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NOTE

Ammonium contribution from boring bivalves to their coral host—a mutualistic symbiosis?

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ABSTRACT: The mytilid bivalve *Lithophaga simplex* is found to inhabit the scleractinian coral *Astreopora myriophthalma* in high densities. This boring bivalve, living inside the $CaCO_3$ skeleton of the coral, produces considerable amounts of ammonium as a nitrogenous waste product. Ammonium production rate by the bivalves and consumption rate by the coral (via the symbiotic algae) were measured in laboratory experiments. The population density of *L. simplex* bivalves in *A. myriophthalma* corals was surveyed in the Nature Reserve Reef, Eilat, Red Sea, Israel. Ammonium production rate by the bivalves, inhabiting the coral at a density of 0.22 ± 0.11 bivalves cm^{-2}, is calculated to be 8.2 ± 3.8 and 3.5 ± 1.6 nmol $(cm^2$ coral$)^{-1}$ h^{-1} during daytime and nighttime, respectively. Under conditions of low ammonium concentration (0.2 to 1.2 µM) the consumption rate of the coral ranged between 5 and 22 nmol cm^{-2} h^{-1}. Thus, under naturally occurring levels of ammonium (<0.15 µM), recycling of nitrogenous waste produced by the bivalves (ammonium) may account for a significant portion of the needs of the coral/zooxanthellae. In contrast to the generally accepted view of boring bivalves as parasites of their coral hosts, it is hypothesized that the association between *L. simplex* and *A. myriophthalma* may also be an example of mutualistic symbiosis. The results indicate a possible pathway in the biogeochemical cycle of nitrogen in the coral reef environment.

KEY WORDS: Ammonium · Boring bivalves · Symbiosis · Nitrogen cycle · Reef ecology

In oligotrophic waters typical of coral reef environments, levels of dissolved N in the water column are very low (Entsch et al. 1983). Thus, biological systems that conserve nitrogen and/or recycle metabolized nitrogen, such as ammonium, have an advantage over systems that do not (Szmant-Froelich & Pilson 1977). The giant clam *Tridacna gigas*, hosting algal symbionts within its tissue, offers an example for such a nitrogen-recycling system (Hawkins & Klumpp 1995).

Aspects of ammonium uptake have been studied in many algae-invertebrate associations (e.g. Wilkerson & Trench 1986, Fitt et al. 1993). The association between hermatypic corals (Order Scleractinia) and the dinoflagellate endosymbiont *Symbiodinium* sp. is a very common symbiotic relationship in tropical and subtropical marine environments (Falkowski et al. 1984). In these symbioses the algae (zooxanthellae) serve as primary producers that translocate organic carbon to their coral host (Muscatine et al. 1989). They also take up dissolved inorganic nutrients, which, together with nutrients obtained from consumption of zooplankton by the coral host, are retained and recycled within the association (Falkowski et al. 1984, Rahav et al. 1989). Mechanisms of ammonium uptake have been studied both in the coral host (Summons et al. 1986) and in the zooxanthellae (Dudler & Miller 1988). It has been shown that assimilation of inorganic nitrogen compounds is done by the zooxanthellae (Muscatine & D'Elia 1978, Muscatine et al. 1979, Burris 1983, Wilkerson & Trench 1986). The involved biochemical pathways have been addressed both in isolated zooxanthellae and in the intact symbiosis (e.g. Gunnersen et al. 1988, Bythell 1990, Wafar et al. 1993, Yellowlees et al. 1994). Physiological effects of ammonium enrichment on corals and their symbionts have also been investigated in many studies (e.g. Hoegh-Guldberg & Smith 1989, Hoegh-Guldberg 1994, Muller-Parker et al. 1994, Stambler et al. 1994).

Excretions of nitrogenous waste products by marine animals may serve as nitrogen sources for organisms that are capable of utilizing them. Meyer et al. (1983) recorded the high level of ammonium excreted by

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haemulid fish schools resting over coral colonies. The excretions of the sea urchin *Diadema antillarum* were suggested to provide ammonium-N for algal turfs upon which the urchin grazes, thus increasing the nutrient-limited primary productivity of the algae (Williams & Carpenter 1988). Spotte (1996) investigated the supply of regenerated nitrogen to sea anemones by their symbiotic shrimps. Dense bivalve populations were shown to play an important role in nitrogen regeneration (Prosch & McLachlan 1984).

