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Chemical *versus* mechanical bioerosion of coral reefs by boring sponges – lessons from *Pione cf. vastifica*

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Summary

Bioerosion by boring sponges is an important mechanism shaping the structure of coral reefs all around the world. To determine the excavation rate by boring sponges, we developed a system in which chemical and mechanical boring rates [calcium carbonate ($CaCO_3$) dissolution and chip production, respectively] were measured simultaneously in experimental tanks containing reefal rock inhabited by a boring sponge. *Pione cf. vastifica* (Hancock 1849) was chosen as a model species to study the erosion rate of boring sponges. It is an abundant species in the coral reefs of the Nature Reserve Reef, Elat, Gulf of Aqaba, northern Red Sea, reaching maximum abundance at 25–30 m. The rate of chemical bioerosion was determined from the increase in tank-seawater alkalinity over time, and the mechanical bioerosion rate was estimated from the total amount of $CaCO_3$ chips produced over the same time interval. The measured bioerosion rate of *P. cf. vastifica* was 2.3 g m^{-2} sponge day^{-1}, showing seasonal but not diurnal variations, suggesting that the zooxanthellae harboring the sponge have no effect on its boring rate. The experiments indicated clearly that per each mass of chips that *P. cf. vastifica* produces during its boring activity, it dissolves three masses of reef $CaCO_3$ framework. Assuming that some additional boring sponges can use a similar strategy of bioerosion, these findings suggest that chips, the most obvious erosion products of boring sponges, represent only a small fraction of boring sponge bioerosion capacity.

Key words: Porifera, excavation, coral reef, dissolution, Clionaidae.

Introduction

The structure and form of the highly complex coral reefs are mainly the result of the interaction between two processes: construction and destruction. Reef growth is mainly attributed to skeletal deposition of organisms having a calcium carbonate ($CaCO_3$) skeleton, such as stony corals, molluscs, polychaetes and crustose coralline algae (Loya, 1990). The agents of destruction are biological, physical and chemical, and in many cases their effect on the erosion is synergistic (Hutchings, 1986). Biological erosion (bioerosion) as a general term refers to the destruction and removal of consolidated minerals of lithic substrate by the direct action of organisms (Neumann, 1966). The most common agents of bioerosion are fish (Risk and Sammarco, 1982), sea urchins (Mokady et al., 1996), algae (Kobluk and Risk, 1977), molluscs (Londono-Cruz et al., 2003; Hutchings et al., 2005), polychaetes and sipunculids (Londono-Cruz et al., 2003) and sponges (Holmes et al., 2000; Hutchings et al., 2005). Physical erosion is caused by wave movement, storms, etc. Chemical erosion involves dissolution of the $CaCO_3$ framework and is mainly mediated by biological activity, either by metabolic acid production or by excretion of ligands and enzymes. The organisms may also contribute to the erosion through their physical boring and scraping activity on the substrate.

Boring sponges, mostly from the family Clionaidae, generally dominate the bioeroder community (Risk et al., 1995; Calcinai et al., 2000). Whereas many sponges are chemically or mechanically defended, some that have no such defenses may have the competitive advantage of using a substrate that other organisms cannot use. One such strategy is to bore into the carbonate substrate that is out of reach of most predators, with the additional advantage of using a space unavailable to their competitors. The activity of boring sponges has far-reaching ecological and economic effects: they can host many organisms inside their water channels; affect settlement of new organisms by changing availability of reef areas; shape the morphology and affect the strength of the reef framework (Risk and Muller, 1983; Neumann, 1966); influence the alkalinity and the dissolved silica of reef-water chemistry; infect cultured clam, oyster, or abalone populations in marine farms (Rosell et al., 1999; Fromont et al., 2005); and bore into the structure of piers and water breakers (Warburton, 1958). Boring sponges

have been used for paleoenvironmental reconstruction, for example, by measuring the size of bore holes in reefs from the geological record (Edinger and Risk, 1996).

