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Cavity-dwelling suspension feeders in coral reefs—a new link in reef trophodynamics

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ABSTRACT: The small-scale distributions of chlorophyll *a* (chl *a*), pheopigments, oxygen and currents were determined in horizontal sections between coral reef cavities and benthic boundary layer waters (BBL) to estimate rates of grazing and respiration by cryptic cavity-dwelling (coelobite) suspension feeders. We investigated 0.5 to 5 m long and 0.1 to 1 m wide cavities in fringing reefs on the western coast of the Gulf of Aqaba (Red Sea), between 2 and 16 m depth. Within cavities net currents averaged 0.9 cm s^{-1}, or 22% of the current speed measured in BBL ~2 m away from the reef. In spite of rapid flushing of cavity waters within a few minutes, we encountered significant chl *a* and oxygen depletions relative to BBL, particularly under oligotrophic conditions. Chl *a* depletions amounted, on average, to 0.10 ± 0.03 mg m^{-3} (median ± median absolute deviation [MAD]) or 54% (max. 86%) of BBL values and showed a positive relation to coelobite suspension feeder densities. Pheopigments, by contrast, remained remarkably constant, indicating selective grazing of the mainly picoplankton-sized food. Oxygen depletions were weak and mainly related to flushing. In sack-shaped cavities they amounted to 13.6 ± 6.1 mmol m^{-3} or 3 to 9% of BBL concentrations. Analyses of water flow and chl *a* distributions show that under oligotrophic summer conditions 0.7 g C m^{-2} d^{-1} of phytoplankton disappears within the upper 1 m of cavernous reef framework. This conservative estimate is about 1 order of magnitude higher than grazing rates of coral-dominated communities on the exposed reef, rendering cryptofauna suspension feeding an important and new pathway of extrinsic organic matter into coral reefs.

KEY WORDS: Cavities · Crevices · Cryptofauna · Coelobites · Phytoplankton · Grazing · Respiration · Coral reefs

INTRODUCTION

Coral reef cavities are believed to constitute between 30 and 75% of the bulk volume of the coral reef (Garrett et al. 1971, Ginsburg 1983, Kobluk & van Soest 1989) and between 60 and 75% of the total available surface (Jackson et al. 1971, Buss & Jackson 1979, Logan et al. 1984), yet hardly anything is known about the ecology of this cryptic habitat. Logistic constraints have until now restricted research mainly to wide caves and caverns, on the one hand, and to the easily accessible cryptofauna communities under living corals and coral rubble, on the other. Only recently with the advent of video-endoscopic techniques has it become possible to investigate the wide-spread small crevices and galleries interlacing the reef framework (Wunsch & Richter 1998).

Framework cavities result from the interaction of growth and erosion of the reef matrix, giving rise to an intricate irregular system of voids (Ginsburg 1983), which may extend several meters into the substrate (Zankl & Schroeder 1972). The cavity walls thus provide a very large living space for low-light adapted organisms or coelobites (Ginsburg & Schroeder 1973) and, hence, a potentially important interface for biogeochemical fluxes between the interior and exterior of the coral reef. Transport of nutrients and organic matter is driven by hydraulic exchange of water through crevices (Wolanski 1994) connecting with the benthic boundary layer waters (BBL) through numerous holes in the limestone (Fig. 1).

Due to the paucity of light, heterotrophs generally dominate coelobite communities, particularly cryptic suspension feeders such as sponges, ascidians or bryo-

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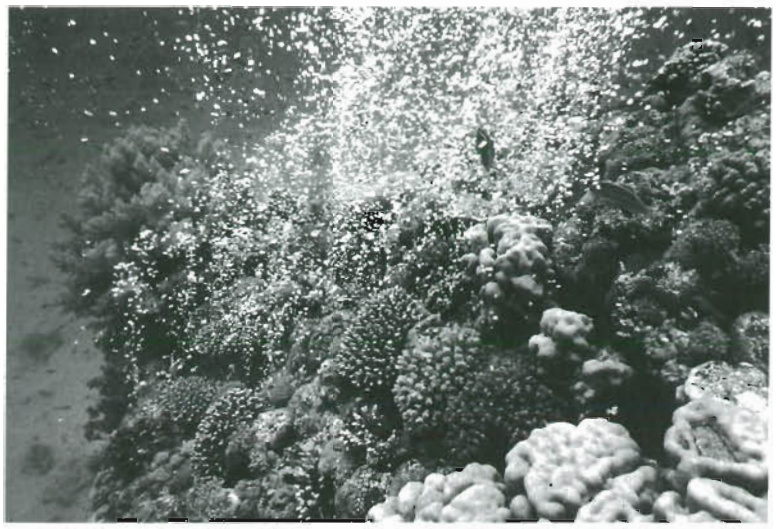

Fig. 1. Curtain of bubbles emerging from air trapped beneath a reef overhang and percolating through 2 m of cavernous reef (Moses Rock, Eilat, Israel)

zoans (Vasseur 1974, 1977, Logan et al. 1984). These groups may reach high biomass levels, comparable to that found on the reef's external surface (Hutchings 1974, Meesters et al. 1991), and cover almost the entire available substratum (Jackson et al. 1971) leaving at the most 1 to 5% unoccupied space (Buss & Jackson 1979). Consequently, competition for space and food is intense (Buss 1979, Buss & Jackson 1979).

Earlier investigations showed substantial depletions of nanoflagellates and bacteria in reef-fouling communities (Buss & Jackson 1981), as well as growth responses of the filtering community to variations in flow conditions (Winston 1976, Wilkinson & Vacelet 1979, Buss & Jackson 1981). Recently, Gast et al. (1998) found significant reductions in bacterial numbers as well as enhanced bacterial growth in small coral reef crevices of Curaçao, and pointed at the possible role of cryptic sponges in filtering and remineralizing the picoplankton (<2 µm) food (Gast et al. 1998). But no attempt has yet been made to quantify the uptake of plankton by the coelobite community.

In oligotrophic waters, most of the plankton in the smallest size classes consists of phytoplankton, mainly of cyanobacteria and prochlorophytes, which constitute more than 50% of the total plankton biomass (Ducklow 1990, Roman et al. 1990, Lindell & Post 1995). For coral reefs, phytoplankton is mainly an extrinsic source of food, particularly on the narrow continental shelves of the Gulf of Aqaba, where steep slopes lead to a constant flushing of the fringing reefs with oceanic waters (Fig. 2, Reiss & Hottinger 1984). In this semi-enclosed sea, the bulk of the phytoplankton biomass is picoplanktonic (>90% at all times, A. F. Post pers. comm.), particularly in summer when prochlorophytes <1 µm predominate (Lindell & Post 1995), albeit at very low total concentrations (usually <0.3 mg chlorophyll *a* (chl *a*) m^{-3}, Genin et al. 1995).

