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Quantifying attributes of boring bivalve populations in corals using micro-computed tomography

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Bioerosion plays a crucial factor in shaping the structure and function of coral reef ecosystems, with bioeroders actively altering both the physical and ecological dynamics of coral substrates. Despite their importance, studying internal bioeroders in corals presents significant challenges owing to their cryptic nature within the skeletal structures. Additionally, invasive methods are often required to reveal the subtle and microscopic bioerosive alterations they induce in calcium carbonate substrates. Here, we demonstrate the effectiveness of high-resolution micro-computed tomography (μ CT) in quantifying the abundance, size, distribution, and growth directions of coral bioeroders such as cryptic calcareous bivalves in the northern Red Sea. We scanned three coral species inhabited by bioeroders, followed by the utilization of three-dimensional image analysis software to identify, count, and measure each bivalve within the coral skeleton, along with quantifying boring cavity volumes. We revealed that μ CT captures small boring cavities ($< 1\text{mm}$), providing more accurate abundance estimates of live and dead boring bivalves than the skeleton decalcification technique, with the added benefits of being rapid and non-destructive in contrast to traditional methods. Furthermore, measurements of empty cavity volumes enabled the estimations of the contribution of bioeroders to the overall coral skeletal porosity. Overall, our study highlights μ CT as a practical and effective tool for studying cryptic coral bioeroders, providing novel ecological insights into bioeroder population ecology and coral-bioeroder interactions.

KEYWORDS

coral reefs, bioerosion, micro-computed tomography, 3D imaging, symbiosis

1 Introduction

Coral reefs, renowned for their vibrant biodiversity and ecological significance, host a rich array of species that occupy various microhabitats within their calcium carbonate formations. The sustainability of coral structures relies on maintaining an equilibrium between reef accretion, primarily driven by hermatypic corals, and processes that break down calcium carbonate substrates (Connell, 1978; Silbiger et al., 2018). While corals are the primary reef builders, they are complemented by the contributions of other organisms such as crustose coralline algae, calcareous sponges, foraminifera, and certain mollusks, all enhancing reef framework formation. This equilibrium faces constant challenges from erosion, occurring in two primary forms: physical erosion from wave action and currents, and bioerosion (often considered the predominant form of erosion), involving organisms that feed on or bore into the reef framework (Connell, 1978; Silbiger et al., 2018). While some reef inhabitants, such as corallivores (dominated by parrotfish and urchin species), directly alter the reef framework through grazing, cryptic “boring” organisms also play important yet hidden roles. Within the calcium carbonate coral skeletons, cryptic communities of bioeroding organisms thrive by actively penetrating and removing the coral’s structural materials through bioerosion activities (Glynn and Manzello, 2015; Fordyce et al., 2021; Rice et al., 2020).

Bioeroders modify the architectural complexity of reefs across multiple spatial scales, ranging from the micron to meter level (Davidson et al., 2018; Fordyce et al., 2020a; Glynn and Manzello, 2015; Roff et al., 2019). These bioeroders are broadly categorized as either surface-dwelling or internal-boring depending on their location and mode of erosive activity. External bioeroders reside on exposed reef surfaces, whereas internal bioeroders reside hidden within the calcium carbonate skeleton (Glynn and Manzello, 2015). Although the majority of internal bioeroders remain cryptic, that is, concealed within the substrates they penetrate, evidence suggests that their abundance and biomass may equal or surpass those of external bioeroders (Ginsburg, 1983; Weinstein et al., 2016). Additionally, internal bioeroders exhibit the highest taxonomic diversity among bioeroding organisms (Glynn and Manzello, 2015). The key taxa among the internal bioeroders that penetrate coral skeletons, also termed macroendoliths, include Porifera, Polychaeta, Sipuncula, Bivalvia, and Cirripedia (MacGeachy and Stearn, 1976). At the microscopic scale, microendolithic communities of cyanobacteria, chlorophytes, rhodophytes, and fungi actively penetrate structural calcium carbonate substrates (Hutchings, 1986; Perry and Harborne, 2016).

