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REPORT

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Phytoplankton grazing by epi- and infauna inhabiting exposed rocks in coral reefs

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Abstract Exposed rocks with no visible macro-fauna are abundant in all coral reefs. Depletion of phytoplankton cells and pigments by the minute crypto fauna inhabiting the outer few centimeters of such rocks was experimentally studied over an annual cycle in the Gulf of Aqaba, Red Sea. Different substrata were introduced into small (3.6 L), well mixed, tanks that were fed by running seawater pumped directly from the reef at a rate of 11 ± 1 L h^{-1}. A steady-state reduction in phytoplankton abundance and chlorophyll *a* concentration of 38 ± 26% (mean ± 1 SD) was found for untreated rocks but not for sand, gravel, or killed controls. Average areal clearance rate by untreated rocks was 17.3 ± 8.0 ml cm^{-2} h^{-1}. Conservative extrapolation of this rate to the whole reef community suggests that the fauna inhabiting exposed rocks clears 2.1 ± 0.9 m^3 m^{-2} d^{-1} at Eilat. Phytoplankton removal by untreated rocks varied from 1.5 ng chlorophyll *a* cm^{-2} h^{-1} during the oligotrophic summer conditions to 6 ng chlorophyll *a* cm^{-2} h^{-1} during the spring bloom. These values correspond to a potential nitrogen gain of 1.3 and 5.2 mmol N m^{-2} day^{-1}, respectively. Cryptic reef-rock fauna can have a key role in the biogeochemical functioning of coral reef communities.

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Introduction

Benthic grazing on phytoplankton is a principal trophic pathway in shallow, temperate coastal habitats (Riisgård et al. 2004 and references therein). The dominant grazers (phytoplanktivores) in those communities include bivalves, ascidians, and polychaetes (Riisgård 1998 and references therein). Studies of pelagic–benthic coupling in coral reefs, where the phytoplanktonic community is dominated by minute prokaryotic cells (Ferrier-Pages and Gattuso 1998), have focused on zooplankton, rather than phytoplankton, as the principal source of prey (reviewed by Yahel et al. 1998). However, following the advent of technologies that allow identification and counting of micron-size picoplankton in aquatic ecosystems, many recent studies demonstrated the significant role of phytoplanktivory and bacteriovory in the trophic dynamics of coral reefs (Ayukai 1995; Ferrier-Pages and Gattuso 1998; Gast et al. 1998; Yahel et al. 1998; Richter and Wunsch 1999; Fabricius and Dommisse 2000; Richter et al. 2001; van Duyl and Gast 2001; van Duyl et al. 2002; Genin et al. 2002; Ribes et al. 2003, 2005). Nevertheless, unlike temperate and boreal coastal habitats, the identification of the key benthic phytoplanktivores and the assessment of their feeding rates have, by and large, remained elusive. To our knowledge, phytoplanktivory has been investigated only in five coral reef dwellers: an Octocoral (Fabricius et al. 1998), two sponges (Pile 1997; Yahel et al. 2003) and commercially reared bivalves (Yukihira et al. 1999; Loret et al. 2000).

Potential sinks for phytoplankton in coral reefs could be physical mechanisms such as entrainment and burial by high-pressure surge in the reef framework (Haberstroh and Sansone 1999) and wave-driven filtration via sand ripples (Huettel and Rusch 2000). However, such mechanisms pertain primarily to the surge zone and cannot account for the removal processes occurring in moderate and low flow environments below the wave action zone (Genin et al. 2002; Yahel et al. 2002). Several biotic guilds have been suggested by various authors to be the dominant phytoplankton grazers in different reefs. For instance, following the discovery of phytoplanktivory in the octocoral *Dendronephthya hemprichi* (Fabricius et al. 1995), phytoplankton depletion over soft coral-dominated reefs was attributed to the corals (Yahel et al. 1998; Fabricius and Dommisse 2000). Yahel et al. (1998) have speculated that epibenthic active suspension-feeders may be responsible for the phytoplankton depletion over fringing reefs at the Gulf of Aqaba where soft corals are scarce. In follow-up studies, Richter and Wunsch (1999) and Richter et al. (2001) suggested that the entire removal of phytoplankton could be accounted for by cavity-dwelling fauna, primarily sponges. A similar suggestion was recently made for epibenthic sponge and tunicates by Ribes et al. (2005). Yet, reef cavities were extremely rare at the experimental sites of Genin et al. (2002) in the Gulf of Aqaba where intense phytoplankton grazing was documented. Moreover, up scaling calculations of individual grazing rate measurements made at the same sites (G. Yahel et al. unpublished) suggest that visible active suspension feeders (including sponges and boring sponges, *Lithophaga* and other bivalves, and tunicates) account for only ~15% of the observed phytoplankton removal.

In a recent compilation of > 1,000 surveys of different coral reefs, Hodgson and Liebeler (2002) reported that "exposed" rocks, that is, hard substratum (excluding recently killed corals) not occupied by live corals, sponges, fleshy algae, or other conspicuous macro-fauna, comprise on average 26% of the Indo-Pacific and 18% of the Atlantic reefs surface area, compared with mean live coral cover of 35% and 23%, respectively. Sand patches and coral rubble (0.5–15 cm) are the two other predominant exposed substrata in coral reefs (Hodgson and Liebeler 2002). Aside from the role in- and epifauna have in reef bioerosion, their ecological functioning in the reef community is poorly understood (Hutchings 1978, 1983; Gischler 1997). Several reports describing the community inhabiting exposed rocks in coral reefs indicated that populations of minute suspension feeders (such as polychaetes, foraminifers, tunicates, and boring sponges) are highly abundant in this micro-habitat (e.g., Bonem 1977; Peyrot-Clausade 1977; Vasseur 1977; Hutchings 1978, 1983; Gischler 1997; Holmes et al. 2000 and references therein). In reefs under stress, where the abundance of dead coral, rocks, and rubble is high (e.g., Edinger et al. 2000) and where sometime anthropogenic eutrophication co-occurs, bioerosion becomes intense and the abundance of boring sponge increases (Holmes et al. 2000 and references therein).

