (Barry et al., 2011). A recent study projected contrasting indirect effects of OA in biogenic habitats: biodiversity may decrease in coral reefs, mussel beds and some macroalgal habitats due to the reduction in structural complexity, but may increase in systems where habitat-forming species benefit from OA (i.e. seagrasses) (Sunday et al., 2017).

Among marine organisms, fish were considered able to cope with low pH due to their well-developed capacity for acid-base regulation (Ishimatsu et al., 2008). However, both direct and indirect effects have been subsequently documented on different fish life stages under higher pCO_2 conditions (reviewed by Cattano et al., 2018; Noor and Das, 2019). For instance, laboratory experiments have found that OA conditions predicted for the end of this century (IPCC et al., 2014; Gattuso et al., 2015) can have a variety of direct effects on fish physiology (Melzner et al., 2009), neurosensory functions (Nilsson et al., 2012) and behaviour (Munday et al., 2014; Nagelkerken and Munday, 2016), otoliths and fish bones (Bignami et al., 2013; Mirasole et al., 2017; Di Franco et al., 2019), reproduction (Miller et al., 2013), survival and growth (Baumann et al., 2011; Stiasny et al., 2016). In particular, early life stages (embryos, larvae and juveniles) are considered more vulnerable to OA than adult stages, due to less efficient capacity for acid-base regulation (Melzner et al., 2009). Indeed, experiments have shown that fish early life stages may have increased predation risk and decreased foraging efficiency (Cattano et al., 2018) with consequences on fish population replenishment (Baumann et al., 2011; Munday et al., 2010; Rossi et al., 2016; Sti-

* Corresponding author. University of Palermo, Department of Earth and Marine Sciences, via Archirafi 18, 90123, Palermo, Italy..
E-mail address: alice.mirasole@szn.it (A. Mirasole)

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asny et al., 2016) under OA conditions. OA has been shown to impair fish larvae's sensory abilities, to affect the morphology of otoliths, and to cause tissue damage that may lead to increased mortality (Cattano et al., 2018; Frommel et al., 2012; Stiasny et al., 2016). On the other hand, indirect effects of OA are caused by habitat alteration, food availability and interactions with other species (Nagelkerken et al., 2015, 2017; Nagelkerken and Munday, 2016). Accordingly, it has been hypothesised that fish biodiversity will be negatively affected by OA by the end of this century (under the RCP 8.5 emission scenario, Gattuso et al., 2015) and decline of catches worldwide is expected (Cheung et al., 2009; Cheung, 2018).

CO_2 vents represent a great opportunity to test the effects of OA at high levels of the biological organization, from single-species to communities (Riebesell and Gattuso, 2015). Nevertheless, so far, most studies in CO_2 vents mainly focused on calcareous species and ecosystem shifts driven by a decline not only in species richness at low pH conditions (Hall-Spencer et al., 2008; Fabricius et al., 2011; Kroeker et al., 2012; Foo et al., 2018), but also by a loss of functional diversity (Teixido et al., 2018). Only recently, a few studies carried out in CO_2 vents addressed the response of fish to OA at species (Nagelkerken et al., 2015; Cattano et al., 2017) and community levels (Munday et al., 2014; Nagelkerken et al., 2017). The latter studies showed contrasting results on changes in community structure and biodiversity, probably influenced by the different habitat use of the fish studied. Although both studies found fish behavioural abnormalities, Nagelkerken et al. (2017) found a loss in biodiversity of highly resident benthic fish, while Munday et al. (2014) found only minor differences in the community structure of more mobile necto-benthic fish. Therefore, it seems that indirect effects may be the major drivers of change in fish community structure at the CO_2 vents studied to date.

This study was conducted at the shallow CO_2 vent located in Vulcano Island (Aeolian Archipelago, Italy) where the seagrass *Cymodocea nodosa* (Ucria) Ascherson, 1870, forms large meadows. In this area, previous studies highlighted lower *C. nodosa* density and biomass close to the CO_2 vent area than in control sites, although overall characterized by a more intense metabolism and photosynthetic activity (Apostolaki et al. 2014). *C. nodosa* has a crucial role in terms of primary production, biodiversity and food web complexity (Cancemi et al., 2002) and is an important habitat-forming species for coastal fish, providing shelter from predators, nursery ground and food (Guidetti and Bussotti, 2000). The main aim of this study was to assess the effect of high pCO_2/low pH on fish assemblages in a coastal area characterised by seagrass meadows. We compared fish assemblages exposed to high pCO_2/low pH conditions (low pH site) to those in normal pH conditions from two control areas, in two periods of the year characterized by different *Cymodocea nodosa* meadow structural complexity (Cancemi et al., 2002). In all sites and periods, we assessed species composition, fish biodiversity, community and size-class structure, as well as *C. nodosa* meadow complexity, in terms of shoot density and leaf canopy height. Accordingly, and consistent with the predictions of Sunday et al. (2017), we hypothesised a decline in fish biodiversity and a homogenization of fish assemblage (over simplification of the community structure through the numerical dominance of only a few species, *sensu* Nagelkerken et al., 2017) due to the combination of the stress effect of low pH and the expected reduction in seagrass structural complexity. We also expected that the detrimental effects were more severe on juveniles due to their higher susceptibility than adults (Melzner et al., 2009; Portner and Peck, 2010).

2. Materials and methods

2.1. Study area and fieldwork

The shallow venting system of Vulcano Island (Aeolian Archipelago, 24 km off the NE coast of Sicily, Italy) is one of the most active and studied vent in the whole Mediterranean Sea. The main venting area occurs at about 1 m depth on the south-western part of Levante Bay, on the eastern side of the Island (Fig. 1) (Boatta et al., 2013). Overall, gas composition is dominated by CO_2 (97–99% vol.), which generates a pH gradient along the northern shore of the bay (Boatta et al., 2013; Italiano, 2009). The area is characterized by acidic and reducing conditions, causing changes in major and trace element geochemical fluxes at the sediment-seawater interface (Vizzini et al., 2013). Emissions include also small quantities of H_2S (< 2.2%), which rapidly decrease with distance from the vent (Boatta et al., 2013). Water composition in terms of major elements and compounds (Cl, SO_4, Na, K, Ca and Mg) is similar to that of Mediterranean surface waters, while greater variability has been recorded for dissolved Fe concentrations, which showed high values close to the vents (Boatta et al., 2013). Seawater carbonate chemistry was studied in the Levante Bay by Boatta et al. (2013). In particular, pH ranged on average from 7.49 ± 0.29 pH_T units to 8.19 ± 0.04 pH_T units, pCO_2 ranged from 3361.7 ± 2971.3 μatm to 424.6 ± 61.5 μatm, whilst total alkalinity was more homogenous in the bay ranging between a minimum of 2.78 to a maximum of 3.17 mmol kg^{-1} (Boatta et al., 2013). Moreover, the same sites used here were previously characterized in the same sampling periods in terms of seawater elemental composition and $\delta^{13}C_{DIC}$ (dissolved inorganic carbon) and revealed significant difference in terms of $\delta^{13}C_{DIC}$ between the vent and the control sites (Mirasole et al., 2017).

