Response to reviewer #1

We thank the reviewer for their valuable and helpful comments which will contribute to improve the quality of our manuscript. All comments have been addressed. Please find our detailed responses below.

The manuscript "High-resolution reconstruction of pH upregulation and its seasonal drivers in the temperate coral Cladocora caespitosa" by Vergotti et al. presents boron isotope and trace element measurements of specimens from two locations in the Mediterranean, which the authors use to reconstruct the carbonate chemistry of the calcification site of this organism. This is of interest as C. caespitosa is the only species of reef-building coral in the Mediterranean, such that understanding the sensitivity of the calcification process to environmental change and environmental variability is a priority. The authors do so using both bulk (solution) and an in situ (femtosecond laser ablation) approach to boron isotope measurement, combining the two to demonstrate the accuracy of the laser ablation data and leveraging the spatially-resolved nature of the laser results to determine seasonal changes in calcification site pH, DIC, and Omega, thus enabling these to be linked to seasonal changes in pH and temperature via trace element-derived individual corralite age models. Ultimately, the data show that this coral appears to maintain an approximate constant calcification site Omega despite large seasonal changes in ambient pH and temperature, which the authors discuss within the context of possible mechanisms of carbon transport to the calcification site.

This thoughtfully constructed manuscript will undoubtedly be of interest to the community and presents a novel and interesting dataset, adding substantially to the small amount of published geochemical information available for this species. I have a few suggestions for the presentation and discussion of the results, especially the impact of temperature versus carbonate chemistry on the calcification site-seawater pH offset and the interpretation of the full range of variance in the laser data, but these are minor in nature and should not be difficult to address - my congratulations to the authors on a really nice piece of work!

- Separation of temperature and upregulation. There is no seasonal d11B signal in (e.g.) the Columbretes data between 2015-2017 or in the Villefranche data in 2020-2021, yet there is nonetheless a clear seasonal pHcf signal reconstructed from these data. This must mean that the seasonal pHcf reconstructions are largely driven by something other than active pH regulation (presumably temperature) which is a really interesting result that could be more clearly stated. E.g., the text on lines 334-336 notes that the seasonality in measured and reconstructed pHcf 'mostly agreed' but this is not surprising if it is in part a temperature effect, and if this is correct, it could be introduced and rephrased in these terms. The impact of temperature on pH is mentioned towards the end of the discussion so no major change is required here, other than to consider rephasing and making the link clearer to the reader earlier in the results and discussion (e.g. by describing the impact of temperature on pKB and pH).

We thank the reviewer for this valuable observation. We agree that the differences between $\delta^{11}B$ and reconstructed pH_{cf} in terms of seasonal signal are likely related to a strong thermodynamic control of temperature particularly on pK_B, resulting on a seasonal signal present in pH_{cf}, but not so much in $\delta^{11}B$. This has been made explicit in the first section of the discussion (line 390: "Additionally, while $\delta^{11}B$ records showed little seasonal oscillation across sites, a clear seasonal signal was present in the reconstructed pH_{cf}. This decoupling indicates that the seasonal variability in pH_{cf} is at least partially driven by thermal effects, through a

strong thermodynamic control of temperature on the dissociation constant of boric acid (pK_B), rather than solely active biological control.").

- Sampling strategy and biases. The discussion starts with a comparison of solution versus fsLA, which is great, but I was left wondering about the degree to which analytical noise in the laser data might bias the comparison (please see a further comment below). Is it possible that some of what you interpret as pHcf variability is analytically derived? And could this be tested by using the variance in the standard measurements to determine the probability of obtaining a dataset with a greater degree of apparent heterogeneity compared to the solution measurements?