The objective of this study was to experimentally test the hypothesis that the cryptic fauna that inhabits exposed rocks in coral reefs removes considerable amounts of phytoplankton from the overlying waters, rendering significant its role in benthic–pelagic coupling in coral reefs.

Methods

Phytoplankton removal by the fauna inhabiting different reef substrata (exposed rocks, gravel, and sand) was studied on the fringing coral reef in front of the Steinitz Marine Laboratory of Eilat, Gulf of Aqaba, Red Sea (29°30′ N, 34°56′ E). Reef substrata were brought to the laboratory and placed in small tanks fed by running water pumped from the reef. Phytoplankton concentration was measured using either chlorophyll *a* or cell counts with a flow cytometer. The sampling period spanned the seasonal variation in the northern tip of the Gulf of Aqaba (Lindell and Post 1995) starting during summer stratification (August 2001) and extending through autumn (September 2001) and the winter mixing (October–December 2001), to the spring bloom (March 2002). See Yahel et al. (1998, 2002) and references therein for a description of the study site.

Experimental setup

The setup included ten polypropylene tanks (3.6 L, Fig. 1) into which different reef substrata (untreated rock, gravel, sand, and controls, see below) were randomly allocated in each experiment (Table 1). Each tank was supplied with running seawater via a 1 m long, 6 mm diameter pipe from a common header tank (20 L) that supplied a constant flow of 11 ± 1 L h^{-1} (mean ± SD). To ensure thorough mixing of the water

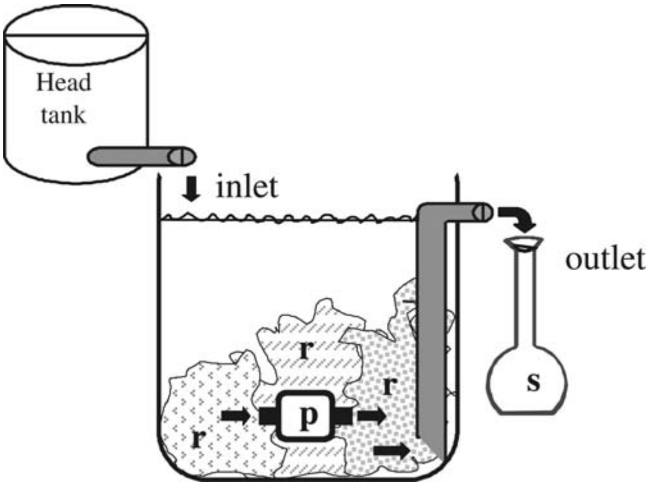


Fig. 1 An illustration (*side view*) of an experimental tank with 3 rocks (*r*). Tank dimensions are 15.5×15.5×15 cm. The water inlet is via a 6 mm hose from a common head tank, water outlet is from near the tank bottom via a 20 mm hose. An electric pump (*p*) ensured thorough mixing of the tank water. Each experiment consisted of ten identical tanks attached to the common head tank

Table 1 The dates and design of the tank experiments carried out during the study

Date	No. of sampling sessions			No. of experimental tanks				
	Day	Night	Total	Rocks	Gravel	Sand	Control	Total
August 2001	4	1	5	4	3	3	[a]	10
September 2001[b]	6	1	7	4	2	2	2[c]	10
October 2001[b]	3	0	3	4	2	2	2[c]	10
December 2001	2	2	4	3	1	1	2[c,d]	7
March 2002	2	2	4	8	0	0	2[d]	10
Total	17	6	23	23	8	8	8	47

[a] In August 2001 sun-dried and empty controls were run prior to substratum experiments

[b] Benthic algae growth experiment

[c] Bleached controls

[d] Combusted controls

in the tanks (Riisgård 2001), an adjustable aquarium pump (100–300 L h^{-1}, Chosen Aquarium Equipment Corp. model AT005) was mounted in each tank, and the tank water outlet was installed near the tank bottom (Fig. 1). To simulate natural flows, the pumps were adjusted so that the flow around the substratum surfaces would be in the natural range encountered in the reef (5–15 cm s^{-1}, Yahel et al. 2002). It took a few seconds for drops of fluorescein dye injected with a syringe into the tanks to be thoroughly mixed. The water was pumped to the header tank from the near bed boundary layer, 0.5 m above the reef surface, in front of the Marine Biology Laboratory of Eilat (Yahel et al. 2002). To minimize the effect of fouling organisms within the pipes, a dual water supply system was installed. Every few days, the systems were switched and the recently used system was flushed for 30–60 min with fresh water to kill the fouling fauna. The tanks were immersed in a shaded water table that was filled by the overflow from the header tank. The temperature and illumination in the tanks were similar to those at the adjacent reef at 5 m depth.

Rocks, sand, and gravel

For each experiment, a fresh set of substrata was collected from 6–14 m depth on the fore reef and transferred submerged in seawater to the tanks. Untreated rocks without visible macro-fauna (mean displacement volume of individual rocks 390 ± 209 ml, range 80–750 ml) covered most of the tank bottom with a vertical relief of 5–15 cm. Whenever possible, the original vertical orientation of the rock was maintained. To facilitate haphazard selection, volunteer divers were asked to collect the rocks from the reef surface. In order to avoid unnecessary damage, no chisels were used so that only loosely attached rocks were collected. Therefore, most rocks were degraded coral skeletons, some still retaining the original coral form, while several were large reef rubble (> 10 cm e.g., Gischler 1997). A very small number of the rocks were of conglomerate composed of dead coral skeleton together with non-carbonated cobbles originating from the nearby mountains. The volume of the rocks in each tank was measured by the displacement volume method. In September 2001 and March 2002, the entire surface area of each rock was also measured by carefully fitting an aluminum foil to the rock surface and subsequently weighing the dried foil. Gravel (408 ± 181 ml per tank) and sand (414 ± 239 ml per tank) were collected by scooping the upper 5 cm of the substratum into a plastic bag at the same site of the rock collection. The gravel (~0.5–5 cm) and sand (0.3–0.05 cm) at our site both contained more than 50% of non-carbonated material. As these substrata are routinely perturbed by burrowing fish (Yahel et al. 2002), no effort was made to retain their original orientation in the tanks.

