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Changes in fish communities due to benthic habitat shifts under ocean acidification conditions

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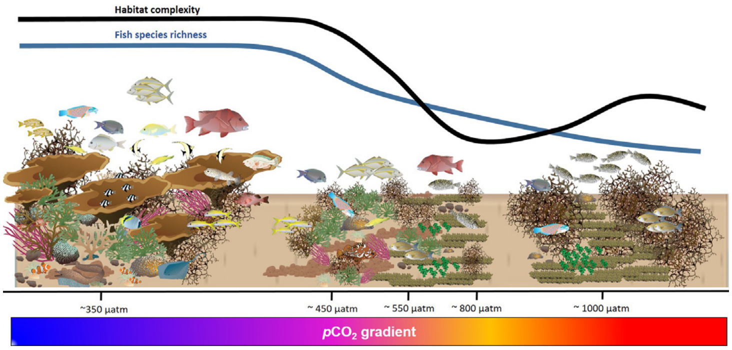
HIGHLIGHTS

- Ocean acidification-mediated habitat shifts and decreased complexity affect associated fish communities.
- Altered fish traits and reduced diversity occurred under near-future ocean acidification levels.
- Ocean acidification may oppose the poleward-shift of tropical fish species under warming.

GRAPHICAL ABSTRACT



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ABSTRACT

Ocean acidification will likely change the structure and function of coastal marine ecosystems over coming decades. Volcanic carbon dioxide seeps generate dissolved CO_2 and pH gradients that provide realistic insights into the direction and magnitude of these changes. Here, we used fish and benthic community surveys to assess the spatio-temporal dynamics of fish community properties off CO_2 seeps in Japan. Adding to previous evidence from ocean acidification ecosystem studies conducted elsewhere, our findings documented shifts from calcified to non-calcified habitats with reduced benthic complexity. In addition, we found that such habitat transition led to decreased diversity of associated fish and to selection of those fish species better adapted to simplified ecosystems dominated by algae. Our data suggest that near-future projected ocean acidification levels will oppose the ongoing range expansion of coral reef-associated fish due to global warming.

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1. Introduction

Shifts in marine biogenic habitats in response to anthropogenic activities and a range of stressors have been documented since the 1960s (Hughes, 1994). In tropical coral reef ecosystems examples include studies of the impacts of overfishing (Jackson et al., 2001), outbreaks of coral-eating predators (De'ath et al., 2012), diseases (Hughes, 1994), pollution (McCulloch et al., 2003), hurricanes (Hughes, 1994), and extreme temperatures (Hoegh-Guldberg, 1999). Ocean warming is changing coastal marine communities, for example due to (1) warm-water species (e.g. corals and tropical fish) moving poleward following their thermal physiological niche, (2) changes in the strength of interspecific interactions (e.g. increase of herbivory from warm-water fish leading to the loss of kelp forests at their low latitude limits), and (3) a decrease in biogenic habitat complexity (e.g. Vergés et al., 2014, 2016; Hall-Spencer and Harvey, 2019).

Ocean Acidification (OA), the alteration of seawater carbonate chemistry due to rising atmospheric CO_2 concentrations, adds an extra set of stressors to those caused by warming. Meta-analyses show that decreased seawater pH due to OA may impair calcification and accelerate dissolution for many calcifying habitat-formers, while rising $p\mathrm{CO_2}$ levels may enhance the primary production and carbon fixation rates of non-calcifying autotrophs (Falkenberg et al., 2013; Harvey et al., 2013; Kroeker et al., 2013; Wittmann and Pörtner, 2013). As a result, there will be losers and winners under OA conditions, with effects on ecosystems documented along gradients in seawater pH at CO_2 seeps around the world (e.g., Hall-Spencer et al., 2008; Fabricius et al., 2011) including reductions in habitat complexity, shifts in competitive interactions and changes in species dominance.

While CO_2 seeps are not perfect analogues for ocean acidification (e.g., Fabricius et al., 2017), they nevertheless comprise one of the very few field-based tools available to assess OA effects on ecosystems and communities (Hall-Spencer and Harvey, 2019). To date, our knowledge about the ecosystem effects of OA is advancing rapidly with increasing evidence from temperate (Hall-Spencer et al., 2008; Nagelkerken et al., 2015; Milazzo et al., 2019), subtropical (Agostini et al., 2018) and tropical (Fabricius et al., 2011, 2014; Inoue et al., 2013; Enochs et al., 2015) CO_2 seeps. The responses of biogenic habitats to OA differ regionally. Shifts from diverse to depauperate scleractinian species assemblages and from hard to soft coral communities have been observed in Papua New Guinea (Fabricius et al., 2011), Palau (Barkley et al., 2015) and in Southern Japan (Inoue et al., 2013). As carbon dioxide levels increase, there is a shift in community dominance from corals to seaweeds in the Northern Mariana Islands (Enochs et al., 2015) and at a subtropical-temperate transition zone in Japan (Agostini et al., 2018). How such OA-induced habitat shifts affect fish requires further study as most work at CO_2 seeps to date at has focused on bacteria, algae and invertebrates (Hall-Spencer et al., 2008; Fabricius et al., 2014; Sunday et al., 2017; Milazzo et al., 2019).

Very few attempts have been made to estimate the effects of OA-induced habitat simplification on fish communities (Munday et al., 2014; Nagelkerken et al., 2015, 2017). A study at three CO_2 seeps in Papua New Guinea reported reduced coral reef complexity at elevated CO_2 respect to control sites. However, there was no difference in fish species richness between seep and control sites, and no difference in fish community structure at two out of the three seep-control groups examined (Munday et al., 2014). The only slight differences detected in fish community structure were mostly driven by small-bodied fish species showing strong habitat preferences (Munday et al., 2014). In another paper, Nagelkerken et al. (2015) documented shifts from kelp/macroalgae and seagrass to low-relief turf-algae at temperate CO_2 seeps that seemed to cause a loss of fish predators and predatory release of prey fish species, even though their antipredator responses were compromised.

At present, how ocean warming and acidification will affect ecosystem properties and functioning is still under debate. Some modelling attempts suggest that declines in aragonite saturation state (Ω_{arag}) will limit the poleward expansion of tropical coral reefs that is underway due to ongoing warming (Yara et al., 2012; van Hooidonk et al., 2014), as will insufficient light in winter for coral algal symbiont photosynthesis (Muir et al., 2015).