Fish assemblage was studied through non-destructive underwater visual censuses (UVCs) (Harmelin-Vivien et al., 1985) along 10 m long × 5 m wide strip transects (total area of each transect: 50 m^2), randomly placed within *Cymodocea nodosa* meadows at a depth of

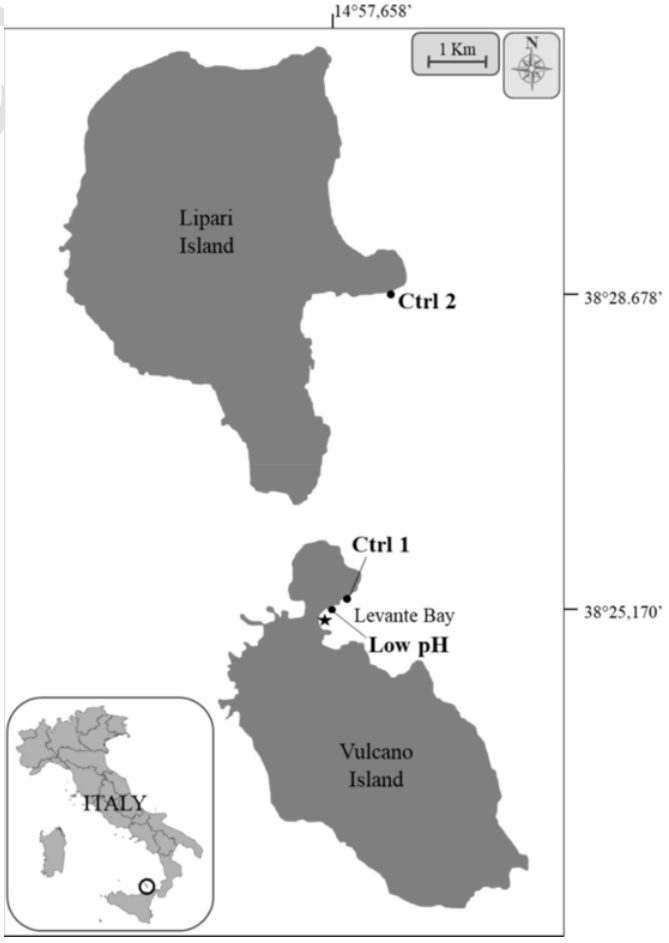

Fig. 1. Map of the study area showing the sampling sites in Vulcano (Low pH and Ctrl 1) and Lipari Islands (Ctrl 2) (Aeolian Archipelago, Italy). The primary vent is located in Levante Bay (Vulcano) and is indicated by the star.

2 and 5 m, and with a space of at least 10 m between two following transects. We chose three sampling sites already used and described in Mirasole et al. (2017). In particular, we chose a low pH site (hereafter Low pH – corresponding to the predicted decrease in surface water pH of 0.4 units by 2100 under the emission scenario RCP 8.5; IPCC et al., 2014, Gattuso et al., 2015) about 250 m far from the primary CO_2 vent in Levante Bay, and two Control sites: Control 1 (Ctrl 1) about 500 m far from the primary vent, and Control 2 (Ctrl 2) in Lipari Island, about 6.5 km far from the primary vent (Fig. 1). Although the presence of a single CO_2 vent in Vulcano Island has driven the choice of just one Low pH site, somehow limiting the possibility to make inferences about the effect of pH on fish assemblages, it must say that control sites were chosen with the same orientation (South-East), depth (2–5 m) and vegetal coverage (*C. nodosa* meadow) as the Low pH site. Moreover, the two islands involved (Vulcano and Lipari) have the same volcanic origin and geomorphological setting (Favalli et al., 2005). Therefore, the most relevant difference between the two controls and the low pH site was the distance from the CO_2 vent and the related changes in the carbonate chemistry.

UVCs were carried out in two periods of the year (Period I: from September to November 2014; Period II: from May to July 2015), between 11.00 a.m. and 3.00 p.m. (18 replicates in total per site and period). Cryptic fish (i.e. Blenniidae, Gobiidae, Scorpaenidae) were not surveyed to avoid underestimation (Willis, 2001). During UVCs, each fish was identified to species level and assigned to three size-classes: small (S), medium (M) and large (L), corresponding each to one-third of the maximum total length reported in the literature, according to FishBase online database (Froese and Pauly, 2016) and Louisy (2015) (for details see the Appendix). In agreement with the literature, we considered small, medium and large size corresponding to different fish life stages, analogues of juveniles, sub-adults and adults (Harmelin-Vivien et al., 1985; Guidetti and Bussotti, 2000, 2002; Azzurro et al., 2007). At the same time, during each transect, fish abundance was estimated for each species censused at each size-class, by using seven pre-established abundance classes (1, 2–5, 6–10, 11–30, 31–50, 51–100, >100 number of individuals) according to Harmelin-Vivien et al. (1985), Guidetti and Bussotti (2000, 2002) and Azzurro et al. (2007). Before data analysis, abundance of each species, at each size-class, was calculated by taking into account the mid-point of each abundance class and expressed as mean fish abundance (ind. 50 m^{-2}). Fish were also grouped into trophic groups following the classification by Guidetti and Sala (2007) (Appendix).

Seawater temperature, salinity, dissolved oxygen (DO), pH and redox potential (Eh) were measured in each site at 2 m depth on the same days as UVC surveys (9 measurements per site and period) using a multiparameter probe (Hanna Instrument, HI98194). The pH sensor was previously calibrated using NIST scale standard buffers with a three points calibration of pH 4.01, 7.00 and 10.01 at 25 °C.

Seagrass (*C. nodosa*) shoot density and leaf canopy height were also measured in the same sites and periods. *C. nodosa* shoot density was estimated by counting shoots (three random replicates per transect) within a 400 cm^2 surface through a 20 × 20 cm frame and then converted to square meter. Leaf canopy height was measured by recording the maximum length of the highest leaf in each shoot analysed (five shoots per square, five replicates per transect).

2.2. Data analysis and statistics

Univariate permutational analysis of variance (PERMANOVA) was used to test for differences among sites (fixed factor with 3 levels: low pH, Ctrl 1 and Ctrl 2) and between periods (fixed factor and orthogonal to Site, with 2 levels: PI and PII) for physico-chemical variables of seawater (temperature, salinity, dissolved oxygen, pH, Eh), *Cymodocea nodosa* features (shoot density and leaf canopy height), fish diversity (species richness S, total abundance N, and size-class abundance N: N_{small}, N_{medium}, N_{large}). Data were previously resembled using Euclidean distance for seawater physico-chemical variables and Bray Curtis similarity for seagrass and fish diversity data (Primer 6/PERMANOVA + software, Plymouth Marine Laboratory). If significant differences occurred, pair-wise *post hoc* tests were carried out and the results (*p* values) were corrected with the Bonferroni method, to counteract the problem of multiple comparisons. Linear regression analysis was run to test the relationship between fish diversity (S, N, N_{small}, N_{medium}, N_{large}) and both *C. nodosa* features (shoot density and leaf canopy height) and pH values, by using Statistica software (Stat Soft V. 10).