Species of the mytilid bivalve *Lithophaga* are found boring inside the skeletons of many species of live scleractinian corals (reviewed by Morton 1983). These bivalve-coral associations are very common in the oligotrophic waters of the reefs of the northern Gulf of Eilat, Red Sea (Loya 1981). The bivalve *L. simplex* Iredale (1939) forms such an association with the massive coral *Astreopora myriophthalma* (Lamarck, 1816). This coral forms large colonies, often carrying dense populations of *L. simplex*. The bivalves are completely enclosed by the coral skeleton, with only the ends of their siphons reaching out to the surrounding seawater (see Fig. 1). Known benefits for the bivalves from this association include protection against predators and the nutritional use of coral mucus (Shafir & Loya 1983). However, possible gains for the coral are less clear at present. We have conducted experiments to examine the possibility that *L. simplex* contributes ammonium to its coral host *A. myriophthalma* (to be utilized by endosymbiotic zooxanthellae), and that the coral-bivalve symbiosis is mutualistic.

Materials and methods. *Astreopora myriophthalma* corals containing *Lithophaga simplex* bivalves were collected in the northern part of the Gulf of Eilat, Red Sea, at a depth of 6 to 12 m. Bivalves were extracted from the coral colonies by gently breaking the coral skeleton. The resulting coral fragments, used in the experiments below, were inspected for infestation by other organisms (including *L. simplex* bivalves). The dead bottom parts of all fragments were partially covered (<10% area) by encrusting organisms (sponges, tunicates, bryozoans). In most cases it was impossible to extract 2 or 3 of the bivalves without excess breakage (see column 1 in Table 1; corals I and II used in the spiking experiments contained 3 and 4 bivalves, respectively). Animals were allowed 12 to 24 h for acclimation and recovery in aquaria with running seawater prior to the experiments. Experiments were typically performed during a period of 3 to 5 d, and the corals were returned to the sea (a flat surface at a depth of 9 m) for long-term storage (several weeks). Laboratory experiments were conducted with surface seawater sampled close to the marine laboratory and filtered through a 0.22 µm Millipore filter (FSW). This seawater contains very low ammonium concentrations [<0.15 µM as measured by Korpal (1991) and <0.1 µM from our own monitoring]. Shortly before the experiments, the experimental vessels (beakers or aquaria) were thoroughly rinsed with 10% HCl and double-distilled water and then rinsed with FSW.

Daytime experiments were conducted under laboratory illumination (ca 10 µE m^{-2} s^{-1}), at 26 to 28°C. Night experiments were carried out in the dark at 24 ± 1°C. In all the experiments described below, analysis of samples for ammonium concentration followed Strickland & Parsons (1972). Briefly, duplicate samples of 25 ml were taken with pre-rinsed syringes at each sampling time and kept in dark-stained bottles for ammonium analysis. The reagents for ammonium analysis were immediately added to the samples, and sample bottles were kept for 2 h in the dark for color development. The reaction results in production of a blue color, the intensity of which is dependent upon the concentration of ammonium. Absorbency at 640 nm was read with a Beckman DU^R-6 spectrophotometer equipped with a 10 cm long optical cell. The average standard deviation between duplicate analyses was 0.13 µM (typically in the range of 1 to 5%). The amount of ammonium present in the experimental vessels (in µmol) at each sampling time was calculated by multiplying the ammonium concentration (in µM) by the volume of FSW (in liters) at the time of sampling.

Three groups of 8 *Lithophaga simplex* each, carefully removed from *Astreopora myriophthalma* corals, were used to measure the rate of ammonium excretion by the bivalves. Each group was placed in a beaker filled with 250 ml FSW. Bivalves quickly relaxed in the experimental vessels, opening their valves and extruding the siphons and mantle-margins within a few minutes. Day and night experiments lasted 6 h and samples were taken at the beginning of the experiment and every 2 h thereafter. Excretion rates were calculated from regression slopes of the total ammonium contents in the experimental vessels versus time. Following the experiments, bivalve tissue was removed from the shell, dried and weighed (each group separately).