For the control, untreated rock fauna was killed by drying the rocks outdoor for several days or baking them at 350°C for 3 h. In September and October 2001, control rocks were treated with 0.5% NaOCl for 24 h to minimize nutrient release from decomposing organic matter (see below).

Water sampling and analysis

Each experiment lasted 2–4 days, with one sampling session during the day (see below), sometimes followed with a second sampling session during the night starting 1–3 h after sunset (Table 1). The only exception was the September experiment where sampling session were disperse over a 3-week time.

After setting up the experimental setup, the substrata were allowed to acclimate within the tanks for at least 24 h. An hour before the beginning of a sampling session, the tanks inflows were cleaned by means of injecting tank water at high pressure through the tubing. Sampling commenced by collecting duplicate water samples from the common header tank. Then duplicate tank water samples were collected from the outflows of all tanks simultaneously into 300 ml opaque BOD glass bottles. A second duplicate water sample was collected from the header tank by the end of the sampling session (~10 min). The mean of the four header-tank water samples was considered representative of the inflow concentration for all tanks. The volume of the BOD bottles was individually measured to the nearest 10 µl. Water samples were immediately transferred to the laboratory, pre-filtered using a 100 µm net to remove large zooplankton and fragments of benthic algae, filtered on GF/F filters and analyzed for chlorophyll *a* by cold acetone extraction and fluorometric determination on a TD-700 (Turner design) fluorometer as in Yahel et al. (1998). The precision of our method (measured as the average deviation of duplicate chlorophyll measurements from their mean) was 5 ng chlorophyll L^{-1} (Coeffcient of variance, $CV < 2\%$, $N = 214$).

In early spring (March 2002), a flow cytometer (FACScan, Becton Dickinson) was used to measure the concentration of the two dominant autotrophic groups (*Synechococcus* and pico-eukaryotes) and the non-photosynthetic bacteria as described by Marie et al. (1999). Taxonomic discrimination was made on the basis of cell side scatter, orange fluorescence of phycoerythrin, and red fluorescence of chlorophyll (Marie et al. 1999).

In order to detect possible remineralization processes, ammonium concentrations were measured during a daytime sampling session in September and October 2001 using the fluorometric method (Holmes et al. 1999). Ammonium concentration was determined by a DyNA Quant 200 fluorometer (Hoffer) after 3 h dark incubation with the reaction mixture in room temperature. To improve the method accuracy, an internal standard curve was obtained for each sample by adding 0, 100, 200, and 300 µl of a standard ammonium solution (2.5 µmol L^{-1}) into 4 ml aliquots of the original water sample (David 2003).

Using a thoroughly mixed system, plankton concentrations in the tanks outflow were equal to the concentration within the tank. Assuming steady-state condition for the duration of the sampling (Riisgård 2001), we could calculate the substratum clearance rate (CR) in each tank (a virtual volume of water filtered clear of plankton per a time unit) as $CR = Q \times (C_i - C_o)/C_o$ (see Eq. 6 in Riisgård 2001) where Q [L h^{-1}] is the flow rate through the system and C_i and C_o are the plankton concentrations in the inflow and outflow, respectively (measured either as nanogram chlorophyll L^{-1} or cell counts with a flow cytometer). Following a standard engineering approach for calculating mass transfer rates (plankton or ammonium) between the rough rock surfaces and the overlying water (Wildish and Kristmanson 1997; Thomas and Atkinson 1997), we scaled the observed clearance rate to the planar area occupied by the rocks in the tank (~240 cm^2). Thus, unless stated otherwise, CR was normalized to the planar tank area and is reported as ml seawater cleared per cm^2 area per hour.

Algal growth experiments

The hypothesis that phytoplankton grazing and subsequent nutrient mineralization by the untreated rock fauna would facilitate the growth of benthic algae was tested in September and October 2001 by incubating four small transparent plastic cylinders within each experimental tank. Cylinders were prepared from cut pieces of 1.5 ml Eppendorf microtubes which were then suspended with small plastic-coated wires 5 cm below the water surface. After 14 or 6 days incubations (in September and October, respectively), the cylinders were removed and the algae chlorophyll was extracted by soaking the cylinder in 90% buffered acetone for 24 h at 4°C in the dark. Chlorophyll was measured fluorometrically as above. Chlorophyll *a* accretion was used as a proxy for the benthic algae standing crop developed on the cylinder during the incubation.

Rock fauna

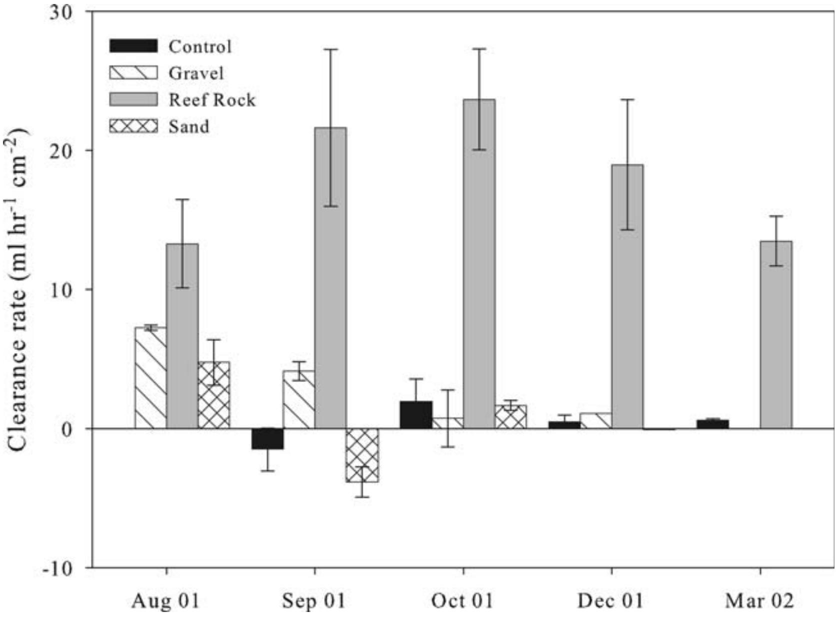
Attaining a full quantitative taxonomic description of the in- and epifauna on the substrata was beyond the scope of this study. In order to quasi-quantitatively describe the fauna, each rock was visually examined and photographed and then a sub-sample (0.5–16 ml) was carefully chiseled from the outer 3 cm of the rock surface and examined under a dissecting microscope. Subsamples were carefully taken apart within a seawater bath, using a small chisel, and the dismantled material was filtered (200 µm) and preserved in 4% buffered formalin for later microscopical analysis. This procedure was repeated for each tank in the first three experiments (August–October 2001). To examine the natural faunistic variability, three rock samples were taken and screened in three cases. No attempt was made to quantify the numerous algae (endolithic, coralline, encrusting) found on the rocks. For sand and gravel, a 10 ml sample was preserved as above and the infauna inhabiting 1 ml aliquot was microscopically counted.