Boring sponges have developed a unique cellular means of penetrating the substrate (see Bergquist, 1978; Pomponi, 1980). The sponge attaches itself onto the substrate and then penetrates by using etching cells to separate $CaCO_3$ chips from the substrate (size range, 15–85 μm). Chip production constitutes the so-called 'mechanical boring' of sponges; however, detachment of chips from the hard substrate requires the use of 'chemical boring' as well. A groove is chemically etched, isolating a chip from the substrate. It is then mechanically transferred out of the sponge body *via* the water channels.

Rates of bioerosion depend on several biotic and abiotic factors, including nutrient and food availability, temperature (Risk et al., 1995; Hill, 1996; Holmes et al., 2000), physiological state of the organism (Rützler, 1975) and the density and type of substrate in which the organism bores (Hutchings, 1986).

The sponge *Pione vastifica* (Hancock 1849) has a cosmopolitan distribution (Warburton, 1958). There is evidence for its distribution in west and east Mediterranean (Bromely et al., 1990; Rosell and Uriz, 2002), Barbados (Holmes, 2000), the Red Sea, Mozambique and the Seychelles (Calcinai et al., 2000). Because of its worldwide distribution, there has been a genuine misconception regarding its true definition (Rützler and Stone, 1986), and recently it has been relocated to the genus *Pione* within the family Clionaidae (Rosell and Uriz, 1997). The sponge hosts many symbiotic organisms, such as zooxanthellae (dinoflagellates) and *Polydorella smurovi* (Tzetlin and Britayev, 1985) (Polychaeta), that live inside its tissue or on its surface, respectively. Despite its high abundance and distribution over a wide depth range on Red Sea reefs, the bioerosion activity of *P. cf. vastifica* has never been studied and quantified.

The aim of the present study was to determine the erosional impact of this sponge on the coral reef as a model for the boring sponge erosion rates. We used *P. cf. vastifica* despite its relatively low abundance (as compared with the abundance of other species of boring sponges) in the studied reefs because of its encrusting (β) growth form. This growth form facilitates measurements of chemical *versus* mechanical boring activity (see below), whereas the papillate (α) growth form of another co-occurring boring species is more complicated for such measurements.

We studied *P. cf. vastifica* distribution and abundance in the coral reef of Elat, measured its bioerosion rate and determined the relative proportion of chemical *versus* mechanical boring mechanisms. The sturdiness of this species facilitated the development of our laboratory experiments and analytical methodology. The experimental set-up we developed for the study can also be easily adapted for other sponge species.

Materials and methods

Field collections and sponge census

The research was conducted in the Nature Reserve Reef (NRR), northern Gulf of Aqaba, Red Sea (31°25′N; 34°53′E), a fringing reef located south of the city of Elat, Israel. Samples of reef rock heavily inhabited by individuals of the sponge *Pione cf. vastifica* were collected by SCUBA diving using a chisel and hammer. The samples were transferred for acclimation into aquaria at the H. Steinitz Marine Biology Laboratory (The Interuniversity Institute for Marine Sciences, Elat, Israel).

Species abundance was estimated using 10×1 m belt transects (Loya, 1972). Arbitrarily placed transects (N=15–20) were performed at depths of: 10, 15, 20, 25 and 30 m. The number of individual sponges and their surface area was recorded for each belt transect. The surface area of each sponge was estimated by covering it with an equivalent surface of aluminum foil and converting the aluminum foil mass (M_{Al}; g) to sponge surface area (A_{sponge}; cm^2) using the calibration curve: $A_{sponge}=227\times M_{Al}$. Analysis of variance (ANOVA) and nonparametric a posteriori LSD tests were used to analyze the results.

Laboratory experiments

Three to five reef rock samples (formerly *Porites* sp. corals, ~15 cm diameter), heavily inhabited by *Pione cf. vastifica* sponges, were collected from 20 m depth once every three months, and were placed for a 24 h acclimation period into Plexiglas containers filled with 2.5 l of filtered (0.2 μm) seawater (total N=24). As a control we used dead coral skeletons (*Porites* sp. maintained out of the water for several months), uninfected by any boring organism, that were immersed in filtered seawater for 48 h prior to the experiments. Prior to immersion, the inhabited rocks and the control fragments were gently cleaned with a brush and washed three times to remove all the epibionts that lived on the substrate and which could affect the water composition. The experiments started after replacing the seawater in the Plexiglas containers and lasted for 24 h. During the experiments the containers were aerated and covered to minimize water evaporation, which can change water condition and composition.

