Gains and losses of coral skeletal porosity changes with ocean acidification acclimation

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Ocean acidification is predicted to impact ecosystems reliant on calcifying organisms, potentially reducing the socioeconomic benefits these habitats provide. Here we investigate the acclimation potential of stony corals living along a pH gradient caused by a Mediterranean CO2 vent that serves as a natural long-term experimental setting. We show that in response to reduced skeletal mineralization at lower pH, corals increase their skeletal macroporosity (features >10 µm) in order to maintain constant linear extension rate, an important criterion for reproductive output. At the nanoscale, the coral skeleton’s structural features are not altered. However, higher skeletal porosity, and reduced bulk density and stiffness may contribute to reduce population density and increase damage susceptibility under low pH conditions. Based on these observations, the almost universally employed measure of coral biomineralization, the rate of linear extension, might not be a reliable metric for assessing coral health and resilience in a warming and acidifying ocean.

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Climate change is among the biggest threats to the health of marine ecosystems. Rising atmospheric carbon dioxide partial pressure (pCO2) increases ocean surface pCO2 due to CO2 diffusion across the air-water interface, leading to ocean acidification (OA). Since global warming and OA are coupled and are predicted to act synergistically, the future health of marine ecosystems and their corresponding long-term economic impacts on human coastal populations remain uncertain. It is therefore of great interest to understand how increasing atmospheric CO2 concentrations will affect these marine habitats and the species that inhabit them.

Since the early 1800s, ocean pH has decreased from 8.2 by ca. 0.1 U and, if CO2 emissions continue at their current rates, the average sea surface pH is predicted to drop to 7.8 by the year 2100 (ref. 1). The Mediterranean Sea, with its closed circulation patterns and limited water exchange with the adjacent Atlantic Ocean, has already undergone a larger decrease in surface pH compared with the global average, making it an ideal site for OA studies.

Near Panarea Island, off the southwestern coast of Italy, lies a series of active volcanic vents in the seabed releasing CO2 emissions that acidify the surrounding seawater, making this location an ideal natural laboratory for OA studies. The underwater CO2 emissions generate a stable pH gradient with levels matching several Intergovernmental Panel on Climate Change (IPCC) sea surface pH predictions associated with different atmospheric CO2 emission scenarios for the end of the century.

The present study investigates the effects of environmental pH on skeletal structures and growth at multiple length scales in the solitary scleractinian coral *Balanophyllia europaea* living along the pH gradient. We studied 74 corals of similar age (mean age of 12 years) that had spent their lives at the CO2-pH gradient. Using a combination of scanning electron microscopy (SEM), atomic force microscopy (AFM), small-angle X-ray scattering (SAXS), micro computed tomography (μCT), nanindentation, hydrostatic weight measurement and time-domain nuclear magnetic resonance (TD-NMR), we document the skeletal mass, bulk volume, pore volume, porosity, biomineral density, bulk density, hardness, stiffness (ratio between elastic stress and strain), biometry data, net calcification rate and linear extension rate for each coral. Weight measurements combined with TD-NMR data represent a non-destructive technique for quantifying skeletal porosity over length scales spanning from tens of nanometres to tens of micrometres, whereas μCT analysis permits a detailed large-scale quantitative 3D analysis of skeletal architecture, including the interseptal regions.

We show that in response to depressed calcification at lower pH, corals increase their skeletal porosity maintaining constant linear extension rate, which is important for reaching critical size at sexual maturity. However, higher skeletal porosity and reduced bulk density and stiffness may contribute to reduced mechanical strength, increasing damage susceptibility, which could result in increased mortality in an acidic environment.

**Results**

**Study site and seawater carbonate chemistry.** The four sites around the main vent are reported in Fig. 1. Site 1 (S1) has an
average total scale pH (pHTS) of 8.1, equivalent to the average surface pH of modern oceans. S2’s average pH of 7.9 aligns with IPCC’s predictions of a conservative CO2 emissions scenario (Representative Concentration Pathway (RCP6.0)), and the average pH of 7.7 for S3 fits the predictions of the ‘business-as-usual’ CO2 emissions scenario (RCP8.5). Since no corals were found at S4 (within the vent crater, pHTS 7.4), only S1–3, which had growing coral populations and pH values ranging from 8.1 to 7.7, were included in the present study. Of the measured parameters at the three sites along the pH gradient (pHTS, total alkalinity, temperature and salinity), only pHTS differed significantly across sites (N = 103–110; P < 0.001, Kruskal–Wallis χ2-test). The changing pH was accompanied by significant shifts in carbonate–bicarbonate equilibria, with aragonite saturation (Ωarag) decreasing by >30% from S1 to S3 (Fig. 1, Supplementary Table 1, Supplementary Note 1).