Here, we evaluate the temporal consistency of changes in fish communities in response to biogenic habitat shifts off CO_2 seeps located in the NW Pacific (Japan), in a region that has naturally low levels of $p\mathrm{CO_2}$, high carbonate saturation levels and elevated local seawater temperatures (Midorikawa et al., 2005). These conditions allow the coexistence of both canopy-forming macroalgae and scleractinian coral communities at ambient CO_2 conditions, while a transition to low-relief algal turf habitats occurs at elevated CO_2 levels (Agostini et al., 2018; Harvey et al., 2019). To assess how fish community properties changed spatially along the $p\mathrm{CO_2}$ gradient, we coupled fish and benthic community assessments (habitat complexity, canopy height, and % cover), along a CO_2 gradient and at control sites off Shikine Island (Eastern Japan). The study was carried out over two time periods (June and September) to investigate whether the effects of OA-mediated habitat shifts on fish community composition and structure are temporally consistent, specifically when acute seasonal typhoons (usually from July to September), may affect benthic community structure and habitat complexity. In addition, we carried out fish trait comparisons between the different CO_2 sites, to assess changes in taxonomic richness and abundance of fish subdivided by geographic distribution (Tropical, Subtropical and Temperate), trophic guilds (Carnivore, Omnivore, Herbivore and Planktivore) and affinity to coral reef habitats.

We expected that fish communities would change in composition and structure as a result of decreasing habitat complexity along a spatial CO_2 gradient and that these changes would be consistent over time. Since it has been suggested that OA may decrease overall habitat complexity (e.g. from complex corals and canopy-forming algae to low-profile algae and turfs; Sunday et al., 2017), we expected that fish community species richness would decrease with increasing levels of CO_2. As CO_2 enrichment acts both as a stressor for scleractinian corals and as a substrate for primary producers, we also expected that the number of species of fish from tropical and subtropical origins would decrease, while the diversity of herbivorous fish would increase in elevated CO_2 conditions.

2. Materials and methods

2.1. Study sites and carbonate chemistry

Shikine is a volcanic island east of the Izu peninsula in Japan (34° 19′ 9“ N, 139° 12’ 18” E) with many CO_2 seeps in shallow waters. Based on previous geochemical investigations (Agostini et al., 2015), our survey locations were selected to avoid potentially confounding geochemical factors (e.g. high sulfides, negative redox potential, altered total alkalinity and elevated temperature). One location (Elevated-CO_2) was within Mikawa Bay and a second location (Control) characterised by ambient CO_2 conditions was positioned in an adjacent bay with similar depths (3–12 m), and exposure to wind and currents (Fig. 1).

To document spatial variation in the carbonate chemistry, a WQC24 multi-parameter logger (DKK-TOA Corporation, Tokyo, Japan) and a HydroC® CO_2 II sensor (Contros System & Solutions GmbH, Germany) were deployed between 9:00 am and 3:00 pm by scuba divers along four and five 100-m transects in the Elevated- and Control CO_2 locations, respectively (Fig. 1). Every 10 m the seawater pH (NBS scale), temperature (T, °C), salinity, and depth (m) were recorded for 5 min with the DKK-TOA, whilst the HydroC® CO_2 II sensor recorded measures of $p\mathrm{CO_2}$ (μatm) every 5 s. The CO_2 sensor detects dissolved CO_2 molecules that diffuse through a thin film composite membrane into an internal gas circuit containing a detector chamber where the $p\mathrm{CO_2}$

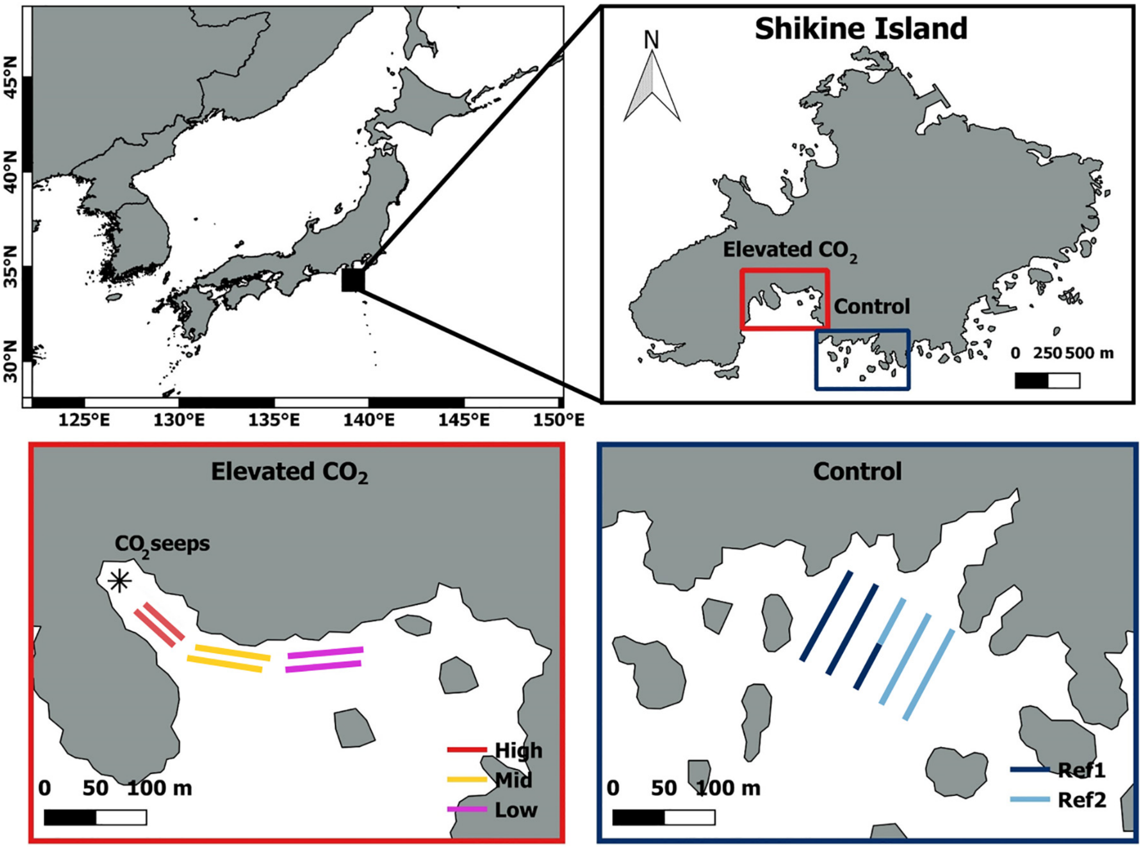

Fig. 1. Map of the study showing Shikine Island, the two CO_2 locations (Elevated and Control) and the five CO_2 sites (High, Mid, Low, Ref1 and Ref2) where the benthic and fish 25 m-transects were positioned.