The dismantled rocks were sorted under a dissecting microscope and identifiable organisms were photographed and counted (Hutchings et al. 1992). The separation and isolation of the organisms were difficult as many animals were fractured or deformed during rock dismantling (Hutchings 1978, 1983). Since colonial organisms could not be quantified (Kiene and Hutchings 1994), only the presence/absence was noted for these taxa. The organisms were identified to the species level whenever possible; however, more often we were able to sort organisms only to order or family. Polychaetes with mouth parts indicating a suspension-feeding mode of feeding were counted separately.

Statistical analysis

Throughout the text, means are reported ±1 standard deviation (SD) unless otherwise stated. Each experiment was analyzed separately using a repeated-measures ANOVA with the sampling sessions as repeated measures crossed with the substratum type. As ANOVA assumptions of homogeneity of variance and normality

Fig. 2 Average areal phytoplankton clearance rate (milliliter of seawater filtered clear of chlorophyll *a* per cm^2 of the tank bottom per hour) in tanks containing three different coral reef substrata (reef-rocks, gravel, and sand) and a control (baked, sun-dried or bleached rocks) during five independent experiments. Averages were calculated over tank mean clearance rate. *Error bars* SE, $N = 3$–8 tanks containing rocks and 2–3 tanks containing sand and gravel per experiment (see Table 1 for more details)



were usually met, no transformation was used. We used planned comparisons to compare the clearance rates of sand and gravel with the control, and of untreated rocks with all other substratum types pooled. Nighttime clearance rates were compared with the preceding daytime results using Wilcoxon match paired test when the comparison was carried only once (experiments 1 and 2) or a two-level repeated-measures ANOVA when the comparison was repeated twice (experiments 4 and 5) with day/night as first repeated measure level and the sampling sessions as a second repeated measure. The abundance of countable organisms in each tank was estimated as the product of normalized abundances of each taxon in the corresponding sub-samples and the rock volume in each tank. To examine possible relationships between the fauna of each tank and the mean tank clearance rate, we used a multiple backward stepwise linear regression analysis. A complete analysis of residuals was performed to validate the robustness of the resulting model. Statistical analysis was undertaken using Statistica 6.0 (2002, Statsoft Inc.). The faunistic composition of the different substratum was compared using the ANOSIM (analysis of similarity) routine and the Primer statistical package (Ver. 5.22, Primer-e Ltd.).

Results

Ambient condition

Typical oligotrophic conditions prevailed at our study site during the summer stratification period (August–October 2001), with surface water temperature (SST) ranging from 25–26°C and chlorophyll concentration ranging from 150 to 220 ng L^{-1}. Prokaryotes dominated the phytoplanktonic community. With the deepening of the winter mixing in the Gulf, eukaryotic algae became more abundant and in December 2001 (SST, 21°C) chlorophyll concentration rose above the annual mean (400 ng L^{-1}). The spring bloom (>600 ng chlorophyll L^{-1}) followed the initiation of water warming in March 2002 (SST, 21.9°C). Typical bloom conditions were evident in March 2002 when the *Prochlorococcus* abundance was extremely low (Lindell and Post 1995; G. Yahel, unpublished data), *Synechococcus* (1.65×10^5 cells ml^{-1}) were 4 to 16-fold the non-bloom concentration (1–4×10^4 *Synechococcus* cells ml^{-1}) and eukaryotic algae (1.1×10^4 cells ml^{-1}) were 3–10 times above the non-bloom concentration (1–4×10^3 cells ml^{-1}, G. Yahel, unpublished).

Phytoplankton removal

Throughout the experiment, substantial phytoplankton removal was evident only in the tanks containing untreated rocks (38 ± 26%, clearance rate of 17.3 ± 8.0 ml cm^{-2} h^{-1}, $N = 23$; Fig. 2). Due to the lack of phytoplankton removal by any of the baked, bleached, or sun dried rocks, these controls were pooled in subsequent analyses. Planned comparisons indicated that the clearance rate in the tanks containing untreated rocks was significantly higher than in the tanks containing other substrata in each of the experiments ($F > 12.5$, $P < 0.05$). The tanks with gravel showed some removal in the summer but barely any later on. In all five experiments, both sand (areal clearance rate: 0.7 ± 7.9 ml cm^{-2} h^{-1}, $N = 8$) and gravel clearance rates (4.5 ± 7.6 ml cm^{-2} h^{-1}, $N = 8$, Fig. 2) were not significantly different from the controls (Planed comparison, $P > 0.1$). Averaging the clearance rates of each tank over all sampling sessions in each experiment ($N = 3$–7) yielded a measure of the mean uptake of the corresponding substratum. A Kruskal–Wallis test over these means