We thank the reviewer for raising this question. The standard deviation for JCp-1-NP for the specific laser session used for the comparison with solution was ± 1.68 ‰, compared to ± 1.15 ‰ across all laser sessions. In both instances, the standard deviation was larger than for bulk powder JCp-1 measured with solution (± 0.09 ‰). We believe this difference reflects the known trade-offs of solid-sample ablation compared to homogeneous liquid nebulization. Additionally, we believe the noise observed in the laser record, and the differences with the solution record are derived largely from the different sample acquisition method and only partially from analytical noise, as detailed below. The sample acquisition process for solution involved micro-milling the corallite perpendicular to the growth axis. However, as the corallite is not always straight, this sampling acquisition may have led to an artificial smoothing by mixing material from different ages. The septa were removed prior to the micro-milling leaving only the theca wall, though remnant septa material could also have contributed to some of the differences between solution and laser ablation. Similarly, and as pointed out in subsequent comments, some of the differences between records may be related to microstructural variability (caused by tracking over centers of calcification or aragonite fibers), which may have been smoothed out by the bulk sampling method used for solution. As such, the noise observed in the laser record is not random, and reflects the variability of the sample composition, combined with environmental signal, rather than analytical noise.

On a similar note, the disadvantages of bulk sampling are stated (again, great) but similar issues could be raised with spatially resolved data depending on the sampling approach. E.g., tracking the laser over a centre of calcification or other structural feature could result in a d11B excursion that has little to do with environmental variability. This could be noted/addressed at the relevant point in the discussion, including whether such structural features are present in the transects and if so, whether they could be/were avoided.

We thank the reviewer for this highlighting this important topic. In *C. caespitosa*, the centers of calcification (COCs) are approximately 10 to 20 μm wide (Montagna et al., 2007). Although we did not actively monitor for the presence of COCs, our laser tracks were located exclusively on the inner wall of the corallites, and operated at a fine spatial resolution (20 μm beam size over 50 μm wide rectangles). As such, while likely tracking mostly on aragonite fiber deposits, the ablation paths are likely sensitive to the microstructural heterogeneity of the wall, which explains some of variability in the laser records, and some of the differences between laser and bulk sampling records. This nuance was noted in the discussion (lines 384: "Nevertheless, it must be noted that the microstructural heterogeneity of the *C. caespitosa* theca wall, including aragonite fibers and centers of calcification (Montagna et al., 2007), may have contributed to the higher variability observed in the records obtained through fsLA").

- I wonder if the first discussion section, focused on the reconstruction seawater pH from coral d11B, misses a really interesting implication of the dataset. While the previous calibration of Trotter et al. (2011) aligns closely with the data presented here on average, that pHsw reconstructed using in situ d11B results in a greater degree of seasonal variability than observed presumably tells us either: i) that the seawater-calcification fluid DpH slope differs depending on whether the coral experience different pH seasonally or on average throughout their life, and/or ii) that seawater pH variability between sites or across seasons is driven mainly by additional factors such as temperature rather than active regulation (please see my earlier comment). This is alluded to in Sec. 4.3, but it might be worth discussing the observation explicitly in these terms, and perhaps the discussion could begin with this observation and/or combined with my second comment above.

We thank the reviewer for this valuable observation. We agree that the greater range of variability in the reconstructed pH_{sw} are likely be explained through a variability in the seasonal dynamic of pH upregulation, and might be constrained by using seasonal slopes of $\Delta pH - pH_{sw}$. A statement addressing this has been added to section 4.1 of the discussion (line 390: "As such, evaluating seasonal ΔpH - pH_{sw} slopes to reconstruct pH_{sw} from pH_{cf} should be considered as a possible way to constrain the seasonal dynamics of pH upregulation"). We also agree that the seasonal and site variability in pH_{cf} (and by extension reconstructed pH_{sw}) may also be linked to a strong temperature effect, as detailed bellow regarding the temperature effect on pK_B.

Minor comments

- line 51. Change 'levels of...' to something like 'relatively high alkalinity concentration'. More broadly, it isn't clear how the second part of the sentence follows from the first. Given all else being equal, TAlk would have almost no effect on the relationship between pH and pCO2, so there must be another cause of the higher than average rate of acidification (likely the higher than average T increase).