is determined by means of an IR absorption spectrometer. Both loggers were positioned at 1 m from the sea-bottom at an average depth range of 3–12 m, and were attached to a floating buoy equipped with a GPS (eTrex30x, Garmin) to record the exact position of each measurement. Total alkalinity (TA) was measured from seawater samples collected underwater at each location ($N = 24$ in June; $N = 25$ in September). Water samples were immediately filtered at 0.45 μm using disposable cellulose acetate filters (Dismic, Advantech, Japan) and stored at room temperature in the dark (for no more than one week) until measurement. TA was measured by titration (TiTouch i915, Metrohm) with HCl at 0.1 mol l^{-1}, and calculated from the Gran function between pH 4.2 and 3.0. The titrations were cross-validated using a working standard (SD: ± 9 μmol kg^{-1}) and against certified reference material purchased from the A.G. Dickson laboratory (Batch 152). The CO_2SYS software (Pierrot et al., 2006) was used to calculate pCO_2 (Table 1) from T, pH, salinity and TA values, and to control in situ continuous measurements of pCO_2 recorded by the HydroC® CO_2 II sensor. The disassociation constants from Mehrbach et al. (1973), as adjusted by Dickson and Millero (1987), HSO_4 using Dickson (1990), and total borate concentrations from Uppström (1974) were used for carbonate chemistry calculations (Table 1). The HydroC® CO_2 II sensor was not employed in the September survey due to logistic constrains.

The carbonate chemistry measurements along the nine 100-m transects were used to identify five sampling CO_2 sites in the rocky subtidal

Table 1

Seawater chemistry of the subtidal sampling sites off Shikine Island. Values from June and September surveys are reported as mean (±SD). Minimum (Min) and maximum (Max) pCO_2 values are also reported. pCO_2 calc. = pCO_2 levels calculated with CO2SYS. pCO_2 meas. = pCO_2 levels measured with the HydroC® CO_2 II logger.

a) June 2016

CO_2 location	CO_2 site	Salinity	T °C	pH nbs	n (pH)	TA (μmol kg^{-1})	pCO_2 calc. (μatm)	pCO_2 meas. (μatm)	n (pCO_2 meas.)
Elevated	High	34.5 (0.05)	19.9 (0.5)	7.87 (0.15)	11	2249.9	971.7 (434.0) Min:591.8 Max:2062.1	952.8 (450.8) Min:567.7 Max:2360.4	417
Elevated	Mid	34.6 (0.07)	19.4 (0.5)	8.09 (0.05)	17	2253.4	497.2 (72.6) Min:373.8 Max:645.8	552.1 (188.2) Min:368.2 Max:1552.1	843
Elevated	Low	34.7 (0.05)	19.5 (0.7)	8.16 (0.05)	16	2270.5	404.9 (54.8) Min:361.2 Max:523.2	402.1 (53.4) Min:358.0 Max:591.1	555
Control	Ref 1	34.7 (0.05)	18.9 (0.3)	8.21 (0.01)	28	2253.1	348.2 (10.6) Min:322.0 Max:367.6	347.9 (13.9) Min:307.2 Max:373.8	994
Control	Ref 2	34.8 (0.05)	19.5 (0.2)	8.25 (0.03)	27	2250.8	311.5 (29.3) Min:255.4 Max:356.7	311.8 (29.1) Min:251.9 Max:357.8	913

b) September 2016

CO_2 location	CO_2 site	Salinity	T °C	pH nbs	n (pH)	TA (μmol kg^{-1})	pCO_2 calc. (μatm)
Elevated	High	33.9 (0.1)	26.0 (0.1)	7.65 (0.09)	4	2267.8	1646.4 (397.3) Min:1220.9 Max:2026.5
Elevated	Mid	33.9 (0.2)	25.1 (1.0)	7.91 (0.12)	6	2257.3	849.7 (291.0) Min:524.4 Max:1372.0
Elevated	Low	33.9 (0.0)	25.6 (0.1)	8.13 (0.01)	4	2269.3	459.3 (12.7) Min:442.7 Max:473.1
Control	Ref 1	33.9 (0.2)	26.3 (1.4)	8.18 (0.01)	4	2249.9	395.4 (11.9) Min:379.3 Max:407.8
Control	Ref 2	33.9 (0.2)	26.2 (1.7)	8.16 (0.01)	4	2249.5	420.8 (13.6) Min:409.2 Max:439.8

zone between 3 and 12 m depth in Mikawa bay and the Control bay: one 'High-CO_2' (High), one 'Mid-CO_2' (Mid) and one 'Low-CO_2' (Low), and two 'Ambient-CO_2' (Ref 1 and Ref 2; Fig. 1; Table 1). In each CO_2 site, both the benthic habitats and the fish communities were characterised as detailed below.

2.2. Benthic habitat characterisation

Average canopy height and percentage cover (% cover) of benthic taxa were recorded in the June and September surveys along 25 m strip transects positioned in the five CO_2 sites (High, Mid, Low, Ref1 and Ref2). Specifically, four transects were deployed in the 'High-CO_2'site (High), six transects within the 'Mid-CO_2' (Mid) site, six transects within the 'Low-CO_2' (Low) site, and nine transects each in the two 'Ambient CO_2' sites (Ref1 and Ref2; Fig. 1). Within each 25 m benthic transect, the canopy height was measured every meter using the point-intercept method, and a Biotic Habitat Profile (BHP) ratio was estimated as a proxy of biotic complexity. BHP, conceptually similar to the well-established chain method, was calculated a posteriori by dividing the contoured distance following the measured canopy profile by the linear distance (i.e. 25 m).

The % cover of benthic taxa was assessed in ten photoquadrats, positioned at ca. 5 m apart along each 25 m transect. An Olympus Stylus Tough TG3 with a PT056 camera housing was mounted on a 1 × 1 m frame. The % cover was estimated using the open-access software Image-J (http://rsb.info.nih.gov/ij/; Schneider et al., 2012) by tracing the 2-dimensional outline of each benthic morphological taxon. For each photoquadrat the % cover of the following benthic groups was recorded: Turf algae, crustose coralline algae (CCA), Non-Canopy-forming fleshy algae (<5 cm canopy height), Canopy-forming algae (≥ 5 cm canopy height), *Caulerpa chemnitzia* var. *peltata*, Table corals, Soft Corals, Encrusting Corals, Massive Corals (i.e. boulder corals with massive growth forms), Anemones and Sponges.