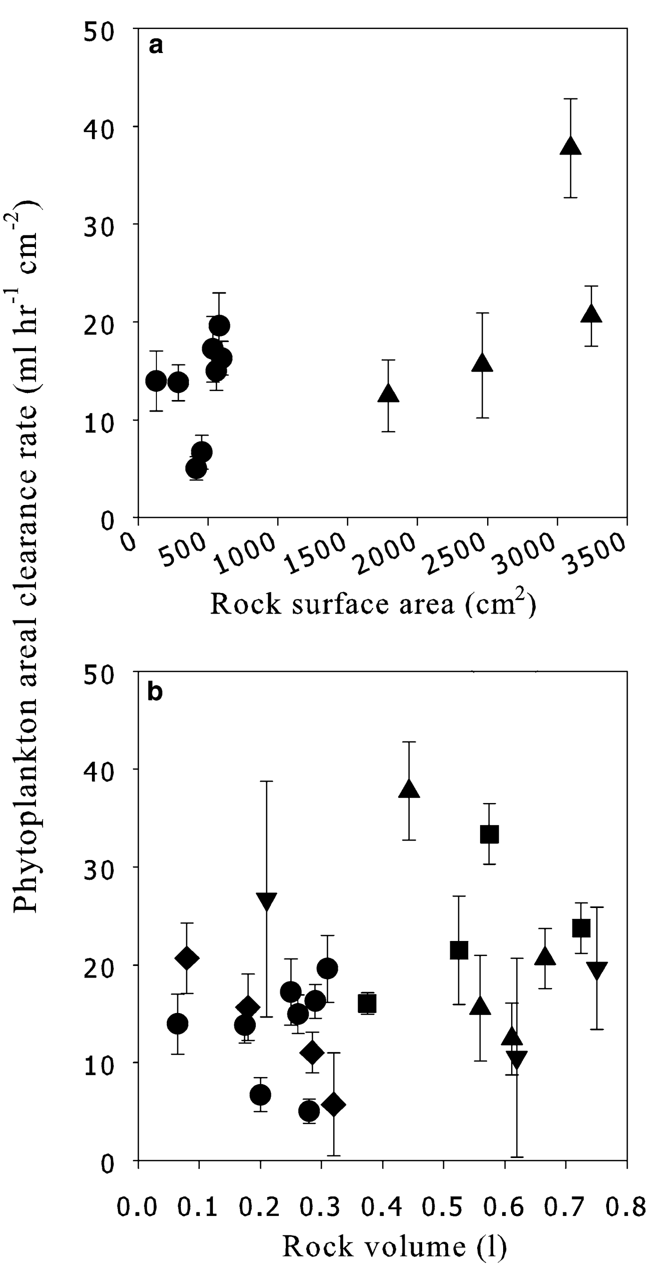


Fig. 3 Areal phytoplankton clearance rate by untreated rocks as a function of: **a** surface area of the untreated rocks and **b** volume of untreated rock in the experimental tanks. *Each point* indicates the average of three to seven repeated measures of the same tank. *Error bars* SE. See Table 1 for number of replicates. Rock displacement volume was measured in all experiments, while surface area was measured only in September and March. *filled diamond* August 2001 *filled triangle* September 2001 *filled square* October 2001 *filled inverted triangle* December 2001 *filled circle* March 2002. Phytoplankton clearance rate was positively correlated with the rock surface area during both September 2001 and March 2002 (Spearman $r > 0.66$) but no correlation with rock volume was found in any of the experiments

indicated a significant difference in the clearance rates of the different substratum types ($H_{3,N=47} = 33.4$, $P < 0.001$). As in the parametric test, a post-hoc, non-parametric (pairwise) multiple comparison of the medians indicated that the clearance in the tanks containing untreated rock was significantly higher than all other treatments ($P < 0.001$) while the gravel and the sand were not significantly different from each other or from the control ($P = 1.0$).

Differences in chlorophyll concentration greater than three times the precision of our method (i.e., >15 ng chlorophyll L^{-1}) occurred in 97 of the total of 103 individual measurements carried with tanks containing untreated rocks. Mean clearance rate in the tanks containing untreated rocks ranged from 5.0 ± 2.5 ml cm^{-2} h^{-1} to 37.8 ± 13.3 ml cm^{-2} h^{-1} and the average difference between inflow and outflow (tank water) concentrations was 86 ± 75 ng chlorophyll L^{-1} (38 ± 26%). Gravel showed detectable phytoplankton removals in 67% of the cases, but the average difference between inflow and outflow was only 9 ± 46 ng chlorophyll L^{-1}.

In March 2002 the removal of *Synechococcus* sp. and eukaryotic algae was highly correlated ($r = 0.90$, $P < 0.001$, $N = 16$). Phytoplankton clearance measured as cell counts was significantly correlated with chlorophyll clearance rate ($r = 0.57$, $P < 0.01$, $N = 16$) and the three measures were not significantly different (Two-level repeated measures ANOVA, $F_{2,47} = 0.4$, $P = 0.69$). Mean clearance rates were 15 ± 8, 13 ± 7, and 14 ± 7 ml cm^{-2} h^{-1} for *Synechococcus*, eukaryotic algae, and chlorophyll, respectively. The grazing rates of non-photosynthetic bacteria was also considerable (8 ± 6 ml cm^{-2} h^{-1}), although significantly lower (Two-level repeated measures ANOVA, $F_{1,7} = 8$, $P = 0.02$) in comparison to phytoplankton grazing. Clearance rates of non-photosynthetic bacteria were well correlated with chlorophyll clearance ($r = 0.60$, $P = 0.01$, $N = 16$) but less so with phytoplankton cell counts ($r = 0.3$, $P > 0.2$, $N = 16$).