PERMANOVA was used also to test for differences among sites and between periods in abundance of the most abundant species (N > 2% in at least one sampling site) taken individually (univariate analysis), all together, and grouped in size-class (N_{small}, N_{medium}, N_{large}) (multivariate analysis). The analysis was carried out after transformation using the log (x + 1) notation to balance the contribution between common and rarer species (Clarke and Warwick, 2001), and resemblance using Bray Curtis similarity matrices. Only in the analysis of size-class abundance, a dummy variable = 1 was added to improve interpretability of displays and significance of tests when denuded samples were found (Clarke et al., 2006). Also in this case, pair-wise *post hoc* tests were carried out once significant differences occurred, and the results (*p* values) were corrected with the Bonferroni method. To visualize the differences in fish abundance (total and size-class abundance) among sites and between periods, a constrained ordination (with the interaction "site x period" as constrained factor) was performed using canonical analysis of principal coordinates (CAP, Anderson and Willis, 2003). A similarity percentage procedure (SIMPER) was used also to identify fish species mostly contributing to dissimilarities among sites (Primer 6/PERMANOVA + software, Plymouth Marine Laboratory).

3. Results

3.1. Environmental features

Temperature did not show among-site and between-period significant differences (Table 1), and was on average 22.3 ± s.d. 2.4 °C (range: 20.1–25.5 °C). Salinity and DO values showed significant differ-

Table 1
Results of univariate PERMANOVA testing for differences among sites and between periods in seawater physico-chemical variables (temperature, salinity, dissolved oxygen - DO, pH and redox potential - Eh). Bonferroni corrected probability levels: n.s. = not significant - p > 0.05; *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001.

Source of variation	Temperature (°C)				Salinity (psu)			DO (mg l^{-1})			pH_{NBS}			Eh (mV)		
	df	MS	Pseudo-F	p	MS	Pseudo- F	p	MS	Pseudo-F	P	MS	Pseudo-F	p	MS	Pseudo-F	p
Site (Si)	2	8.07	1.14	n.s.	0.00	0.00	n.s.	0.00	0.00	n.s.	0.98	302.59	**	5273.1	49.5	**
Period (Pe)	1	0.81	0.11	n.s.	2.54	20.58	**	7.68	22.28	**	0.00	1.16	n.s.	182.6	1.7	n.s.
Si*Pe	2	15.00	2.11	n.s.	0.00	0.00	n.s.	0.00	0.00	n.s.	0.00	0.42	n.s.	136.5	1.3	n.s.
Residuals	48	7.10			0.12			0.34			0.00			106.5		
Pair-wise test results		n.s.			PII < PI			PII < PI			Low pH < C1 = C2			Low pH < C1 = C2		

ences between periods, with lower values in PII (salinity: 38.5 ± 0.3 psμ; DO: 7.0 ± 0.5 mg l^{-1}) than in PI (salinity: 38.9 ± 0.4 psμ; DO: 7.7 ± 0.6 mg l^{-1}). On the other hand, pH showed the expected among-site significant variation, being significantly lower in the Low pH site (7.80 ± 0.09 pH_{NBS} units) than in both Controls (8.19 ± 0.03 pH_{NBS} units in Ctrl 1 and 8.22 ± 0.02 pH_{NBS} units in Ctrl 2). Accordingly, Eh was significantly lower in the Low pH (79.3 ± 5.6 mV) than in Ctrl 1 (85.6 ± 8.3 mV) and Ctrl 2 (111.6 ± 13.7 mV) (Table 1).

Cymodocea nodosa shoot density showed significant differences for the interaction 'site x period' (Pseudo-$F_{(2, 318)} = 25.76$, $p \leq 0.001$). Pair-wise tests highlighted significantly lower densities in the Low pH site than in both Controls in Period I ($p \leq 0.05$), and significantly lower densities were also highlighted in Period I than in Period II at all sites (Fig. 2a). No among-site and between-period differences in *C. nodosa* leaf canopy height were detected (Fig. 2b).

3.2. Fish assemblages

Overall, nineteen fish species belonging to six different families were recorded. Assemblages were dominated by Labridae (10 species) and Sparidae (5 species), followed by Mullidae, Mugilidae, Pomacentridae and Serranidae (Appendix). Most species belonged to the invertivorous trophic group with the exception of one herbivore (*Sarpa salpa*), one detritivore (*Mugil cephalus*), one piscivore (*Serranus scriba*) and two planktivores (*Chromis chromis* and *Oblada melanura*). In general, the most abundant species belonged to the families Labridae (i.e. *Coris julis* and *Symphodus ocellatus*), Pomacentridae (*C. chromis*) and Sparidae (i.e. *Diplodus vulgaris* and *S. salpa*).

At the multivariate level, fish assemblage showed significant differences for the factors site (Pseudo-$F_{(2,102)} = 10.25$, $p \leq 0.001$) and period (Pseudo-$F_{(2,102)} = 542$, $p \leq 0.001$), but not for their interaction. Pair-wise tests revealed that all the three sites were significantly differed. Furthermore, site seems the main factor discriminating the three groups in the CAP ordination (Fig. 3). Specifically, the CAP ordination separated the Low pH site from the Ctrl 2 site along the first canonical axis. The position of the Ctrl 1 site was neutral being interspersed between the other two sites, and no evident separation occurred between periods within each site. The canonical correlations of the first two axes with the resulted ordination were large ($\delta_1 = 0.76$ and $\delta_2 = 0.59$), indicating a strong association between the multivariate data cloud and the hypothesis of fish assemblage's differences. Vectors superimposed onto the graph, showed that the main species contributing to the ordination were *C. chromis, C. julis* and *Symphodus tinca* for samples from Low pH and Ctrl 1, and *D. vulgaris* and *Thalassoma pavo* mainly for samples from Ctrl 2. Furthermore, SIMPER analysis highlighted the lowest dissimilarity between Low pH and Ctrl 1, and the highest dissimilarity between Low pH and Ctrl 2, due to the species *C. chromis*, *S. salpa*, *D. vulgaris* and *T. pavo*. On the other hand, the dissimilarity between the two controls was due mainly to *C. chromis* and *D. vulgaris* (Table 2).

Accordingly, at the univariate level, the most abundant fish species (N > 2% in at least one site) showed significant differences among the three sites, except for *M. surmuletus* and *S. ocellatus* (Table 3). In particular, three species showed comparable abundances in Low pH and Ctrl 1 sites, and lower (*D. vulgaris*) or higher (*C. chromis* and *C. julis*) than in Ctrl 2. One species (*S. tinca*) showed similar abundances in Low pH and Ctrl 2, while only one species showed lower abundance in Low pH than both Controls (*O. melanura*), and another species differed among the three sites with a marked increase from Low pH to Ctrl 1 and Ctrl 2 (*T. pavo*). Finally, *S. salpa* showed an opposite trend (higher in Low pH than in both Controls). By comparing periods, only three species (*C. julis*, *S. tinca* and *T. pavo*) showed a significantly higher abundance in Period I than in Period II, while one species (*S. salpa*) showed the opposite trend.