Multi-scale analysis of coral skeletal properties. Combined results of SEM, μCT, AFM and TD-NMR skeletal analyses of corals growing at each study site revealed the detailed, multi-scale structural organization of the skeletons of *B. europaea* (Fig. 2, Supplementary Figs 1–3).

At the macroscale (relating to feature sizes >10 μm), linear extension rate (averaging ca. 1 mm per year) did not vary among sites (Supplementary Table 2), whereas net calcification rate (N = 44; P < 0.01, robust t-statistics test) and skeletal bulk density (N = 44; P < 0.001, robust t-statistics test) significantly declined (Fig. 3, Supplementary Table 3) and skeletal porosity and macroscale porosity increased (N = 44; P < 0.001, robust t-statistics test, Fig. 3, Supplementary Fig. 1, and Supplementary Table 3). The differences between S1 and S3 were ca. −18% for net calcification rate, ca. −7% for bulk density, ca. +21% for porosity and ca. +30% for macroscale porosity (Supplementary Table 2). The coralite interseptal volume fraction from μCT (Supplementary Fig. 4) showed a difference among sites (N = 30; P < 0.05, F and Kruskal–Wallis χ2-tests, Supplementary Table 4) but no significant dependence on pH (Supplementary Fig. 5). The biometric data for the coralites (Supplementary Table 5) did not vary among sites.

At the micro/macroscale, skeletal stiffness significantly declined with decreasing pH (n = 122; P < 0.001, robust t-statistics test, Fig. 3, Supplementary Fig. 6, Supplementary Tables 4 and 6), whereas skeletal microscale porosity did not vary among sites (Supplementary Table 2 and Supplementary Fig. 1).

At smaller length scales (at the micro and nanoscales), SEM and AFM showed that the organization of the aragonite fibre bundles (Fig. 2c,g,k) and the morphology and packing of the constituent mineral grains (Fig. 2d,h,l) appeared similar among corals from the three different sites, confirming that the basic biomineralization products were not affected by reduced pH13 (Fig. 2 and Supplementary Fig. 2). Skeletal biomineral hardness did not change among sites (Supplementary Fig. 7, Supplementary Table 4). Also, skeletal biomineral density values were similar across sites and consistent with those measured in previous studies16 (Supplementary Table 2). Similar results were obtained from both SAXS and TD-NMR analyses, which revealed that nanoscale porosity did not change significantly with changing pH (Supplementary Figs 8–10 and Supplementary Tables 2 and 4).

The principal component analysis identified three major components: growth, skeletal porosity and biomineral density (Supplementary Tables 7 and 8). Only the first two components depended significantly on pH (Supplementary Table 9).

Figure 2 | Skeletal morphology of *Balanophyllia europaea* growing under different pH conditions from the macroscale to the nanoscale. Each row in the figure corresponds to a different study site and sample age is 9–11 years. Images are representative of all observed skeletons. (a,e,i) Low magnification SEM images of coral skeletons, marker 5 mm. (b,f,j) Internal sections of coralites from μCT images, marker 5 mm. (c,g,k) SEM images of entire skeletal fibres from fractured septae, marker 10 μm. (d,h,l) AFM images of mineral grains on the skeletal fibre surfaces, marker 50 nm.
In summary, skeletal nano and microstructural features, linear extension rate, interseptal volume fraction and corallite biometry of *B. europaea* did not change significantly with decreasing pH, despite a clear reduction in net calcification rates. This reduction in net calcification rate was accompanied by an increase in skeletal porosity (Fig. 3f, \( N = 44; P < 0.001 \), robust t-statistics test) and a consequent decrease in skeletal bulk density and stiffness.

**Discussion**

Results of the present study complement previous research on *B. europaea* at this same vent site, which revealed no changes in skeletal calcium carbonate polymorph, organic matrix content, aragonite fibre thickness and skeletal hardness in corals growing along the pH gradient. There was, however, a significant reduction in population density along the pH gradient, decreasing by a factor of 3 with increasing proximity to the vent crater centre (that is, from S1 to S3).