2.3. Fish surveys

Species composition and relative abundance of fish were visually censused within standard linear 25 × 5 m transects (Harmelin-Vivien et al., 1985). A total of 73 and 37 transects were carried out on June and September 2016, respectively. Fish transects were located haphazardly within each sampling CO_2 site at 4–10 m depth, and were conducted between 09.00 am and 03.00 pm by a scuba diver leaving behind a 25 m measure tape, while counting and identifying all the fish encountered 2.5 m either side of the tape (125 m^2; Harmelin-Vivien et al., 1985). Water visibility exceeded 15 m for all counts. Each sampling day, only two spatially separated transects (at >20 m distance each other) were gathered at each CO_2 site to avoid temporal dependence of data (Stewart-Oaten et al., 1986).

To make trait-mediated comparisons among different CO_2 conditions, the different fish species were also subdivided by geographical origin (Tropical, Subtropical and Temperate), by trophic guild (Carnivore, Omnivore, Herbivore and Planktivore), and by their association with coral reefs (i.e. coral reef associated and non-associated species) following Nakamura et al. (2013) and FishBase (http://www.fishbase.org/).

2.4. Data analyses

Changes in benthic habitat composition among CO_2 sites were analysed using non-metric multidimensional scaling technique (nMDS) and tested with Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson and Braak, 2003) using the software PRIMER 6 and PERMANOVA+ β3 package (Clarke and Gorley, 2006). The analysis was performed on Bray-Curtis measures in a multivariate context of untransformed % cover data, using 9999 permutations of the appropriate units. Two fixed factors were considered: "CO_2 site" with 5 levels (High, Mid, Low, Ref 1 and Ref 2) and "Season" with two 2 levels (June and September).

To identify the relevant variables characterising the benthic habitat which were responsible for the variation in fish community structure and composition, we used a Multivariate Distance Based Linear Model [DISTLM, Anderson et al., 2008]. Both the fish community and the benthic datasets were square root transformed and the step-wise model selection method based on the AIC criterion was performed to assess the benthic variables related with Bray-Curtis resemblance matrix of the fish dataset. To visualise the fish community data as a biplot, the Distance-based redundancy analysis (dbRDA; Legendre and Anderson, 1999; McArdle and Anderson, 2001) using the benthic variables identified by the DISTLM routine was used.

To investigate the potential relationship between pCO_2 and habitat complexity (as BHP index, log transformed) we used an Additive Mixed Model (AMM) with a Gaussian distribution and the identity link. AMM was used because it allows for the modelling of the non-linear effects of continuous explanatory variables by incorporating smooth functions (Wood, 2011). Specifically, the cubic regression spline was used as a one-dimensional non-parametric smoothing function and the number of knots k was set to 6, to prevent the models from producing complex non-linear relationships of little biological significance (Wood, 2006). To account for the lack of independence of the BHP data of the same Site per Season we used Site x Season as random intercept, which is assumed to be normally distributed with mean 0 and variance σ^2. Data for both sampling campaigns (June and September) were combined into a single data set and Season was modelled as a factor. The model was fitted using maximum likelihood (ML) parameter estimation. The analysis was performed using the R (R Core Team, 2018) package 'mgcv' (Wood, 2011).

We also used a method derived from meta-analysis to assess the effects of the different CO_2 conditions on the number (S) and abundance (N) of fish species, also considering their classification by geographical distribution (S_{origin}), trophic guild ($N_{trophic}$) and coral reef association (S_{coral}). To this aim, we calculated the effect size (a metric that quantifies the difference between the control and experimental groups) as the response ratio, i.e. the natural logarithm of the ratio between the averaged response variable values (S, N, S_{origin}, $N_{trophic}$, S_{coral}) recorded at the Elevated CO_2 (High, Mid and Low CO_2 sites) and Control (Ref1 and Ref2 sites) locations. These analyses were performed using the R (R Core Team, 2018) package 'metafor' (Viechtbauer, 2010).

3. Results and discussion

Benthic communities changed from rocky habitats dominated by scleractinian corals and canopy-forming macroalgae to rocky reefs covered in low-profile and turf algae from Control (Ref1 and Ref2) to Elevated CO_2 sites (Low, Mid and High) and this observation was consistent in both of the considered time periods (Fig. 2; PERMANOVA: CO_2 site x Season, Pseudo-F = 7781.2; P(perm) = 0.0001). Composition and structure of benthic communities did not differ between sites within ambient CO_2 condition both in June (i.e., Ref1 = Ref 2; Pair-wise *t*-test, $t = 1.52$; P(perm) = 0.08) and September (Pair-wise t-test, $t = 1.20$; P(perm) = 0.28) surveys, whilst they did significantly differ in most of the pair-wise comparisons of sites within the elevated CO_2 sites (Table S1).

Table, massive and encrusting corals were common at control sites in both sampling periods. They are able to survive at this high latitude (34° N) in the NW Pacific due to the warm northward flow of the Kuroshio Current (Veron and Minchin, 1992). Hard corals were absent along transects taken at elevated CO_2 conditions. In contrast to some other CO_2 seep systems (Suggett et al., 2012; Inoue et al., 2013), soft corals were rare and were absent in our elevated CO_2 transects. Instead, dense mats of *Caulerpa chemnitzia* var. *peltata* and the diatom *Biddulphia biddulphiana* covered most of the rocky substrata at the elevated CO_2 sites in June. These species were not seen in our transects in September,