The relationship between bivalve ammonium supply rate and coral consumption rate was determined *in vitro* using ammonium excretion by live bivalves and ammonium supply controlled with a peristaltic pump. The pump enabled us to increase (double) the bivalve supply rate without extracting more bivalves from corals. Live bivalve experiments were conducted by incubating each of 4 *Astreopora myriophthalma* colonies with a group of 10 to 14 *Lithophaga simplex* bivalves (a total of 4 independent experiments) in 750 to 1000 ml FSW. Ammonium production rate was measured for the bivalve groups serving as an ammonium

source prior to the experiment, as described above. Both phases (pre-measurement of production by bivalves and incubation with coral) were run for 3 h each, and samples were taken at the beginning of the experiment and every 1 h thereafter. These experiments were done during daytime, when ammonium production of the bivalves was found to be significantly higher (see below). Experiments with the peristaltic pump (LKB 2232 Microperpex S) were conducted by continuously pumping NH_4Cl solution into an aquarium containing a coral colony in an initial FSW volume of 1800 ml. Each experiment was run during daytime with each of 2 coral colonies (a total of 3 experiments, 2 of which employed the same coral colony). Different supply rates/concentrations were achieved by varying (1) the NH_4Cl solution concentration between 20 and 50 µM and (2) the pumping rate between 20 and 100 ml h^{-1} Sampling and analysis followed the same steps as above.

Pulse chase experiments provided by discrete ammonium spikes enabled us to expose corals to high initial concentrations of ammonium (1.6 to 4.1 µM). The experiments were conducted at night, when coral tissue is typically extruded and potential uptake rates were assumed to be higher. In these experiments each of 3 *Astreopora myriophthalma* colonies was placed in a separate aquarium of FSW (2000 ml) and spiked with a single aliquot of NH_4Cl solution (7.2 ml of a 0.55 mM stock solution). Samples were taken every 0.5 h for a period of 1.5 h, and then a second, 15 ml spike was added. The same sampling was repeated for an additional 1.5 h. This procedure exposes the corals to higher ammonium concentrations than in the previous setups and was used in order to explore higher potential uptake rates.

Following the experiments, coral surface area was calculated by geometric approximation (partitioning of the surface of the coral fragment into rectangles and triangles) using a caliper. This procedure, carried out independently by 2 people for each fragment does not provide the actual surface area (does not take polyp topography into account), but does yield accurate and repeatable measures of flat-surface area. Thus, the 100 cm^2 field samples used for estimating bivalve population density (see below), could be readily used in conjunction with consumption rates measured in the laboratory.

Field studies with a fluorescent dye were carried out in the Eilat Coral Nature Reserve in order to investigate possible pathways of fluids excreted by the bivalves near the surface of their coral host (Fig. 1). The influence of ambient currents was studied by carefully injecting dye at the coral surface, and at varying distances from the surface. The siphonal currents were studied by gently injecting dye directly into the inhalant siphon. Throughout the procedure, siphons were observed to remain normally extruded out of the burrow. Three sessions were carried out on a single day (early July, calm sea throughout day and night), in the early afternoon (full daylight), early night (23:00 h) and late night (04:00 h).

In order to estimate the natural population density of *Lithophaga simplex* in the studied area, colonies of *Astreopora myriophthalma* were examined with a wire square of 100 cm^2. The square was randomly placed on the coral colony and all the *L. simplex* openings within it were counted (at least 20 cm between adjacent placements of the square). Fifteen corals were examined at a depth of 6 to 8 m, to give a total of 65 squares (2 to 10 counts per coral, depending on the size of the colony). The downward-facing surfaces of the coral colonies are usually very poorly populated and were excluded from this survey. Average and standard deviation were first calculated for each coral separately, and were subsequently used to calculate a grand average and a weighted average standard deviation (Sokal & Rohlf 1969).