Clearance rates in the untreated rock tanks varied significantly among sampling sessions in all but the spring experiment. The comparison of the night- and daytime clearance rates did not reveal any difference except in December 2002 when nocturnal grazing was significantly higher ($F_{1,2} = 39$, $P = 0.02$, data not shown). It should be noted that the statistical power associated with this null observation is low due to the small number of day/night comparison (1–2 per experiment). Clearance rates were positively correlated with rock surface area (Fig. 3a, Spearman rank order correlation $r_s = 0.65$, $N = 12$, $P = 0.02$), but not with its displacement volume (Fig. 3b, $r_s = 0.25$, $N = 23$, $P = 0.2$) or ambient (inflow) chlorophyll ($r_s = -0.22$, $N = 23$, $P = 0.3$). The same trend was also evident when each experiment was analyzed separately. Since clearance rates were not correlated with ambient chlorophyll, the phytoplanktonic biomass gained by the rock fauna (ng chlorophyll *a* cm^{-2} h^{-1}, calculated as the product of clearance rate and the average chlorophyll concentration in the tank) was mainly determined by ambient concentration (Fig. 4, $r_s = 0.78$, $N = 23$, $P < 0.001$). Thus, during the spring bloom, the rock fauna removed four times more phytoplankton than during the oligotrophic summer (Fig. 4).

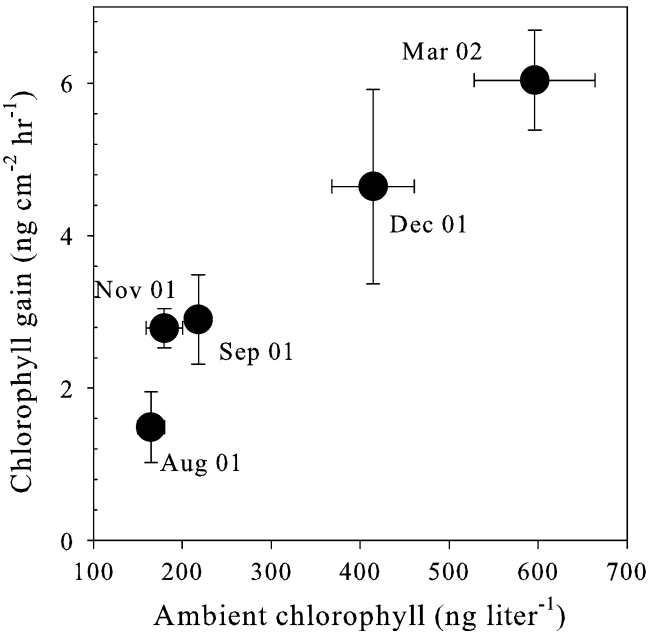


Fig. 4 Average rate of phytoplankton grazing by the rocks fauna (nanogram chlorophyll *a* cm^{-2} h^{-1}), calculated as the product of clearance rate and the average chlorophyll concentration in the tank, as a function of ambient phytoplanktonic biomass. *Vertical error bars* are SE calculated over tank means. *Horizontal error bars* are SE calculated over the mean ambient chlorophyll of all sampling sessions in an experiment (period). See Table 1 for number of replicates

Rock fauna

The rocks were inhabited with a highly diverse and rich fauna (Table 2, Fig. 5). Most of the animals were found in the outer ~3 cm. The average density of individual animals (excluding colonial taxa) in samples taken from the outer (<3 cm) layer was 15.6 per ml, reaching up to 60 individuals per ml. Foraminifera and polychaetes were the most abundant non-colonial taxa ($>80\%$ occurrence), followed by nematodes, gastropods, and other worms. The abundances of nematodes and polychaetes were highly correlated (Spearman $r=0.80$, $P<0.05$). Encrusting sponges had an overall low coverage with high abundance ($>30\%$ cover) found only in 3 of the 18 rocks examined. Boring sponges were present in 88% of the sub-samples microscopically examined (Table 2) but were absent in five of the tanks showing clear phytoplankton removal. Boring bivalves, a highly abundant occupant on living corals (Yahel et al. 1998; Holmes et al 2000), were almost absent in the rocks. Different rocks varied in their faunistic composition (Fig. 5), with no correlation between the abundances of the different taxa (except nematodes and polychaetes). However, similarity analysis (Bray Curtis similarity of untransformed counts, Clarke 1993) indicated that the rock surface fauna (average similarity 40.5%) had unique characteristics that differed significantly from the communities living in both the sand and gravel (analysis of similarity, $R=0.3$, $P=0.001$, Clarke 1993). The sand and gravel communities were more diverse (within groups similarity $<23\%$) and thus, the two groups were not significantly different from each other at the crude taxonomic resolution used (analysis of similarity, pairwise comparison $P>0.5$). The gravel, dominated by pebbles of magmatic origin, was the poorest substratum in our study site. The fauna of the few non-carbonate rocks examined was also rather sparse with very few infaunal organisms.

Despite the low taxonomic resolution employed, multiple regression analysis indicated the existence of a relationship between the faunistic composition of the tanks (estimated as the product of organism densities in sub-samples and the substratum volume) and the clearance rate (Adjusted $R^2=0.39$, $F_{2,23}=9.0$, $P=0.001$). When the entire data set was analyzed, regression analysis suggested that the abundance of polychaetes ($\beta=1.39$) and crustaceans ($\beta=-1.1$) accounted for 39% of the observed clearance rate variability between tanks. When untreated rock tanks were considered separately, polychaete ($\beta=1.7$) and crustacean ($\beta={}^{-}1.6$) abundances accounted for 50% of the variability (Adjusted $R^2=0.50$, $F_{2,9}=6.7$, $P=0.016$).

Ammonium

Ammonium concentrations in the inflow were in the typical range of the reef bottom water during the stratified season (Rasheed et al. 2002). In September, ammonium concentrations were somewhat higher (median 205 nmol NH_4 L^{-1}) than in October (181 nmol NH_4 L^{-1}). Chlorophyll *a* concentration showed the same trend (197 and 156 ng L^{-1}, respectively). Three of the four untreated rock tanks examined in each experiment showed small ammonium regeneration (median 0.5 and 7.4 nmol cm^{-2} h^{-1} for September and October, respectively), whereas a fourth tank showed net uptake (<3.8 nmol NH_4 cm^{-2} h^{-1}). These values corresponded to a regeneration of 0.3 and 2.0 nmol NH_4 per ng chlorophyll removed in the September and October experiments, respectively. Gravel and sand (n = 4 for each treatment) showed net NH_4 uptake in one experiment and net increase in the other.

