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# Coral hosts provide more than shelter to boring bivalves

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Coral reefs are slow-growing, calcareous, and biodiversity hotspots (see Stella et al., 2011 for review). Bioerosion of living corals may accelerate the loss of coral skeletons and prevent reef accretion (Harriott & Banks, 2002). Despite their impact on coral reef resilience and stability, adequate knowledge of the ecophysiology of bioeroders is lacking (Schönberg et al., 2017). To better understand the nature of the relationship between bioeroding (boring) bivalves and their coral hosts, we conducted field studies over 12 months to compare the physiological parameters of *Leiosolenus simplex* residing in live coral hosts and in corals stripped of their live tissue (therefore considered “dead”). Surprisingly, 1 year after the experiment, the survival rate of bivalves living within dead coral hosts was similar (<5% difference) to that of the bivalves in live coral hosts, and the diet composition of the bivalves residing in both live and dead coral hosts was quite similar. Nonetheless, several other indicators of physiological condition, such as pumping rate and O<sub>2</sub> consumption of bivalves residing in dead coral hosts, were considerably lower (31%) than those residing in live coral hosts.

Most bioeroding species are cryptobiotic (Timmers et al., 2021). Large endolithic bivalves constantly keep

pace with the outward growth of their coral hosts by sustained outward mechanical and chemical burrowing (Lazar & Loya, 1991; Soliman, 1969), allowing them to maintain contact with the surrounding water. Additionally, both live corals and their endolithic bivalves are suspension feeders, raising the possibility of trophic overlap and competition. Therefore, it may be advantageous for coral-boring bivalves to inhabit dead coral hosts, thereby receiving the benefit of mechanical protection without the energy costs of continuous burrowing or competition resulting from trophic overlap. Indeed, boring into dead substrates is assumed to be the ancestral condition that persists into the present in many coral-boring species (Kleemann, 2008; Morton, 1990). Some species, such as those of the mytilid genus *Leiosolenus* (formerly of the genus *Lithophaga*), preferentially or exclusively inhabit living corals (Mokady et al., 1992; Scott, 1988), suggesting that the bivalve may derive essential benefits from this relationship. Such benefits may include active protection provided by the stinging coral cnidocytes (Morton, 1990; Morton & Scott, 1980; T. Amit, personal observations over 10 years of fieldwork) or the consumption of mucus for nutritional

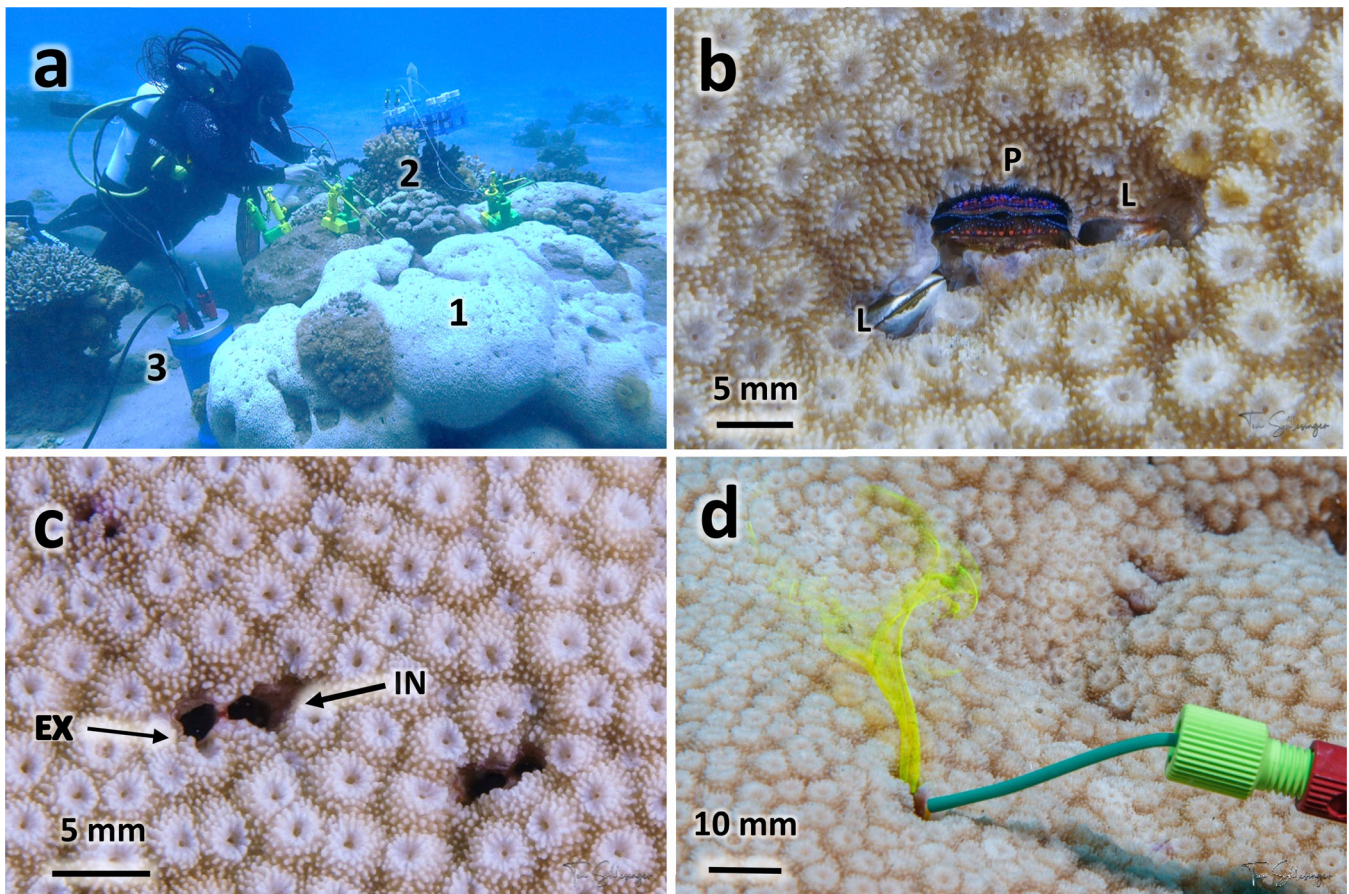
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needs (Shafir & Loya, 1983). The nature of the relationship of the boring bivalve to its coral host is thus an intriguing question; however, aside from Yahel et al. (2009) and Amit et al. (2023), the extreme inaccessibility of these cryptobionts has seriously hampered research on their ecophysiology.