Our main objective was to see if and to what extent the cryptofauna community is able to tap this dilute suspension of minute particulate food and to assess the magnitude of this potential pathway of extrinsic food into the coral reef. The specific objectives were (1) to determine the fluxes of chl *a* and pheopigments between reef cavities and BBL as proxies for picoplankton removal and digestion by the suspension-feeding community and (2) to compare the carbon input channeled through the suspension feeders with the oxygen uptake of the total cryptic community.

MATERIAL AND METHODS

Site description. A total of 22 cavity transects were sampled at 4 fringing reef locations on the Egyptian and Israeli coast of the Gulf of Aqaba, a northeastern extension of the Red Sea (Table 1, Fig 2). Detailed descriptions of the sites and the biological and physical characteristics of the study area are found in Reiss & Hottinger (1984), Yahel et al. (1998) and references therein. They represent typical flourishing reef sections of the western Gulf characterized by a narrow shelf, moderate slopes and a fairly open unconsolidated framework with little sediment infilling (Barnes & Lazar 1993). Coastal currents are generally longshore and weak (<20 cm s^{-1}), with semi-diurnal flow reversals during summer (Yahel et al. 1998). A weak (<2 cm s^{-1}) cross-shore circulation transports offshore water and plankton to the coast in the upper 10 to 20 m, with subsequent downwelling and offshore flow near the bottom (Yahel et al. 1998). This cross-shore circulation onto the narrow shelf leads to a continuous, albeit weak, flushing of the reef slope with offshore waters.

At all sites we found the reef riddled with holes of various sizes connecting the framework cavities with the reef exterior (Fig. 1). Observations with an endoscopic videocamera ('CaveCam', Wunsch & Richter 1998) support previous estimates that at least 30% of the volume of the upper reef framework is made up of cavities harbouring cryptic coelobite communities (Gischler & Ginsburg 1996). Most cavities examined were densely covered with coelobites including many suspension feeding forms, such as encrusting sponges, ascidians and bryozoans (Wunsch & Richter 1998,

Fig. 2. Fringing reef locations (arrows) studied in the Gulf of Aqaba, Red Sea

Wunsch unpubl.). Coralline algae predominated near the cavity entrances.

Sampling and sample processing. Sampling was carried out in summer, when phytoplankton concentrations are at their annual minimum (Genin et al. 1995, Lindell & Post 1995), and hence, most likely to be limiting to cryptic suspension feeders.

Different cavities were selected on exploratory SCUBA dives between 2 and 16 m depth. They primarily consisted of crevices and galleries in the framework of the reef slope, pinnacles and reef patches, but also of voids under coral overhangs and within coral thickets. Cavities were typically 0.1 to 1 m wide and extended 0.5 to 5 m horizontally or obliquely into the framework (Table 1). Dye

Table 1. List of coral reef cavities sampled. Cavity Type A: sack type, weak flushing, low connectivity; B: obstructed tunnel, moderately flushed, medium connectivity; C: tunnel cavity, well flushed, high connectivity. Orientations n and p: cavity axes perpendicular and parallel to prevailing flow, respectively

Transect no.	Date	Time	Site	Water depth (m)	Name	Length (m)	Type	Orientation	Coelobite cover	Remarks
1	4 Aug 1996	6:30	Ras Abu Galum	2	*Acropora* table	5.0	C	n	High	Red algae, sponges, tunicates, hydrozoa, gorgonians, *Tubastrea*
2	5 Aug 1996	8:00	Ras Abu Galum	2	*Acropora* table	5.0	C	n	High	Red algae, sponges, tunicates, hydrozoa, gorgonians, *Tubastrea*
3	5 Aug 1996	18:00	Ras Abu Galum	5	Pinnacle	4.4	B	p	High	Encrusting and boring sponges, bivalves, gorgonians, fish
4	6 Aug 1996	7:00	Ras Abu Galum	5	Pinnacle	4.4	B	p	High	Encrusting and boring sponges, bivalves, gorgonians, fish
5	7 Aug 1996	7:00	Hibiq	4	Lobster cave	2.0	A	n	Medium	Sediment bottom, high siltation
6	7 Aug 1996	21:00	Hibiq	4	Fore reef	2.0	C	n	Medium	Encrusting organisms, high siltation
7	7 Aug 1996	21:00	Hibiq	3	Back reef	2.0	C	n	Medium	Encrusting organisms, high siltation
8	8 Aug 1996	12:00	Hibiq	4	Cavern	2.0	C	n	Low	Spaceous cave, low coelobite cover, red algae
9	8 Aug 1996	12:00	Hibiq	4	*Acropora* thicket	2.0	B	p	Medium	–
10	10 Aug 1997	13:00	Eilat	5	Moses Rock	4.0	C	p	High	Extremely rich, all groups, *Scleronephthya*
11	11 Aug 1997	10:00	Eilat	5	Moses Rock	4.0	C	p	High	Extremely rich, all groups, *Scleronephthya*
12	11 Aug 1997	19:00	Eilat	5	Moses Rock	4.0	C	p	High	Extremely rich, all groups, *Scleronephthya*
13	19 Aug 1997	9:00	Ras Burka	16	Patch reef	2.0	B	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
14	19 Aug 1997	17:00	Ras Burka	16	Patch reef-Cave 1	0.6	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
15	19 Aug 1997	17:00	Ras Burka	16	Patch reef-Cave 2	0.6	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
16	19 Aug 1997	17:00	Ras Burka	16	Patch reef-Cave 3	0.6	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
17	20 Aug 1997	17:00	Ras Burka	16	Patch reef-Cave 1	0.6	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
18	20 Aug 1997	17:00	Ras Burka	16	Patch reef-Cave 2	0.6	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
19	20 Aug 1997	17:00	Ras Burka	16	Patch reef-Cave 4	0.7	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
20	21 Aug 1997	11:00	Ras Burka	16	Patch reef-Cave 1	0.6	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
21	21 Aug 1997	11:00	Ras Burka	16	Patch reef-Cave 2	0.6	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish
22	21 Aug 1997	11:00	Ras Burka	16	Patch reef-Cave 4	0.7	A	p	High	Red algae, solitary and encr. tunicates, sponges, sheltering fish

and air experiments revealed numerous secondary vertical connections between cavities and BBL (Fig 1). Based on their degree of connectivity with BBL we broadly classified the voids into 'low' connectivity sack-shape cavities with little water exchange through small cracks and fissures, 'medium' connectivity obstructed tunnel cavities with moderate exchange of water through a cavernous framework, and 'high' connectivity tunnel cavities with free water exchange between opposite openings (Table 1).

Cavities were inspected using the CaveCam fitted with a 3.5 mm super-wide angle lens (cf. Wunsch & Richter 1998 for details). A preliminary assessment of cryptofauna densities was undertaken on site, identifying cavities with 'high', 'moderate' and 'low' densities of coelobite suspension feeders, corresponding to an estimated <10%, 10 to 30% and >30% cover. A detailed quantitative analysis of coelobite communities in the Gulf of Aqaba is in progress and will be given elsewhere (Wunsch unpubl.). Cavities were marked with numbered buoys for later re-identification.