Algae growth experiments

Benthic algal growth rate on plastic cylinders in the untreated rock tanks (56 ± 40 ng chlorophyll cylinder^{-1} day^{-1}) were the lowest, compared with 107 ± 70, 148 ± 135, and 211 ± 184 ng chlorophyll cylinder^{-1} day^{-1} on cylinders in tanks containing sand, bleached control, and gravel, respectively (two-way ANOVA over tank's means, $F_{3,54}=11.5$, $P<0.001$). The latter three substrata were not significantly different from each other (Tukey Unequal *N* HSD post-hoc pairwise comparison, $P>0.8$).

Discussion

The crypto fauna that inhabits exposed reef rocks removed up to 60% of the phytoplankton from the water flowing above it in our laboratory tanks (Figs. 2, 3). The 95% confidence interval for the annual mean clearance rate of untreated rock was 13.9–20.7 ml cm^{-2} h^{-1}. The lack of removal by the control (killed) rocks (Fig. 2) clearly ruled out hydraulic filtration or other abiotic removal mechanisms as a significant phytoplankton sink under the experimental conditions. Such mechanisms may, however, have a significant role in situ, primarily within the wave action zone and in high flow environments (Haberstroh and Sansone 1999; Huettel and Rusch 2000). We therefore conclude that the observed plankton removal in the tanks was due to a biotic process, most likely grazing (phytoplanktivory) by minute, unidentified, phytoplanktivorous suspension-feeders that inhabit the outer few centimeters of the rocks. Due to the small sample size, the statistical power of our experimental design was insufficient to reject the hypothesis (H_1) of significant plankton removal by the gravel or sand. However, the low to null removals recorded for these substrata indicate that they are far less important sinks for phytoplankton in comparison with exposed rock surfaces on the Eilat fringing reef.

The reef rocks we studied were selected by many volunteer divers when asked to choose rock samples with no visible macro-fauna cover (e.g., corals, sponges, tunicates, and fleshy algae). Thus it is most probable that these rocks would have been classified as ‘rock’ in most reef surveys (e.g., Reef Check, Hodgson and Liebeler 2002). As in previous reports (e.g., Bonem 1977; Peyrot-Clausade 1977; Vasseur 1977; Hutchings 1978, 1983; Gischler 1997; Holmes et al. 2000 and references therein), close examination of the surface of the rocks under the dissecting microscope revealed a highly diverse and rich fauna (Table 2, Fig. 5) with a mean total density of 15.6 individuals per ml of rock surface (outer 3 cm, excluding colonial forms). However, the cryptic nature of many rock dwellers precluded accurate visual counts of all the specimens present in a sample (Hutchings 1983). For example, serpulid polychaetes create a maze of microscopic tubes within minute rock crevices. It was sometimes impossible to separate individual tubes or to verify whether the tube contained a living worm. Boring sponges (e.g., *Cliona* spp.) posed another complication as there was no simple measure for their abundance (Kiene and Hutchings 1994). Moreover, due to methodological limitations (Wickham et al. 2000), ciliates and flagellates were not enumerated. Thus, data reported here should be considered conservative. As indicated by the multivariate analysis, rock surface fauna had unique characteristics and was both richer and more diverse in comparison with the gravel and sand communities. The regression analysis suggests a dependence of removal rate on the substratum community composition.

Robust inference from the experimental results to the field should rely on a proper measure of the amount of rock surface or phytoplanktivorous grazers in the experimental tanks, establishing proper methodology for measuring these parameters in the field, and good replication of field hydrodynamics in the laboratory. Unfortunately, none of the above can be easily established. Rock volume was clearly irrelevant as the vast majority of the fauna was found within 5 cm from the rock surface (see also Hutchings et al. 1992 and references therein). Indeed, rock volume and clearance rate were not correlated (Fig. 3b). Rock surface area is probably a better predictor of the grazing rates as indicated by the significant, albeit not very high ($r_s = 0.65$), correlation with clearance rates (Fig. 3a). This low correlation may have partly been a result of the inclusion of rocks bases and measurement inaccuracies; however, the most likely explanation is the high variability of the grazer’s abundance and community composition (Fig. 5).

Table 2 Average (SE) and maximum densities (# ml^{-1} of rock) of the fauna identified in sub-samples taken from the outer 3 cm of reef rocks surfaces used in the August, September, and October 2001 experiments. Percent values indicate the proportion of the sub-samples in which the taxon was present (sub-sample volume ranged 0.5–16 ml). Colonial organisms, such as sponges, ascidians, and bryozoans were not quantified, thus only the presence/absence data are reported for these taxa. Endolithic, encrusting, and coralline algae were present in most rocks but were not quantified. Visual observations of the rocks indicated the occurrence of additional taxa that were absent in the sub-samples, including: boring bivalves (*Lithophaga* spp.), holothurians, unidentified ophiuroids, nemerteans, small sea anemones, and a few coral polyps (new recruits)

Taxon	Untreated rock ($N = 18$)			Gravel ($N = 7$)			Sand ($N = 7$)		
	Density	Max	Percentage	Density	Max	Percentage	Density	Max	Percentage
Foraminifers	5.4 (1.7)	21	82	0.4 (0.2)	1	43	4.7 (2.2)	15	71
Polychaetes	3.8 (1.0)	19	94	0	0	0	2.6 (1.1)	6	57
Filter-feeding Polychaetes	0.8 (0.2)	3	59	0.3 (0.2)	1	29	0.3 (0.3)	2	14
Nematodes	3.4 (1.4)	19	76	0.3 (0.2)	1	29	0.6 (0.3)	2	43
Other worms	0.7 (0.2)	3	59	0.1 (0.1)	1	14	0.3 (0.2)	1	29
Mollusks	0.8 (0.2)	4	71	0.1 (0.1)	1	14	1.7 (0.8)	5	43
Crustaceans	1.1 (0.5)	8	76	0.1 (0.1)	1	14	0.6 (0.2)	1	57
Sponges			88			29			0
Tunicates			47			29			0
Bryozoans			23			0			0