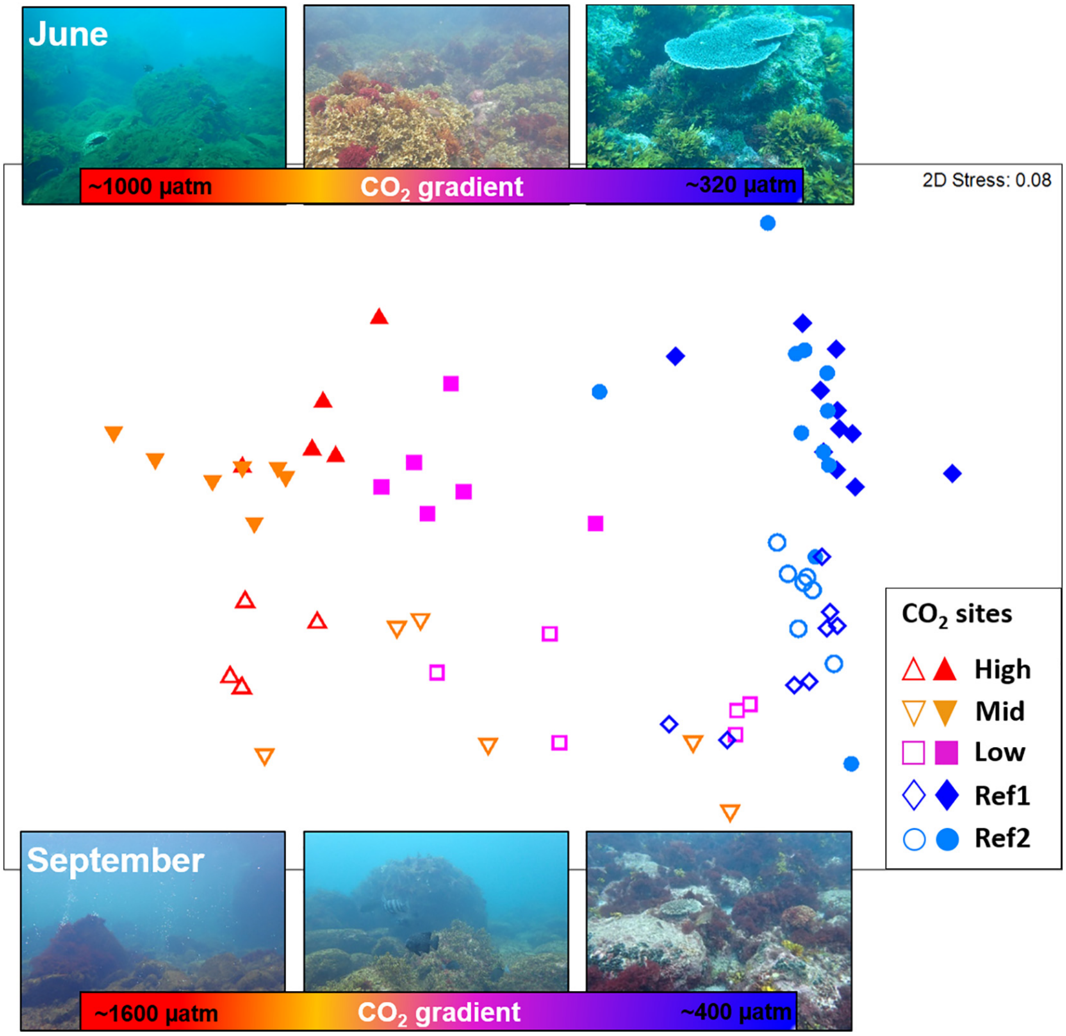

Fig. 2. Non-metric multidimensional scaling (nMDS) on benthic habitats at the five CO$_2$ sampling sites (High, Mid, Low, Ref1 and Ref2) in June (filled symbols) and September (empty symbols). Photomosaics of benthic community shifts observed in June and September along the CO$_2$ gradient are also reported. The figure shows a clear community shifts in both seasons from zooxanthellate scleractinian corals and canopy-forming macroalgae at Control CO$_2$ location (Ref1 and Ref2) to macroalgae at the Low and Mid CO$_2$ sites and turf algae at the High CO$_2$ site.

often revealing a covering of crustose coralline algae or low profile turf algae on the rocks (Fig. 2). As recently suggested, this was likely due to strong wave energy during typhoon activity that occurs in summer and early autumn (from late July to early October each year) on Shikine Island (Harvey et al., 2019). This major seasonal habitat shift resulted in an overall loss of canopy height due to the increase in the abundance of a few low profile algal and turf species which may outcompete large and slow-growing species under ocean acidification conditions (Harley et al., 2012; O'Brien and Scheibling, 2018; Harvey et al., 2019). The ability of a few opportunistic species to withstand OA effects, benefit from CO$_2$ enrichment and displace dominant habitat-forming species (such as canopy-forming algae or coral early stages), has been previously documented (e.g. Connell et al., 2018; Agostini et al., 2018) and can be attributed to stunted successional development (Gaylord et al., 2015).

Previous CO$_2$ seeps studies revealed both detrimental and no effects of elevated CO$_2$ levels on the eco-physiological and behavioral performances of fish (e.g. Munday et al., 2014; Nagelkerken et al., 2015; Milazzo et al., 2016; Cattano et al., 2017; Di Franco et al., 2019). Here we focus on fish responses at the community level.

Fish assemblages changed significantly between sites along the CO$_2$ gradient, and between elevated CO$_2$ and reference sites. The DISTLM procedure revealed differences in fish assemblage composition and structure, and identified five variables that best explained such patterns: the table and massive corals, the turf, the non-canopy forming algae and the CCA. The dbRDA ordination of the dataset constrained by these variables showed that the difference in the fish communities along the CO$_2$ gradient was best explained by turf, massive and non-canopy algae, while the differences between June and September were best explained by table corals and CCA (Fig. 3). Thus, the clear change of fish communities from ambient to elevated CO$_2$ conditions was associated with a biogenic habitat shift under OA conditions.

To date, few studies have documented the effects of OA-induced habitat changes on the structure and composition of fish communities. Munday et al. (2014) found that fish communities differed little between CO$_2$ seeps and nearby control reefs in Papua New Guinea, suggesting that such similarities were due to the contribution of highly mobile fish species, which are able to move in and out of small CO$_2$ seep areas. The few observed differences in the abundance of certain fish species were related to coral community changes (from branched to massive corals) between CO$_2$ exposed and un-exposed reefs (see Fabricius et al., 2014) rather than by the direct effects of high CO$_2$ on fish. Nagelkerken et al. (2015) described habitat characteristics and fish species composition at two different CO$_2$ seeps, documenting predator reductions and habitat shifts at elevated CO$_2$ conditions, which together led to an increase of a few territorial fish species. A more recent