Determination of chemical boring rate

Rate of chemical boring was determined by measuring changes in total alkalinity (A_T) in the seawater during the experiments. Total alkalinity of 'normal' seawater is defined as (Stumm and Morgan, 1981):

$$A_T = [HCO_3^-] + 2[CO_3^{-2}] + [B(OH)_4^-] + [OH^-] - [H^+] , \quad (1)$$

which in effect is the number of equivalents of strong acid added to a seawater sample in order to reach the H_2CO_3 endpoint. In our experiments, changes in total alkalinity resulted almost entirely from precipitation or dissolution of $CaCO_3$ (Lazar and Loya, 1991). The molar amount of $CaCO_3$ dissolved by the sponge was half of the observed A_T increase in the experimental aquarium. Effects on total alkalinity other than $CaCO_3$ dissolution or precipitation may result, for example, from A_T decrease due to aerobic respiration and production of HNO_3, and the opposite effect may result from photosynthesis and NO_3^- assimilation. In our experimental system these non-conservative

effects on A_T were negligible. A_T was measured by potentiometric titration and by fitting a Gran function. The mass of $CaCO_3$ dissolved by the sponge, $M_{(CaCO_3)}$ (in g), was calculated from the change in total alkalinity [ΔA_T (eq kg^{-1})] during the experiment (A_T at the end of the experiment minus A_T at the beginning, ~24 h earlier) as follows:

$$M_{(CaCO_3)} = 0.5 \text{ (mol eq}^{-1}) \times \Delta A_T \times 100 \times V_{sw} \times \rho_{sw} , \quad (2)$$

where 100 is the molecular mass of $CaCO_3$; V_{sw} is volume (l) of seawater in the experimental aquarium; and ρ_{sw} is the seawater density (~1.028 kg l^{-1}).

The boring activity was measured both during day time and at night, since it has previously been shown that distribution of some *Cliona* species correlated with light irradiance (Lopez-Victoria and Zea, 2005), and *Cliona varians* (Duchassaing and Michelotti 1864) boring rate was correlated with zooxanthellae abundance and light irradiance (Hill, 1996).

Determination of mechanical boring rate

At the end of each experiment the aquarium was stirred, the $CaCO_3$ chips produced by the sponge and settled on the bottom were resuspended and the seawater was filtered through a glass fiber filter (3 μm) to collect all the chips. The filter with the chips was combusted at 450°C for 6 h to remove all organic matter. After cooling, the residues were passed through 200 μm and 100 μm sieves, removing large particles, assuming that the sponge-produced chips lie within a smaller fraction <100 μm (see above). The filtered chips were cooled to –70°C, freeze-dried to remove any traces of water and weighed.

Electron microscopy

Small fragments (~2×3×3 mm) of rocks containing sponges were gently broken using sharp knives as chisels. The samples were immersed for 24 h in diluted sodium hypochlorite. The clean fragments were rinsed three times for 30 min in distilled water and then three times for 30 min in ethanol (100%). The samples were then air dried and glued on stubs for examination with a scanning electron microscope. The fragments were critical-point dried and sputtered with gold. The preparations were viewed with a JEOL JSM 840A SEM-microscope (Tokyo, Japan).

Clean sponge spicules for electron microscope examination were obtained by decalcifying sponge samples (immersing the samples overnight in diluted sodium citrate and formic acid) and digesting the tissue (12 h immersion in sodium hypochlorite). The residues were rinsed three times in water and three times in ethanol (100%), mounted on stubs, gold coated and inspected on a JEOL JSM 840A SEM-microscope. The length (N=40) and width (N=25) of complete spicules from each type were measured.