Results and discussion. ***Ammonium release:*** Fig. 2 shows an example of a time course of ammonium production by *Lithophaga simplex* bivalves as measured in day and night experiments. Production rate of ammonium during the day (37 nmol $bivalve^{-1}$ h^{-1}) is much higher than that measured during the night (16 nmol bivalve ^{1} h^{-1}; $p < 0.025$ for each regression slope). The considerable increase in ammonium production rate (>2-fold) is statistically significant [com-

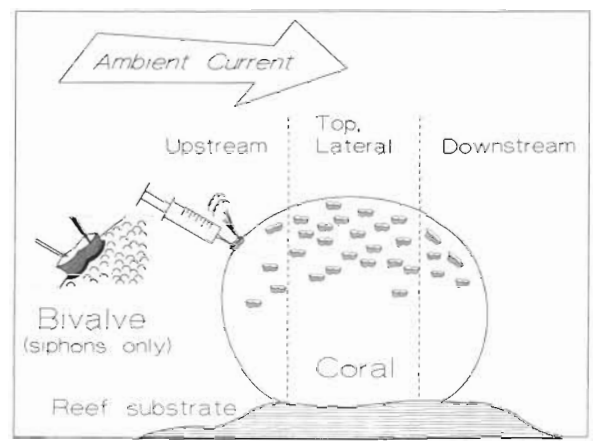

Fig 1. Coral *Astreopora myriophthalma* populated by the boring bivalve *Lithophaga simplex* in the reefs of the northern Gulf of Eilat, Red Sea, Israel. Upstream and downstream portions constitute ca 20% of the surface area of the coral colony, each. Top and lateral faces comprise ca 60% of the surface area. The siphons of the bivalves appear on the coral's surface in their natural posture (see enlargement). Measurement of the plume generated by the exhalant siphon is depicted (see 'Materials and methods')

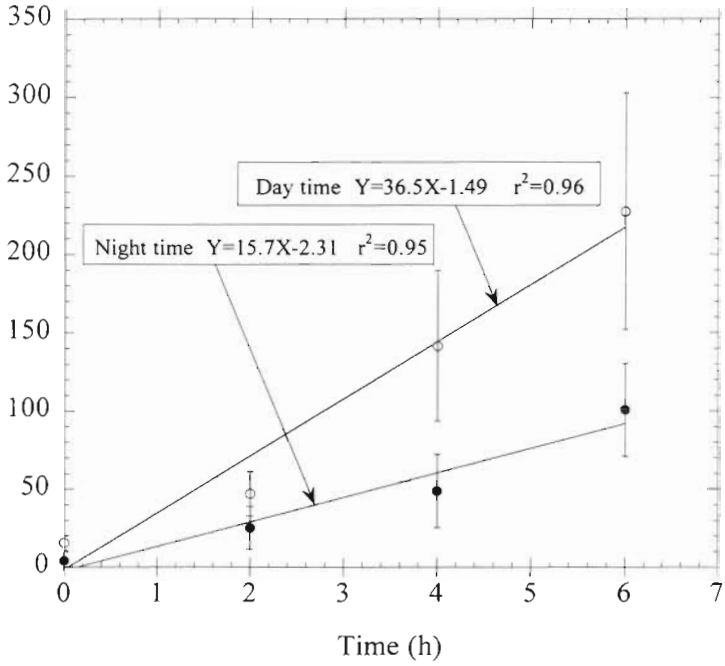

Fig. 2. *Lithophaga simplex*. Average nighttime (●) and daytime (○) ammonium production by bivalves pooled from 3 experiments with a group of 8 bivalves each. Error bars represent ±1 SD. Linear curves were fitted by regression analysis

parison of slopes, (Sokal & Rohlf 1969); $F_s = 13.73$ (df = 1, 4); $p < 0.025$]. Much larger differences between minimum and maximum rates of ammonium release were recorded in some cases for marine bivalves (see Table 5 in Smaal & Prins 1993). The average ammonium production rates measured for *L. simplex* in day and night experiments were 0.81 ± 0.4 and 0.36 ± 0.15 µmol (g dry weight)$^{-1}$ h^{-1}, respectively. These values are comparable to the rates reported by Hawkins et al. (1983) for the bivalve *Mytilus edulis*.