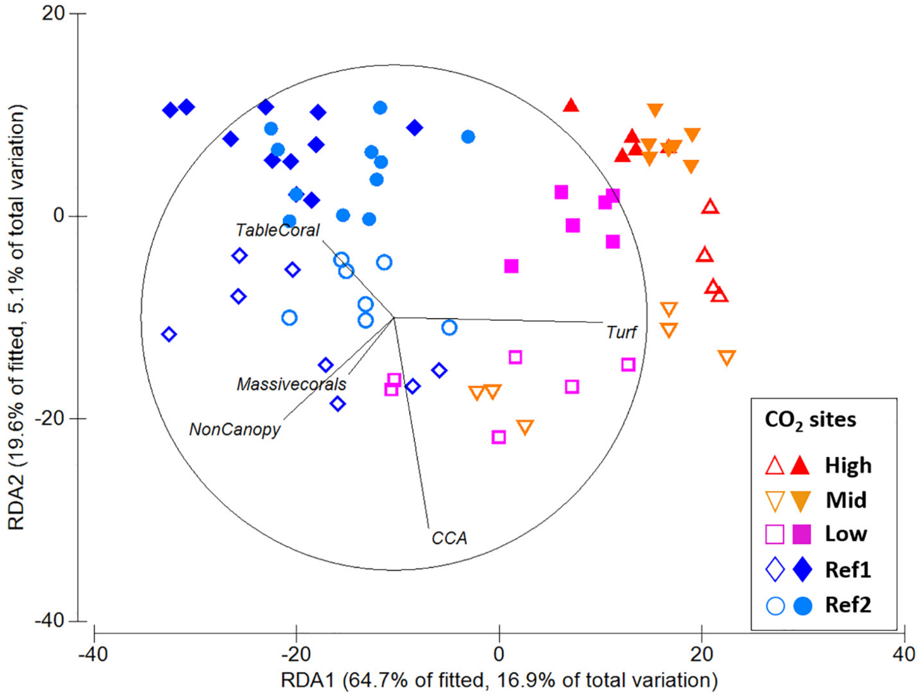

Fig. 3. dbRDA ordination of fish community data from five sampling CO_2 sites (High, Mid, Low, Ref1 and Ref2) constrained by five environmental variables (CCA, Massive corals, table corals, Turf and non canopy algae) identified by DISTLM as significant in explaining 84,3% of fitted and 22% of total variation. Vectors represent strength of variables in the model. Their length in relation to the circle radius (radius = 1.0) and their direction indicate the strength and the sign, respectively, of the relationship between the variable and the axes. Filled and empty symbols represent data from June and September, respectively.

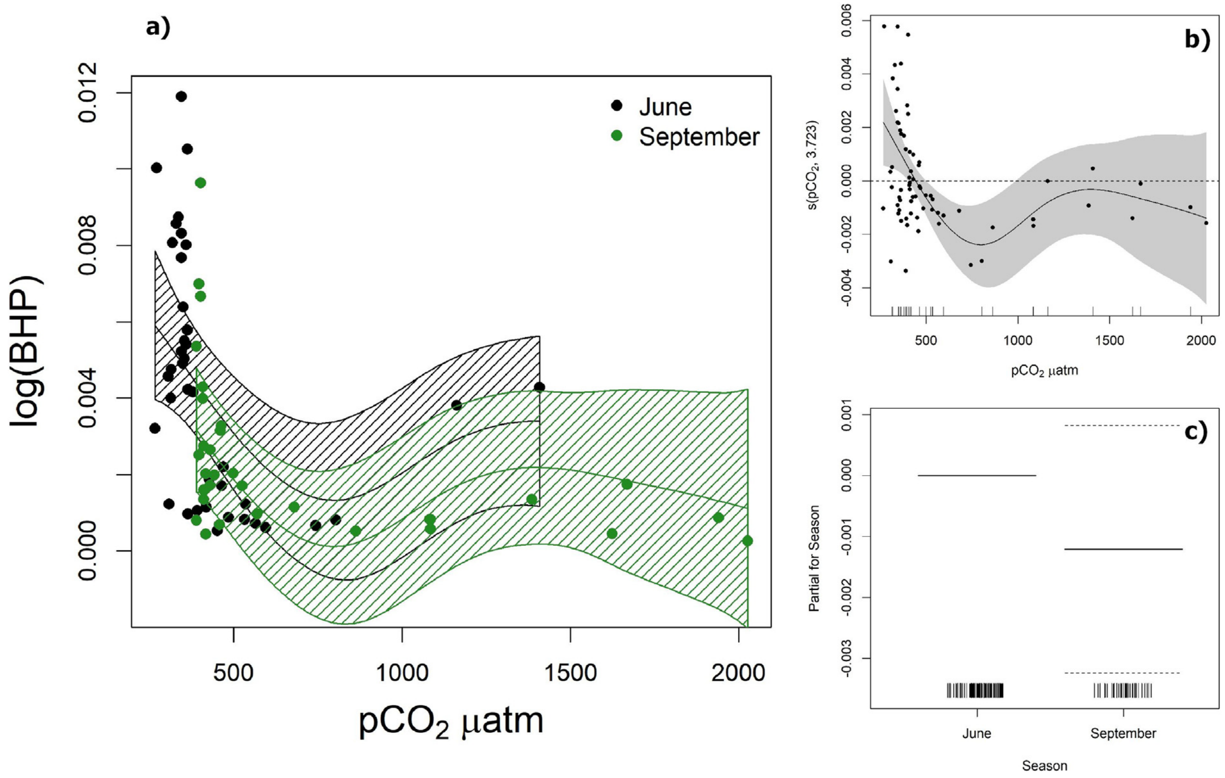

Fig. 4. AMM (Additive Mixed Model) showing the relationship between pCO_2 values and habitat complexity (BHP). a) Fitted values (±95% confidence intervals) of pCO_2 values and habitat complexity (log-transformed BHP index) for June (black dots) and September (green dots); b) model residuals (black dots) and estimated smoothing curve (solid line with ±95% confidence interval) showing the pCO_2 effects on BHP. The effect is significant (i.e. positive or negative) when the CI (grey area) does not overlap the zero (dashed line); c) partial effect (solid lines) of the factor Season on the BHP index (dashed lines indicate the ±95% confidence interval for September). The vertical lines reported on the x-axis of panels b and c represent the observations from the different pCO_2 values and from the two seasons, respectively.

study carried out off the White Island CO_2 seeps in New Zealand documented loss of fish diversity and homogenisation of fish communities under OA conditions, suggesting that elevated CO_2 indirectly boosted the abundance of a single species thus altering the competitive relationships among species and suppressing the abundance of the competitive subordinates (Nagelkerken et al., 2017). Contrary to these previous studies, where fish community differences between CO_2 exposed and unexposed reefs were evaluated focusing on a few species with narrow home ranges, here we compared the structure and the composition of entire fish communities finding significant differences among the four CO_2 conditions considered.

The effects of OA on fish communities may depend on how elevated CO_2 affects the different species directly and indirectly. By altering acid-base balance and the processing of sensory information, elevated CO_2 concentrations affect physiological and behavioral performance in fish, although such effects are species- and trait-specific (reviewed in Cattano et al., 2018). In addition, by promoting shifts in biogenic habitat (Milazzo et al., 2019), habitat simplification (Sunday et al., 2017) and food web simplification (Fabricius et al., 2014; Vizzini et al., 2017), high CO_2 conditions may indirectly affect some fish species, especially those with highly specialised habitat and resource use. Conversely, generalist species could cope better with the predicted effects of OA on habitat and resources (e.g. Wilson et al., 2008a). This inter-specific variability in the extent to which fish may respond to OA-driven habitat modifications could play a role in shaping the direction of community shift and the composition of novel fish communities under elevated CO_2 conditions (Nagelkerken et al., 2017).