Fish grouped in size-classes also differed among sites (N_{small}: Pseudo-$F_{(2,102)} = 3.20$, $p \leq 0.01$; N_{medium}: Pseudo-$F_{(2,102)} = 4.58$, $p \leq 0.001$; N_{large}: Pseudo-$F_{(2,102)} = 5.20$, $p \leq 0.001$) and between periods (N_{small}: Pseudo-$F_{(1,102)} = 7.88$, $p \leq 0.001$; N_{medium}: Pseudo-$F_{(1,102)} = 2.61$, $p \leq 0.05$; N_{large}: Pseudo-$F_{(1,102)} = 2.50$, $p \leq 0.05$). Pair wise tests showed that the small and the large fish size-classes differed among the three sites, while the medium class differed only between Ctrl 2 and the other sites. According to the CAP ordination of the whole assemblage, CAP of size-class abundance did not highlight any temporal separation, but partial spatial separations along the first canonical axis. In particular, small and medium-sized fish from Low pH and Ctrl 2 clustered in the positive and negative portion of the first axis respectively, with Ctrl 1 partially overlapped to both Low pH and Ctrl 2 in the central position (Fig. 4a and b). Large-sized fish from the three sites were even more distinct along the first axis and the three sites were more overlapped each other (Fig. 4c). Moreover, the main species contributing to discriminate the sites were *C. julis* and *D. vulgaris* for small-sized fish, *D. vulgaris* and *S. ocellatus* for medium-sized fish, and *C. chromis* and *C. julis* for large-sized fish.

Fish biodiversity, in terms of species richness (S) and total abundance (N), showed different patterns when comparing sites and periods. Overall, S differed among sites (Pseudo-$F_{(2,102)} = 4.79$, $p \leq 0.01$) and periods (Pseudo-$F_{(1,102)} = 5.97$, $p \leq 0.05$), but not for their interaction. In more detail, significantly higher S values were observed in Ctrl 1 than in the other sites, and in Period I than in Period II (Fig. 5a). Despite the high spatial variability of N in Period I, no significant difference was detected, nor clear spatial or temporal patterns (Fig. 5b). Results of the regression analysis between fish diversity (S and N) and environmental variables (*C. nodosa* shoot density, leaf canopy height, pH) revealed a significant positive relationship only between both S and N and leaf canopy height (S: $n = 108$, $r = 0.22$, $p \leq 0.05$; N: $n = 108$, $r = 0.33$, $p \leq 0.01$).

Regarding size-class abundance (N_{small}, N_{medium}, N_{large}), small- and large-sized individuals showed contrasting temporal trends (Fig. 6a, c): N_{small} decreased significantly from Period I to Period II (Pseudo-$F_{(1,102)} = 4.88$; $p \leq 0.05$), when N_{large} increased (Pseudo-$F_{(1,102)} = 5.07$; $p \leq 0.05$). Abundance of medium-sized fish, N_{medium}, did not differ between periods, but was higher in Ctrl 1 than in the other sites (Pseudo-$F_{(2,102)} = 5.43$; $p \leq 0.01$) (Fig. 6b). N_{small} was positively correlated with *C. nodosa* leaf canopy height ($n = 108$, $r = 0.37$; $p \leq 0.001$)

4. Discussion

The forecasted 0.4 units decrease in ocean pH by 2100 (IPCC et al., 2014) is predicted to negatively affect marine ecosystems and biodiversity through direct and indirect effects (Cheung et al., 2009; Sunday et al., 2017). Even though calcareous organisms are considered more susceptible (Doney et al., 2009), fish are expected to be directly and/or indirectly affected by ocean acidification (OA), with consequences on their distribution, abundance and biodiversity (Portner and Peck, 2010; Nagelkerken and Munday, 2016; Cattano et al., 2018).

In the shallow volcanic CO_2 vent of Vulcano Island (Aeolian Archipelago, Italy), although a few species were more abundant at the low pH site than in both controls, we did not find the expected reduction in fish biodiversity or the homogenization of the community structure. Our findings highlighted, instead, a well-structured nekto-benthic fish assemblage in the acidified site, probably driven by higher resources availability close to the CO_2 vent.

In particular, our findings revealed that fish diversity, in terms of species richness and abundance, did not show a unique spatial pattern and significant relationships with pH. However, fish assemblages changed among sites with important species like *Chromis chromis* and *Coris julis* higher in both the acidified site and the close control than in the far control, and *Diplodus vulgaris* and *Thalassoma pavo* showing an opposite trend and clearly dominating the fish assemblage in the far control. Moreover, *Sarpa salpa* dominated the assemblages in the low pH site in both periods, and *Oblada melanura* showed a lower abun-

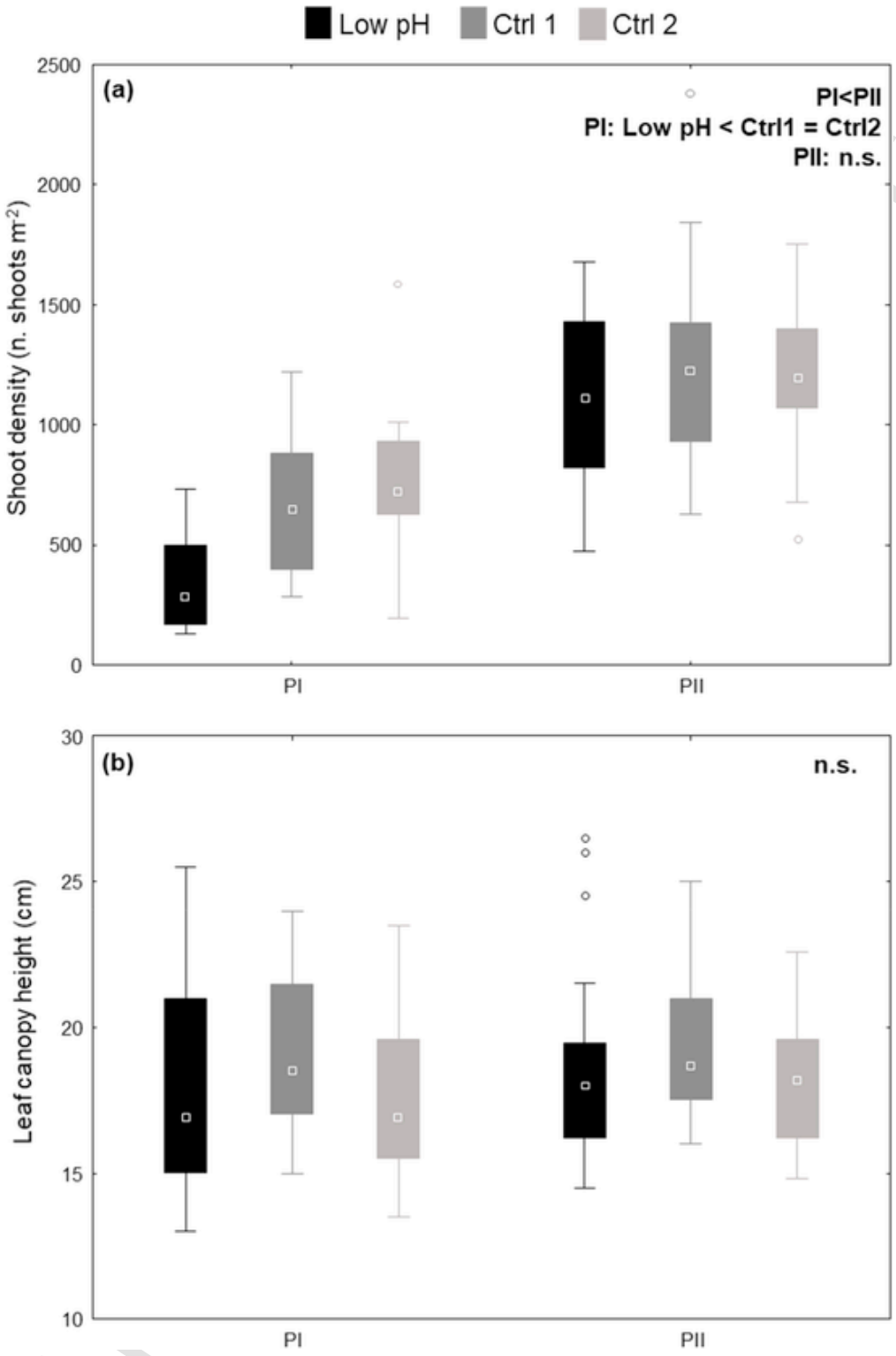

Fig. 2. a) *Cymodocea nodosa* shoot density (n. shoots m^{-2}) and b) leaf canopy height (cm) in the three sites (Low pH, Ctrl 1 and Ctrl 2) and the two periods (PI and PII). Whiskers indicate the non-outlier range of variation; boxes: 25th to 75th percentiles. The small circles outside the boxes indicate the outliers. Results of univariate PERMANOVA pair-wise tests are also showed on each panel (n.s. = not significant difference).