On subsequent dives, we sampled the small-scale distribution of phytoplankton pigments and oxygen between cavities and BBL. To this effect we carried out horizontal transects along the main axes of the cavities, and along (pinnacle and patch reef transects) or perpendicular (fore-reef transects) to the prevailing current direction. Pressure gradients due to vertical flow speed differences (cf. Vogel 1994) between the deeper main and the shallower secondary cavity openings resulted in weak net currents directed into the cavities. Thus, in general, water sampled at the distal end of a given cavity had passed over an assemblage of suspension feeders before reaching the sampling point. This sampling scheme is similar to the classical Eulerian design used in earlier plankton depletion studies over reef flats (Glynn 1973, Ayukai 1995), but different from the one used by Yahel et al. (1998), who studied *inter alia* the phytoplankton distribution over the reef normal to the prevailing flow.

Each transect was aligned with the center axis of the cavity. It was composed of a first sampling point in the outer bottom boundary layer (*sensu* Shashar et al. 1996) 1 to 2 m off the reef, outside the direct influence of corals. A second sampling point was centered in the cavity entrance and a variable number of further sampling points spaced evenly over the length of the cavity (Table 2). In addition, we collected water from the downstream ends of tunnel cavities and from the leeward sides of pinnacles.

On every sampling point we took triplicate water samples for both, phytoplankton pigments and oxygen, yielding a total of 18 to 42 samples per transect. Water was collected with 100 ml polyethylene syringes fitted with 100 µm screened silicone tubing mounted on a rod. The system was rinsed between samplings to

Table 2. Mean concentrations and standard deviations (SD) of phytoplankton pigment and oxygen concentrations and current speeds in bottom boundary layer (BBL) and cavity (Cav.) waters. k gives the number of sampling points on every transect. Significant gradients, according to the Page-test are denoted with asterisks (*p < 0.05, **p < 0.01, ns: not significant). Positive current values are directed into the cavities

Transect		Chlorophyll *a* (ng l^{-1})					Pheopigments (ng l^{-1})					Oxygen (µmol l^{-1})					Currents (cm s^{-1})			
No.	k	BBL	SD	Cav.	SD	p	BBL	SD	Cav.	SD	p	BBL	SD	Cav.	SD	p	BBL	SD	Cav.	SD
1	5	99	14	51	18	*	65	10	66	5	ns	220.5	0.6	216.7	6.4	ns				
2	7	151	7	82	20	**	88	10	72	16	ns	214.0	7.6	203.9	1.2	*				
3	6	162	14	115	37	**	56	17	48	12	*	211.4	1.1	207.3	1.3	**				
4	6	188	16	96	45	**	45	6	50	27	ns	207.8	3.9	206.4	3.9	*				
5	4	170	3	165	24	ns	81	4	97	7	*	190.8	0.8	187.5	3.5	ns				
6	4	120	8	79	9	**	71	10	102	30	*	204.1	1.6	200.8	2.8	*				
7	3	97	7	79	17	ns	92	9	104	64	ns	194.4	7.0	198.8	2.3	**				
8	4	158	2	169	14	ns	67	3	69	4	ns	209.1	2.5	210.0	1.2	ns				
9	4	156	5	112	22	**	74	4	87	10	ns	211.3	0.5	207.2	2.7	**				
10	7	1732	173	1708	166	ns	296	52	349	67	ns	226.8	0.6	218.1	7.6	**	2.7	1.2	1.2	0.9
11	7	269	25	258	14	ns	74	16	70	5	ns	206.5	1.1	204.9	1.1	**	8.9	1.2	6.7	1.1
12	7	1237	84	982	213	**	384	37	314	44	**	215.0	3.0	211.3	2.5	**	2.6	0.5	1.4	0.7
13	5	249	4	140	77	**	123	10	88	28	ns	207.8	2.2	206.6	2.8	ns	8.9	2.3	1.6	2.0
14	3	184	6	67	7	**	94	3	72	4	ns	215.8	2.2	202.6	1.9	**	3.4	0.2	1.0	0.3
15	3	128	24	68	13	**	100	7	77	5	ns	208.8	0.4	197.4	4.0	ns	3.4	0.2	0.4	0.2
16	3	191	21	42	6	**	106	6	97	3	*	201.8	0.7	195.9	0.3	ns	3.4	0.2	0.2	0.2
17	3	207	10	44	5	**	82	7	80	9	ns	220.1	4.7	201.6	0.5	ns	4.6	0.9	0.2	0.6
18	3	118	26	103	10	**	105	10	87	4	ns	206.6	4.3	209.1	1.6	ns	4.6	0.9	0.8	0.7
19	3	210	20	49	18	ns	105	17	109	6	ns	203.1	2.5	202.0	3.5	*	10.6	0.8	1.1	0.2
20	3	211	45	91	26	*	99	18	81	13	ns	214.0	0.9	205.5	0.5	ns	4.0	0.6	1.1	0.4
21	3	109	6	86	7	**	118	34	90	11	ns	207.4	0.6	211.6	6.0	ns	4.0	0.6	1.5	0.6
22	3	209	2	67	13	*	83	12	82	11	ns	182.1	3.2	188.3	1.6	ns	6.3	1.1	3.2	0.9

avoid contamination from previous samples. Syringes were stored in a shaded box, transferred into the laboratory immediately after every dive and kept at ambient temperature until processing within 2 h of collection. The impermeability of the syringe pistons was tested fluorometrically, using distilled water drawn into syringes submerged in a bucket of fluorescein dye. The impermeability of the sampling system for oxygen was confirmed using seawater scrubbed with nitrogen measured immediately and 3 h after collection. No differences in chl *a* and pheopigment concentrations were detected in syringes processed immediately and 3 h after collection.

Chl *a* and pheopigments were measured with a fluorometer (Turner Designs Mod. AU-10) using the acidification method (Parsons et al. 1984) after filtering 100 ml of the sample on 25 mm diameter Whatman GF/F filter and extracting the pigments in 90% acetone over a 24 h period at 4°C in the dark. Oxygen was measured by Winkler titration (Grasshoff et al. 1976).

Current speed data are available for the 1997 investigations only. The net displacement of suspended particles in the water was recorded simultaneously by video in BBL and inside the cavities. The BBL camera (a digital SONY VX1000E in a Seacam housing) was mounted on a tripod ~2 m upstream of the cavity entrances and oriented perpendicular to the current direction. The CaveCam was fitted with a small mirror at 45° angle in front of the lens to record currents inside the narrow cavities (Wunsch & Richter 1998). Both cameras used ambient light in conjunction with a narrow depth of field to trace the trajectories of advected particles against a dark background. For both the BBL camera and CaveCam, the focal plane was 10 to 30 cm away from the lens, far enough for the camera body not to affect the streamlines. CaveCam recordings were performed after syringe samplings to rule out the possibility of affecting the pigment and oxygen samples. BBL currents, which were recorded continuously on every dive, remained stable during the ~1 h sampling periods. We processed the video tapes by counting the number of frames it took a particle to cross the known distance between the left and right margins of the monitor screen. The current speed (cm s^{-1}) was calculated by dividing the recording frequency (25 frames s^{-1}) by the number of frames per unit length (frames cm^{-1}).