Despite the high biomass, diversity, and prevalence of internal bioeroders observed in many scleractinian corals, a comprehensive understanding of these cryptic organisms remains elusive (Schönberg et al., 2017). The profound inaccessibility of internal bioeroders significantly impedes research efforts, contributing to this knowledge gap. Moreover, the complexity of bioerosion processes, which intricately shape various facets of reef ecological functions (Fordyce et al., 2020a), poses additional challenges to understanding this phenomena. For instance, in contrast to the apparent detrimental impact on reef substrata strength, cavities

generated by internal bioeroders augment habitat complexity, thereby enhancing the diversity and biomass of organisms associated with reefs (Glynn and Manzello, 2015). There is a critical need to enhance our understanding of bioeroders’ abundance, burrowing activities, and potential impacts on coral skeletal properties, as these organisms play a pivotal role in influencing coral reef resilience and stability (Schönberg et al., 2017).

To date, various methodologies have been employed to assess the abundance of internal bioeroders, including the cross-sectioning of bioeroder cavities, coral skeletal decalcification, and *in situ* surveys (Maher et al., 2018; Rice et al., 2019; Risk et al., 1995; Scott, 1988). While these approaches enable the direct quantification of living bioeroders in their natural habitat, they are limited in identifying cavities blocked by coral overgrowth, which may result from the death of bioeroders during the coral lifespan or coverage by other settlements. These methods provide limited data on the abundance of living bioeroders and lack information on cavity volume or the impact of bioeroders on substrate properties such as skeleton density and porosity.

Another technique utilized to gain insights into the extent and characteristic patterns of skeletal excavation by diverse organisms is the use of X-ray scans (Hein and Risk, 1975; MacGeachy and Stearn, 1976; Highsmith et al., 1983; Risk and Sammarco, 1991). However, simple X-ray radiography offers limited insights, as it is a two-dimensional imaging technique and is typically characterized by lower resolution. Computed Tomography (CT), on the other hand, offers exceptional three-dimensional (3D) high-resolution imaging, facilitating the non-destructive analysis of intricate microstructural details within coral skeletons without physically altering or destroying the original skeleton (DeCarlo et al., 2015; Fordyce et al., 2020b; Kramer et al., 2022). Previous studies utilizing CT for non-destructive analysis have quantified carbonate production, bioeroding activities, and net accretion on coral substrates (Silbiger et al., 2014, 2016, 2017; DeCarlo et al., 2015; Enochs et al., 2016, 2021; Newman et al., 2023). However, detailed methodological evaluations of CT for quantitative analysis of cryptic internal coral bioeroders, such as calcareous bivalves, are insufficient.

Here, we present a case study that evaluates the effectiveness of μ CT scanning in conducting high-resolution morphometric analyses of common coral-boring species in the northern Red Sea, and present evidence of the advantages of this technique over traditional methods. Furthermore, we address potential concerns regarding the use of preserved coral samples for μ CT scanning. Our complementary approach provides precise quantification of internal calcareous bioeroders that can be applied to advance our understanding of the interactions between these organisms and their calcifying hosts.

2 Materials and methods

2.1 Coral collection and preparation

We selected three reef-building coral species from the Gulf of Eilat/Aqaba, Red Sea, due to their known associations with boring

organisms and distinct growth forms. These species include: *Stylophora pistillata* (branching) associated with *Leiosolenus lessepsianus* (formerly *Lithophaga*) (Mokady et al., 1991), *Astreopora myriophthalma* (massive) associated with *Leiosolenus simplex* (Mokady et al., 1998), *Echinopora forskaliana* (encrusting) associated with *Leiosolenus* spp (Goreau et al., 1970). Coral fragments were collected using recreational and technical diving in front of the Interuniversity Institute for Marine Sciences (IUI). *A. myriophthalma* and *E. forskaliana* colonies ($n=1$ fragment per species) were collected at 5m, while *S. pistillata* samples ($n=12$ fragments, 1 per colony) was collected at mesophotic depths (45m) due to the high prevalence of *L. lessepsianus* compared to shallow specimen (unpublished data). Additionally, fragments of *S. pistillata* were used to assess the suitability of preserved, complete, formalin-fixed samples for histological examination after X-ray scanning, compared to samples that were not scanned. These samples were fixed with 4% formaldehyde solution in seawater for 24h, rinsed in running tap water, and preserved in 70% ethanol, following Rapuano et al. (2017).