We thank the reviewer for pointing this out. Indeed, according to the literature, the projected higher rate of OA is attributed to the higher warming rate, and CO_2 incorporation, together with low exchange rates with other basins. The sentence has been amended for clarity ("Driven by its accelerated warming rate and unique oceanographic features…").

- lines 89-90. It might be worth noting that this is not unique to C. caespitosa and also the case for many other species.

Clarified as requested.

- lines 100-101. And presumably, no in situ studies that avoid complications such as acclimatisation to aquarium conditions etc.

We thank the reviewer for underlining this. This nuance has been reflected in the statement.

- lines 103-107. There is no problem with this paragraph but it could be rephrased for stylistic purposes. E.g., I'm not sure the last sentence is necessary at the end of the introduction (it would

fit better in the abstract or conclusions) and the first two sentences could be combined. Either way, line 106 needs to be edited to 'corals' ' or ideally something like 'the growth of temperate corals'

We thank the reviewer for these suggestions. We have combined the opening sentences, and removed the closing sentence for better flow.

- line 113. State the approximate NaOCl concentration before it was diluted with DI.

We have specified the initial concentration of NaOCl (12%) prior to dilution.

- lines 118-119. Rephrase to avoid using X-ray as a verb.

Changed as requested.

- Section 2.2. Please add or comment on the following details if possible:

- What is the magnitude of diurnal pH variation at Columbretes Islands (to give a sense of whether the choice of time is important - I imagine not)

The average magnitude of diurnal pH variation in Columbretes is of approximately 0.14 ± 0.05 units. While this diurnal variation is small, we believe it is still substantial enough to be accounted for in inter-site comparison. Because of this, we filter the Columbretes data specifically for the 9:00 AM time slots, to ensure a robust comparison with the data from Villefranche which relies on CTD casts performed consistently at 9:00.

- How was the pH data calibrated/state some estimate of data quality and how it was determined

The pH sensor used in the Columbretes Islands was calibrated using standard certified buffer solutions prior to deployment and checked post-recovery to ensure data stability and quantify any drift. The pH_{sw} for Villefranche was gathered from the PANGAEA database (https://doi.pangaea.de/10.1594/PANGAEA.727120; Gattuso et al., 2021). These details have been added to the method section 2.2 of the manuscript.

- line 142. The unit of resistivity is MOhm cm.

Corrected.

- lines 151-152. I didn't understand how this laser path geometry aligns with what is written about the beam diameter a few sentences below. If the laser spot size was 20 um, why were the paths 50 um wide? Please clarify.

The paths were 50 µm wide as the laser beam (20 µm in diameter) was swept over the 50 x 600 µm rectangle in a rasterized grid pattern. This has been clarified in the text.

- Line 156. Please also state representative sensitivity and gas blank voltages.

Indicated in the text as requested.

- Line 167. Please clarify whether the in-house pressed pellets were 'nanopellets' (Garbe-Schoenberg & Muller, 2014) or pressed powders with a larger grain size.

The in-house pressed pellets were pressed powders in each case, and not the "nanopellets". Corresponding clarification has been added to the text.

- line 174 onwards. If I understand, this implies that all standards were used to generate the Dd11B-11/10.066 ratio with the exception of the JCp-NP, is that correct? If so, I would suggest taking one of the standards out of the calibration line in order to give an estimate of data quality, or otherwise please state data quality (accuracy and precision) and how it was determined.

Yes, this is correct: JCp-NP was not included in the interference correction curve, and was used solely as a means to monitor performance and reproducibility. The set of standards was chosen by design so that the standards spread deliberately across a range in the X-axis. Consequently, removing one standard might change the form of the matrix calibration. Data quality following interference correction was assessed by comparing the $\delta^{11}B$ data obtained with laser ablation with solution (detailed in method sections 2.3.3 and 2.4.1, and Figure 4).

