



FEATURE ARTICLE: NOTE

The perks of being endolithic

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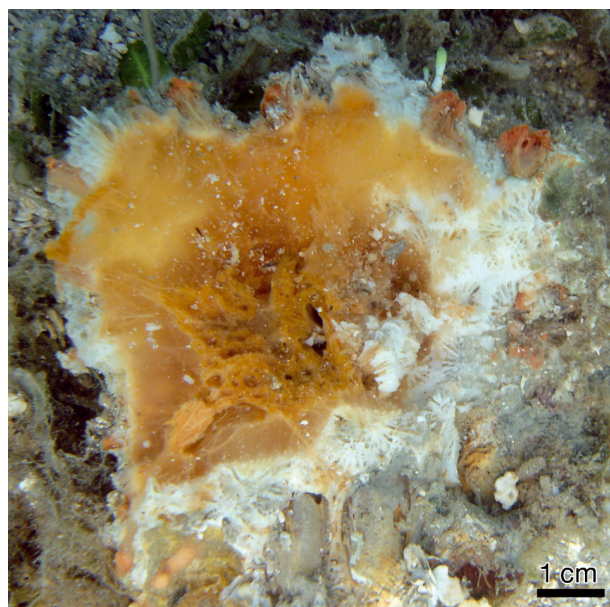
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ABSTRACT: Bioeroding sponges erode and live in calcium carbonate substrates such as coral skeleton. The most obvious reason for this lifestyle is shelter from grazers and predators, but this has never been conclusively shown. To investigate this we collected *Siphonodictyon mucosum* Bergquist, 1965 and *Cliothosa aurivillii* (Lindgren, 1898), 2 lesser-studied bioeroding sponges common in coral rock at Orpheus Island, central Great Barrier Reef, Australia. During sampling we broke up blocks of dead coral that contained the sponges and observed post-fracture healing processes. Even though both sponges produce large erosion chambers and their endolithic tissue is soft and easily ruptured, they initially displayed early signs of healing, showing some scarring after only 3 to 4 days. However, endolithic tissue of *S. mucosum* specimens exposed to direct sunlight did not continue to heal, but rotted away, while shaded tissue fully healed, toughened and turned brown-black like the external fistules. Likewise, endolithic tissue of *C. aurivillii* showed signs of healing by contracting, toughening and flattening, but after about 2 wk, some *C. aurivillii* individuals nevertheless began to rot and had patches of orange sediment underneath them. Their undersides were teeming with copepods. A closer investigation revealed that the copepods had orange stomach contents the colour of the sponge tissue and produced rust-coloured faeces collecting underneath the sponges. Hence, being endolithic has multiple sheltering functions beyond the obvious escape from grazers and predators, very likely including shading, shielding from parasites and disease, and saving on maintenance costs.

KEY WORDS: *Siphonodictyon* · *Cliothosa* · Macroendoliths · Healing · Disease · Parasitism

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Cross-section through a colony of the bioeroding sponge *Cliothosa aurivillii*. Endolithic tissue is very soft and vulnerable, while exposed papillae are dense with spicules

Photo: Christine Schönberg

INTRODUCTION

Most bioeroding sponges are obligatory macroendoliths, i.e. they inhabit calcium carbonate materials, such as coral skeleton and mollusc shells, in which they spread, producing new or widening existing cavities that are connected to the surface by exhalant and inhalant canals terminating in pores (e.g. Schönberg 2008). While free-living forms exist, they appear to retain bioerosion capabilities (Hatch 1980). Sev-

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eral authors have speculated as to why these sponges expend energy to erode and what they gain from this lifestyle. Ward & Risk (1977) proposed that they may obtain nutrition from the removed material, but similar to free-living sponges, bioeroding sponges actively move water through their bodies and can be assumed to be efficient filter feeders (Fig. 1a; C. H. L. Schönberg & A. J. Pile unpubl. data for Australian *Cliona orientalis*, *Cliona celata* and *Siphonodictyon mucosum*). Moreover, some of the most aggressive bioeroding sponges harbour symbiotic dinoflagellates that apparently support their hosts with photosynthates (Rosell & Uriz 1992, Hill 1996, Schönberg 2006, Weisz et al. 2010). It seems to be more plausible to explain the bioeroding habit of sponges with sheltering and shaping functions afforded by the surrounding hard substrate. Water retained in the erosion chambers may provide protection from desiccation in the intertidal (Schönberg 2000, 2001), and the substrate also supplies shade for photosynthetic symbionts and the sponge itself (Schönberg & Suwa 2007).