Our scans encompassed coral samples with both bare skeletons and tissues (i.e., preserved complete formalin-fixed samples, only for *S. pistillata*). Although extended exposure to X-rays during μ CT scanning may theoretically induce a minor temperature increase within the sample, it is important to note that this heating effect is typically minimal and not a primary concern for most applications. Nevertheless, since our samples retained tissues intended for later histological analysis (not included in the scope of this study), we conducted a comparative histological examination between fixed samples that underwent μ CT scanning with those that did not. This comparison aimed to assess the impact of μ CT scanning on tissue integrity for subsequent histological analyses. As a precautionary measure, we immersed the sample in distilled water, as ethanol, being highly volatile, was previously present in the solution. The coral tissues were then sealed with parafilm to create an airtight enclosure, thereby maintaining tissue moisture.

Except for these fragments, all the samples were bleached in 6% sodium hypochlorite solution for 24h for tissue removal, followed by thorough rinsing with deionized running water to remove the remaining organic matter. Finally, they were left to air-dry at room temperature for an additional 24h.

2.2 μ CT scanning and quantitative analysis

High-resolution micro-computed tomography (μ CT) was performed using a Nikon XT H 225ST μ CT (Nikon Metrology Inc., USA) at The Steinhardt Museum of Natural History, Tel Aviv University. The coral samples were scanned in a 360° rotation (in 0.5° increments, scan time = 40 min) at an isotropic voxel size of 50 μ m, 0.25mm stainless steel filter, voltage of 65 kV, amperage of 123 μ A, and exposure time of 1.15s. The reconstructions into image stacks were conducted with VGSTUDIO MAX software (Volume Graphics © 2024) which were then saved in TIFF image format for 3D volume rendering and quantitative analysis using Dragonfly software (© 2023 Object Research System (ORS) Inc.). The Range tools were used to define threshold radiodensity values to create a new region of interest (ROI) for only the CaCO₃ skeleton, in which all

voxels within the selected range were labeled. A label analysis was conducted on the segmented dataset to determine the surface area and bulk volume of the coral samples. Other measurements were made manually: using the Ruler tool, the length and width of each bivalve were determined by scaling the two-dimensional (2D) axes along their longitudinal and lateral dimensions, and their boring cavity volume was estimated by distinguishing and outlining the boundaries between air and solid CaCO₃, segmented using the ROI Painter in Multi-slice mode, and applying a Multi-ROI to label each burrow separately.

2.3 Skeleton decalcification for bivalve abundance

The skeletal samples were utilized to evaluate and compare the efficiency and accuracy of the μ CT compared to the skeleton decalcification technique for the measurement and enumeration of internal bioeroders. Initially, μ CT scans were conducted on these fragments, followed by quantitative measurements, as previously described. Then, to physically evaluate bivalve abundance per sample, decalcification was conducted using a sodium citrate buffered 25% formic acid solution prepared by combining equal volumes of 50% formic acid in distilled water and 20% sodium citrate in distilled water. This specific solution decalcifies the coral skeletons efficiently while minimizing potential damage to the bivalve shells. Despite both being made of calcium carbonate, bivalve shells differ in structure from coral skeletons. Specifically, Mytilidae bivalve shells consist of three distinct layers: the periostracum, the calcium carbonate-based prismatic, and the nacreous layers (Albano, 2021). The prismatic and nacreous layers are susceptible to dissolution in a 25% formic acid solution. However, the outer organic layer (the periostracum), mainly composed of conchiolin, a proteinaceous material, serves as a protective barrier that is comparatively more resistant to the decalcifying solution (Al-Hosney et al., 2005), thereby ensuring shell integrity. Following the completion of decalcification, bivalves were carefully extracted and counted.

3 Results and discussion

Modern 3D imaging techniques, such as computed tomography, are gaining popularity in the study of calcifying organisms as this tool facilitates ecologically relevant examinations of internal structural changes (Silbiger et al., 2016; Gutiérrez et al., 2018; Fordyce et al., 2020b; Kramer et al., 2023). However, coral reef research has not yet fully harnessed its potential to provide novel ecological insights. Here, we demonstrate that μ CT serves as a powerful, precise, and non-destructive tool to study quantitative demographical and morphological aspects of bioeroders in their coral hosts, and provide spatial visualization of the of the internal bioeroder population within the host skeleton.