Results

Sponge identification and description

The sponges studied here were tentatively identified as *Pione cf. vastifica* based on the brightly orange-red colors of the sponge and the spicule types. The spicules found within this sponge (Fig. 1) were of three types: tylostyles to subtylostyles (length: range 155–241 μm, mean 230±30 μm; width: range 2.0–4.0 μm, mean 3.6±0.6 μm), acantho microxea (length: range 77–125 μm, mean 103±13 μm; width: range 2.0–3.5 μm, mean 2.8±0.4 μm) and acantho microrhabds (length: range 6.3–10.0 μm, mean 8.5±1.1; width: range 2.0–4.0 μm, mean 2.5±0.5). However, the clionaid's encrusting growth form, where the sponge covers the dead surface skeleton of usually massive corals, has not been reported for *P. vastifica* (Schönberg, 2002a), and hence the current identification as *P. cf. vastifica* indicating its affiliation with this species complex.

Sponge distribution in the reef

In the depth range of this study (down to 30 m depth), the abundance of *P. cf. vastifica* increased linearly with depth by ~2 individuals per 10 m^2 per 10 m depth (Fig. 2). This finding was corroborated by an ANOVA test, which showed a significant difference in abundance between the various depths (P<0.001), and an *a-posteriori* test, which revealed three main depth-related abundance groups (10, 15 and 20, and 25 and 30 m) in which the abundance increased with depth.

Surface area of individual sponges varied at all depths

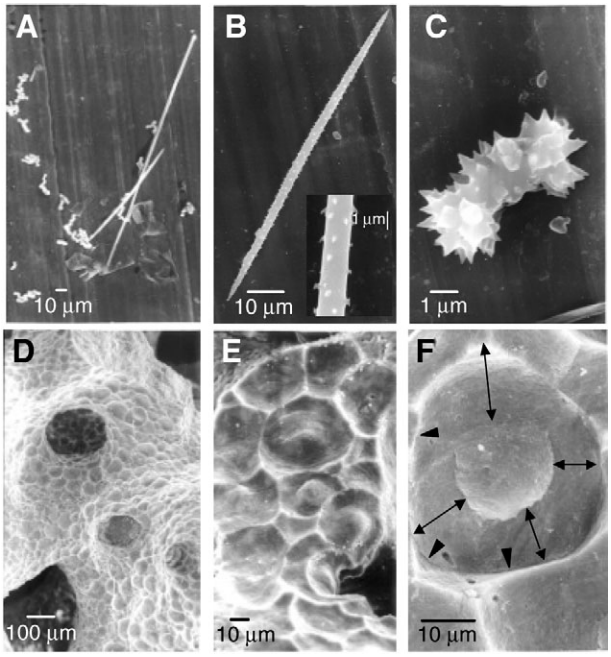

Fig. 1. *Pione cf. vastifica* spicules and erosion scars. (A) All three types of spicules. The longest one is a tylostyle. (B) An acantho microxea. (C) An acantho microrhabd. (D) Wall of sponge excavation in coral, covered with erosion scars. (E) A few erosion scars of different shapes. Of note are the projections in the center of some of them, where no substrate dissolution occurred. (F) A single erosion scar with a small projection in the middle. Signs of penetration beneath the projection are evident in its perimeter (arrowheads). Arrow indicates the area assumed to have been chemically removed.

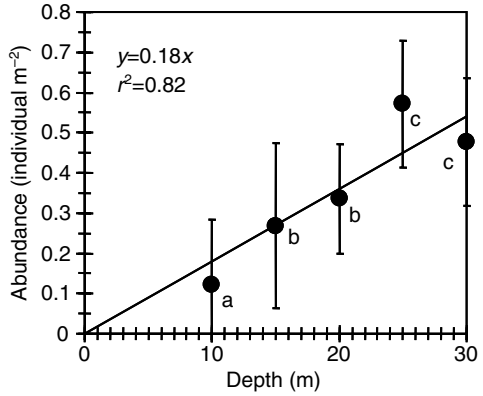

Fig. 2. Abundance of *Pione cf. vastifica* at different depths (mean ± s.d.). a, b and c show statistically different groups (ANOVA and LSD a-posteriori test; $P<0.001$).