dance in the low pH than in both control sites. These results suggest that pH played a role in shaping fish assemblage, with a few species overlapping between the low pH site and the close control, although the latter was characterised by boosted species richness.

S. salpa (commonly known as salema), which was one of the most influential species in discriminating sites, is one of the most important herbivorous fish in the Mediterranean Sea. The minor content of phenolic substances, which are deterrent to herbivory (Arnold et al., 2012), and the greater palatability of *Cymodocea nodosa* long-term exposed to high pCO_2 (Apostolaki et al. 2014) may have led to a higher attractiveness of the acidified site for the highly mobile *S. salpa*. Moreover, it was the only species whose abundance showed a similar temporal trend together with the seagrass shoot density, revealing an important role of the meadow structure for the salema species. This re-

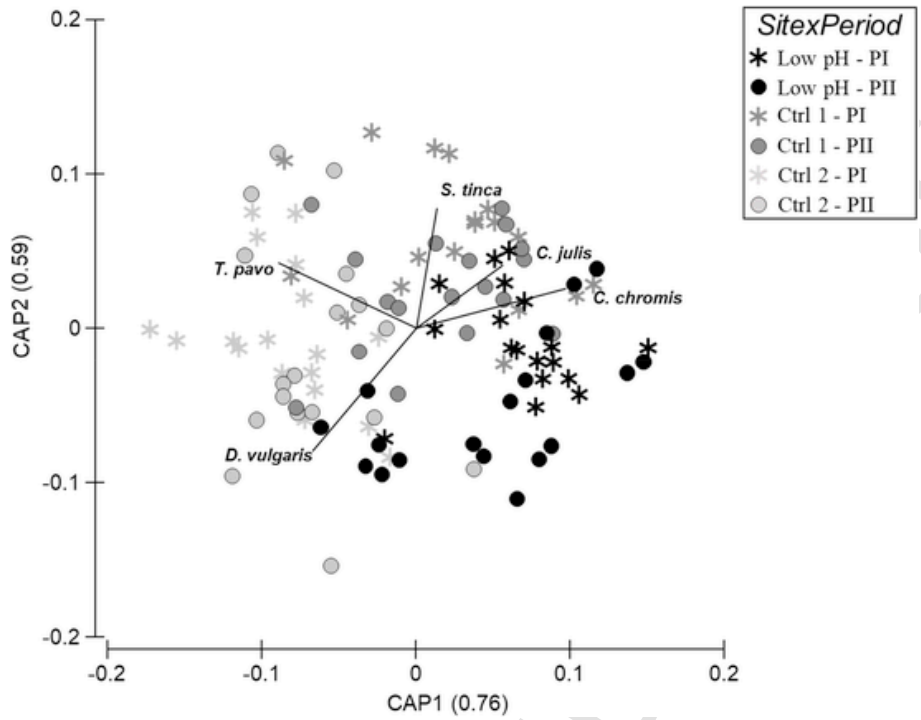

Fig. 3. Canonical analysis of principal coordinates (CAP) of abundance of the most abundant species (> 2%) in the three sites (Low pH, Ctrl 1 and Ctrl 2) and the two periods (PI and PII). Vectors of the species contributing most to the ordination (Pearson correlation > 0.4) are superimposed. See the appendix for the whole scientific name of the species. The correlation of each axis with the resulted ordination is also indicated.

Table 2
SIMPER analysis showing fish species contributing most to the dissimilarity among sites and average abundance at each site (Low pH, Ctrl 1 and Ctrl 2). Av. Ab.: Average abundances; Contr.%: dissimilarity contribution; Av. Dis.: Average dissimilarity.

Species	Contr. %	Av. Ab.		Contr. %	Av. Ab.		Contr. %	Av. Ab.	
		Low pH	Ctrl 1		Low pH	Ctrl 2		Ctrl 1	Ctrl 2
C. chromis	17.32	1.35	1.33	15.79	1.35	0.27	14.8	1.33	0.27
C. julis	8.53	1.27	1.25	9.07	1.27	0.79	9.29	1.25	0.79
D. vulgaris	7.21	0.49	0.30	13.38	0.49	1.19	12.95	0.30	1.19
M. surmuletus	6.76	0.39	0.32	6.68	0.39	0.37	6.07	0.32	0.37
O. melanura	8.20	0.02	0.71	5.92	0.02	0.50	9.84	0.71	0.50
S. ocellatus	12.23	0.47	0.92	8.01	0.47	0.40	12.00	0.92	0.40
S. salpa	12.77	1.08	0.27	14.00	1.08	0.77	9.69	0.27	0.77
S. tinca	10.70	0.58	1.03	8.78	0.58	0.57	9.69	1.03	0.57
T. pavo	7.30	0.18	0.56	11.02	0.18	0.98	9.13	0.56	0.98
	Av. Dis. = 61.59			**Av. Dis. = 67.41**			**Av. Dis. = 66.42**		

sult opens interesting scenarios about the role that herbivores may have in future acidified oceans, because of their control on primary producers through top-down forces (Poore et al., 2012), which may lead to a potential compensatory effect to maintain communities' resistance under high CO_2 conditions (Ghedini et al., 2015).

Like *S. salpa*, the spatial patterns observed for the damselfish *C. chromis,* namely a clear dominance and a significantly higher abundance in both the low pH and close control, than in the further control site, confirm its high tolerance to OA. Ferrari et al. (2011) reported considerable variation in the sensitivity of damselfish to elevated CO_2, with some species much more sensitive than others. More recently, a high resistance to OA (Kwan et al., 2017), as well as an improved aerobic performance (Rummer et al., 2013) and an unaffected gregarious behavior (group cohesion) were highlighted in damselfish under high pCO_2 levels (Cattano et al., 2019).

Among the species that mainly discriminate between sites, the case of the two Labridae the rainbow wrasse *C. julis* and the ornate wrasse *T. pavo* was particularly interesting. Here, their different spatial distribution was striking: *C. julis* abundance was higher in the low pH and the adjacent control site than in the far control, while *T. pavo* showed the highest abundance in the far control and the lowest in the acidified site. These findings suggest that *C. julis* is more tolerant to acidified conditions compared to *T. pavo* and open a new question regarding the combined effects of warming and acidification. Indeed, recent studies showed that the interaction of these species is potentially exacerbated by seawater warming and that their distribution differs according to water temperature (Milazzo et al., 2013, 2016).