While prior studies share the use of volumetric μ CT analysis for quantifying overall bioerosion patterns and processes in coral skeletons, including that of macro bioeroders (Silbiger et al., 2014, 2016, 2017; DeCarlo et al., 2015; Enochs et al., 2016, 2021; Newman et al., 2023), a key distinction lies in our focus on specific cryptic calcareous bivalves

species rather than general bioerosion measures or broader taxonomical level. By targeting these major yet understudied bioeroders, we evaluate μ CT's ability to precisely quantify their abundance, size structure, spatial distribution, and the geometry of their individual boring cavities - aspects not explicitly examined in previous studies. Moreover, our direct comparative analysis between μ CT and decalcification techniques highlights μ CT's advantages as a rapid, non-destructive method for assessing bioeroder population demographics and impacts on skeletal porosity. Overall, our work provides a complementary, fine-scale perspective on coral-bioeroder interactions, demonstrating μ CT as a practical tool for advanced ecological investigations in this area.

μ CT was advantageous for locating lithophagid bivalves and their boreholes (Figure 1). This group plays a significant role in internal bioerosion and contributes to the destruction of diverse calcareous substrates (Glynn and Manzello, 2015; Morton, 1983; Rice et al., 2019). Specifically, genera such as *Leiosolenus* and *Lithophaga* engage in boring activities within live and dead coral structures, respectively. These cryptic molluscs achieve peak abundances in subtidal reef zones, with certain species extending their bioerosive activities to the lower depth limits of reef-building corals (Glynn and Manzello, 2015). Our 3D analyses of coral specimens provide detailed insights into the impacts of boring bivalves on coral skeletons, enabling accurate assessments of

bioerosion processes by locating the precise location, distribution, growth angle, and abundance of bioeroders within corals (Figures 1, 2), and to measure their body size with microscale precision (Figure 3). We were able to detect bivalves ranging in size from 0.5mm to 28mm, with varying sizes among the *Leiosolenus* species (Figure 1; Table 1). This size variation aligns with the skeletal polyp dimensions of the different coral morphologies examined. In contrast to small-polyp corals (<1.2mm in diameter for *S. pistillata*), large-polyp corals (5mm and 2.5mm in diameter for *E. forskaliana* and *A. myriophthalma*, respectively) are typically associated with larger skeletal features, thus providing more space for larger bivalves to settle and bore.

Assessing the body size of boring bivalve assemblages could provide unprecedented information regarding their demographic characteristics, including recruitment events, reproductive maturity, and longevity (Dietzel et al., 2020; Kramer et al., 2020). However, reports of the size-frequency distribution of boring organisms, let alone of lithophagid bivalves, are lacking and non-existent in many species. Scott (1988) sought to assess the abundance of the internal bioeroder *Leiosolenus bisulcatus* within live and dead coral hosts. Coral host fragments were collected, and counts were made of both living and deceased *Leiosolenus* individuals. However, aside from the clear destructive and irreversible drawbacks associated with this method, it lacks the