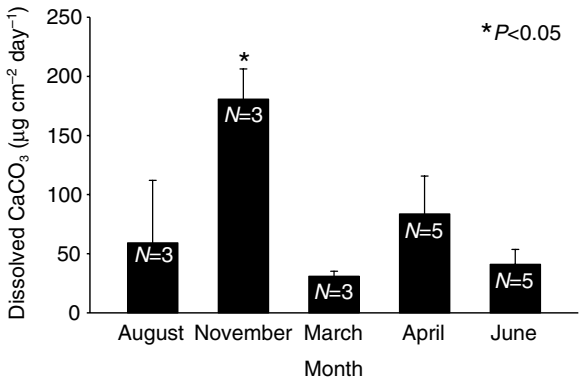

Fig. 4. Chemical boring rate of *Pione cf. vastifica* in different months (mean + s.d.), (ANOVA, $P<0.05$).

ranging from 20 to 1000 cm^2. No significant difference was found in a one-way ANOVA between sponge sizes at different depths, and the mean sponge area was approximately 400 cm^2 with only a small number of small individuals (Fig. 3).

Sponge chemical bioerosion

Rate of chemical boring was measured from three to five individual sponges for five different months, at water temperatures ranging from 28.1°C in August to 21.5°C in November (Fig. 4). In a one-way ANOVA test, a significant difference was found between the rates of chemical boring during these months ($P<0.05$). When analyzed by an LSD a-posteriori test, the highest boring rate was measured in November, in which the amount of $CaCO_3$ dissolved by the sponges was 180±30 μg $CaCO_3$ cm^{-2} sponge day^{-1}, and the lowest rate was during March, with a rate of 30±4 μg $CaCO_3$ cm^{-2} sponge day^{-1}. The mean chemical bioerosion rate (calculated by annual integration) was 74±16 μg $CaCO_3$ cm^{-2} sponge day^{-1}, with no significant difference (according to a paired *t*-test) between day and night (Fig. 5).

Sponge mechanical bioerosion

Electron microscope examination of the substrate excavated by *P. cf. vastifica* showed the smooth erosion scars (length: range 36–97 μm, mean 59±18 μm; width: range 17–73 μm, mean 40±13 μm; $N=15$) to be polygonal to oval (often round) in shape (Fig. 1). Closer observation revealed that the excavated pit frequently had a small projection in the middle (Fig. 1E,F), suggesting that the entire surrounding of this projection had already been dissolved.

Discussion

Remarks on the species

The spicule types and the sponge color support its placement within the genus *Pione* close to the *P. cf. vastifica* (Hancock) species complex. However, we have previously found that this Red Sea *P. cf. vastifica* always harbors photosynthetic symbiotic algae (Beer and Ilan, 1998; Steindler et al., 2001). Thus, the encrusting (β) growth form and the presence of symbiotic algae do not fit this species (Rützler, 2002a). Recently, material from another previously recognized *P. cf. vastifica* from Western Australia was reassigned to *P. velans* (Fromont et al., 2005). Further systematic treatment of the

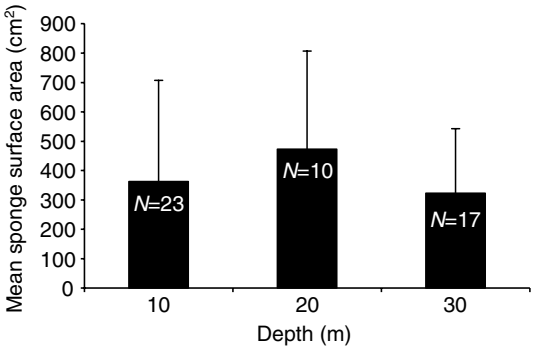

Fig. 3. Surface area of individual *Pione cf. vastifica* at different depths (mean + s.d.).