It has been assumed by a number of authors that the main reason for bioerosion is creating refuge from grazers and predators (e.g. González-Rivero et al. 2012; our Fig. 1b), but interactions with predators and grazers are poorly studied, and some observations suggest that predation can even be positive for the sponges by removing coral tissue along with sponge tissue from the zone of interaction, stimulating sponge growth rates (Márquez & Zea 2012). Endolithic clionoids usually have a lower spicule:tissue ratio than their free-living relatives (C. H. L. Schönberg pers. obs.), and the physical support by the hard substrate may save them costs for structural enforcement with spicules. During an extended research program on the central Great Barrier Reef, Australia, 2 comparatively understudied sponge species were sampled, and further aspects to explain this endolithic lifestyle became apparent.

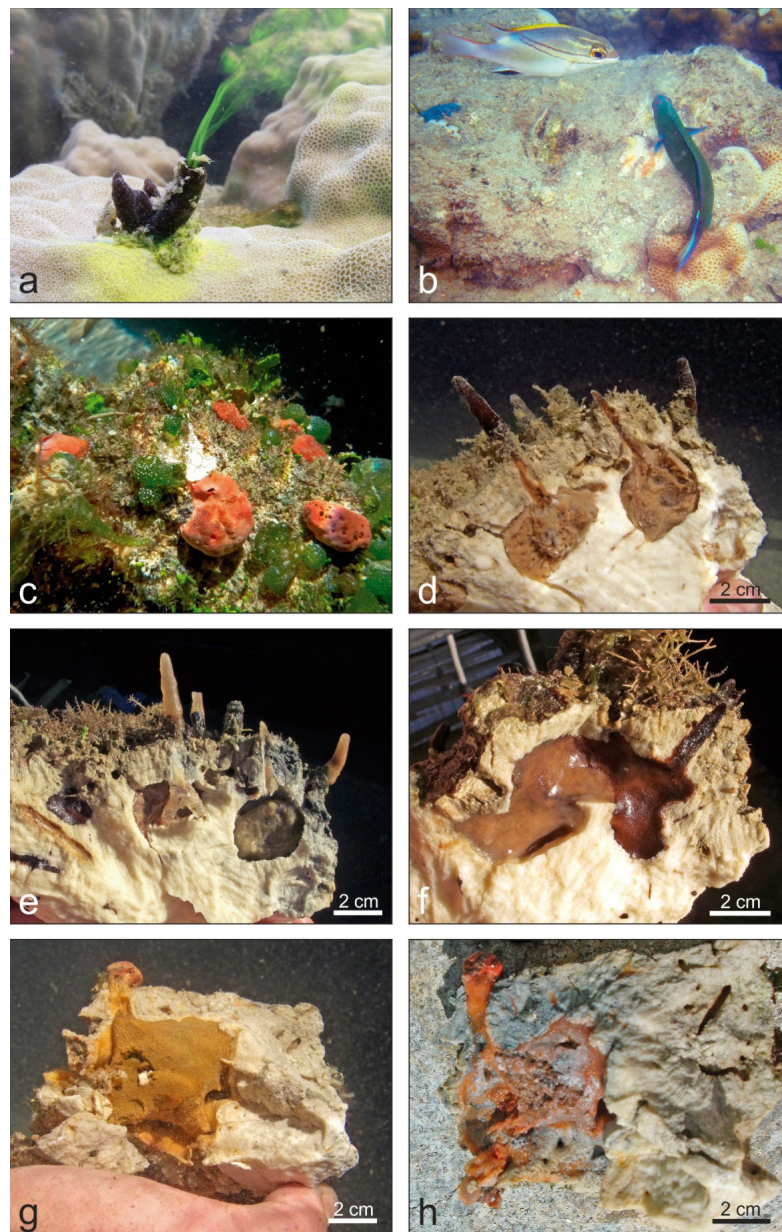


Fig. 1. *Siphonodictyon mucosum* and *Clionothosa aurivillii* from Orpheus Island, central Great Barrier Reef. (a) Intact *S. mucosum* treated with fluorescent dye to visualise its pumping currents; (b) soft endolithic tissue of *C. aurivillii* damaged by sampling is immediately attacked by fish. Here a goatfish and a moon wrasse; (c) *C. aurivillii* in a block of calcareous material in the sandy intertidal before sampling (*S. mucosum* can be found in the same conditions); (d) freshly sampled fragment of *S. mucosum*; (e) same fragment of *S. mucosum* after 4 d, having been exposed to sunlight. Big erosion chamber on the right with 'black rot', middle chamber with macerated fistular base and small chamber on the left with contracted, healed, dark-coloured tissue. Note that all fistules either lost their dark colour or were largely macerated; (f) fully healed tissue in an especially large erosion chamber of a different specimen of *S. mucosum* after 13 d. The tissue significantly contracted, toughened and darkened over time; (g) sample of *C. aurivillii* in the tank on the day of sampling. The tissue already had contracted to some degree; (h) the same sample of *C. aurivillii* with symptoms of 'black rot', 13 d after sampling, with the typical white layer signifying the onset of the disease

MATERIALS AND METHODS

Observations were made at Orpheus Island Research Station, Palm Island Group, central Great Barrier Reef, Australia. We sampled several specimens each of the 2 sponges *Siphonodictyon mucosum* Bergquist, 1965 and *Cliothosa aurivillii* (Lindgren, 1898) from the sandy intertidal of Pioneer Bay, where they commonly inhabit old coral blocks that are partially buried in sand and regularly exposed to air at low tide (Fig. 1c). Blocks were broken up with hammer and chisel, and sponge-containing fragments were carried back to the research station in a bucket with seawater with the aim to assess their recovery capabilities, and thus their suitability for possible future parameter-controlled tank experiments. Both species have large, cavernous erosion chambers