Looking at the whole assemblage, the close control site had a fish community structure partially overlapped to that of both the low pH site and the far control, and showed the lowest dissimilarity with the low pH site. This result, together with the among-site similarity in fish total abundance, provides evidence that fish do not avoid the low pH site, possibly driven by the boosted food resources (low-order invertebrates; Vizzini et al., 2017) that allow to maintain a well-struc-

Table 3
Results of univariate PERMANOVA testing for differences among sites and between periods in abundance of the most abundant species (>2%). Bonferroni corrected probability levels: n.s. = not significant difference; p > 0.05; *p ≤ 0.05; **p ≤ 0.01; ***p ≤ 0.001.

Source of variation		*C. chromis*			*C. julis*			*D. vulgaris*		
	df	MS	Pseudo-F	p	MS	Pseudo-F	p	MS	Pseudo-F	p
Site (Si)	2	6895.3	13.0	***	1622.8	8.8	***	5783.3	19.2	***
Period (Pe)	1	1318.9	2.5	n.s.	4858.9	26.4	***	494.3	1.6	n.s.
Si*Pe	2	493.7	0.9	n.s.	411.1	2.2	n.s.	701.0	2.3	n.s.
Residuals	102	528.9			183.8			300.8		
Pair-wise test results		C2 < Low pH = C1			C2 < Low pH = C1 PII < PI			C1 = Low pH < C2		
Source of variation		***M. surmuletus***			***O. melanura***			***S. ocellatus***		
	df	**MS**	**Pseudo-F**	**p**	**MS**	**Pseudo-F**	**p**	**MS**	**Pseudo-F**	**p**
Site (Si)	2	120.0	0.4	n.s.	2714.9	8.0	***	1516.6	3.0	n.s.
Period (Pe)	1	187.9	0.6	n.s.	93.5	0.3	n.s.	252.6	0.5	n.s.
Si*Pe	2	657.3	2.3	n.s.	395.8	1.2	n.s.	758.4	1.5	n.s.
Residuals	102	285.2			338.6			498.7		
Pair-wise test results					Low pH < C2 = C1					
Source of variation		***S. salpa***			***S. tinca***			***T. pavo***		
	df	**MS**	**Pseudo-F**	**p**	**MS**	**Pseudo-F**	**p**	**MS**	**Pseudo-F**	**p**
Site (Si)	2	2175.1	4.0	*	1799.1	5.4	**	4387.1	16.8	***
Period (Pe)	1	3040.8	5.6	*	2061.3	6.2	*	1011.4	3.9	*
Si*Pe	2	840.9	1.5	n.s.	387.3	1.2	n.s.	587.8	2.2	n.s.
Residuals	102	542.8			332.5			260.7		
Pair-wise test results		C2 = C1 < Low pH PI < PII			Low pH = C2 < C1 PII < PI			Low pH < C1 < C2 PII < PI		

tured assemblage also in terms of trophic structure and diversity (Mirasole, 2017). The expected higher energetic cost for the acid-base regulation under acidified conditions (Lefevre, 2016) may be therefore compensated by the higher availability of prey associated to macrophytes in the acidified area (Vizzini et al., 2017), corroborating the results found by Nagelkerken et al. (2015, 2017) where the increase in fish density found close to CO_2 vent was driven by higher resource abundances. This hypothesis is supported also by the high percentage of invertivorous fish (~75%) in the low pH site and the similar isotopic ($\delta^{13}C$, $\delta^{15}N$) composition and niches of fish (Mirasole, 2017) between the low pH site and the close control site, which may represent an adjacent 'recovery area' where fish move to escape the acidified conditions.

The geo-morphological settings of the Levante Bay may also play a role in the overall similarity of fish assemblage between the low pH and adjacent control site. The pH gradient created by the primary vent along the northern shore of the bay is predominant when north-western winds blow, but it is reduced or deleted when south-east (Sirocco wind) winds blow (Boatta et al., 2013). As suggested by Kroeker et al. (2012), natural fluctuations in carbonate chemistry in vent areas may allow organisms to better tolerate or locally acclimate to these particular conditions. On the other hand, most species analysed in the present study have a long pelagic larval stage ranging between 10 and 30 days (Raventos and Macpherson, 2001) and fish population replenishment at vent may occur from "non-acidified populations", as already suggested by Kroeker et al. (2012) and Munday et al. (2014). This may also explain the similar abundance of juveniles found across sites, contrary to the expected negative effects of OA on fish early life stages, as previously found both in laboratory experiments (Baumann et al., 2011) and field studies (Rossi et al., 2016). Indeed, considering fish size-classes, we observed the same spatial pattern as the whole assemblage and only sub-adults showed among-site differences in abundance, with significantly higher values in the close control site than in both the acidified and the far control site. The contrasting results with the literature may be due to a species-specific vulnerability (Ferrari et al., 2011) and/or constrained experimental conditions, such as limited exposure time and high pCO_2 levels (Ishimatsu et al., 2008).

Regarding the relation between fish assemblage and seagrass meadows, species richness, total and juvenile abundances correlated positively only with *C. nodosa* leaf canopy height, which however did not change between low pH site and controls. This pattern confirms the role of seagrass meadow structure in supporting fish diversity, and, in particular, juveniles (Guidetti and Bussotti, 2000, 2002; Hori et al., 2009; Cuadros et al., 2017), regardless of pH conditions. On the other hand, consistently with Apostolaki at al. (2014), *C. nodosa* shoot density was overall lower in the Low pH site, and in the first sampling period (i.e. autumn) when fish species richness reached higher values. These results may indicate a stronger effect of low pH conditions on *C. nodosa* density in autumn/winter when the seagrass is featured by low structural complexity (Guidetti and Bussotti, 2000; Cancemi et al., 2002), and suggests a lower effect of density than leaf canopy height in shaping fish diversity, consistent with the literature (Bell and Westoby, 1986; Hori et al., 2009).

An overall assessment of the patterns observed in this study were only partially consistent with those found in other shallow CO_2 vents in the southern hemisphere. In New Zealand, Nagelkerken et al. (2017) found a strong homogenization of community structure due to a reduction of predatory pressure coupled with an increase of behaviourally dominant fish in the acidified site compared with the control site. Here, we did not find a loss in species richness, nor a simplification of the assemblage composition, although a few species were prevalent in the low pH site. The different mobility and habitat use of the fish addressed, highly territorial benthic fish in Nagelkerken et al. (2017) *vs.* nekto-benthic fish in this study, may explain the contrasting results. On the other hand, in another CO_2 vent (Papua New Guinea), diversity and community structure of the reef nekton-benthic fish differed little between acidified and control sites (Munday et al., 2014), consistent with the present study. However, while Munday et al. (2014) attributed this pattern to a different habitat complexity and composition in corals, rather than to a direct effect of high CO_2, we cannot at-