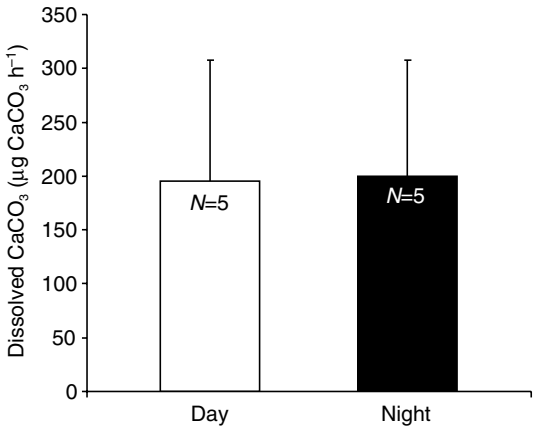

Fig. 5. *Pione cf. vastifica* chemical boring rate during the day and at night (mean + s.d.).

present species from the Red Sea, such as a comparison with *P. mussae* (Keller, 1891), will reveal its proper assignment. In this paper, however, for lack of strong counter-characteristics, this species is still called *P. cf. vastifica.*

Sponge abundance and distribution

The abundance of *Pione cf. vastifica* was found to increase linearly with depth in the range of 10–30 m (Fig. 2), with no difference in individual size at the different depths. The increase in population density was two individuals per 10 m^2 for a depth interval of 10 m (the slope of the trend-line in Fig. 2). No transects were performed in the depth range of 0–10 m because *P. cf. vastifica* abundance in this range was very low and the sponge was found mainly in deeper waters. No systematic transects were performed below 30 m due to logistical difficulties, but sporadic dives indicated that sponge abundance below 30 m depth was high. Such a pattern of population distribution could be the result of several pre- and post-settlement processes that were not examined in the course of the present study.

The scarcity of small individuals in the reef is rather puzzling, especially because individual sponge tissue was found to contain oocytes (A.Z., unpublished). This may suggest a long period with no recruitment prior to the present study or that young individuals grow very fast and after reaching a certain size (>100 cm^2) their growth rate slows substantially. Alternatively, it might be that the smaller individuals grew within the substrate and took the encrusting growth form only after reaching a larger size. Since in the present study we concentrated on the encrusting growth form, a situation as described above would have been overlooked.

Sponge bioerosion rates

Many studies have examined boring sponges and their activity because of their unique and important role in the shaping of hard-bottom environments (e.g. Rützler and Rieger, 1973; Acker and Risk, 1985; Thomas, 1996). Most of these studies, however, measured total $CaCO_3$ disappearance and frequently focused on the mechanical boring rates, i.e. the production of $CaCO_3$ chips, while guessing the amount of the chemical boring rate (Warburton, 1958) or calculating (Rützler and Rieger, 1973) it to be 10–2% of the total bioerosion, respectively. The present study is the first to simultaneously quantify both the chemical and mechanical bioerosion rates. The mean amount of $CaCO_3$ that was chemically removed from the substrate was 260 g m^{-2} sponge $year^{-1}$ (Fig. 4), which is approximately three times more than that mechanically eroded by the same sponge over the same period (80 g m^{-2} sponge $year^{-1}$). The chemical and mechanical erosion rates correlate positively (Fig. 6) with a chemical/mechanical boring rate ratio of ~3, reflecting dissolution of three volumes of $CaCO_3$ during production of one volume of chips. Indeed, the pattern of the erosion scars seen in pits with incomplete chip removal (Fig. 1D-F) indicates that most of the scar has been chemically dissolved, which has not been previously noted in any other bioeroding sponge. The total bioerosion rate (chemical plus mechanical) is 340±170 g m^{-2} sponge $year^{-1}$,