Figure 4 summarizes these results at the ocean, population, macro, micro and nanoscales for *B. europaea*. At the macroscale, increasing acidity was associated with a reduction in net calcification rate and a parallel increase in skeletal porosity, coupled with a decrease in skeletal bulk density. Linear extension rate and corallite shape (biometry and interseptal volume fraction) did not depend on pH, probably as a result of the compensation of reduced net calcification rate by increased skeletal porosity. At the micro/macro scale, the declining skeletal stiffness with decreasing pH could be coupled to an increased volume fraction of pores having a size comparable to the indentation area (that is, at the border between the micro and macroscales). At the nanoscale, porosity, biominal hardness and density were not significantly affected by pH. These results, bolstered by qualitative SEM and AFM analyses, suggest that the ‘building blocks’ produced by the biomineralization process are substantially unaffected, but the increase in skeletal porosity is both a gain and a loss for the coral. In fact, in an acidic

![Figure 3](image-url) **Figure 3 | Scatterplots of skeletal parameters, and correlation analysis between porosity and net calcification rate.** Site 1 = blue, Site 2 = green, Site 3 = red. Straight lines represent the best-fit linear regression (mean, solid line), 25% quantile and 75% quantile (dashed lines). **(a-e)** Skeletal parameters (y-axes) plotted against pH<sub>TS</sub>. (f) Scatterplot of porosity (Pa) versus net calcification rate in corals from Sites 1 to 3. For a-d,f \( N = 44 \); for e \( n = 122 \). ** *P < 0.001; ** P < 0.01; * P < 0.05, robust t-statistics test.**
The decrease of bulk density with decreasing pH depends on the increase of macroporosity, leaving the linear extension rate constant.

Our findings, together with the well-described detrimental effects of heat stress on the scleractinian zooxanthellate coral *B. europaea*<sup>16,20–23</sup>, provide several independent and consistent clues regarding the sensitivity of this species to global climate change predicted for the coming decades. Together with results from previous studies<sup>24</sup>, we demonstrate that the almost universally employed measure of coral biomineralization, namely the rate of linear extension, might not be a reliable metric for assessing coral health and resilience in a warming and acidifying ocean. Indeed, although the coral’s ability to maintain linear extension rate and gross skeletal morphology under conditions of decreasing oceanic pH could allow it to reach sexual maturity, it could reduce skeletal resistance to environmental challenges, affecting the long-term survivability of the species.

**Methods**

**Study site.** Off the southwestern coast of Italy, near the island of Panarea, an area delimited by the islets of Dattilo, Bottaro, Liscia Nera and Liscia Bianca (Fig. 1) is characterized by underwater volcanic CO2 vents. The main vent, a crater measuring 20 m × 14 m and ~10-m deep, generates a persistent column of CO2 bubbles that rise from the seabed to the sea surface. In this hydrothermally stable setting with ambient temperature, CO2 emissions establish a pH gradient that extends ~34 m from the centre of this crater to its periphery<sup>13</sup>. Three sites along this pH gradient were chosen for study. Distances (*d*) from the main crater centre and mean pH<sub>15</sub> values of the three sites from which corals were collected are: S1 (the control site), *d* = 34 m, pH<sub>15</sub> = 8.07; S2, *d* = 13 m, pH<sub>15</sub> = 7.87; S3, *d* = 9 m, pH<sub>15</sub> = 7.74. Water depth varies from 11.6 m within the crater to 8.8 m at the crater edge (S2) to 9.2 m at the outer margins (S1), where the local pH matches that of the surrounding seawater. The study site has stable hydrothermal–chemical properties<sup>25</sup>.

**The corals.** *B. europaea* (Fig. 1) is a solitary zooxanthellate scleractinian coral endemic to the Mediterranean Sea found at depths ranging from 0 to 50 m<sup>26</sup>. Specimens of *B. europaea* were randomly collected by SCUBA diving at three study sites along the pH gradient (26 from S1, 26 from S2 and 22 from S3) between November 2010 and May 2013. This sample size was chosen to limit damage on the study sites along the pH gradient (26 from S1, 26 from S2 and 22 from S3). Biometric data were recorded for the specimens (that is, width-to-length, width-to-height and height-to-length ratios, Supplementary Table 5). Nanotomography, hydrostatic weight measurement, SEM, AFM, SAXS, TD-NMR and TD-NMR analyses were performed on a subsample of specimens from each site.

**Coral sample cleaning.** Coral skeletons were submerged in 1% solution of sodium hypochlorite for 3 days to dissolve poly tissue. After washing with deionized water and drying at 50 °C for 3–4 days, each coral was examined under a binocular microscope to remove fragments of sediment, rock and encrusting organisms<sup>16</sup>.