These direct observations were complemented with water flushing experiments using fluorescent dye. We injected fluorescein homogenously into the given cavity and recorded the dilution of the fluorescence signal over time in 100 ml syringe samples taken in given time intervals (seconds to minutes) in its center. Raw blank-corrected fluorescence was measured on a TD-700 fluorometer equipped with a fluorescein filter kit (486 nm excitation, 510 to 700 nm emission). At Moses Rock, a 4 m diameter pinnacle in the Coral Reserve of Eilat, Israel, the dilution of the dye was observed at 4 sampling points spanning the full length of a tunnel cavity facing into the current. Fluorescein is a nontoxic and conservative tracer with negligible adsorption properties (Turner Associates 1971). Yet, fluorescein experiments were always carried out last to rule out the possibility of interference with the phytoplankton pigment measurements.

Statistical analysis. Data were analyzed using standard statistical tests (Sachs 1992 and references therein).

To test for spatial gradients in the pigment and oxygen concentrations of the individual transects we ran the Page-test for N = 22 transects with k = 3 to 7 sampling points and n = 3 replicates each. This nonparametric test for ordered alternatives is based on Friedman rank sums and tests for monotonously increasing (or decreasing) treatment effects (here: coelobite grazing and respiration) against the null-hypothesis of no treatment effects on the distributions of chl *a*, pheopigments and oxygen. The distal sections of tunnel and pinnacle transects (cavity exits, leeward sides of pinnacles) were excluded from analysis, because vagarious mixing with BBL would obliterate the test results.

In a second step we grouped the data into k = 4 transect sections and examined the distributions of pigments and oxygen between BBL, cavity entrance, cavity and cavity exit by means of box-plots. Skewed distributions led us to report median and median absolute deviations (MAD) and to transform the data for subsequent analyses.

ANOVA was carried out to determine the effects of sampling sites, flushing, suspension feeder cover, etc. on the distributions of chl *a* and oxygen in BBL and cavities. Raw data were log-normalized, percentages were arcsine-transformed. Scheffé's F procedure was used for *a posteriori* multiple comparison of means.

To explore the effects of water renewal and phytoplankton availability on the amount of phytoplankton grazed in the cavities, we carried out a multiple linear regression analysis with the average current speed in the cavity and chl *a* concentration in BBL as independent variables and the percent concentration difference of chl *a* between BBL and cavity as a dependent variable.

RESULTS

In all but 1 of the 22 transects carried out, chl *a* concentrations were lower in coral reef cavities than in BBL; in 16 transects examined the observed depletions

were significant according to the Page-test ($p < 0.05$, Table 2). In contrast to the chl *a*, no clear pattern emerged for the pheopigments; higher and lower cavity concentrations compared to ambient values were found in roughly the same number of cases, and the few significant gradients featured opposite signs (Table 2). Oxygen values were lower in the cavities than in BBL in 17 out of 22 transects examined, and significantly so in 10—as opposed to only 1 significant positive gradient ($p < 0.05$, Table 2).

Transects 3 and 4 are given as examples for typical upstream-downstream distributions of chl *a*, pheopigments and oxygen between BBL and a cavernous fore-reef pinnacle in Ras Abu Galum, visited twice under strong (~20 cm s^{-1} in BBL) and weak (~3 cm s^{-1}) current conditions (Fig. 3A,B). On the day with a strong current, we found a linear decrease of chl *a* concentrations along the 4.4 m section of the pinnacle down to one-third of the upstream values at its leeward end (Fig. 3A, shaded area, left to right). During weak currents, chl *a* values plummeted to minimum values

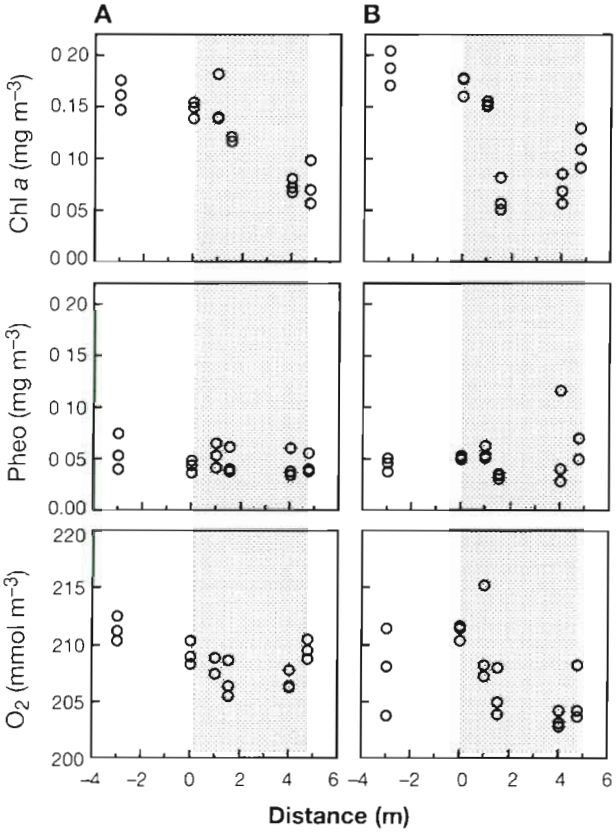

Fig 3 Cross-section through a fore-reef pinnacle in Ras Abu Galum, Egypt, with upstream (negative values on abscissa) and cavity (shaded area) concentrations of chlorophyll *a* (chl *a*), pheopigments and oxygen (O_2) during (A) strong (~20 cm s^{-1}) and (B) weak (~3 cm s^{-1}) current conditions in the bottom boundary layer. Chl *a* and O_2 gradients were significant according to the Page-test

already in the upstream third of the transect and rose again towards the leeward end to about 50% of BBL concentrations (Fig. 3B). Pheopigments remained virtually unchanged along the first transect and displayed some inconsistent scatter on the second. Oxygen profiles showed weak but clear depressions in the inner reaches of the pinnacle of 4 and 7 mmol m^{-3}, respectively. A maximum at the upstream entrance was apparent under weak current conditions only. It coincided with a high cover of coralline algae.

Chl *a* concentrations were <0.3 mg m^{-3} throughout the study ('normal summer' conditions, Fig. 4A, Table 2), with the exception of Transects 10 and 12 at Moses Rock, Eilat, where we encountered, between tides, a bloom with very high pigment concentrations in the BBL ranging between 1.1 and 2.0 mg chl *a* m^{-3} (Fig. 4B, Table 2).