often only containing a single body of endolithic tissue, which becomes exposed and severely damaged during sampling. This may result in slower healing and a reduced likelihood of recovery in comparison to sponges with small erosion chambers and porous erosion patterns, for which the proportion of chambers with undamaged tissue after sampling is higher. Rock fragments containing *S. mucosum* and *C. aurivillii* were placed into flowthrough outdoor raceway tanks with unfiltered seawater to recover, and were not further treated, but visually checked every 3 or 4 d for 3 wk. Adverse developments towards the end of this study required investigations by microscopy which were conducted on an Olympus BX41 light microscope equipped with an Olympus DP70 camera and the Olympus software DP Manager. Subsamples of copepods found during the study were either preserved in 70 % ethanol or 3 % formalin, and specimens were made available for further research at the German Centre for Marine Biodiversity at Senckenberg am Meer in Wilhelmshaven, Germany.

RESULTS AND DISCUSSION

Even though *Siphonodictyon mucosum* and *Cliothosa aurivillii* produce large erosion cavities and their soft tissue was ruptured and torn during sampling (Fig. 1d,g), the sponges initially healed very quickly, showing clear evidence of recovery and scarring after only 3 to 4 d. For these 2 species this demonstrates healing capabilities almost as strong as in the case of *Cliona orientalis*, which has small bioerosion chambers in finely-porous distribution and is generally fully healed 4 d after sampling and ready

for use in any experimental work (e.g. Wisshak et al. 2012). However, where the delicate, endolithic, light-coloured tissue of *S. mucosum* was situated on upper parts of the samples and exposed to full sunlight, it became putrid, showing black patches and a white overlying film (Fig. 1e). Affected tissue continued to rot away until 2 wk after sampling, when some erosion chambers were empty and only spongin-reinforced tubes at the bases of the fistules as well as the macerated fistules remained behind (Fig. 1e). In the same time span shaded tissue in neighbouring chambers on lower parts of the samples which faced the bottom of the holding tank further contracted, became firmer, toughened, hardened and darkened to the same brown-black as the fistules and were thus considered fully healed (Fig. 1f). While in the field this process may be prevented by predators taking advantage of any exposure of the tissue, in the tank the healing process changed the properties of the light-coloured and soft endolithic tissue to resemble those of external fistules, thereby giving it a firmer texture putatively less vulnerable to predation, and adapting it to the higher light levels that affect exposed parts of *S. mucosum*. Other *Siphonodictyon* spp. have been described to occur in the intertidal where they need to be adapted to high irradiation levels at low tide, and dark pigmentation appears to be important (Rützler 1971, Schönberg 2001).