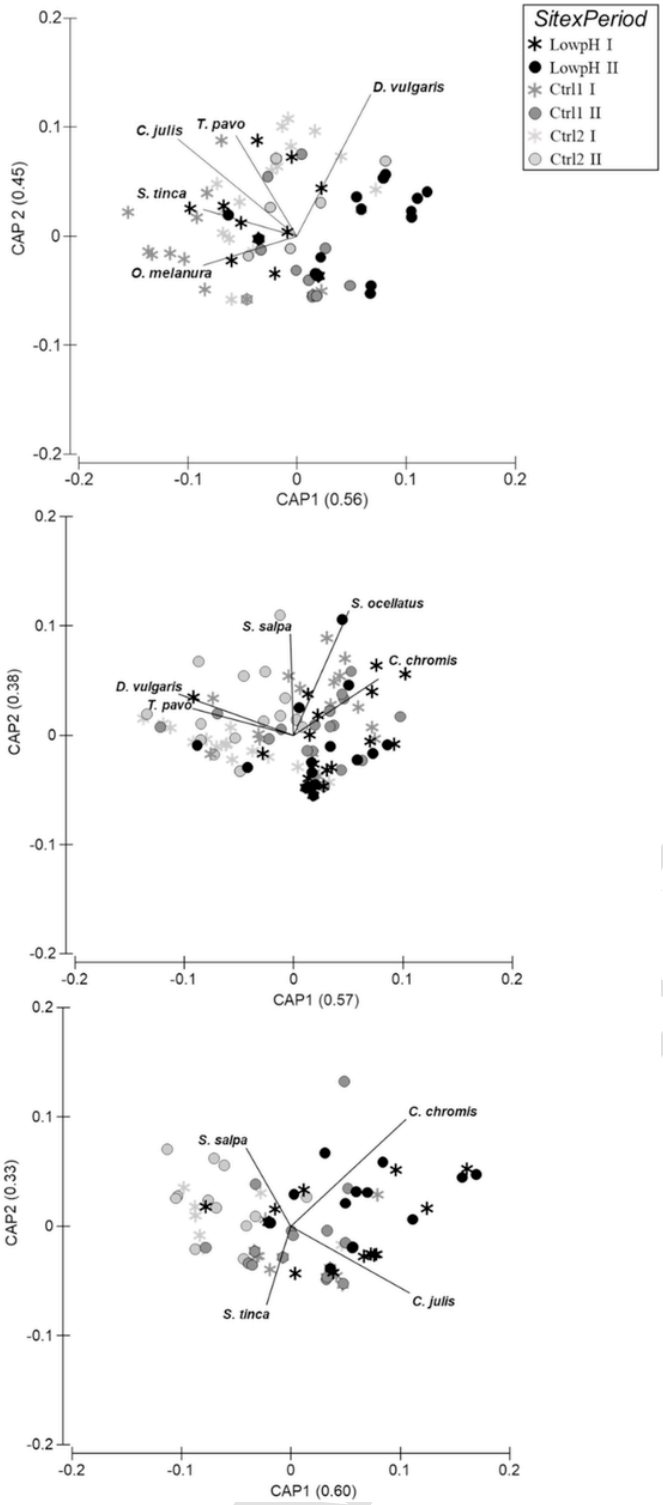

Fig. 4. Canonical analysis of principal coordinates (CAP) of density of the most abundant species (>2%) grouped per size-class: a) N_{small}, b) N_{medium} and c) N_{large} in the three sites (Low pH, Ctrl 1 and Ctrl 2) and the two periods (PI and PII). Vectors of the species contributing most to the ordination (Pearson correlation > 0.4) are superimposed. See the appendix for the whole scientific name of the species. The correlation of each axis with the resulted ordination is also indicated.

tribute the spatial changes found in fish communities to differences in the seagrass meadow structural complexity, but pH seems an important driver of the fish assemblage close to Vulcano vent.

5. Conclusions

Nekto-benthic fish assemblages from CO_2 vents seem to be able to cope with OA under the CO_2 emission scenarios forecasted for the end of the century (IPCC et al., 2014), by forming well-structured fish assemblages, despite dominated by high-tolerant species, and seem to benefit from an adjacent 'recovery area'. Therefore, because of their behavioural and physiological features (mobile habitus, capacity of acid-base regulation) and indirect effects at CO_2 vents (i.e. greater food availability), fish can balance the potential higher energetic cost to live under high pCO_2/low pH environments without major changes in community structure. Being habitat use crucial in influencing fish response to environmental stressors, further investigations are needed to assess if this pattern is exacerbated in highly territorial benthic fish exposed to high pCO_2/low pH conditions. In addition, further data are needed to predict the species-specific responses of other seagrass systems and the resulting effects on associated fauna. Finally, although the presence of a single CO_2 vent in Vulcano Island may have represented a limitation to fully infer the effect of pH to fish assemblages, our findings give insights about fish community structure and biodiversity under high pCO_2/low pH conditions, confirming also the importance of naturally acidified environments to study the responses of whole communities exposed to OA.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Author statement

This study was designed by S.V. and A.M. A.M. was involved with fieldwork. A.M and G.S. analysed the environmental and the fish data. S.V. and A.M. drafted the initial manuscript and all authors contributed discussion, writing and interpretation.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Appendix. List of all fish species censused in the three sites (Low pH, Ctrl 1 and Ctrl 2) and their small, medium and large range size-classes (in cm) according to FishBase online database (Froese and Pauly, 2016) and Louisy (2015). Trophic group and total relative abundance (%) of each species in the two periods (PI and PII) and in total (Tot) are indicated. Trophic groups: Invertivore (INV); Detritivore (DET); Planktivore (PLK); Small piscivore (PISC); Herbivore (HER).

Family	Species	Trophic Group	Low pH			Ctrl 1	
			PI	PII	Tot	PI	PII
Labridae	*Coris julis*	INV	7.7	3.5	11.2	6.8	
	Labrus viridis	INV	<2	<2	<2	<2	