The normal summer situation (Fig. 4A) was characterized by significant chl *a* differences along the 'average' transect (ANOVA, log-normalized data, $F_{3,225} = 22.43$, $p < 0.0001$). The strongest depletion occurred between BBL and the cavity section (–54%, Scheffé's $p < 0.0001$), with average (median ± MAD) concentrations of 0.188 ± 0.028 and 0.086 ± 0.030 mg m^{-3}, respectively. No spatial differences were detectable for either pheopigments ($F_{3,225} = 1.96$, $p = 0.12$) or oxygen ($F_{3,201} = 2.52$, $p = 0.06$, Fig. 4A). Net flow inside the cavities averaged 0.89 ± 0.27 cm s^{-1} or 21.6% of the current speed measured in BBL (Fig. 4A). This corresponds to a mean water passage time of less than 4 min (225 s) over the average 2.0 ± 1.4 m length of the investigated cavities.

During the bloom at Moses Rock (Fig. 4B), we detected no significant differences for either chl *a* or pheopigments along the transect (ANOVA, log-normalized data: $F_{3,38} = 1.54$, $p = 0.22$; and $F_{3,38} = 2.06$, $p = 0.12$; respectively). Oxygen did, however, show significant differences between transect sections (ANOVA, log-normalized data: $F_{3,38} = 6.34$, $p < 0.01$), notably between BBL and the leeward exit of the tunnel cavity (Scheffé's $p < 0.01$), but not between BBL and the cavity itself (Scheffé's $p = 0.10$). The average net current in this relatively open tunnel cavity (1.04 ± 0.78 cm s^{-1}, Fig. 4B) was 36.8% of the average speed in the BBL.

A closer examination of the normal summer distributions revealed marked differences in BBL chl *a* between sampling sites and times (Fig. 5A to D). Lowest concentrations were found at the southern sites of Ras Abu Galum and Hibiq, and highest values in Eilat at the northern tip of the Gulf of Aqaba. Nighttime concentrations were significantly lower than daytime concentrations (ANOVA, log-normalized data: $F_{2,45} = 21.31$, $p < 0.0001$). The apparent differences in BBL chl *a* relating to 'coelobite cover' turned out to be effectively 'site' effects: this is because low coelobite cover was restricted to Hibiq, and because at the same time Hibiq

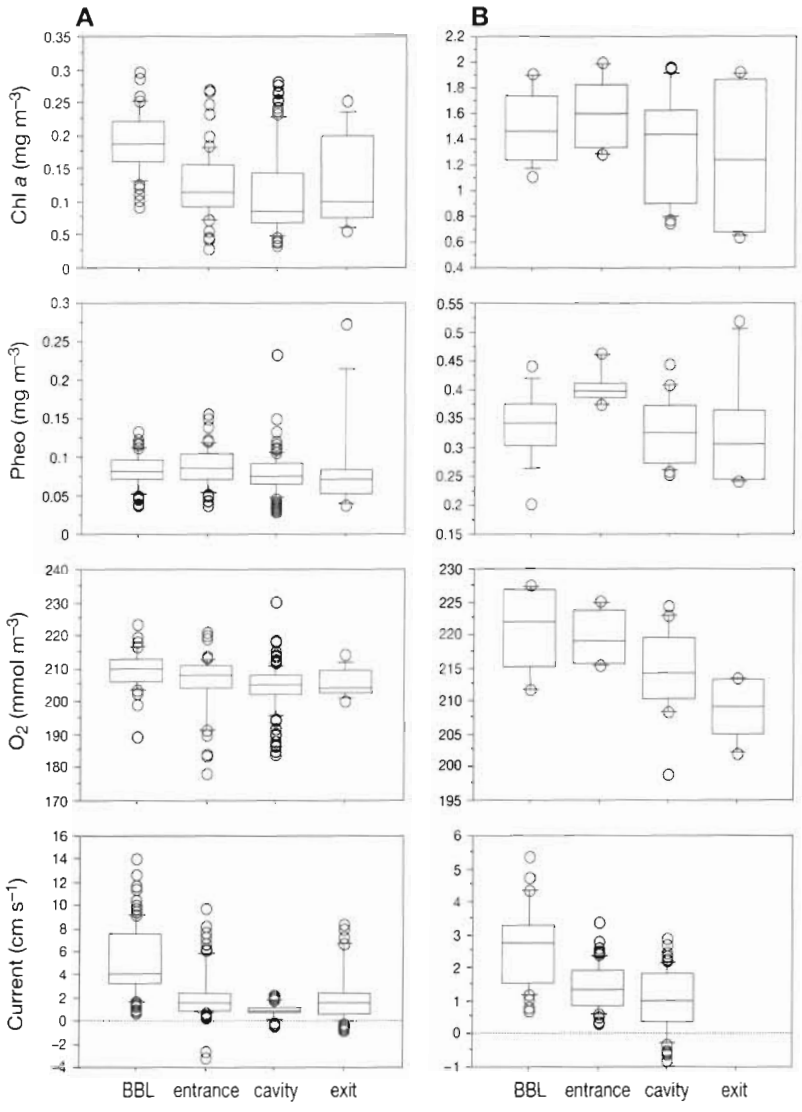

Fig. 4. Distributions (top to bottom panels) of chl *a*, pheopigments, oxygen and currents between the the bottom boundary layer (BBL), cavity entrance, cavity and cavity exits of 20 transects carried out under (A) normal summer and 2 transects carried out under (B) bloom conditions (>0.3 mg chl *a* m^{-3}). Boxes encompass 50% of the data between the 25th and 75th percentile, center lines display the medians. The upper and lower horizontal lines delimit the 10th and 90th percentiles, outliers are shown as open circles

coincided with the lowest chl *a* concentrations in BBL (Table 1). Cavity connectivity (i.e. whether the cavities were closed, semi-closed or open) did not affect BBL chl *a* levels (ANOVA, log-normalized data: $F_{2,45} = 1.19$, $p = 0.31$; Fig. 5C).

Chl *a* consumption in the cavities (Fig. 5E to H) appeared to be non-linearly related to chl *a* availability in BBL at the different sites: the effectiveness of removal increased from 18% at the low-chlorophyll site Hibiq to 62% in Ras Burka with moderate chl *a* levels. At higher chlorophyll levels, however, this trend reversed: in Moses Rock, Eilat, removal was effectively zero, even though this cavity was virtually carpeted with filter feeders (Table 1). Two-way ANOVA showed that connectivity and coelobite cover significantly affected chl *a* removal, as did the interaction term of the 2 factors (ANOVA, arcsine-transformed data: $F_{1,105} = 6.71$, $p < 0.05$): strongest depletions (>60%) occurred where both coelobite cover was high and water exchange reduced. We found no significant temporal differences in chl *a* retention efficiency (ANOVA, arcsine-transformed data: $F_{2,45} = 2.85$, $p = 0.06$; Fig. 5F).