- Section 2.3.2. I appreciate the data given in Table B5, although some of the measured values are substantially offset from the reported values for this material, which is a bit surprising given that it is a nanopellet standard. It would be good to report the percentage accuracies in the methods section if possible and to briefly comment on whether the relatively large B/Ca inaccuracies are a source of concern when interpreting the sample data. You could also compare to the NP data reported in Jochum et al. (2019) & https://www.nature.com/articles/s41597-026-07812-0 - a bit circular in the first case given these were measured using fsLA, but it would give a sense of whether the data quality is driven by the standard versus analytical approach.

We thank the reviewer for pointing this out. We believe that the differences in the E/Ca ratios compared to those reported by Hathorne et al. (2013) for the JCp-1 powder standard, and for JCp-1-NP measured with the different instruments used in this study likely result from the alteration originating from the pellet production process, as indicated recently by Flöter et al. (2026). Additionally, the alteration occurring during nano-pellets production process may not be homogeneous, due to agate-milling silicate particles having different sizes and distributions, and we used different pellets of JCp-1-NP for each instrumental setup used in our study, explaining some of the differences between our sessions. For this reason, we decided not to use JCp-1-NP for instrument bias correction, and applied instead a site-specific mean-centering approach to correct against any instrumental bias that might affect sample data. Additional lines were added to Table B5 with the values reported by Flöter et al. (2026) and Jochum et al. (2019) for JCp-1-NP, for further comparison, and a note was added to method section 2.3.2: "However, we note that offsets between laser sessions and bulk values measured by Hathorne et al. (2013) likely reflect preparation artifacts related to agate-milling alteration inherent to the nano-pellet production (Flöter et al., 2026)". For transparency, we

also included percentage accuracies for B/Ca relative to the values reported by Jochum et al. (2019) (ranging from 11 to 34 %), in the methods.

- Line 209. I think the correct term is 'intermediate precision', but this may depend on whether the data were measured over multiple analytical sessions (which intermediate precision would imply).

Changed to intermediate precision.

- Line 214. It would be great to show the age models in the appendix or a supplement, including the details of how these were pieced together using different elemental ratios.

The age models for each corallite are now indicated on their corresponding X-rays, in the modified Figure B1. An additional figure was added to appendix B (Figure B4) showing the time series of the trace element ratios used for the elaboration of each sample's age model, and the steps followed to this effect are detailed in the figure caption. Briefly, preliminary age models were established using the skeletal density and growth bands revealed in the X-rays, by tying the low density bands with temperature maxima (summers), and high density bands with temperature minima (winters), starting from the date of collection. These preliminary age models established a rough relation between the distance from the calix and the age of the corallite, which were refined using two trace element ratios per sample showing the clearest seasonal oscillation, and tying their minima to temperature maxima, and their maxima to temperature minima.

- Line 283. 'reconstructed pHsw' should not appear here if I understand as you're (I think) comparing reconstructed calcification site pH to seawater measurements, rather than reconstructing seawater pH.

We thank the reviewer for their suggestion. We agree that the mention of "reconstructed pH_{sw}" at this point is confusing and redundant, since the comparison at line 283 focuses on inter-site differences in calcification site parameters and environmental measurements. The text has been corrected accordingly.

- Figure 3. Given that you've gone to the effort of reconstructing individual corralite age models and making spatially resolved measurements, it seems a shame not to show the complete dataset on this figure. I know that further details are given in subsequent sections/figures, but this could be a two panel figure showing both the corralite averages as well as the seasonal/monthly average pHsw and d11B data, which would give an immediate sense of whether seasonal pH change impact pHcf (perhaps tying into my main comment above).

We thank the reviewer for this suggestion. The figure and its caption have been modified accordingly to include an additional panel (B) showing monthly average $\delta^{11}B$ per sample and site, relative to monthly average in situ pH_{sw}.

- Figure 3. Please also state which conditions the reference curve is shown for (T,S).

Klochko's borate curve shown in figure 3 corresponds to a temperature of 25 °C and a salinity of 35 PSU, which are now indicated accordingly in the new figure caption.