Our field study aimed to elucidate the relationship between the boring bivalve *L. simplex* (Iredale, 1939) and its coral host species *Astreopora myriophthalma* (Lamarck, 1816) in the Gulf of Eilat/Aqaba, Red Sea, Israel. We used purpose-built watertight instrumentation and scuba manipulations to compare, in situ, key physiological and trophic status indicators for *L. simplex* inhabiting 12 similar-sized, haphazardly chosen coral heads sampled in December 2017 (under Israel Nature and Parks Authority permit number 41787). Six of the sampled coral heads were stripped of their live tissue using the PAASCHE airbrush system (Alamaru

et al., 2009). The bivalves in the live and stripped coral colonies were allowed to acclimate in the field for 1 month prior to the beginning of the measurements. The oxygen consumption of the bivalves (an indicator of metabolic activity) was quantified in situ, using optodes (FireSting-O2 system, PyroScience, Germany) and an automatic logger (Figure 1a, see Moskovich et al., 2023 for a detailed description of the methodology). The proportion of actively pumping *L. simplex* was quantified monthly using fluorescein dye released at the inhalant siphon opening of the boreholes (Figure 1b–d, see Video S1 for demonstration). Pumping rates were measured using a modified version of the dye front speed (DFS) method described by Yahel et al. (2005); for a demonstration, see Video S2. To elucidate the putative food sources of the bivalves, we measured the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope ratios of *L. simplex* tissues and of the particulate organic matter (POM, <100  $\mu\text{m}$ ) in the