Oxygen concentrations in the BBL (Fig. 5I to L) varied significantly between sites and daytime hours, but also upstream of cavities of differing connectivity and coelobite cover. Diel changes of ~8 mmol m^{-3} (ANOVA, log-transformed data: $F_{2,32} = 6.35$, $p < 0.01$; Fig. 5J) due to light-dependent variations in the ratio between production and respiration of the reef community explain much of the variability between sites and cavity types. Thus, we find that measurements carried out in Ras Burka and closed cavities (low connectivity) are biassed towards daytime, while tunnel cavities with moderate coelobite cover hold a higher-than-average number of nighttime observations (Table 1). Yet, in spite of the higher BBL levels, oxygen consumption in the cavities (Fig. 5M to P) was significantly higher in sack-type (low connectivity) than in tunnel (medium and high connectivity) cavities (ANOVA, arcsine-transformed data: $F_{1,99} = 44.14$, $p < 0.0001$; Fig. 5P), underlining the importance of water exchange on the observed depletions. Suspension feeder cover, by contrast, seemed to have little effect on the magnitude of depletion when comparing cavities with high and moderate cover (Scheffé's $p = 0.82$). The interaction, however, between connectivity and coelobite cover was significant (2-way ANOVA, arcsine-normalized data: $F_{1,99} = 12.29$, $p < 0.001$). Net oxygen production (negative values in Fig. 5M to P) in cavities was encountered on 2 occasions (Table 1).

Multiple linear regression analysis (normal summer conditions) confirmed that the magnitude of chl *a* depletions depended on the flow of water through the

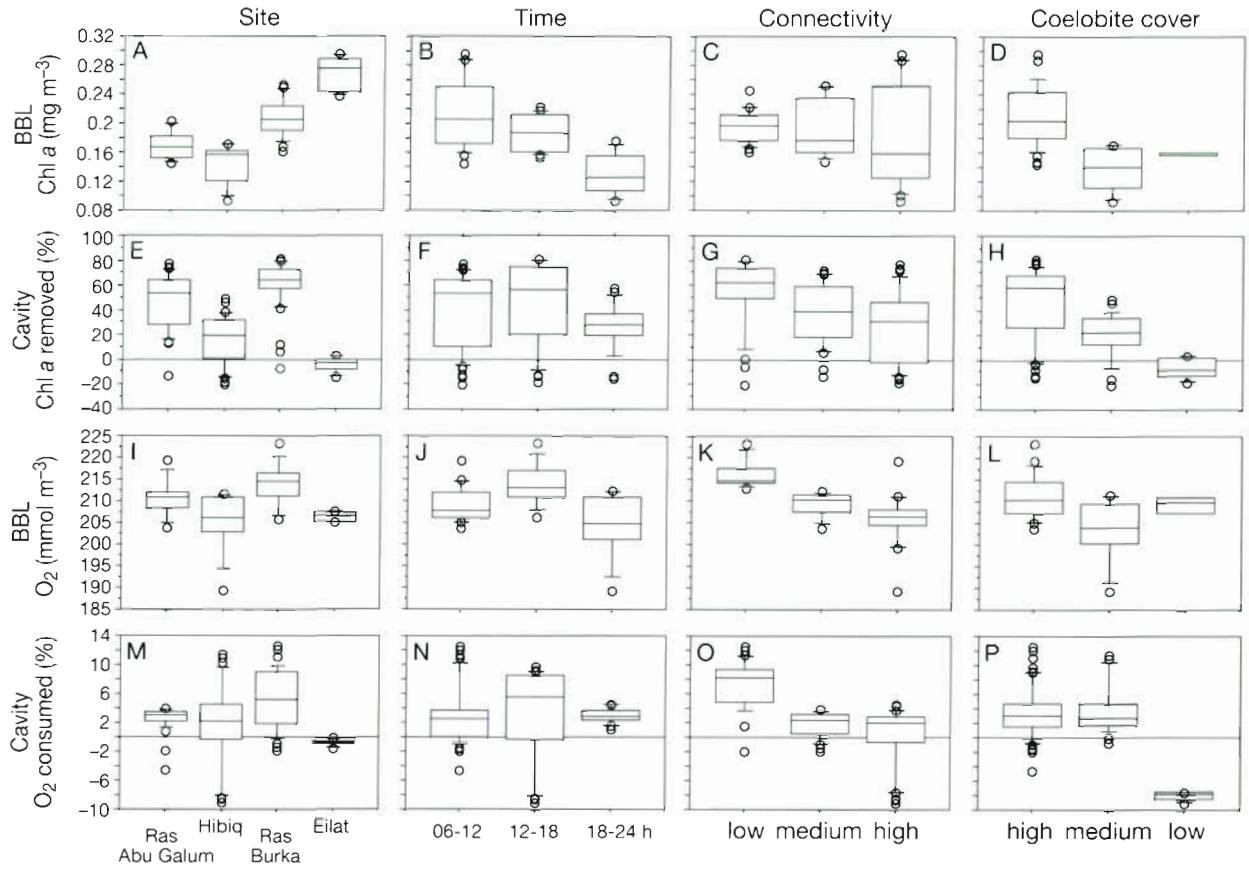

Fig. 5. Average distributions (20 transects, excluding 2 blooms >0.3 mg chl *a* m^{-3}) of (A to D) chl *a* concentrations in the bottom boundary layer (BBL), (E to H) chl *a* depletions in cavities, (I to L) oxygen concentrations in the BBL, and (M to P) oxygen consumption in the cavities, as a function of sampling sites, sampling time (hours), degree of connectivity of cavity with BBL (low: sack-shaped, medium: obstructed tunnel, high: open tunnel cavity), and coelobite suspension feeder cover (high: >30%, medium: 10 to 30%, low: <10% suspension feeder cover). See Fig. 4 for explanation of box plots

cavities, as well as on the amount of chl *a* present in BBL, according to the equation

$$\%\Delta c = -13.9\, v_c + 375.6\, c_{BBL}$$

Multiple adjusted $R^2 = 0.91$, $F_{2,9} = 53.14$, $p < 0.0001$

where %Δc is the relative concentration difference of chl *a* between BBL and cavity (in % of c_{BBL}), v_c is the average current speed (cm s^{-1}) in the cavity and c_{BBL} is the chl *a* concentration in BBL (Table 2).

When applied to the entire data set (normal and bloom conditions), multiple linear regression yielded no fit at all ($R^2 = 0.26$, $F_{2,9} = 3.24$, $p = 0.08$).

Pheopigments were positively correlated with chl *a* under bloom conditions (Fig. 6B). Under normal summer conditions, however, pheopigment concentrations remained virtually constant while chl *a* levels progressively declined from BBL to cavities (Fig. 6A), indicating selective removal of chl *a* in the cavities.

Fluorescent dye experiments revealed rapid flushing of cavity waters in the order of only minutes (Fig. 7). Fluorescein injected into the upstream entrance of Moses Rock took 3:20 min (corresponding to a travel speed of 2.0 cm s^{-1}) to reach the leeward end of the 4 m tunnel cavity and was diluted to threshold concentrations in 10 min (Fig. 7A). Ambient speed in the BBL at that time was 8.2 cm s^{-1}. In 36 flushing experiments carried out to date, 90% of the fluorescein injected into the cavity was washed out in about 3 min and 99% in about 8 min (Fig. 7B). In Ras Burka, where we found the highest chl *a* depletions (>60%, Fig. 5E), the dye travelled through the 2.5 m diameter patch reef at 0.8 cm s^{-1} after which it was found seeping out of several downstream openings before being carried away by the BBL current at 2.9 cm s^{-1}.