- Lines 308-309. This is interesting, although to interpret this in terms of a larger range in pHcf identified in Fig. 4 requires the analytical noise in the laser measurements to be accounted for. Was an attempt made to take this into account?

To allow the reader to distinguish between true data variability and analytical noise, we have modified Figure 4 to include the error bars (2SE) to the $\delta^{11}B$ data, now showing similar levels of 2SE between laser and solution. In the case of the laser records, the uncertainty is small compared to the range of variation of laser record. Additionally, we believe the larger range present in the laser records is largely driven by differences in microstructural heterogeneity and sampling volume between each analytical approach (detailed in the following comment).

- Figure 4. It may simply be that the in situ data align in a slightly unintuitive way, but I struggled to understand why the curves in the upper and lower panels of Fig. 4 do not look more similar. For example, solution d11B is approximately constant between 2015 and 2016 while there is a relatively large pHcf decrease in the middle of the year (presumably driven by the effect of T on pKB?). However, the lowest laser d11B data point has been corrected upwards in terms of pHcf, which isn't visible in the solution data. Is this correct?

We believe the differences between the laser and solution $\delta^{11}B$ records, and their specific behavior when converted to pH_{cf} are driven by a combination of i) spatial integration and ii) non-linear mathematical conversion. i) While the same spatial resolution was used when sampling for the laser and for solution (every 0.5 mm along the skeletal wall), the sampling methods differ slightly. The laser and the solution analyze complementary halves of the same corallite. Additionally, solution evaluates a larger volume of milled corallite wall, integrating the full microstructural heterogeneity (centers of calcification and aragonite fibers), thereby smoothing out variability at the microstructural scale. Conversely, laser only sampled a 50 by 600 µm rectangle, and is likely sensitive to microstructural variability. As detailed above, we believe microstructural heterogeneity (centers of the calcification and aragonite fibers) may explain some of the differences between solution and laser records. As such, differences in sampling would account for some of the differences between laser and solution records. ii) As the reviewer points out, we agree that the main driver in the seasonal oscillation of pH_{cf} (which is not so visible in the $\delta^{11}B$ records, particularly with solution) is the seasonality in temperature (detailed above). Additionally, the conversion to a logarithmic scale, when converting $\delta^{11}B$ to pH, implies a non-linear conversion. As such, combined with the temperature effect, this would result in non-intuitive "corrections" in pH_{cf} which may be different when dealing with the laser or the solution records.

- Figure 5. Please correct the y axis labels - B/Ca in panel (c) should not contain a cf subscript and Omega (e) is unitless. You could also give the pH scale. Note the incorrect (b) on line 320 too

We thank the reviewer for pointing out these corrections, which have been applied to the figure and its caption accordingly. The pH shown in this figure is in total scale (this has been specified in the figure caption).

- Figure 5. I would suggest changing 'reconstructed records...' to simply 'reconstructed pHcf).

Changed accordingly.

- Lines 412-414. I appreciate that references are provided but wonder if this confuses cause and effect - perhaps they grow more slowly because they are less able to maintain the cf carbonate chemistry that they need to do so.

We thank the reviewer for this interesting insight. We have assessed this aspect using the approach proposed by Burton and Walter (1987) and applied in McCulloch et al. (2017), where coral calcification rate (G) is estimated from Ω_{cf} using the formula: $G = k \cdot (\Omega_{cf} - 1)^n \cdot 8.77 \cdot 10^{-5}$ (in $g \cdot cm^{-2} \cdot yr^{-1}$). Using the data from our study, we calculated an average estimated calcification rate of 0.13 $g \cdot cm^{-2} \cdot yr^{-1}$ for the Columbretes Islands and 0.10 $g \cdot cm^{-2} \cdot yr^{-1}$ for Villefranche, which is lower than the calcification rates measured from the X-rays (on average 0.27 and 0.20 $g \cdot cm^{-2} \cdot yr^{-1}$ respectively), indicating that Ω_{cf} is not the only parameter driving calcification. We believe this outcome could support further the notion that calcification in this coral is limited by environmental conditions (chiefly temperature), rather than by CF chemistry, and have added this argumentation to the manuscript, in the methods (line 225, and appendix A), results (section 3.2, line 283) and discussion (line 435: "Additionally, calcification rates estimated from Ω_{cf} yielded lower averages (0.13 $g \cdot cm^{-2} \cdot yr^{-1}$ in the Columbretes Islands and 0.10 $g \cdot cm^{-2} \cdot yr^{-1}$ in Villefranche) than those measured directly from the coral X-rays (0.27 $g \cdot cm^{-2} \cdot yr^{-1}$ in the Columbretes Islands and 0.20 $g \cdot cm^{-2} \cdot yr^{-1}$ in Villefranche), indicating that Ω_{cf} and CF chemistry alone do not fully explain coral calcification rates").