Our findings support the prediction that OA simplifies habitat composition and reduces habitat complexity (Sunday et al., 2017). Biogenic habitat complexity (BHP) decreased with increasing pCO_2 levels, in a non-linear relationship (Fig. 4a). When looking at model residuals including both seasons, habitat complexity was high at pCO_2 values below ~500 μatm, whilst this relationship was significantly negative for values up to ~ 1000 μatm (i.e. decreased complexity with increasing pCO_2), after which no significant effects were detected probably due to the low sample size (Fig. 4b). Overall, this trend was consistent in the two sampling campaigns (Fig. 4c). The minimum index values were reached between ~500 and ~1000 μatm, where table corals disappeared being replaced mainly by turf, non-canopy algae and *Caulerpa chemnitzia* var. *peltata*, and where the only calcifying groups were represented by CCA or a few encrusting corals. The consistent complexity reduction in the elevated CO_2 sites compared to control conditions matches the habitat shift from corals and canopy-forming macroalgae to turf dominated reefs, which indeed provides fewer structure and habitat functions than corals (Filbee-Dexter and Wernberg, 2018). Such transition to less complex habitats may lead to the loss of a suite

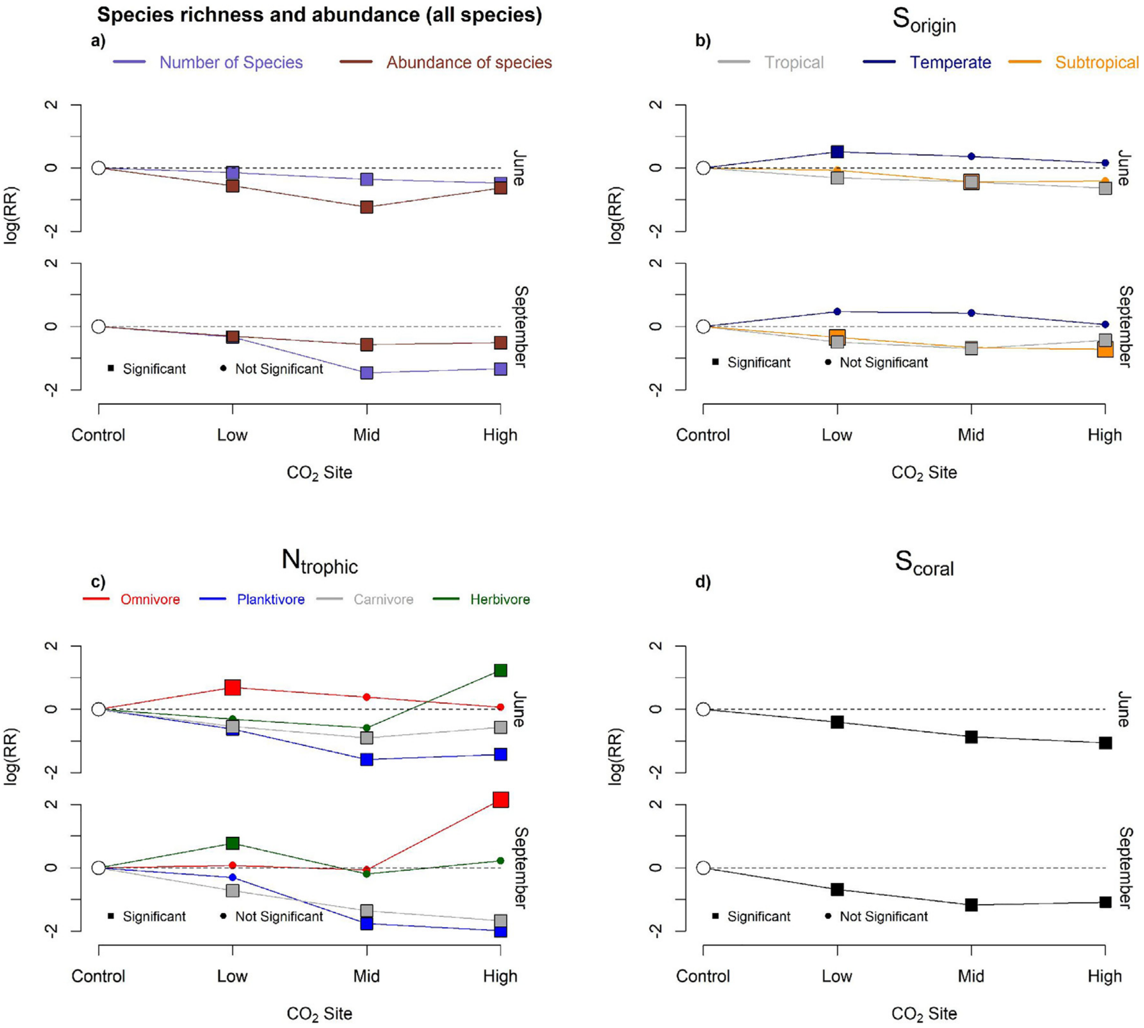

Fig. 5. Meta-analysis-derived approach to assess overall and trait-based changes of fish community at the different elevated CO_2 sites, both in June and September. Each point represents the log response ratio (LnRR) of the average value for the different fish community variables recorded at Low, Mid and High CO_2 sites relative to the ambient CO_2 condition (i.e. Control location: Ref1 and Ref2 together), indicating the sign and the strength of change. a) Number and abundance of fish species (all the censused species); b) S_{origin}: number of species by their geographic distribution (Tropical, Sub-tropical or Temperate); c) $N_{trophic}$: abundance of species by their trophic guild (Omnivore, Planktivore, Carnivore or Herbivore); d) S_{coral}: number of coral-reef associated fish species. Squares indicate significant effects per $p < 0.05$. Small circles indicate no significant differences.

of resources for fish (e.g. food and space availability) and to the alteration of important ecological processes, such as foraging, settlement and predation avoidance. OA research in CO_2 seeps has documented altered properties and non-linear responses for invertebrate communities along CO_2 gradients (e.g. Fabricius et al., 2014; Milazzo et al., 2019), whilst no effects were detected in fish communities despite lower habitat complexity under elevated CO_2 conditions (Munday et al., 2014).

Here for the first time, a consistent temporal response of the fish fauna to the OA-mediated habitat shift was documented. Overall, the number of species declined by 35% and 57% when comparing fish species richness at Control vs High CO_2 sites in June and September, respectively (see Table S3). In addition, average species richness and abundance significantly decreased from Control to elevated CO_2 conditions, with the lowest values recorded at the High and Mid CO_2 sites (Fig. 5a; Table S3). Such a pattern was consistent in both June and September (Fig. 5a; Table S3) and confirms previous evidence that shifts toward less complex habitat causes decreased fish diversity and abundance (e.g. Wilson et al., 2008b), as well as simplified and homogenised fish communities under OA conditions (Nagelkerken et al., 2017).