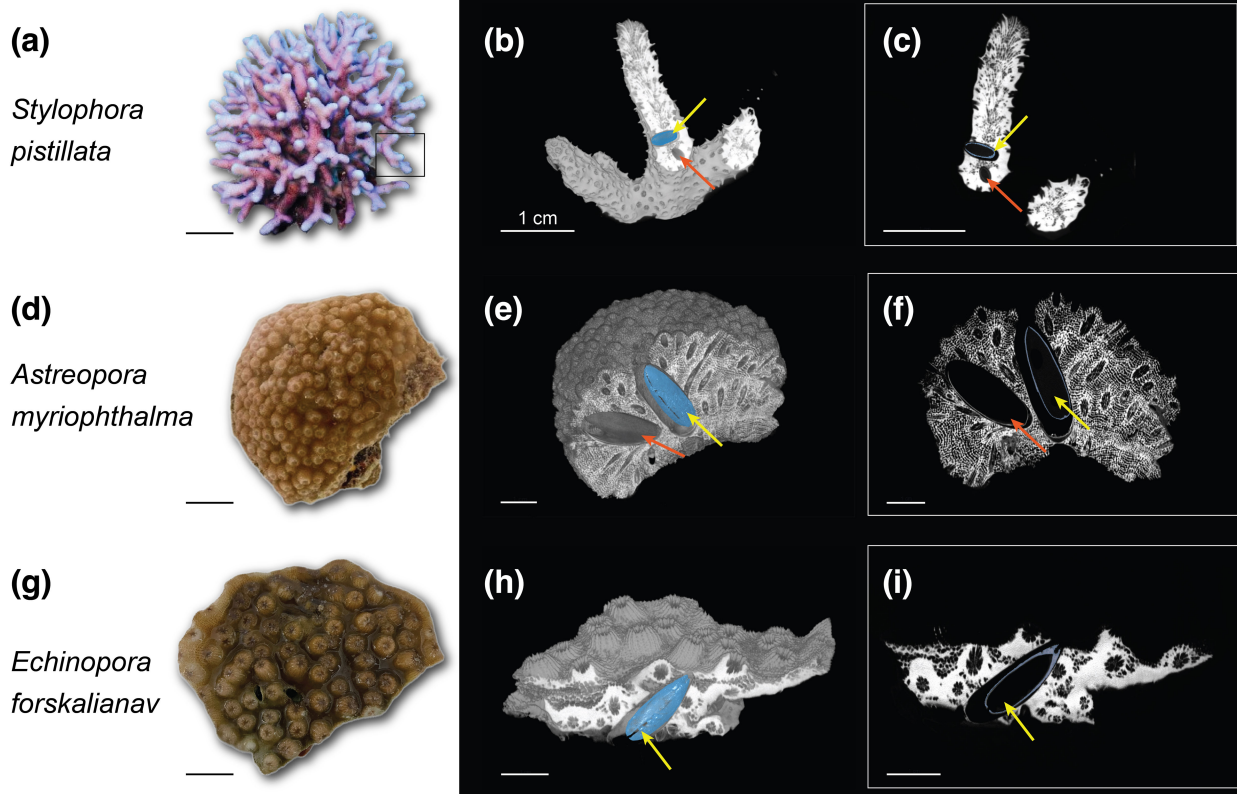


FIGURE 1

Three-dimensional rendering based on μ CT data of three reef-building corals *Stylophora pistillata*, *Astreopora myriophthalma*, and *Echinopora forskaliana*. (A, D, G) Live corals; (B, E, H) 3D surface reconstructions of coral skeletons vertically clipped in the center of a bioeroder (segmented in blue) and (C, F, I) 2D reconstructions of the clipped area. Yellow arrows indicate segmented bioeroders and red arrows indicate non-segmented bioeroders. Scale bars = 1 cm.