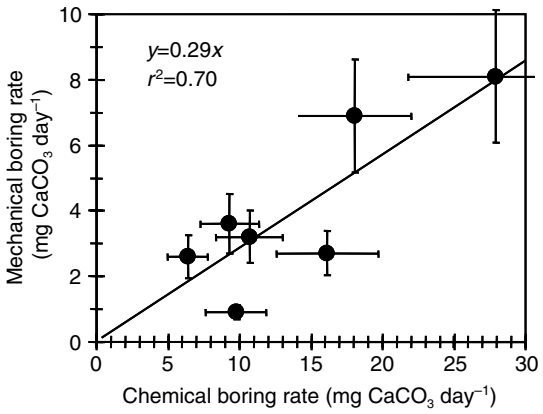

Fig. 6. *Pione cf. vastifica* rates of chemical boring *versus* mechanical boring by individual sponges (mean ± s.d.).

which is equivalent to sponge bioerosion per reef area of 68±34 g m^{-2} $year^{-1}$. Boring activity during November was significantly higher than during the rest of the examined months (Fig. 4). The total erosion of the reef by this *Pione* species is estimated to be rather small compared with clionaids (0.2–23.8 kg m^{-2} $year^{-1}$ results given per sponge surface area and not reef area) and other bioeroders (11–724 g m^{-2} $year^{-1}$ for sea urchins) reported from the same reef and from reefs elsewhere [see Schönberg (Schönberg, 2002b) and Mokady et al. (Mokady et al., 1996), respectively].

The large variability between studies in the measured sponge erosion rates may stem from: (1) Variability in type and density of the substrate. We used skeletons of dead *Porites* sp. coral whereas other studies used other coral species and much denser bricks of $CaCO_3$ or skeletons of molluscs, as reviewed, for example, in Schönberg (Schönberg, 2002b). The latter study found that the measured $CaCO_3$ erosion per unit volume increased with substrate density. Substrate type may yield erosion rate variability of up to six times the values for measurements performed on the same sponge species in the same locality [see, for example, table 4 in Schönberg (Schönberg, 2002b)]. (2) Differences in the species of sponges studied (Schönberg, 2002b). The present research used only one species, *P. cf. vastifica*. (3) Variability in sponge age. All specimens studied in this study were mature individuals, which bore more slowly, whereas other studies used young sponges or fragments that bore faster (Rützler, 1975). (4) The length of the sponge's water canals. It was shown that the boring activity decreases when the water canals pass a certain threshold length (Neumann, 1966). (5) Variability in nutrient levels. It was argued that high nutrient levels stimulate boring rate in sponges (Holmes, 2000). The surface water of the northern Gulf of Aqaba, northern Red Sea, is depleted of nutrients during summer and may contain relatively high nutrient levels during spring. (6) Variability in water temperature. The sponge boring activity that might be temperature-dependent (Rützler, 2002b) is low in the cooler water of the northern Gulf of Aqaba (sea surface temperature ranges of between 20°C and 28°C).

The results of this study indicate that the chemical boring rates of *P. cf. vastifica* are constant during a diurnal cycle, showing no change between night and day (Fig. 5). Light intensity, the daytime net photosynthesis of the symbiotic zooxanthellae and the night-time net respiration of the sponge were apparently not reflected by a change in the boring rate of *P. cf. vastifica*. This finding is in contrast to the results of an earlier study showing that the boring rates of the sponge *Cliona varians* forma *varians* correlated with zooxanthellae abundance and light irradiance (Hill, 1996). However, it was shown that for the sponge species studied here, *P. cf. vastifica*, the zooxanthella abundance did not correlate with light intensity (Steindler et al., 2001), supporting the findings of the present study.

In summary, the present study demonstrated the feasibility of simultaneously measuring chemical and mechanical boring rates. The combined chemical and mechanical boring rate of the sponge *P. cf. vastifica* in the reefs of the northern Gulf of Aqaba was estimated to be 70 g m^{-2} $year^{-1}$, which is ~1–2% of the total growth (calcification) rate on these reefs (Barnes and Lazar, 1983). The abundance of *P. cf. vastifica* in these reefs is much lower than that of other clionaid sponges. Therefore, the actual role of boring sponges in northern Red Sea reef bioerosion is most probably much larger than the rate cited above.

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