Trait-based approaches are increasingly being used to characterise ecological changes in disturbed ecosystems (Mouillot et al., 2013). Environmental alterations may not only lead to biodiversity loss, but also to changes in community function, through the selection of species with traits well-adapted to the new environmental conditions. Since functional groups may show specific habitat requirements and preferences, the occurrence and abundance of certain species can be strongly influenced by habitat composition and characteristics. As expected, trait-based comparisons of fish communities along the CO_2 gradient reveal a change in composition toward fish species of less tropical and subtropical origin (Fig. 5b), which is very likely related to the observed loss of scleractinian corals at >400 ppm CO_2 and to the disappearance of the more specialised associated fish fauna they support. Therefore, the observed transitions from corals/high-profile algae to low-profile/turf algae support the available models suggesting that OA will hold temperature-induced poleward expansion of coral habitats (Yara et al., 2012), and this will cascade on the composition of the associated fish fauna with a decreasing pool of tropical, sub-tropical and coral reef associated species under elevated CO_2 conditions. In this regard, Nakamura et al. (2013) documented an increase of warm-water tropical fish along the Japan high-latitude waters. Our findings rather suggest that if ongoing OA will act as a supplementary game-changer in the near future, this could not be the case.

When looking at fish trophic guilds we found that, relative to ambient CO_2 conditions, the abundance of herbivorous fish was significantly higher at the High CO_2 site in June, but not in September when seasonal typhoons caused the removal of macroalgal and turf cover particularly from the high CO_2 area (Fig. 5c). Conversely, omnivorous species showed the opposite pattern being more abundant after the typhoon season. These results support previous evidence showing that an increased abundance of herbivore species at elevated CO_2 conditions can be driven by the greater biomass of primary producers associated with enhanced nutritional quality (Vizzini et al., 2017). When turf and algae are removed by wave action, the availability and type of food changes, with repercussions on trophic guild composition (i.e., less herbivorous and more omnivorous species). In addition to this, results from recent experiments suggest that by increasing their macrophyte consumption and defecation rates, herbivore population growth could further modify trophic processes in benthic systems under OA conditions, hence amplifying detritus biomass production and potentially altering energy pathways and ecosystem functioning (Zarco-Perello et al., 2019).

By contrast, a consistent decrease in the abundance of carnivore species was observed along the CO_2 gradient in both the sampling seasons (Fig. 5c). Such switches in the composition of functional groups (i.e., increase of herbivore and reduction in carnivores) appears to be a common community property in elevated CO_2 systems and has been described by other ecosystem studies carried out in temperate natural CO_2 vent systems (Vizzini et al., 2017; Nagelkerken et al., 2015; Milazzo et al., 2019). In this regard, we speculate that piscivorous species may be attracted to more complex habitat characterised by higher prey abundance, while herbivores may prefer less complex areas where primary production is higher and this resource can be accessed more easily. We also found a consistent decline in the abundance of planktivorous fish and in the number of coral reef associated species from ambient to elevated CO_2 conditions (Fig. 5c and d). Again, this seems to be related to the loss of coral species at the more elevated CO_2 sites, which provide structural complexity and represent the preferred habitat for many coral fish species and their prey (Coker et al., 2014; Smith et al., 2016). Our findings add to previous evidence from ocean warming studies showing fish diversity declines following extensive coral loss due to bleaching events (e.g. Pratchett et al., 2011). In this regard, we suggest that OA may act as an additional bottleneck for fish community resilience under predicted ocean change scenarios.

Natural analogues have many benefits for furthering knowledge about the responses of fish to OA conditions, but they are not perfect analogues for acidifying oceans. The seep areas are localised and so fish can move in and out, complicating dose-response assessments (Hurlbert, 1984; Munday et al., 2014; Cornwall and Hurd, 2015). Moreover, carbonate chemistry can be highly variable at CO_2 seeps (Cattano et al., 2016; Cattano et al., 2017; Agostini et al., 2018) and toxic areas around volcanic vents need to be avoided in studies of the effects of ocean acidification (Vizzini et al., 2013). Nonetheless, the seeps allow studies of the ecosystem effects of OA and over time, using multiple CO_2 seep locations, a pattern is beginning to emerge about the effects of OA on fish communities. An additional caveat with volcanic CO_2 seeps is that ocean acidification is occurring concurrently with warming, thus preventing their use as analogues for future oceans (Rastrick et al., 2018). This issue can be addressed by assessing ecosystem responses at CO_2 seep in different biogeographic regions, or by manipulating temperature along CO_2 gradients (Alessi et al., 2019), or by exploiting marine heat waves to assess the combined stress of rising temperature and elevated CO_2 (Rodolfo-Metalpa et al., 2011). In this context, recent evidence combining laboratory, mesocosm and meta-analyses of CO_2 seep research suggests that OA affects the outcome of ocean warming (Goldenberg et al., 2018).

In summary, our data provide direct evidence that shifts in biogenic habitat and complexity reduction underpin a major loss (35–57%) of marine fish diversity as levels of carbon dioxide in seawater increase in coastal waters off Japan. Ocean acidification is expected to limit the poleward range expansion of coral reef-associated fish that is now occurring due to warming in Japan (Yamano et al., 2011; Agostini et al., 2018; Kumagai et al., 2018) and elsewhere (Baird et al., 2012; Serrano et al., 2013; Denis et al., 2015; Tuckett et al., 2017). By enhancing the competitive strength of algae at the expense of structurally complex calcifying organisms, such as corals, our surveys indicate that ocean acidification will change fish community function with a greater abundance of herbivorous fish species but fewer carnivores and planktivores. Such changes in fish communities would cause major changes in trophic processes and energy pathways, as well as affecting fisheries. We conclude that the indirect effects of rising CO_2 levels on coastal ecosystems will have a profound impact on reef fish communities.

CRediT authorship contribution statement

Carlo Cattano: Conceptualization, Writing - original draft, Investigation. **Sylvain Agostini:** Investigation. **Ben P. Harvey:** Investigation. **Shigeki Wada:** Investigation. **Federico Quattrocchi:** Formal analysis. **Gabriele Turco:** Formal analysis. **Kazuo Inaba:** Investigation. **Jason M. Hall-Spencer:** Investigation. **Marco Milazzo:** Conceptualization, Writing - original draft, Investigation.

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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.scitotenv.2020.138501.

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