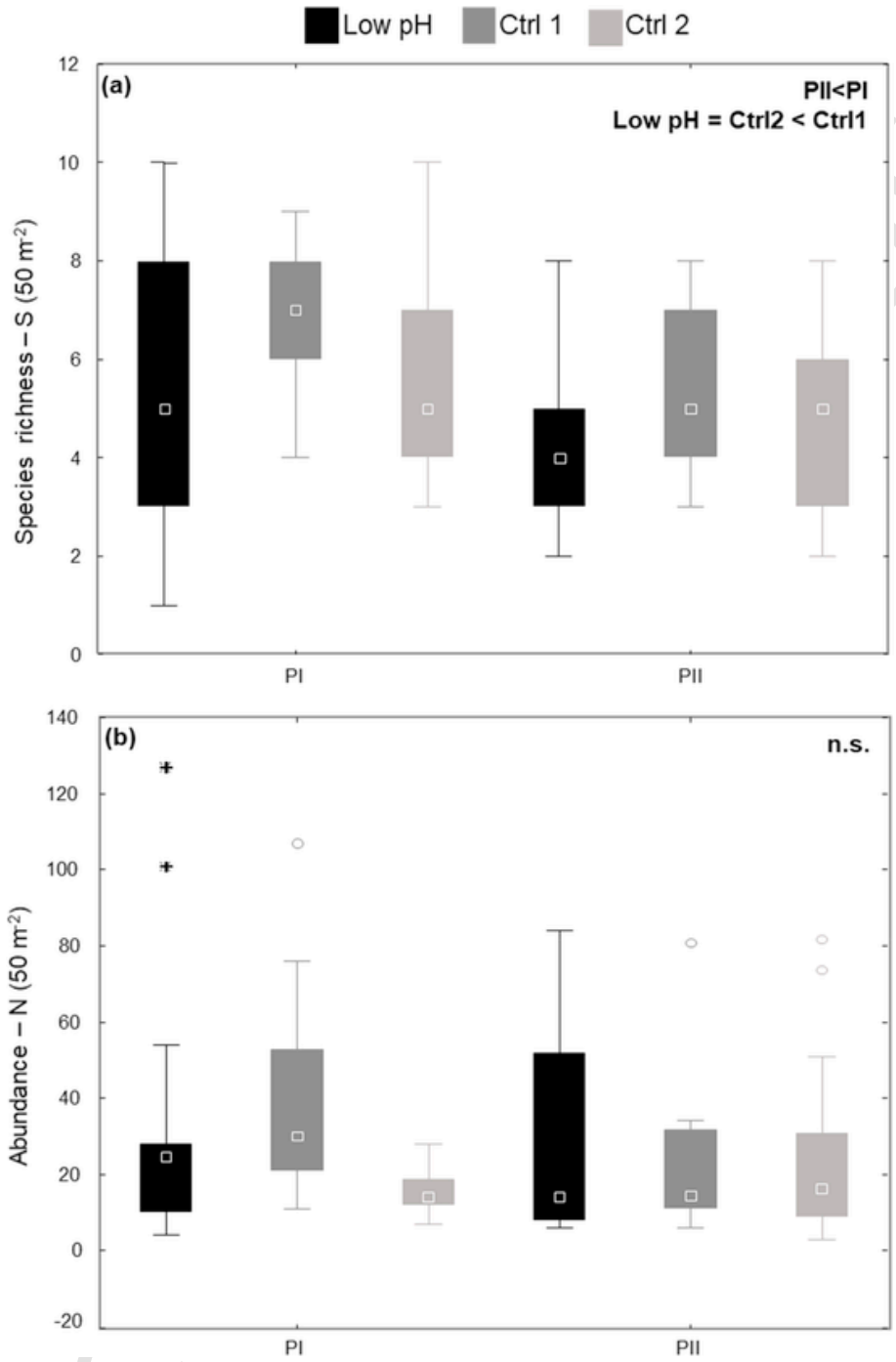

Fig. 5. a) Species richness (S) and b) abundance (N) of fish in the three sites (Low pH, Ctrl 1 and Ctrl 2) and the two periods (PI and PII). Whiskers indicate the non-outlier range of variation; boxes: 25th to 75th percentiles. The small circles and asterisks outside the boxes indicate the outliers and the extreme values respectively. Results of univariate PERMANOVA pair-wise tests are also showed on each panel (n.s. = not significant difference).

	Symphodus cinereus	INV	<2	<2	2.1	<2	<2
	Symphodus doderleini	INV	<2	<2	<2	<2	<2
	Symphodus mediterraneus	INV	<2	<2	<2	<2	<2
	Symphodus ocellatus	INV	7.2	<2	8.7	15.6	2.5
	Symphodus roissali	INV	<2	<2	<2	<2	<2
	Symphodus rostratus	INV	<2	<2	<2	<2	<2
	Symphodus tinca	INV	3.1	<2	4.9	6.1	2.7
	Thalassoma pavo	INV	<2	<2	<2	2.2	<2
Mugilidae	*Mugil cephalus*	DET	<2	<2	<2	<2	<2

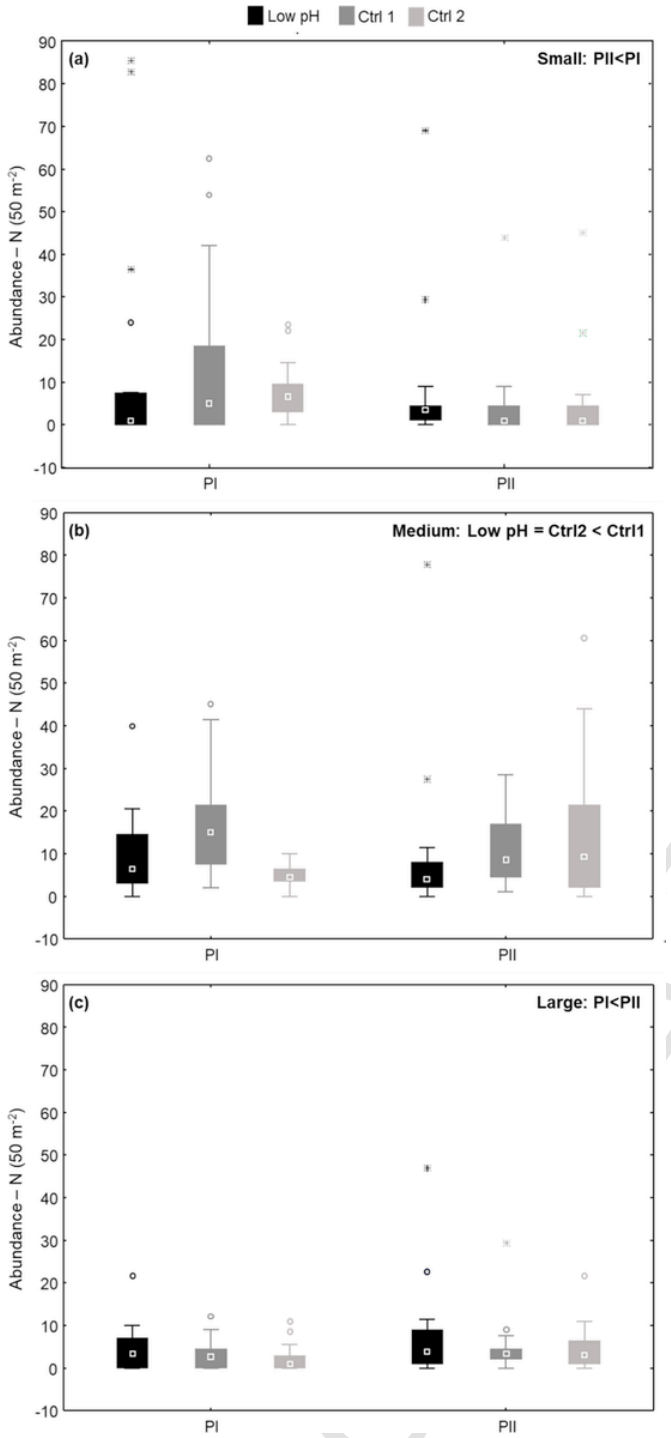

Fig. 6. Size-class abundance (N) of a) Small (N_{small}), b) Medium (N_{medium}) and c) Large (N_{large}) fish in the three sites (Low pH, Ctrl 1 and Ctrl 2) and the two periods (PI and PII). Whiskers indicate the non-outlier range of variation; boxes: 25th to 75th percentiles. The small circles and asterisks outside the boxes indicate the outliers and the extreme values respectively. Results of univariate PERMANOVA pair-wise tests are also showed.

Mullidae	*Mullus surmuletus*	INV	<2	4.5	5.4	<2	<2
Pomacentridae	*Chromis chromis*	PLK	12.1	9.5	21.6	12.0	12.
Serranidae	*Serranus scriba*	PISC	<2	<2	1.3	<2	<2
Sparidae	*Diplodus annularis*	INV	<2	<2	<2	<2	<2
	Diplodus sargus	INV	<2	<2	<2	<2	<2
	Diplodus vulgaris	INV	<2	3.1	4.0	<2	<2
	Oblada melanura	PLK	<2	<2	<2	9.6	<2
	Sarpa salpa	HER	16.4	21.4	37.8	<2	4.7

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