In most bivalves, feeding and the different processes of digestion are to varying degrees rhythmic or phasic (Barnes 1980). The diurnal rhythm of night and day was found to be the main environmental factor controlling the rhythm of activity in freshwater and sublittoral marine bivalves (Morton 1978), including the rock-boring *Lithophaga lithophaga*. The constancy of ammonium production rates observed in this study within each experimental period and the differences between the results obtained during night and day experiments (see Fig. 2) may reflect a physiological rhythm of this sort. The illumination provided in daytime experiments was lower than that usually prevailing at the depth from which corals were collected. This may have had an effect on our results, as light intensity influences the relevant physiological processes. Elevated levels of activity during daytime have been reported for several marine bivalves (Morton 1978). It should be noted that the observed differences were significant in spite of the low illumination provided in daytime experiments (see 'Materials and methods'). Therefore, we may underestimate the daytime ammonium release by the bivalves.

The population density of *Lithophaga simplex* in *Astreopora myriophthalma* was measured to be 22.4 ± 10.5 bivalves (100 cm^2 coral)$^{-1}$. The maximum density observed was 55 bivalves (100 cm^2 coral)$^{-1}$. Based on ammonium production rates measured in this study, *L. simplex* bivalves produce about 8.2 ± 3.8 and 3.5 ± 1.6 nmol (cm^2 coral)$^{-1}$ h^{-1} during daytime and nighttime, respectively.

Ammonium uptake: The experimental setup in which supply rates were the lowest was that involving ammonium supply by *Lithophaga simplex* bivalves (Table 1). The bivalves which were not extracted from the experimental corals constituted ≤23% of the total number of bivalves in the experimental vessel. Since in all cases we observed no increase in ammonium levels over the course of the experiment, the potential effect

Table 1. Laboratory measurements of ammonium uptake rate by colonies of the coral *Astreopora myriophthalma* (number of bivalves not extracted from the coral is shown in parentheses; see 'Materials and methods') under a continuous supply of ammonium. In the experiments involving *Lithophaga simplex* bivalves, specified supply rate is based on earlier measurements of excretion rate of each bivalve group (see 'Materials and methods')

Coral colony	Surface area (cm^2)	Ammonium source	Supply rate (nmol cm^{-2} h^{-1})	Measured concentration Initial (nM)	Final (nM)	Uptake rate (nmol cm^{-2} h^{-1})
Coral IV (0)	83	*L. simplex*	1	1200	640	5
Coral V (3)	48	*L. simplex*	2	950	120	11
Coral VI (3)	57	*L. simplex*	2	1200	190	9
Coral VII (3)	35	*L. simplex*	12	870	930	12
Coral VII (3)	35	Continuous pumping	15	340	360	15
Coral VII (3)	35	Continuous pumping	30	360	620	22
Coral VIII (2)	150	Continuous pumping	33	210	3000	21

of these bivalves could not change any of the interpretations below. It is clear, therefore, that the potential contribution of these bivalves in the experimental setup involving continuous pumping of an ammonium stock solution was negligible.

With the exception of the spiking experiments (Fig. 3), most experiments in which ammonium uptake was measured were carried out in the presence of low initial ammonium concentrations (0.2 to 1.2 µM; Table 1). Despite the fact that the highest uptake rates were recorded under high concentrations (see results of 'spiking experiments' below), a correlation between uptake rates and ammonium concentrations was not observed. This is in contrast to other studies dealing with ammonium uptake by marine invertebrates (e.g. Burris 1983, Atkinson et al. 1994) in which such a correlation was established, often involving the use of extremely high ammonium concentrations (e.g. 20 µM; see Atkinson et al. 1994).