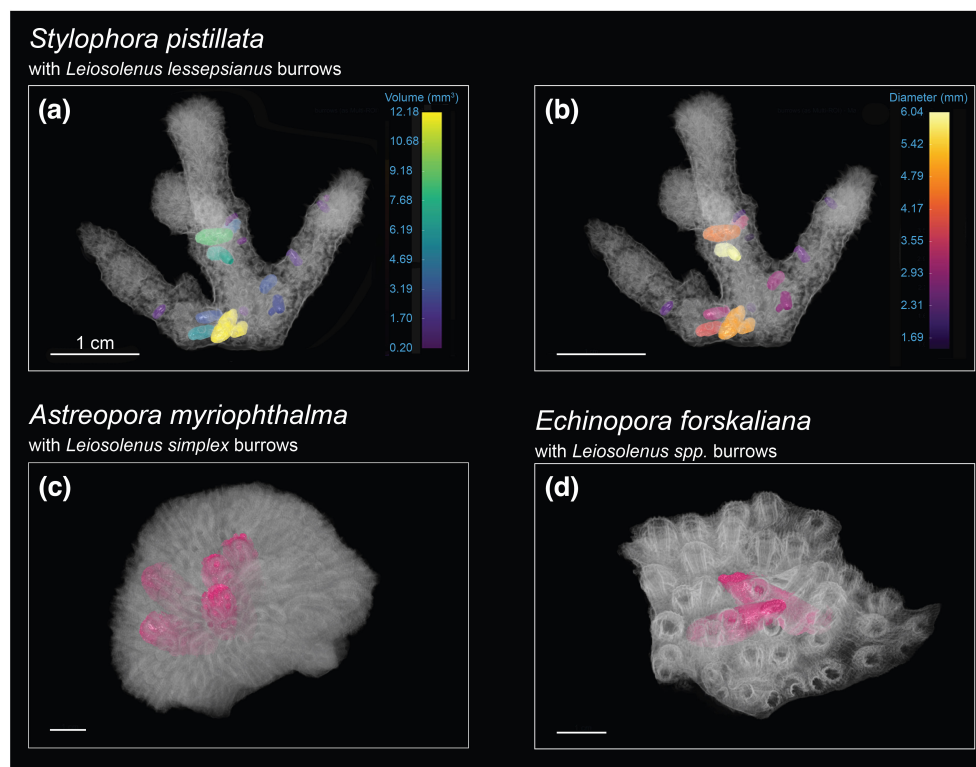


FIGURE 2

Volumetric μ CT visualization of the location, distribution, and growth direction of active boring cavities in three coral hosts and their associated bivalves. *S. pistillata* borrows are colored based on (A) volume (mm³) and (B) maximum diameter (mm). (C, D) Borrows in other species are colored in pink. Scale bars = 1 cm.

capacity to furnish details regarding burrow volume and its effect on coral porosity.

Bioerosion by bivalves is caused by the secretion of acid, which dissolves the substrate and allows them to create a burrow, typically occupying polyp spaces (Lazar and Loya, 1991). Utilizing μ CT scans, we segmented and measured individual burrow volumes created by the bioeroders within the host skeleton (Figure 2). Measuring these volumes provides insights into the impact of internal bioerosion on skeletal integrity and porosity, which varies among coral species owing to factors such as morphological groups and environmental conditions (Foster et al., 2016; Hughes, 1987; Kramer et al., 2023). We showed that boring cavities in the encrusting *E. forskaliana* accounted for over 60% of the total porosity, boring cavities in the massive *A. myriophthalma* contributed nearly one-third of the coral porosity, and boring cavities in the branching *S. pistillata* reached up to 25% of the coral porosity (Table 1). Associating these findings with bivalve size and abundance suggests that the extent of internal bioerosion is influenced by bivalve size and coral morphology, namely, larger bivalve species create expansive boring cavities that contribute substantially to skeletal porosity.

Additionally, examining the internal coral skeleton in 3D provided flexibility in identifying bivalves that were “blocked” (Table 1) by the coral skeletal overgrowth, obstructing their burrowing progress towards the coral surface. Such information can easily be overlooked during field observations of live boring

bivalves or when examining a predetermined 2D slice angle of the skeleton since these approaches offer inadequate estimation for macroborers (Silbiger et al., 2016). A comparison between μ CT scan examination and bivalve counting after skeleton decalcification revealed that μ CT scans yielded more accurate bivalve abundance estimates in 9 of 12 *S. pistillata* samples (Table 1). This superiority is attributed to the ability of μ CT to capture very small bivalves (< 1 mm) effectively, which is especially beneficial in corals inhabited by mostly small-sized bioeroders, such as *S. pistillata*. In contrast, using the skeleton decalcification method proved insufficient as it can be prone to human error and oversight in identifying and locating bivalves hidden within the tissue, and there is a risk of losing very small bivalves during the process (Figure 4). Furthermore, skeletal decalcification is significantly more time-consuming than X-ray scanning, taking up to 24h (depending on skeletal density) compared to just 1h in μ CT. However, while reducing processing time, μ CT scanning may potentially increase costs. Therefore, to balance accuracy and affordability, it is important to clearly state the research objective. If μ CT is required, it is necessary to predetermine the optimal scan parameters required to identify and measure the structures of interest. Lastly, we demonstrated the ability to scan corals with fixed tissues as a powerful tool for advancing comprehensive research, eliminating the need for additional sampling efforts. Our investigation revealed that X-ray tomography had no adverse effects on tissue integrity compared to samples that had not undergone scanning, ensuring the