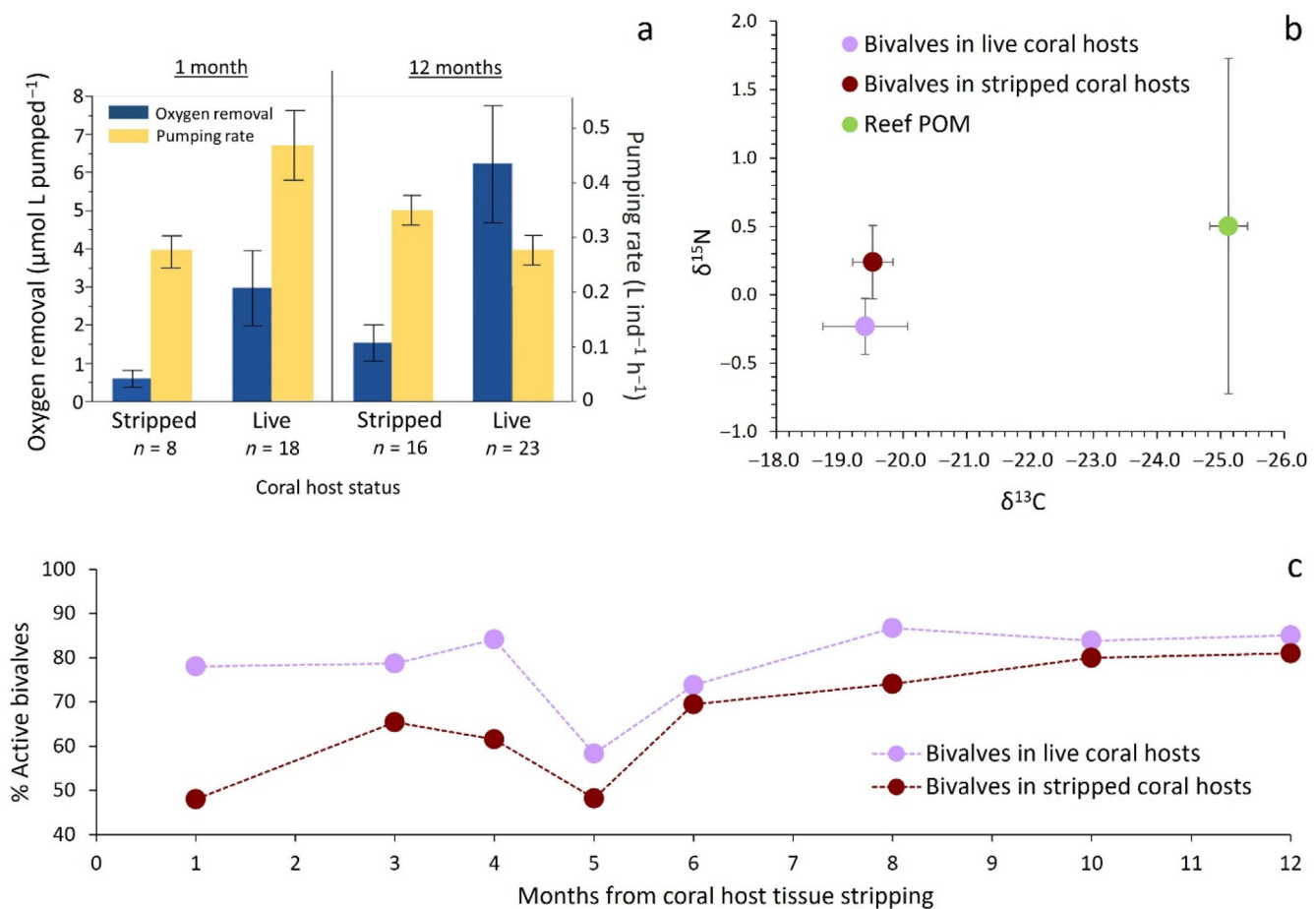
**FIGURE 1** In situ sampling of coral-boring bivalves in the coral reef of Eilat. (a) Installation of  $\text{O}_2$  measurement and recording system. (1) *Astreopora myriophthalma* coral head hosting >100 boring bivalves; (2) oxygen optodes; (3) data logger. (b) Coral colony showing two boring bivalve species, *Leiosolenus simplex* (L) and *Pedum spondyloideum* (P). (c) The usual appearance of *L. simplex* in the coral head shows a larger, more oval, inhalant siphon aperture (IN) and a smaller, rounder, exhalant siphon aperture (EX). (d) Fluorescein dye emerging from the exhalant siphon aperture of *L. simplex*, indicating active pumping. Photo credits: (a) Rei Diga, 5 May 2021; (b–d) Tom Shlesinger, 7 December 2022. All photographs were taken at the reef in front of the Inter-University Institute for Marine Science in the Gulf of Eilat/Aqaba.

overlying water, using standard methodology (Sharp, 2017). Plastic nets deployed on top of the experimental setup protected the coral colonies from predation.

The O<sub>2</sub> consumption of *L. simplex* was markedly reduced in the stripped coral hosts compared with that of *L. simplex* in the live coral hosts at both 1 and 12 months post-manipulation (Figure 2a). After 12 months, the percentages of actively pumping (i.e., known living) bivalves were relatively high (80%–85%) in both the living and stripped coral hosts. However, the percentage of actively pumping bivalves in the stripped coral hosts remained consistently lower in comparison with that of the live coral hosts throughout the 12-month observation period (Figure 2c). Thus, the reduced percentage of pumping bivalves in the stripped hosts before the 12-month mark did not signify higher mortality, but rather a lower frequency/duration of pumping activity than those in the live hosts. At the 12-month mark, *L. simplex* residing in live coral hosts

pumped at the same rate as those in the dead coral hosts, indicating that the high oxygen removal was not the result of a lower pumping rate but rather of higher oxidation of organic matter indicative of superior feeding (Figure 2a).