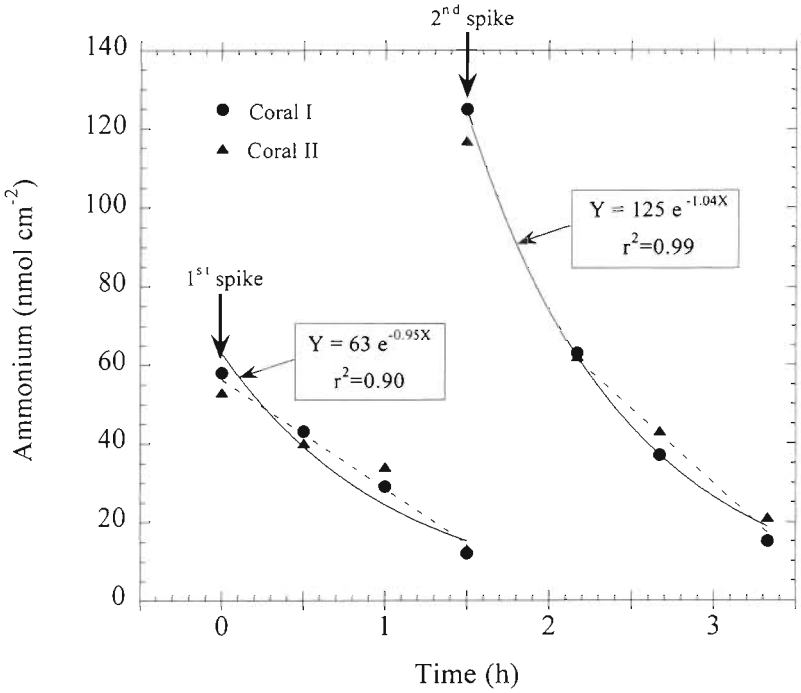

Fig. 3. *Astreopora myriophthalma*. Ammonium consumption by 2 coral colonies (I and II) Ammonium spikes were added twice during the experiment. Exponential curves were fitted by Kaleidagraph™ 3.0 (Abelbeck software

A significant correlation was observed in this study between supply rate and uptake rate under continuous supply, either by *Lithophaga simplex* bivalves or by continuous pumping (all entries in Table 1, $r^2 = 0.92$, $p < 0.01$). In these experiments we measured uptake rates in the range 5 to 22 nmol cm^{-2} h^{-1}.

The pulse chase ammonium spiking experiment (Fig. 3) provided important information on the potential uptake rate of the corals. An exponential fit of the data yields an uptake coefficient (λ) of 0.95 h^{-1} (r^2 = 0.90) and 1.04 h^{-1} (r^2 = 0.99) for the first and second spikes, respectively. λ is the uptake coefficient in an equation of the form:

$$A_t = A_0 e^{-\lambda t}$$

where A_t is the instantaneous specific ammonium availability (nmol cm^{-2}), A_0 is the initial specific ammonium availability (just after spiking), and t is the time (h) after spiking. The meaning of λ is that after a characteristic time $t = \lambda^{-1}$, 63% of the spike A_0 is absorbed by the coral, or that ammonium half life is $-\lambda^{-1}$ ln(0.5). In this case $\lambda \approx 1$, which implies that the corals were able to take up half of the available ammonium in ca 40 min.

A 2-fold increase in the spike resulted in ca 2-fold increase in initial specific uptake (U_0 = 60 nmol cm^{-2} for the first spike; U_0 = 130 nmol cm^{-2} for the second spike). It is clear, therefore, that even under the highest specific ammonium concentrations utilized the corals were not saturated. Under lower ammonium availability, the uptake seems to behave almost linearly (dashed lines in Fig. 3). The uptake rate calculated by linear regression during this quasi-linear phase is lower in the first spike (28 nmol cm^{-2} h^{-1}, $p < 0.01$, $r^2 = 0.97$) than in the second spike (38 nmol cm^{-2} h^{-1}, $p < 0.01$, $r^2 = 0.97$). However, this difference is not significant [comparison of slopes, (Sokal & Rohlf 1969); $F_s = 6.36$ (df = 1,3); $0.05 < p < 0.1$].

It should be noted that these experiments were conducted under relatively high ambient ammonium concentrations [initial concentration ranging from 1.6 to 4.1 µM, which is more than an order of magnitude higher than the concentrations found by Korpal (1991) in the natural reef environment]. These experiments clearly demonstrate that the host corals can easily take up all the ammonium supplied by their burrowing bivalves.