- Lines 417-420. I think this interpretation might be a bit simplistic. What you show is that this species maintains an approximately constant calcification site Omega through the year, so the DIC data could be interpreted to suggest that a lower degree of CO2 diffusion/transport is required when the pH is higher. These processes of course do not take place in isolation however, a greater pHcf and therefore steeper pH gradient to the cytosol will impact CO2 diffusion, which will result in a higher Omega if pH can be maintained and a lower Omega if not. Overall it is perhaps more likely that the organism prioritises maintaining Omega in the face of seasonally varying light, temperature (impacting pH and metabolism), and carbonate chemistry, in which case DIC increase responds to, rather than drives, the trends you see.

We thank the reviewer for this insightful comment, and for helping us refine our interpretation, and agree that our original phrasing does not reflect the complexity of the relation between DIC_{cf} and pH_{cf}. We have reviewed the first paragraph of section 4.2 of the discussion to better reflect this relation. Briefly, we agree with the reviewer that the regulation of the CF prioritizes the maintenance of a relatively constant Ω_{cf} throughout the year, as is argued in subsequent paragraphs of the manuscript. In *Cladocora caespitosa*, the lower DIC_{cf} compared to tropical corals likely reflects the environmental constraints of the Mediterranean (lower temperature and light availability compared to tropical settings) resulting in a lower metabolic activity of the coral-endosymbiont. As such, the higher pH upregulation (evidenced by the higher ΔpH compared to tropical corals) is a likely a compensatory mechanisms to the lower DIC input to the CF. In agreement with the reviewer, we believe that the lower seasonal oscillation of DIC_{cf} reflects a complex interplay of different mechanisms involving the interaction with pH_{cf}, as well as seasonal variability in coral-endosymbiont metabolism, and active carbon transport to the CF. The upregulated and stable Ω_{cf} through the year is a result of the coordination of each of these mechanisms.

- Lines 432-433. Please see my earlier comment - it is perhaps more likely that they grow more slowly because they are not able to maintain a higher cf Omega.

Answered in the prior comment at lines 412-414.

- Line 438. 'products required for calcification'? I'm not sure I understand though. Aragonite precipiation is ultimately driven by cf carbonate chemistry (essentially the same between the two populations) and the only way to decouple this from growth rate on longer timescales is to cycle more seawater. So, the population may be more efficient in that they can do more with the same resources, if indeed the resources are the same (food, nutrients etc. - are they?), but not that they can use the products of or required for calcification more efficiently.

We thank the reviewer for pointing this out, and agree that the current formulation is misleading. The statement has been amended to "…a more efficient use from the coral of the resources necessary for calcification extracted from the environment …".

Typos/phrasing

- line 162. 'the signal'

- line 170. 'Section 2.3.3'

- line 315. Delete 'composition'

- line 344. The reference to panel b is incorrect and perhaps replace 'soft' with 'gradual'

- line 347. Multiplication symbols needed

- line 375. Change 'in' to 'using'.

- line 377. 'indicating that the measurements were accurate'

We thank the reviewer for indicating these typos, which have been corrected accordingly in the manuscript.

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