DISCUSSION

This study is the first account, to our knowledge, of significant depletions of chl *a* between BBL and coral reef cavities.

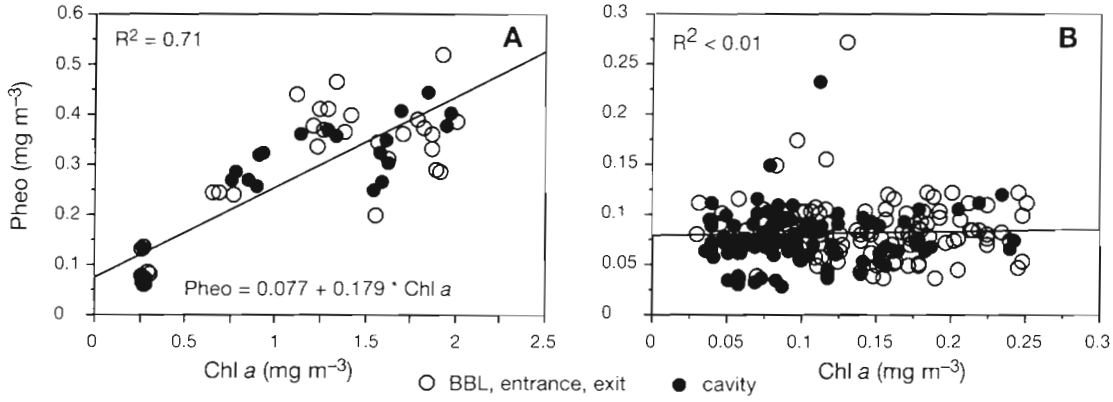

Fig. 6. Pheopigment versus chl *a* concentrations for (A) bloom (>0.3 mg chl *a* m^{-3}) and (B) oligotrophic summer conditions in the Gulf of Aqaba. (○) Bottom boundary layer (BBL) waters, cavity entrances and exits; (●) cavity values

Contrary to the gradients described from the large Mediterranean caverns, which feature long water residence times (days, Fichez 1991) and successive impoverishment of the fauna towards their inner reaches (Riedl 1966, Gili et al. 1986), the much smaller-scale gradients we measured in coral reef cavities during this study were accompanied by very short water residence times (minutes) and flourishing coelobite communities. In fact, almost all cavities inspected at our sites and elsewhere in the Gulf of Aqaba (Wunsch unpubl.) harboured dense cryptic communities. Only in Hibiq, for one reason or another, we found less developed assemblages. This shows that food supply to the cavity system is sufficient to nourish a generally rich cryptic suspension feeding benthos, in spite of the general paucity of suspended organic matter in oligotrophic reef waters (Sargent & Austin 1949, Odum & Odum 1955).

In order to produce a conservative estimate for phytoplankton removal by the coelobite community, we modelled the water flow (m s^{-1}) and chl *a* (mg m^{-3}) changes across an idealized section of cavernous fore-reef slope, under normal summer conditions (<0.3 mg chl *a* m^{-3}), according to the equation

$$F = \bar{v}_c \times \Delta c \times \Delta L^{-1} \times p_c \times k$$

F is the amount of phytoplankton carbon retained per unit volume of cavernous reef (g C m^{-3} d^{-1} or g C m^{-2} d^{-1} normalized to the upper 1 m framework), $\bar{v}_c$ is the median net flow through cavities (8.9×10^{-3} m s^{-1}, Fig. 4A), Δc is the chl *a* concentration difference between BBL and cavity (1.0×10^{-4} g chl *a* m^{-3}, Fig. 4A), ΔL is the median cavity length (2 m, Table 1), p_c is a conservative estimate for the fraction of cavities per unit volume of reef (0.3, Gischler & Ginsburg 1996, Wunsch & Richter unpubl.), and k is a constant (5.184×10^6 g C [g chl *a*]$^{-1}$ s d^{-1}), assuming a carbon:chl *a* ratio of 60 for phytoplankton in oligotrophic waters near the reef (Legendre et al. 1988). This model yields a substantial retention of 0.70 g C m^{-2} d^{-1}, roughly 1 order of magnitude higher than previous estimates of pico-

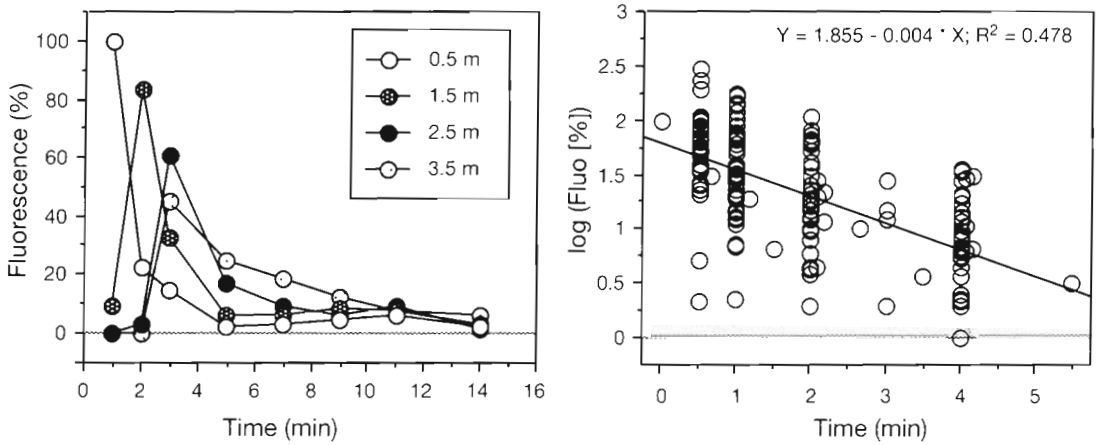

Fig. 7. Fluorescent dye dilution experiments. (A) Propagation of the dye patch from the upstream to the downstream end of a 4 m tunnel cavity pinnacle in Moses Rock, Eilat, showing the exponential decay of the fluorescence signal over time at the 4 sampling points (0.5 to 3.5 m from upstream entrance). (B) Exponential decay of the dye fluorescence signal in coral reef cavities of the Gulf of Aqaba (36 experiments)

plankton retention in waters flowing over the reef flat (Ayukai 1995). Our average figure is thus in the range of maximum rates reported so far for epibenthic reef communities (Fabricius et al. 1998, Yahel et al. 1998), highlighting the importance of cavity-dwelling suspension feeders in channeling suspended food from the BBL into the coral reef.