Cliothosa aurivillii also showed rapid signs of healing after sampling (Fig. 1g), with tissue contracting, flattening, firming and toughening. After about 2 wk, however, some fragments displayed early stages of the same 'black rot' disease as observed in *Siphonodictyon mucosum*, this time on exposed, but shaded portions of the endolithic tissue (Fig. 1h). There were also some patches of dull-orange sediment directly underneath tissue portions with 'black rot'. Upon closer investigation, we found exposed tissue on the undersides of the fragments teeming with tiny organisms which were concentrated on the sponge tissue and not on the surrounding substrate. These organisms were identified under the microscope as copepods of the genus *Tisbe* (subsample of 72 individuals: 96 % *Tisbe* sp., 3 % *Delavalia* sp. and 1 specimen of the Thalestridae), and all adults had orange stomach contents of the same colour as endolithic tissue of *C. aurivillii* (Fig. 1c,g,h, Fig. 2a). The copepods produced rust-coloured faeces that collected underneath the sponges (Fig. 2b), resulting in the dull-orange sediment patches. On exposed external tissue of the same sample, i.e. on the papillae of *C. aurivillii* we found only very few of the same copepods and here no damage to the sponge was apparent. By



Fig. 2. Microscopy photographs of parasitic copepods feeding on *Cliothisa aurivillii* and of a few threads of the black disease affecting the sponge. (a) Adult copepod of the genus *Tisbe* with orange stomach contents; (b) a pellet of copepod faeces; (c) microbial threads attached to a tylostyle spicule sampled from a rotting specimen of *C. aurivillii*

opening the erosion chambers during sampling, the obviously parasitic copepods thus obtained access to the softer and possibly less well chemically defended endolithic tissue of *C. aurivillii*, fed and multiplied, and eventually reversed the healing process by reopening the sponges' newly established ectosome, preventing proper scarring, and finally also allowing the disease to infect the sponge tissue. *S. mucosum* was not affected by the parasitic copepods, but the genus is well known for its antibiotic properties (e.g. Sullivan et al. 1986).

We have previously observed 'black rot' disease in samples of *Cliona orientalis* and *C. celata* in experimental situations where the specimens were subjected to extremely stressful conditions, often resulting in death or at least in partial tissue loss (authors' pers. obs.). In a few occasions it has also been encountered in *C. orientalis* in the field (C. H. L. Schönberg pers. obs.). The disease starts with small patches of a spreading white film that can form a delicate cocoon around the sample, underneath which black, stinking patches of dead tissue develop that usually grow across the entire sample. The same aetiology has been described for a bacterial disease found in coral (Jones et al. 2004), but our microscope images of *Cliothisa aurivillii* were insufficient to discriminate between bacteria and fungi (Fig. 2c). If healthy and diseased specimens of *C. orientalis* are kept together in a small tank, the disease can occasionally spread and afflict previously unstressed specimens (authors' pers. obs.). In the rare cases where samples recover, the disease runs its course, finally leaving empty patches of clean substrate behind, while endolithic tissue and some surface tissue of *C. orientalis* persist, scar and heal (authors' pers. obs.).

We conclude that, for sponges, the endolithic habit has multiple sheltering functions beyond the obvious

escape from severe damage by grazers and predators. According to our observations, being endolithic creates shade for light-sensitive tissue and cover for insufficiently defended soft tissue that contains fewer spicules than that of free-living congeners. While intact, the sponges do not need to produce as much skeleton as they have to embed in their scar tissue, now open to the environment. And maybe most importantly, the surrounding substrate potentially provides a shield against parasites, diseases and vectors of disease. Therefore, an endolithic life style results in savings in maintenance costs, which would adequately compensate for the costs of the bioerosion process.

Acknowledgements. We thank the staff at Orpheus Island Research Station for their outstanding and cheerful support, and C. Ansell and N. Lee for field assistance. We are indebted to K. H. George from the German Centre for Marine Biodiversity at Senckenberg am Meer for kindly identifying our sponge-eating copepods. Fieldwork was part of the German Science Foundation project Fr 1134/19 and was co-funded by The Australian Institute of Marine Science.

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Editorial responsibility: Paul Sammarco,
Chauvin, Louisiana, USA

Submitted: April 18, 2012; Accepted: August 23, 2012
Proofs received from author(s): September 10, 2012