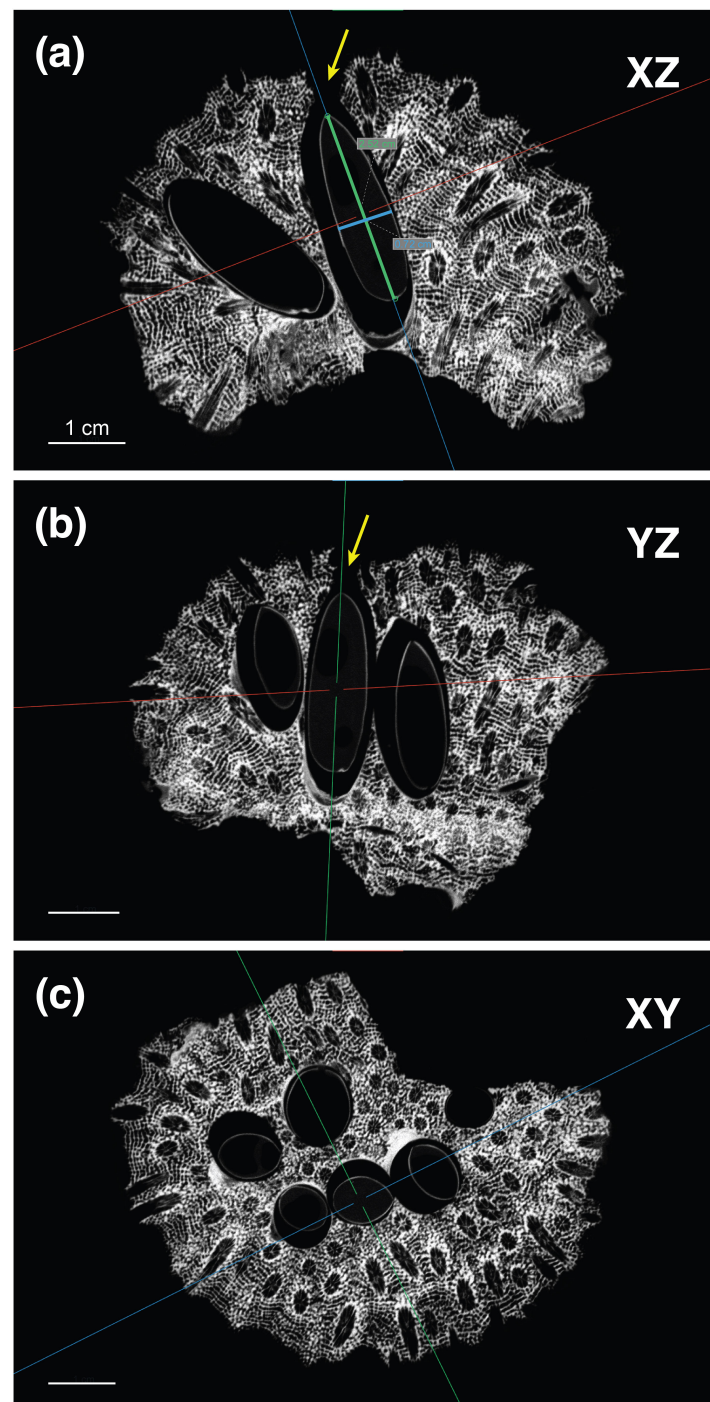


FIGURE 3

Example of 2D reconstructions of μ CT data for *Astreopora myriophthalma* showing 3D cuts in the center of a bivalve. (A) The XZ (vertical), (B) YZ (vertical), and (C) XY (horizontal) planes were oriented along the given bivalve's longitudinal axis to examine its dimensions [A: length (green line) and width (blue line)] and whether it has an opening (A, B: yellow arrows) indicating a live bivalve. Scale bars = 1 cm.

suitability of the samples for subsequent histological analysis. This finding carries significant implications, offering valuable opportunities for utilizing existing sample collections and museum specimens more effectively. Traditionally, formalin-fixed coral specimens have been primarily utilized to investigate cellular

composition and other histological characteristics from the preserved tissues. However, we highlight that the non-destructive nature of μ CT allows to visualize and analyze their internal calcareous structures without compromising on the integrity of the tissue, thereby allowing for subsequent analyses.

TABLE 1 Volume measurements of the three coral species, including their total void space (pores) within the skeleton and boreholes, and their bivalve measurements, including abundance estimations as detected by the μ CT (blocked bivalves in parenthesis) and by visual inspection of decalcified samples, and their mean shell length (mean $\pm$ SE; in mm).