Given that both the boring bivalve and its coral host are suspension feeders, with the possibility of trophic niche overlap, the obvious next question was “How did removing the live coral tissue affect the diet of *L. simplex*?” The stable isotope data showed that the diet composition and trophic position of *L. simplex* were similar in live and dead coral hosts, with nearly identical δ<sup>13</sup>C values (indicating similar nutritional sources), and an observed δ<sup>15</sup>N difference ≈1‰, indicating a slight increase in trophic level of diet items in bivalves inhabiting dead corals (a difference of 3‰ signifying a change in trophic level; Adams & Sterner, 2000) (Figure 2b). The slight increase in the trophic level (δ<sup>15</sup>N) of bivalves inhabiting dead corals supports the possibility that the lack of competition from the coral polyps for zooplankton may be at play (Figure 2b). Although bivalves



**FIGURE 2** Physiological status and stable isotope trophic indicators of *Leiosolenus simplex* in live and stripped host corals. (a) Oxygen removal and pumping rates by *L. simplex* at 1 and 12 months post-stripping. (b) Stable isotope ratios (δ) of particulate organic matter (POM) suspended in reef water and tissue of *L. simplex* from live and stripped host corals 12 months post-stripping. (c) The percentage of actively pumping *L. simplex* from live and stripped host corals over the 12-month observation period. Error bars in (a) and (b) represent 95% confidence intervals for the mean. ind, individuals.

in both the live and the dead coral hosts showed typical stable isotope fractionation relative to reef POM (Duarte et al., 2018; Hondula & Pace, 2014), which they have been observed to capture (Amit et al., 2023; Yahel et al., 2009), the  $\delta^{13}\text{C}$  signature of the reef POM at the study site was much lighter ( $-25.1\text{‰}$ ) than that of the bivalve tissue ( $-19.4\text{‰}$ ) (Figure 2b). Coral tissue and mucus  $\delta^{13}\text{C}$  values in the Gulf of Eilat/Aqaba range from  $-10\text{‰}$  to  $-19\text{‰}$  (Alamaru et al., 2009; Muscatine et al., 1989; Naumann, Mayr, et al., 2010), suggesting that some fraction of the bivalve diet was derived from live corals, potentially coral mucus (Marshall, 1968; Naumann, Haas, et al., 2010; Shafir & Loya, 1983). Living within mucus-generating (i.e., live) corals may thus confer a trophic advantage to the boring habit of *L. simplex*. Coral mucus was likely also indirectly available to the individuals inhabiting the stripped corals in our experiment due to their physical proximity to the live corals (Johannes, 1967), thereby contributing to the similar  $\delta^{13}\text{C}$  values in both groups.

Because aerobic respiration is the metabolic pathway for obtaining energy from assimilated food, it appears likely that the difference in  $\text{O}_2$  consumption signaled an overall reduction in the quantity of food assimilated by the bivalves inhabiting the stripped coral. This interpretation is supported by the pumping rate data, which showed reduced  $\text{O}_2$  consumption even when the bivalves inhabiting stripped coral hosts had a higher pumping rate than those inhabiting live coral hosts (Figure 2a). Whereas the stable isotope data only inform as to the origin of the food and do not allow a quantitative comparison of the amount of each food type consumed/assimilated, the  $\text{O}_2$  consumption data argue for a greater amount of food being metabolized by the bivalves in the live coral heads, suggesting superior physiological condition.

Taken together, these data show that there were small differences in mortality or diet composition between *L. simplex* in stripped versus live coral hosts, compared to the larger differences in pumping rate and  $\text{O}_2$  consumption, during the 1-year experiment. The data indicated that live coral hosts provide a greater food supply, thus providing scope for a greater investment in growth and reproduction (Figure 2a,c). Hence, while it is possible for *L. simplex* to survive within a dead coral host for an extended period, a live coral host enhances the physiological state of this boring bivalve. It should be noted that over hundreds of survey dives in the natural reefs of the Red Sea, we did not observe any *L. simplex* living in naturally dead corals (T. Amit, G. Yahel, and Y. Loya, personal observations), underscoring the additional role of live corals in the protection of both the coral host and *L. simplex* from predation.

This study demonstrates the potential for advances in understanding interactions between cryptic reef species

by augmenting natural history observations with in situ experimental manipulations using appropriate underwater instrumentation. We plan to use a similar field deployment to examine how live coral hosts influence the reproductive biology and growth of boring bivalves and vice versa. The data presented here suggest that the perks of life within a live coral host go well beyond the provision of shelter.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Amit, 2023) are available in Zenodo at <https://doi.org/10.5281/zenodo.7965711>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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