In order to validate our model, we carried out a separate analysis for phytoplankton retention in Moses Rock, according to the equation

$$F_c = v_e \times A_e \times \Delta c \times A_c^{-1} \times k$$

where F_c is the amount of phytoplankton carbon retained per square meter of cavity wall (g C m^{-2} d^{-1}), $v_e \times A_e$ is the volume flux of water across the cavity entrance (0.01 m s^{-1} × 0.44 m^2), Δc is the chl *a* concentration difference between BBL and cavity (6.58×10^{-4} g chl *a* m^{-3}), A_c is the surface area of the tunnel cavity, approximated by a cylinder (9.4 m^2), and k is the above constant. This mass-balance model yields an uptake of 1.60 g C d^{-1} per square meter cavity wall. Assuming a conservative factor of 2 between cavity area and that of the reef surface (Buss & Jackson 1979, Logan et al. 1984), this translates into an uptake of 0.80 g C d^{-1} on a square meter reef basis, reasonably close to the previous figure for the cavity system.

The models support the at first counterintuitive notion of high pelagic-benthic coupling in oligotrophic waters, where a rich albeit hidden suspension feeding benthos thrives on a dilute suspension of particulate food. They show how short residence times (Dill 1977, the present study) and high filter efficiencies (Reiswig 1971, Pile et al. 1996, Pile 1997) combine to give rise to community retention rates, which are comparable in magnitude to those measured over dense aggregations of suspension feeders in other marine and freshwater habitats (Jørgensen 1990, Petersen & Riisgård 1992, Riisgård et al. 1996, Pile et al. 1997, Gili & Coma 1998).

The short residence time of water over the narrow shelf (hours) and the short phytoplankton doubling times (0.4 to 3 d^{-1}; Ayukai 1992, Ferrier-Pagès & Gattuso 1998) show that the phytoplankton is mainly an allochthonous source of food to the coelobite suspension feeders. It enters the cavernous framework through flow speed differences in the BBL. The resulting pressure difference between the intake openings and the elevated output openings creates a secondary flow through the cavity system, much like the wind-induced ventilation of termite mounds (Weir 1973) or the current-induced flow through living sponges (Vogel 1974, 1977). It should be noted that the direction of flow is not so important as the speed difference between intake and exhaust. The increase in the cross-sectional area between the single large cavity entrance and the numerous smaller exhaust openings results in a deceleration of flow in the inner reaches of the cavity (Fig. 4). It is in this area of reduced flow where we found the strongest depletions (Fig. 3) and highest proportions of active suspension feeders (Wunsch & Richter 1998, Wunsch unpubl.). By analogy, the coral reef framework may thus be seen as a giant 'sponge' (J.-M. Gili pers. comm.), where the cavities take the role of the internal channels and the coelobite suspension feeders the function of the choanocyte chambers retaining phytoplankton (the present study), bacteria (Gast et al. 1998), heterotrophic nanoflagellates (Buss & Jackson 1981) and likely other suspended and dissolved organic matter (e.g. mucus, as suggested by Pérès & Picard 1969). In this regard it is interesting to note that the maximum community filtration efficiencies we report in our study (86%) approach that of filter-feeding individuals (Reiswig 1971, Pile et al. 1996).

Curiously, the pheopigment concentrations in the cavities did not increase in response to phytoplankton-derived production of feces (Currie 1962), nor did they decrease as a result of unselective grazing of both chl *a* and pheopigment-rich particles, as optimum foraging theory would predict for active suspension feeders (Gili & Coma 1998). Instead, pheopigment concentrations remained surprisingly constant, in contrast to the strong depletions of chl *a*. This points to an efficient selection mechanism between high- and low-value food (chl *a* and pheopigments), as was shown to occur even in ancestral organisms such as sponges (Kilian 1980, Wolfrath & Barthel 1989). A similar decoupling of chl *a* and pheopigments was described for community grazing by a fouling community on harbour pilings in Eilat (Yahel et al. 1998). In both instances, grazed chl *a* was probably broken down into non-fluorescent units or compacted into larger fecal units which escaped detection. Whatever the cause, the differential retention of the 2 pigments discredits mucus scavenging, wall adsorption or other non-biological mechanisms in explaining the notorious phytoplankton depletions near coral reefs (Glynn 1973, Legendre et al. 1988, Ayukai 1995, Yahel et al. 1998).

Zooplankton which may abound locally near the reef (Emery 1968, Hamner & Carleton 1979) did not occur in conspicuous aggregations in the cavities in the course of our study, and the limited data on reef-associated plankton available for the Gulf of Aqaba suggest that zooplankton would have an insignificant effect on phytoplankton pigment concentrations near the reef (Yahel et al. 1998).

Although flow through the cavernous framework is largely limited to macroscopic cavities, crevices and cracks (Andrews & Pickard 1990, Wolanski 1994), flow also occurs through the porous carbonate matrix, albeit at 1 to several orders of magnitude lower pore-water velocities (Buddemeier 1981, Roberts et al. 1988, Wo-

lanski 1994), and water residence times in the order of days rather than minutes (Tribble et al. 1992). Seepage from the framework is unlikely to affect the large chl *a* concentration differences we measured between BBL and cavities, but it may well affect the small differences we detected in the oxygen concentrations: 1 to 2 orders of magnitude lower oxygen concentrations (Sansone et al. 1988) and 3 to 4 orders of magnitude slower porewater flows (Tribble et al. 1992), may explain a few percent lower oxygen values in the cavity system. The effect of seepage may thus outweigh the effect due to the respiratory demand of the sessile coelobite community, because the respiratory cost of capture in suspension feeders is very low (Gili & Coma 1998).

Various interacting antagonistic physical and biological processes (e.g. wave action, advection, photosynthesis by sciaphilic algae, respiration by vagrant organisms, remineralization of their feces, etc.) working on different spatial and temporal scales, as well as high background levels and large diurnal variations in the BBL render the interpretation of the oxygen data difficult. Yet, in spite of these limitations, we saw that, with the exception of occasional oxygen peaks in the sun-lit cavity entrances, heterotrophic processes dominate over autotrophic processes in this light-protected habitat.

The animal-dominated coelobite community led Pérès & Picard (1969) to postulate that large amounts of the coral reef primary production were 'wasted' in the 'mesh-like' framework. Our study shows that in addition to reef-derived material which is deposited and remineralized in the cavities, a significant input occurs in terms of phytoplankton and likely other suspended and dissolved organic matter. This largely allochthonous material is trapped by the cryptic suspension feeders, effectively providing new nutrients and energy to the coral reef ecosystem.

The magnitude of this flux on the one hand, and the low densities (22 m^{-2}, Yahel et al. 1998) and small size (cm) of the dominant epi-reefal phytoplankton grazers on the other (Maier 1998, Yahel et al. 1998), as well as reported phytoplankton depletions over denuded reef sections (B. Lazar pers. comm.), give us reason to assume that coelobite suspension feeders may account for much if not most of the ultraphytoplankton depletions observed near coral reefs in the Red Sea (Yahel et al. 1998) and possibly also other parts of the world (Glynn 1973, Ayukai 1995). A comparative investigation of epi-reefal and coelobite community grazing is therefore highly needed.

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