Sample	Volume measurements			Bivalve measurements		
	Coral Volume (cm ³)	Total Pore Volume (cm ³)	Borehole Volume (cm ³)	μ CT count	Visual count	Shell length (mm; mean $\pm$ SE)
<i>A. myriophthalma</i>	104.76	27.59	8.10	6 (0)	6	24.61 $\pm$ 1.56
<i>E. forskaliana</i>	14.77	2.25	1.38	2 (0)	2	19.90 $\pm$ 1.16
<i>S. pistillata</i> 1	2.21	0.38	0.031	8 (4)	8	2.82 $\pm$ 0.47
<i>S. pistillata</i> 2	1.67	0.32	0.019	7 (0)	3	2.24 $\pm$ 0.38
<i>S. pistillata</i> 3	5.57	1.82	0.12	19 (3)	11	2.70 $\pm$ 0.32
<i>S. pistillata</i> 4	1.87	0.49	0.01	1 (0)	1	9.10 $\pm$ 0.00
<i>S. pistillata</i> 5	4.66	1.041	0.027	32 (12)	18	3.29 $\pm$ 0.27
<i>S. pistillata</i> 6	4.52	0.62	0.15	40 (3)	29	2.14 $\pm$ 0.20
<i>S. pistillata</i> 7	1.20	0.32	0.03	13 (1)	4	2.25 $\pm$ 0.40
<i>S. pistillata</i> 8	1.14	0.52	0.08	3 (1)	3	3.20 $\pm$ 2.36
<i>S. pistillata</i> 9	1.28	0.61	0.1	14 (0)	8	2.47 $\pm$ 0.25
<i>S. pistillata</i> 10	1.35	0.32	0.06	12 (3)	7	3.58 $\pm$ 0.31
<i>S. pistillata</i> 11	1.29	0.48	0.06	15 (5)	14	1.96 $\pm$ 1.20
<i>S. pistillata</i> 12	1.36	0.53	0.13	14 (1)	9	3.03 $\pm$ 0.41

4 Conclusions

Our approach demonstrated that utilizing μ CT for bioeroder analysis in corals surpasses the traditional 2D X-ray radiography technique, sectioning, and/or skeletal decalcification owing to its non-destructive nature, time efficiency, precision, and provision of high-resolution 3D reconstructions of internal and external coral-bivalve features. Our study highlights the advantages of μ CT in quantifying bore-holes down to the sub-millimeter scale and offering high-resolution 3D visualization of their distribution within coral skeletons. Additionally, we demonstrated that with proper sample preparation, μ CT can be used with fixed coral tissues,

which is important for studying delicate structures or samples that need to be preserved.

As we navigate an era of climate change, investigating the impact of shifting oceanic conditions on marine calcifiers has become increasingly imperative (Fordyce et al., 2020b). Incorporating this powerful tool into our toolkit fills essential gaps in our understanding of the interaction between internal bioeroders and their coral hosts, which is necessary for unraveling the factors influencing coral health and resilience. Lastly, μ CT generates digital image data that can be readily shared among researchers, fostering collaboration and advancing our collective understanding of coral ecosystems.

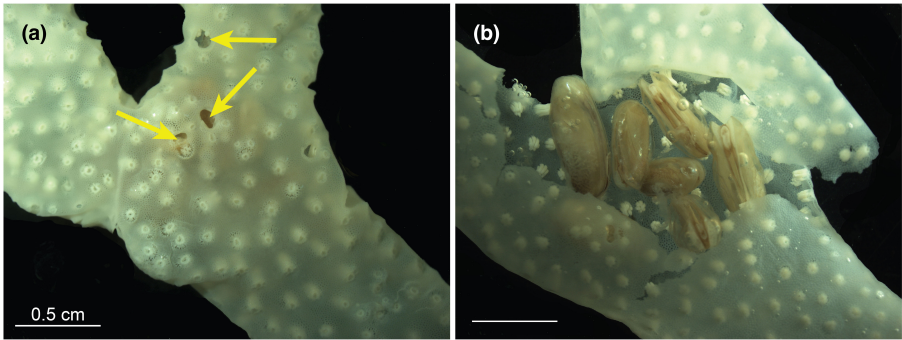


FIGURE 4
A decalcified *S. pistillata* sample (A) before and (B) after tissue examination. Scale bars = 0.5 cm. Arrows indicate burrow openings.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material and figshare repository (DOI: <https://doi.org/10.6084/m9.figshare.27046294.v1>). Further inquiries can be directed to the corresponding author/s.

Ethics statement

The animal study was approved by The Israel Nature and Parks Authority, permit 2022/43141. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

NK: Conceptualization, Formal analysis, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing, Data curation. TA: Conceptualization, Data curation, Writing – review & editing. NG: Data curation, Writing – review & editing. MG: Data curation, Writing – review & editing. DW: Funding acquisition, Supervision, Writing – review & editing. YL: Conceptualization, Funding acquisition, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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