Ammonium availability: Since ammonium is exported from the bivalves through their exhalant siphons, its availability depends upon the siphonal currents and the ambient current regime adjacent to the surface of the coral. Siphonal currents produced by the bivalves, as measured by application of fluorescent dye (see Fig. 1), were strongest during daytime, when dye plumes reached a distance of about 3 cm from the coral surface. In the early hours of the night the intensity of the currents was reduced, with seawater being

ejected from the siphonal aperture to about 1.5 cm. Late at night, no siphonal currents were observed, but rather a feeble stream leaving the exhalant siphon and adhering to the coral surface.

In terms of the effect of ambient currents on the availability of bivalve-produced ammonium for the coral, our observations indicate 3 distinct regions within the coral colony. (1) At the upstream side of the colony, constituting approximately 20% of the surface area (Fig. 1), seawater is pushed toward the coral. (2) The downstream side of the colony experiences steady vortices, vortex shedding or turbulent flow (depending on the ambient flow velocity, see Fig. 5.5 in Vogel 1983). As a result, excreted plumes are partly pushed back toward the coral surface, although it is very difficult to determine the exact fraction being pushed back under varying flow regimes. (3) The top and lateral faces of the colony, constituting ca 60% of the surface area (Fig. 1), are effectively flushed by ambient currents.

These preliminary observations of ambient flow regimes and siphonal currents do not permit a quantitative estimate of the potential importance of ammonium contribution by the bivalves to the coral. In particular, typical diffusion boundary layers have to be examined in detail and under different flow regimes (see Shashar et al. 1996). It is, however, very likely that substantial amounts of bivalve-produced ammonium are available to the coral host, especially during nighttime, when the feeble stream leaving the exhalant siphon adheres to the coral surface. Nighttime ammonium uptake by the coral and production by the bivalves were clearly demonstrated in this study.

Our laboratory results should be verified in the field, preferably *in situ* (bivalves in their natural burrows). The use of labeled nitrogen for tracing a hypothesized transfer of ammonium from the bivalves to the coral is also desirable. Nevertheless, our data regarding ammonium production, potential consumption rates and the population density of the bivalves suggest that such a contribution is significant in the natural reef environment (even if the corals can effectively take up only that ammonium which is produced during nighttime). The following discussion considers potential biogeochemical and ecological significance of ammonium recycling between the bivalves and the coral.

Potential significance: Filter feeding on plankton by the bivalves and excretion of nitrogenous metabolic products transforms particulate organic nitrogen, which is an important limiting nutrient (Erez 1990), into its mineralized form. Hence, the described interaction between *Astreopora myriophthalma* and *Lithophaga simplex* may serve as a pathway in the nitrogen biogeochemical budget of the reef. Similar nitrogen-cycling has been studied in other invertebrate-algae symbioses (e.g. Wilkerson & Trench 1986). However, most of the existing examples are bipartite, most notably coral-algae (e.g. Muscatine & D'Elia 1978) or clam-algae (e.g. Fitt et al. 1993, Hawkins & Klumpp 1995). The tripartite bivalve-coral-algae system studied here features both phytoplankton filter-feeding (*L. simplex*) and zooplankton predation (*A. myriophthalma*) together, as in the shrimp-anemone symbiosis described by Spotte (1996). The studied system may thus convert nitrogen from both plankton sources into readily available nitrogenous compounds.

Lithophaga simplex bivalves boring into the skeletons of living coral colonies are usually considered to be parasites. This view of the bivalves is based on the 'obvious' damage associated with bioerosion of the coral skeleton. Acknowledged benefits for the bivalves include physical protection and the use of coral mucus as a nutritional source (Shafir & Loya 1983), but no potential benefit for the coral has yet been pointed out. The results presented in this study suggest a possible benefit for the coral host from the association with the bivalves. One of the implications of this suggestion is that the symbiotic relationships between the boring bivalve *L. simplex* and the coral *Astreopora myriophthalma* may be mutualistic. One should be cautious, however, about such interpretations, as the important issue is not the presence or absence of benefits and damages to each of the participants, but the balance between them, i.e. whether the gains for a given participant *outweigh* the costs or vise versa. Current knowledge is not sufficient for answering this question, and the suggestion of mutualism remains hypothetical at this stage.

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