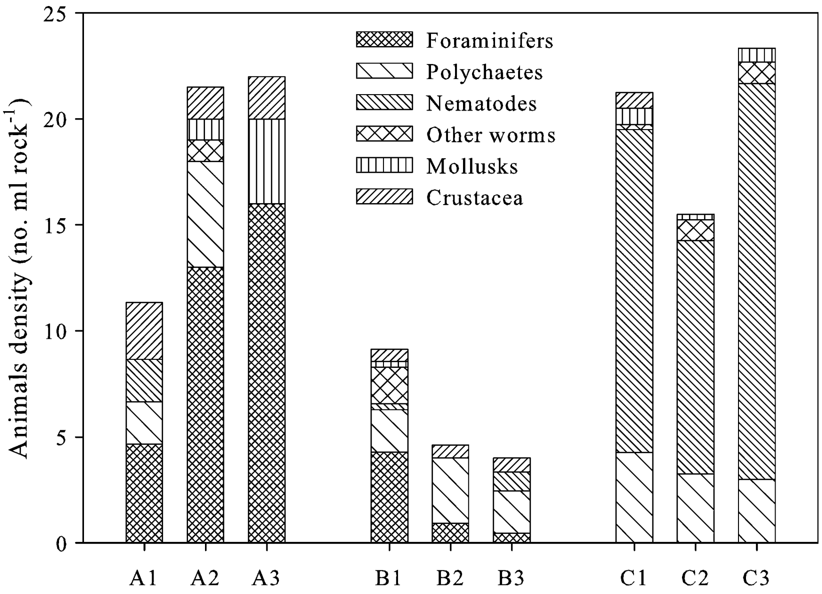


Fig. 5 An example of the faunistic composition in sub-samples (one to three) taken from the untreated rock surface of tanks 7(A), 8(B), and 10(C) used in the August 2000 experiment. Note the high intra-rock variability

Due to the aforementioned limitations, our laboratory data cannot be directly applied to infer grazing rates in the field. Nevertheless, scaling the observed clearance rate to the planar area occupied by the rocks in the tank can provide reasonable first-order estimate for the *potential* of reef rock fauna to remove phytoplankton at the field. However, as the relief of the rocks within the tanks was limited to 0.15 m, our calculated areal clearance rates for the reef should be considered as a lower bound estimate. Moreover, the rather large difference in phytoplankton concentration between the inflow and outflow waters (38 ± 26%) may indicate that the rate of consumption by the fauna in the tanks was limited by phytoplankton availability. If the feeding by the rock surface fauna was indeed limited by insufficient supply of planktonic food (as suggested by Fig. 4), then potential grazing rates were further underestimated.

Scaled up, the annual mean clearance rate by untreated rock fauna was 4.2 ± 1.9 m^3 m^{-2} day^{-1} (95% confidence interval: 3.3–5.0 m^3 m^{-2} day^{-1}). Considering a 50% rock cover at our study site (Yahel et al. 1998) and boundary layer flow similar to the field (Yahel et al 2002; M. A. Reidenbach et al., unpublished), the exposed rock fauna may be estimated to have cleared 1.6–2.5 m^3 m^{-2} day^{-1}. This clearance rate is in the lower range of reported values for the beds of benthic suspension feeders in temperate eutrophic waters (e.g., Riisgård 1998) and accounts for a small percentage of the observed phytoplankton removal reported by Genin et al. (2002) for the same study site. Clearly, other suspension feeders such as macro-sponges and tunicates and the fauna inhabit live corals (e.g., *Lithophaga* spp.) contribute substantially to the total grazing by the reef community (Ribes et al. 2005). In March 2001 when direct cell counts were available, nitrogen and carbon gain via plankton removal (including bacteria) could be estimated using published conversion factors (Caron et al. 1995). The nitrogen removal rate was 5.27 mmol m^{-2} reef day^{-1}, exceeding values reported by Fabricius and Dommisse (2000) for the total particulate nitrogen removal by a soft coral dominated reef, and comparable to values reported by Ribes et al. (2003) for natural assemblages of coral reef benthos (8–10 mmol m^{-2} reef day^{-1}). The phytoplanktonic carbon removal rate was 0.14 g C m^{-2} reef day^{-1}, about half the Fabricius and Dommisse (2000) value. It should be noted that the March experiment was done during a spring bloom with elevated plankton concentrations. A more realistic estimate of the annual carbon gain was calculated using the annual chlorophyll average for 1988–1998 (353 ± 91 ng L^{-1}, measured daily at the reef, Genin et al. 1995) and chlorophyll: carbon ratio of 60 (Yahel et al. 1998). Using these values the estimated annual import of phytoplanktonic carbon to the reef via rock surfaces fauna was at least 16 g C m^{-2} year^{-1}. While this value is an order of magnitude lower than those recorded over soft coral-dominated reefs (Yahel et al. 1998; Fabricius and Dommisse 2000), it is comparable to values reported for oligotrophic barrier reefs in Australia (4–20 g C m^{-2} year^{A1}, Ayukai 1995).

In contrast to the reports of nutrient release in coral reef rock cavities (Gast et al. 1998; Richter and Wunsch 1999), ammonium regeneration within the untreated rock tanks was marginal, and no enhancement of benthic algae growth could be detected. Dense populations of epi- and endolithic algae were present in all the rocks examined. Such algal population is usually absent or diminished in reef cavities (Richter et al. 2001). It is therefore possible that the majority of the remineralized nitrogen (and phosphorus) was consumed by autotrophic and microbial communities on the untreated rocks and could not be available to the experimental plastic tubes located few centimeters from the rocks.

In areal terms, exposed rock is the second most important niche in coral reefs worldwide (Hodgson and Liebeler 2002). Although the presence of a diverse infauna in these rocks had been known for several decades (reviewed by Hutchings 1983; Holmes et al. 2000), only little attention had been devoted to its ecological function. This study demonstrates the potential importance of rock surface fauna in importing allochtoneous nutrients (as phytoplankton) into the reef. Further studies are required to establish the role of different taxa and the overall contribution of reef rocks fauna to biogeochemical fluxes in coral reefs.

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