**Weight measurements.** The buoyant method, usually applied for corals<sup>27–29</sup>, was used to measure the total volume occupied by the coral skeleton (called bulk volume, *V<sub>b</sub>*), the density (*d*) ratio of the mass to *V<sub>b</sub>*; the biomineral density (*d<sub>r</sub>*) ratio of the biomineral mass to biomineral volume; excluding pore volume connected to the external surface, also called real density or micro-density) and the apparent porosity (or effective or connected porosity, *p<sub>a</sub>*)<sup>30</sup> (ratio of the pore volume connected to the external surface (*V<sub>p</sub>*) to *V<sub>b</sub>*). This method is based on the Archimedean principle applied to the specimen after full saturation with the same fluid in which it is fully submerged (water in our case). It is worth to underline that the pore volume (*V<sub>p</sub>*), measured by the buoyant method is only the volume of the pores that can be saturated with water, that is, connected with the external surface. Pores inside the biomineral that are not connected to the external surface (occluded pores) are not measured. An estimate of the occluded porosity gave a negligible maximum value of ~3% (in porosity units) (Supplementary Note 2), which was homogenous among sites. For coherence with coral literature, for the apparent porosity we use the term porosity.

The skeletons were weighed with a precision balance to determine the dry mass (*m*) and then placed inside a dryer chamber and evacuated with a rotary mechanical pump down to a vacuum of 10<sup>−2</sup> mbar. After 6 hours, water was gently introduced to fully saturate the samples. The pump was switched off, the chamber was vented to the ambient atmosphere, and the masses of the fully water-saturated samples (*m<sub>v</sub>*<sub>0</sub>) determined. With a hydrostatic balance, the masses of saturated samples fully immersed in water (*m<sub>v</sub>*) were determined. The skeletal parameters were calculated (Supplementary Table 2) by means of the following operational definitions: *ρ<sub>aw</sub>* = water density, *V<sub>a</sub>* = (*m* − *m<sub>v</sub>)/*ρ<sub>aw</sub>*; *V<sub>b</sub>* = (*m* − *m<sub>v</sub>)/*ρ<sub>aw</sub>*; *p<sub>a</sub>* = *V<sub>p</sub>/V<sub>b</sub> = (m<sub>0</sub> − m)/m<sub>0</sub> = (m<sub>0</sub> − m<sub>v</sub>)/m<sub>0</sub>; *d<sub>r</sub>* = m<sub>v</sub>/V<sub>b</sub> = d<sub>r</sub>/V<sub>b</sub>.
After weight measurement, the fully saturated samples were removed from the water container and rapidly placed on wet paper to remove excess water on the external surface. Each specimen was then placed in the bottom of a glass tube, which was then sealed for TD-NMR measurements.

**TD-NMR method and parameter definitions.** This technique (Supplementary Note 3) was applied to obtain skeletal ‘ pore-size’ distributions by the analysis of quasi-continuous distributions of the transverse relaxation time $T_2$ (ref. 14) by means of the algorithm UPEND, implemented in the OpenWin software package. To test the significance of the differences among sites, parametric (F) or non-parametric (Kruskal–Wallis $\chi^2$) tests were run. Non-parametric tests were performed for data that did not assume normal distributions. Multivariate regression analyses were performed to investigate the relationships between one independent and one or several independent variables, using ordinary least squares robust to outliers. The model is described by the equation (1):

$$y_i = a + \sum_{j=1}^{M} b_j x_{ij} + e_i$$  

(1)

where the index $i$ refers to the $i$-observation, $x_j$ is an independent variable, $y_i$ is the value of the dependent variable and $e_i$ is the corresponding error. The constants $a, b_j (j = 1, M)$ are the best-fit parameters, to be determined by the best fit. Quantile analysis was performed to study the previous relationships for homogeneous groups of values of the dependent variable. This analysis was used to give a more comprehensive picture of the effect of the independent variable (pH) on the dependent variables of Fig. 3 and Supplementary Fig. 1, as it can show different effects of the independent variable in different ranges of the dependent variable.

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**Author contributions**

S.G., G.F., P.F. and Z.D. conceived and designed the research. E.C., F.P., S.G. and B.C. collected the samples and performed the diving field work. L.B., M.M., M.D.G., E.C., F.P., P.K., J.U.H., Y.D., J.P.C., J.C.W., W.W. and G.F. performed the laboratory analyses. P.F., S.M., L.P., Y.B., L.B., M.M., E.C., F.P., J.A.K., P.K., J.U.H., Y.D., J.P.C., J.C.W., W.W., P.F., G.F. and S.G. analysed the data. All authors wrote the manuscript and participated in the scientific discussion.

**Additional information**

Supplementary Information accompanies this paper at http://www.nature.com/naturecommunications

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